

Activation of writing-specific brain regions when reading Chinese as a second language

Effects of training modality and transfer to novel characters

Aurélie Lagarrigue^{1,2}, Marieke Longcamp², Jean Luc Anton³, Bruno Nazarian³, Laurent Prévot¹,

Jean-Luc Velay², Fan Cao⁴, Cheryl Frenck-Mestre¹

1 Aix-Marseille Université, CNRS, LPL-UMR 7309, 13100 Aix-en-Provence France

2 Aix-Marseille Université, CNRS, LNC-UMR 7291, 13005 Marseille, France

3 Centre IRM Fonctionnelle de Marseille, INT-UMR 7289, CNRS Université Aix Marseille, France

4 Michigan State University, East Lansing, MI, USA

Corresponding author :

Aurélie Lagarrigue

Laboratoire Parole et Langage, CNRS, UMR 7309

5, Avenue Pasteur

13100 Aix en Provence, France

email : aurelie.lagarrigue@blri.fr

Keywords : Handwriting ; reading ; second language learning ; Chinese characters ; fMRI

Corresponding author : Aurelie Lagarrigue

Highlights :

- Training modality effect on brain representation of Chinese words in French learners
- Overlap between neural substrates of reading and motor processing involved in writing
- Writing neural network is differentially involved in reading depend on stored knowledge
- Kinematic handwriting quality positively correlate to the stored knowledge of words
- Stored knowledge of words impacts the response of the left mid-fusiform

ABSTRACT

We examined the implication of training modality on the cortical representation of Chinese words in adult learners of Chinese. In particular, we tested the implication of the neural substrates of writing in a reading task. The brain network sustaining writing was defined neuroanatomically based on an independent functional localizer, and brain activations during reading were analysed according to the position of the activation peaks in this localizer. We compared the brain activation elicited by Chinese words learned via writing vs. pronunciation. Our results in the reading task showed that activations of the brain network were in close vicinity to the main activation peaks of the writing localizer. Notably, common activation peaks were found in the left superior frontal sulcus, right middle temporal gyrus, bilaterally for superior parietal lobule/intraparietal sulcus, the right cerebellum and thalamus. Moreover, the response of several parts of the writing network varied according to training modality and type of character (learned vs. novel). Finally, the response of the left mid-fusiform region, known to be elicited during orthographic processing, was also affected by training modality and the linguistic properties of stimuli. At the behavioral level, global handwriting quality during the training sessions was correlated to the final translation performance. Our results demonstrate substantial overlap in the neural substrates of reading and writing, and indicate that some parietofrontal and subcortical regions sustaining handwriting are differentially involved in reading depending on the type of knowledge associated with words (semantic vs. phonological).

1 Introduction

Reading and writing are highly related skills, which are nonetheless most often studied independently in neuroscience. There are, however, a handful of studies that have examined the links between the two and whether knowledge of writing movements impacts upon reading. Results from these studies show a close relationship between cortical activation in regions related to handwriting and the visual perception of known single letters (Anderson, Damasio, & Damasio, 1990; James & Gauthier, 2006, 2009; Longcamp et al., 2008; Longcamp, Anton, Roth, & Velay, 2003, 2005; Longcamp, Hlushchuk, & Hari, 2011). In one of the earliest fMRI investigations involving alphabetic languages, Longcamp et al. (2003) showed, in right-handed French adults, that passively viewing letters of the Roman alphabet elicited activation in the left premotor cortex (Brodmann Area 6, BA6) whereas passively viewing pseudo-letters, for which the participants had no stored motor programs, did not. Moreover, passively viewing letters activated areas of the left premotor cortex in common with those activated by the actual writing of letters. The fact that the activation of premotor areas during letter perception was linked to the retrieval of stored information about writing versus other possible motor activities such as sub-vocalization was demonstrated in a subsequent study (Longcamp et al., 2005). Using the same paradigm but with left-handed adults Longcamp et al. (2005) found activation in the homologous right hemisphere of the pre-motor cortex. The finding of overlapping cortical activation during passive viewing and actual writing of known letters has since been replicated in adults (James & Gauthier, 2006) as well as in children (James & Engelhardt, 2012).

In like fashion to what has been found for alphabetic languages, there is a strong link between writing knowledge and stored visual representations of Chinese characters as well as Japanese kanji. In a seminal study, Flores d'Arcais (1994) showed that priming Chinese characters with a partial character facilitated subsequent recognition when the prime was consistent with the sequence of strokes normally used to write the character. This suggests that the specific motor schema for a given character may be an essential component of its representation. In line with this hypothesis, two imaging studies in Japanese, where participants had to recall the number of strokes of a kanji character when shown its syllabic transcription (Hirigana script) without performing finger movements, showed activation of sensorimotor areas activated during writing. Notably, BA6/9 was activated as was the rostral part of the supplementary motor area and the intraparietal sulcus (IPS) (Kato et al., 1999; Matsuo et al., 2003). The activation of a left premotor area during the visual processing of characters, whether alphabetic or morpho-syllabic, has been attributed to the neural representation of known letters, which is hypothesized to be distributed and to involve not only visual representations but motor patterns specific to their production as well (James & Engelhardt,

2012; James & Gauthier, 2006, 2009, Longcamp et al., 2003, 2005, 2011). This may occur, in part, due to the coupled learning of reading and handwriting during childhood.

To examine how visual and motor representations of characters may interact, various studies have manipulated learning modality. These studies have opposed producing new characters by hand to typing or simply viewing them and have shown that handwriting strongly impacts the later recognition of learned characters (Cao, Vu, et al., 2013; James & Atwood, 2009; James & Engelhardt, 2012; Kersey & James, 2013; Longcamp et al., 2008, 2005; Longcamp, Boucard, Gilhodes, & Velay, 2006). In adults, learning new characters by actually writing them versus typing on a keyboard improves both recognition and retrieval, as shown in a behavioral study (Longcamp et al., 2006) and replicated both behaviorally and in an fMRI protocol (Longcamp et al., 2008). Training characters by hand as opposed to on a keyboard led to stronger activation in several cortical regions known to be involved in motor preparation and execution. Both Longcamp et al. (2008) and James and Atwood (2009) showed that following writing practice, neural activation patterns to newly trained characters resembled patterns observed for known letters. In addition, both studies identified a dorsal premotor region that was more strongly activated when participants viewed characters trained by hand. James and Atwood (2009) also identified increased neural activation in the left fusiform gyrus.

In pre-literate children, writing but not visual-only training produced increased activation in bilateral anterior fusiform gyri from pre- to post-training scans in a letter recognition task (James, 2010). Moreover, activation in the left fusiform gyrus was specific to writing training, which calls into question the specificity of this area for visual word processing (see also Devlin, Jamison, Gonnerman, & Matthews, 2006). These findings were corroborated in a subsequent study, which compared the effect of freely producing letters to tracing or typing them on the cortical network activated during letter perception (James & Engelhardt, 2012). Only letters that were freely written during training elicited activation in areas related to letter recognition in a subsequent passive viewing task. Hence, even early in learning, when motor programs are not yet highly automated, writing training leads to the subsequent activation of cortical areas related to letter perception. To account for these results, James and Engelhardt (2012) have suggested that the production of numerous “noisy” outputs, i.e. semi-accurate productions of the intended character, enables the extraction of invariant features and hence the creation of an abstract exemplar (see also, Li & James, 2016).

While the above mentioned studies showed clear effects of writing on both the learning of the visuospatial features of characters and their cortical representation, they were not designed to examine the effect of handwriting on linguistic processing per se. That is, they all looked at processing at the sublexical level, whether letters in alphabetic languages or strokes in morpho-syllabic languages. Neither isolated

letters nor stroke information generally convey lexical or semantic information. While one study on alphabetic languages (James & Gauthier, 2009) showed that writing letters interfered more with letter perception than did drawing shapes, and that this motor effect was indeed specific to linguistic stimuli (i.e., drawing shapes did not interfere with perceiving shapes), the results remain at the pre-lexical level. The question thus remains open as to whether the same type of motor reactivation will occur during the processing of stored higher level units, i.e. during lexical processing.

To examine how writing may impact the learning and subsequent retrieval of higher level linguistic units, several studies have looked at whole character processing in Chinese. This question has been approached both behaviorally (Guan, Liu, Chan, Ye, & Perfetti, 2011; Guan, Perfetti, & Meng, 2015; Tan, Laird, Li, & Fox, 2005; for a recent review, see Perfetti & Tan, 2013) and using electrophysiology to track the time course of cortical processing (Cao, Rickles, et al., 2013). In an fMRI study, Cao, Vu, et al. (2013) used a training protocol based on that of Guan et al. (2011) to examine the effect of training modality on brain activation for learned characters in adult L2 learners of Chinese. They found that handwriting led to stronger activation of the bilateral superior parietal lobule (SPL) and right postcentral gyrus than did pinyin typing. In addition, for characters learned by hand, the amount of activation in the left sensorimotor cortex was correlated with accuracy in lexical processing. Cao, Vu, et al. (2013) argued that writing is an active encoding mechanism that accelerates the establishment of stable orthographic patterns, and therefore impacts higher-level linguistic processing in reading.

A limitation of all the above mentioned studies, which partially motivated the present study, is the absence of a direct comparison between the spatial location of the brain regions activated in either the visual perception of characters or in reading and the actual network sustaining handwriting. Apart from Longcamp et al. (2003) and James et Gauthier (2006) who used a functional localizer to evaluate the overlap of premotor activations, other studies have inferred that the gestural representations of handwriting are reactivated based on observed premotor or sensorimotor activation triggered by the visual presentation of characters. Direct mapping of the brain regions involved in writing is essential because other motor functions, especially those involved in the retrieval of phonological codes and articulation in speech production, could also be mobilized in reading and explain possible premotor, parietal or subcortical activations that would therefore incorrectly be attributed to writing knowledge reactivation.

The aim of the present experiment was to investigate the implication of the neural substrates of writing in a reading task that required lexical processing of single words in an ecological situation. In this aim, the brain network sustaining writing was defined neuroanatomically based on an independent functional localizer, and brain activations observed during reading were referred to the position of the activation peaks in the writing

localizer. Producing a writing gesture involves specific brain regions, as revealed by neuropsychological data from brain-damaged patients with agraphia or dysgraphia (Alexander, Friedman, Loverso, & Fischer, 1992; Anderson et al., 1990; Han & Bi, 2009; Ishihara et al., 2010) as well as brain imaging experiments (James & Gauthier, 2006; Longcamp et al., 2014; Planton, Jucla, Roux, & Démonet, 2013; Purcell, Turkeltaub, Eden, & Rapp, 2011; Sugihara, Kaminaga, & Sugishita, 2006). In a meta-analysis of 18 neuroimaging studies, Planton et al. (2013) highlighted several cortical regions of the left hemisphere that are crucially implicated in the control of handwriting, in the superior parietal cortex at the level of the SPL/IPS, and the premotor cortex at the level of the superior frontal sulcus (SFS), the ventral premotor cortex, the right cerebellum and the left thalamus.

The protocol used in the current study was partially based on that by Cao, Vu, et al. (2013) in which English speaking adults learned Chinese characters either by writing them or typing their pinyin equivalent. In the present study, French students of Chinese learned new characters by either writing them or simply pronouncing them. Following training sessions, we compared the impact of training modalities on brain activations during a reading task. In addition, we examined whether learned characters would generalize to novel characters bearing the same semantic or phonetic radicals, and whether training modality affected generalization. We hypothesized that if motor representations are part and parcel of learned characters, as suggested by both Longcamp et al. (2003, 2005) and James and Gauthier (2006, 2009), then we should see this in the pattern of brain activations observed during reading the learned characters included in actual words with known semantic and phonological properties. Moreover, if training modality plays a role, then the effect should be stronger for characters learned via writing.

To examine the capacity to generalize from learned to new characters, we examined the brain activations involved in processing novel characters that contained learned semantic or phonetic radicals. Processing novel characters that contain the same information as learned characters may also be supported by motor knowledge and therefore also rely on writing-related brain regions. Modern Chinese characters are generally composed of two sub-lexical units or radicals. Semantic radicals, which are generally to the left of the character, afford information about meaning although at a gross level. For example, the semantic radical 女 is used in various characters related to the concept of “femaleness” (i.e. “woman” “marriage” “aunt” “pretty” etc.). Phonetic radicals, which vary more in position, provide information about the phonological realization of a character but again, at a gross level. Upon reading the phonetic radical 羊 one knows that the corresponding pronunciation is “yang” but the exact tone can only be retrieved from memory.

We hypothesized that learning by writing should, first, affect the understanding and memorization of the radical structure of characters. Participants should therefore create motor representations of the characters. Said motor representations and their corresponding neural correlates might therefore play a role in the transfer to novel, related characters.

2 **Material and methods**

2.1 ***Participants***

Twenty-four French students of Chinese (17 female, mean age =19.6 years, range 18-25) participated for monetary compensation. All were recruited from the elementary level Chinese classes offered by Aix-Marseille University (France). Pre-scan questionnaires ensured that all participants were native speakers of French and had basic knowledge of Chinese. All had learned both how Chinese characters are formed (radical composition) and the principles of writing Chinese characters (i.e. stroke order). They all had normal or corrected-to-normal vision and no known hearing deficits, language or movement disorders. All participants consistently used their right hand to write and for daily manual activities (Edinburgh questionnaire ratios mean 86.7; Oldfield, 1971). Participants' displayed normal linguistic skills in their native language as ensured by language background questionnaires. Three participants (1 female) were excluded either due to either excessive head movement in the fMRI session (n=2) or poor performance over the training sessions (n=1). The study had prior approval by the Ethics Committee of the Aix-Marseille University (N° RCB 2010-A00155-34) and the CNRS. Participants signed a written informed consent form prior to the study. They were fully debriefed following their participation.

2.2 ***Stimulus materials***

A total of 96 Chinese characters were selected based on the type of radical (semantic or phonetic). There were 6 semantic and 6 phonetic radicals and, for each type, 8 characters were selected that contained a given radical. There were thus 6 sets of 8 characters (N=48) that shared a common semantic radical and 6 sets of 8 characters (N=48) that shared a common phonetic radical. While some of the radicals were known to participants, none of the characters were known prior to the experiment. For each set and each type of radical, half were learned during training (N=48) and later presented during the fMRI scan while the other half (N=48) were not learned but were presented during scanning (novel generalizations). Two counterbalanced lists were created such that all characters were seen in both conditions (generalization :

learned or novel). In addition, as show in Figure 1, two counterbalanced lists were created, each list being assigned either to the handwriting condition or to the pronunciation condition (described below). In each list, characters were matched across phonetic and semantic radicals for their spatial structure and complexity as well as for the number of strokes and word class.

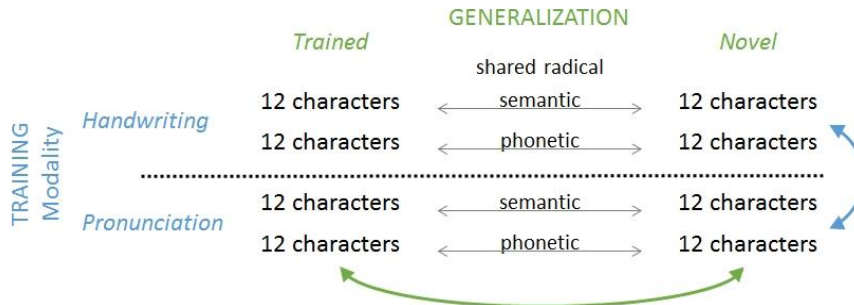


Figure 1. Design. The assignment of a given list of 24 characters to a given training modality, or to the trained/novel conditions was counterbalanced between participants.

2.3 Procedure

2.3.1 Behavioral procedures

The behavioral protocol comprised 5 one-hour sessions over 5 consecutive days. Participants learned a total of 48 characters (described above), half of which (24) were presented in one of 2 training conditions: writing or pronunciation. In each training condition, there were 3 sets of 4 characters that shared a common phonetic radical and 3 sets of 4 that shared a semantic radical. The sequence of the two training conditions was counterbalanced between participants and days.

For both training conditions, the presentation sequence of each character took 18s divided into 4 steps, as follows. The Chinese character was presented in the center of the computer screen for 1 second followed by its pinyin translation for 1 second along with its pronunciation by a native Chinese speaker; subsequently the French written translation was presented for 1 second. At the end, the Chinese character was again presented for 15 seconds along with its pinyin and French translation and participants were required to either write the character or to pronounce the corresponding syllable. Participants were asked to write the character twice and to pronounce it no more than 2 times while staring at the character on screen.

In a given session each character was presented three times. The order of presentation of characters was randomized by participants and days, with the restriction that two characters sharing the same radical did not directly follow each other, nor was a given character immediately repeated. Chinese characters (250x188 pixel bitmap image) and pinyin translations (24 point lower case Arial font) were written in white on a black background.

The behavioral experiment was conducted with E-prime software. In the writing training condition, participants had to write each character with a pencil on a specific square paper usually used in Chinese class. In the pronunciation training condition, participants spoke into a head-microphone; their productions were recorded. No feedback was provided for either condition.

On days one, three and five, participants performed a pencil and paper translation test of learned Chinese characters. Participants were instructed to provide the French translation of each learned character in writing or, if they were not able to translate the whole character, to provide the translation of the radical. On days one and five, we also recorded handwriting production in the course of the training session, to evaluate any improvement in handwriting quality. Fifteen participants of the original sample had exploitable data. Recordings and subsequent analysis were conducted using MovAlyzeR[®] software (<http://www.neuroscript.net>), with an Inking Pen on a graphic tablet (Wacom Intuos 4 A4; sampling frequency 200 Hz, accuracy 0.02 mm) connected to a computer.

Participants were scanned at the fMRI Centre in Marseille two days following the end of training.

A final oral translation test was performed immediately after the fMRI recordings using E-prime software. Learned Chinese characters (250x188 pixel bitmap image, displayed in white on a black background) were randomly presented in the center of the computer screen for 5 seconds and the participants had to produce the French translation orally. We recorded productions by means of a head-microphone. Characters were considered learned when participants were able to produce their exact translation.

2.3.2 *fMRI procedure*

2.3.2.1 *Localizer*. Brain regions supporting writing and pronunciation were assessed in a separate session, performed after the main reading task. Forty simple and frequent Chinese characters, repeated twice, served as stimuli, in blocks of 4 trials. Characters were chosen from those learned in the first year of Chinese classes and were assumed to be known by participants. Depending on the instruction at the beginning of a block participants had to either trace the visually displayed character in the air with their right index finger, or pronounce it overtly while trying to minimize jaw and head movements. Blocks of writing, pronunciation and rest were alternated randomly. The total run time was roughly 8.5 minutes (3.5 sec presentation per item, 3 sec mean ISI (min: 1.6s – max: 8s))

2.3.2.2 *Main reading task*. Prior to the fMRI recordings, participants were familiarized with the task using a set of known Chinese characters (learned in class). During scanning, an event-related design was used in each of 4 runs. Runs 1 and 2 involved trained characters and runs 3 and 4 the novel characters (generalization). We manipulated 2 factors per experimental run: Training (handwriting vs. pronunciation) and Radical (semantic vs. phonetic), with an equal number of trials per condition.

The fMRI session consisted of a reading task. To ensure that participants retrieved all knowledge they had about a character upon its visual presentation, they were asked to prepare for a question that tapped into either semantic or phonological knowledge. On 25% of trials of the experimental run (catch trials), the character was followed by a question. On 75% of trials, the characters were presented without a subsequent probe question. Each of the 48 characters was seen 4 times in all, once as a catch trial. On catch trials, subjects had to choose between two alternatives presented above and below the fixation cross, immediately after the presentation of the character. On fifty percent of catch trials, the alternatives were possible translations in French; on the other half of trials, the alternatives were possible pinyin correspondences. This design ensured that participants had to retrieve all stored semantic and phonological information about a character on each trial. There were thus 192 characters in all, randomly divided in two runs of 96 characters. The total run time was roughly 9 minutes (2 sec presentation per item, 3 sec mean ISI (min: 1.6s – max: 8s); for catch trials: 4.8 sec (2 sec presentation, 1.3 sec mean ISI (min: 0.8s – max: 1.8s), 1.5 sec for the question period).

2.3.3 *fMRI data recording and analysis*

All images were acquired using a 3-T MEDSPEC 30/80 AVANCE whole-body imager (Bruker, Ettlingen, Germany), equipped with a circular polarized head coil.

First, we acquired a high-resolution structural T1-weighted image (3D sagittal volume using MPRAGE sequence). Then, for functional imaging, we used a T2*-weighted FID-echo planar sequence (EPI), covering the whole brain with 36 interleaved 3-mm-thick axial slices with a 1 mm gap, parallel to the AC-PC plane (repetition time - 2400 ms, echo time - 30 ms, flip angle 82°, field of view 192 x 192 mm- matrix 64 x 64 of 3 x 3 voxels). We acquired 256 functional images per session. A fieldmap acquisition was acquired to correct geometrical deformations on EPI images. A 3D gradient echo sequence with two echoes (echo times 3.7 ms and 8.252 ms) was used.

Data were processed using spm8 software (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>), according to the general linear model (Friston et al., 1995). The first three functional volumes of each session were removed to eliminate nonequilibrium effects of magnetization. The remaining 253 images were corrected for differences in slice acquisition time. Fieldmaps were processed for each participant using the FieldMap toolbox implemented in SPM8 (Hutton et al., 2002). The images were then realigned to the first image and corrected for interactions between movements and field inhomogeneities using the fieldmap (Anderson, 2001), which allows the measured static distortions to be included in the estimation of distortion changes associated with head motion. Each participant's structural image was then co-registered to the mean of the motion-corrected functional images using normalized mutual information, and segmented using affine

registration to an ICBM/MNI template space. The spatial normalization parameters resulting from the previous step were then applied to the functional images to allow for inter-subject analysis, and finally the images were smoothed using a 5 mm FWHM Gaussian kernel.

2.3.4 *fMRI statistical analysis*

After pre-processing, individual functional images were entered in a first level general linear model.

For the localizer, we modeled the tasks of writing and pronunciation as box-cars convolved with the HRF. At the second level, we defined the brain network involved in writing and in pronunciation by performing one-sample t-tests of the contrasts between the writing and pronunciation tasks. Because the input (visual display of the characters) was identical in both tasks, the writing - pronunciation contrast reveals the neural substrates of both orthographic and manual-motor processing of the characters (Table I.A), while the pronunciation – writing contrast reveals the neural substrates of phonological and articulatory-motor processing of characters (Table II.A). Corresponding maps were thresholded at $p < 0.05$, FWE-corrected for multiple comparisons at the voxel-level.

For the main reading task (Table III), trials were modeled as events convolved with the HRF. Separate general linear models were constructed for the trained and the novel characters. For both trained and novel characters, we used the same 4 regressors per session according to a 2x2 design: Training (writing vs. pronunciation) x Radical (semantic vs. phonetic). An additional regressor accounting for the motor response in the catch trials, as well as the head movement parameters were also entered in the individual models. At the second level, we implemented a full factorial ANOVA with the factors Training modality, Radical and Generalization as within-subject factors. We also ran one-sample t-tests using the contrasts between writing-trained and pronunciation-trained characters with the corresponding behavioral effect (difference of the translation performance in both training modalities in the post-fMRI test) as a covariate (Table V). Then, for all activation peaks, we calculated the correlations between BOLD signal and behavioral data. We performed this analysis for the trained characters only, since the behavioral measures concerned only these characters.

The statistical maps corresponding to the reading task were examined using small volume correction (SVC). We defined the loci of interest based on the peaks of highest significance in the writing localizer (from bilateral parietal, left dorsal premotor and primary motor cortices, occipito-temporal regions, right cerebellum and subcortical regions; Table IV), and conducted the ANOVA and t-tests on the reading data with SVC centered on those peaks ($p < 0.05$, FWE-corrected at the voxel-level; 10-mm-radius sphere). The same procedure was used to evaluate effects localized in the vicinity of maximal activations in the pronunciation localizer (bilateral inferior frontal and superior temporal regions). Significant activations were localized using

a computerized atlas (Talairach Client, version 2,4,3; Lancaster et al., 2000) and a paper atlas (Duvernoy & Bourguin, 1999).

In line with the literature and our hypotheses concerning expected effects, one additional analysis was focused specifically on the activation of the mid-fusiform gyrus in the reading task. To this end, using the writing localizer we calculated the conjunction of the contrasts Write vs. Rest and Pronounce vs. Rest because both tasks were performed using the visual display of characters. This conjunction revealed an extended cluster of activation in the left and right occipital-temporal regions and from this cluster we chose the activation peak that was the closest to the coordinates determined previously in a meta analysis of reading studies (Jobard, Crivello, & Tzourio-Mazoyer, 2003). This led to Montreal Neurological Institute (MNI) coordinates of -36 -54 -12 (compared to -44 -58 -15 in Jobard et al., 2003). We constructed a sphere 6 mm in radius around this point. We checked that the extent of this Region of Interest (ROI) covered tissue of the fusiform gyrus only, and did not cover part of the underlying cerebellum (see Figure 7). We then applied the full-factorial ANOVA described above to the mean signal value in this ROI during the reading task, thresholded at $p < 0.05$.

3 Results

3.1 Behavioral performance

3.1.1 Evolution of performance as a function of training session:

3.1.1.1 Pen and paper tests. An ANOVA involving Training modality (writing vs. pronunciation), Radical (phonologic vs. semantic) and Session (Days 1, 3 and 5) revealed a significant main effect Session ($F(2, 40) = 61.08$; $p < 0.0001$). Neither Training modality, Radical nor their interaction produced significant effects. The percentage of learned characters steadily increased across learning sessions: beginning day 1: 0%, day 3: 28%, day 5: 70%, and post-hoc comparisons confirmed the difference between all contrasts.

3.1.1.2 Computerized translation test (post-fMRI). An ANOVA with the factors Training modality (writing vs. pronunciation) and Radical (phonologic vs. semantic) did not reveal any significant main effects or interaction. The percentage of learned characters was equal to 74% across modalities.

3.1.2 Kinematic data and correlation between handwriting quality and Translation performance

Data representing the proficiency of hand movements were summarized into movement fluency as assessed by the Normalized Jerk per character. Normalized jerk (Teulings, Contreras-Vidal, Stelmach, & Adler, 1997) reflects the smoothness of the pen movement (normalized of the third time derivate of displacement) and

characterizes the quality of the movement execution (a low score corresponds to less jerk in the movement, and therefore to a smooth movement). For each recording session we took into account the mean for the two productions of the character. A t-test between day 1 and day 5 revealed a significant decrease for fluency ($t(14)= 3.02, p < .01$), with a more accurate gesture at day 5 (304.72 Normalized Jerk) than at day 1 (1070.03 Normalized Jerk).

We calculated a Pearson's Correlation Coefficient between the gain score of fluency (Normalized Jerk in session 5 minus session 1) and the ratio of correct responses in the translation test_post-fMRI. As show in Figure 2, the gain score positively correlated with the translation performance ($r(13)= 0.60, p < .02$). The more fluency improved in the course of training, the better the subsequent performance in the translation task. In addition, we calculated Pearson's Correlation Coefficient between global movement fluency per participant (average between the 2 session) and the ratio of correct responses in the translation test at post-fMRI. As show in Figure 2, the Normalized Jerk ($r(13)= -0.64, p < .01$) negatively correlated with the translation performance. The more fluent subjects were when writing (so the less jerk), the better their performance in the translation task.

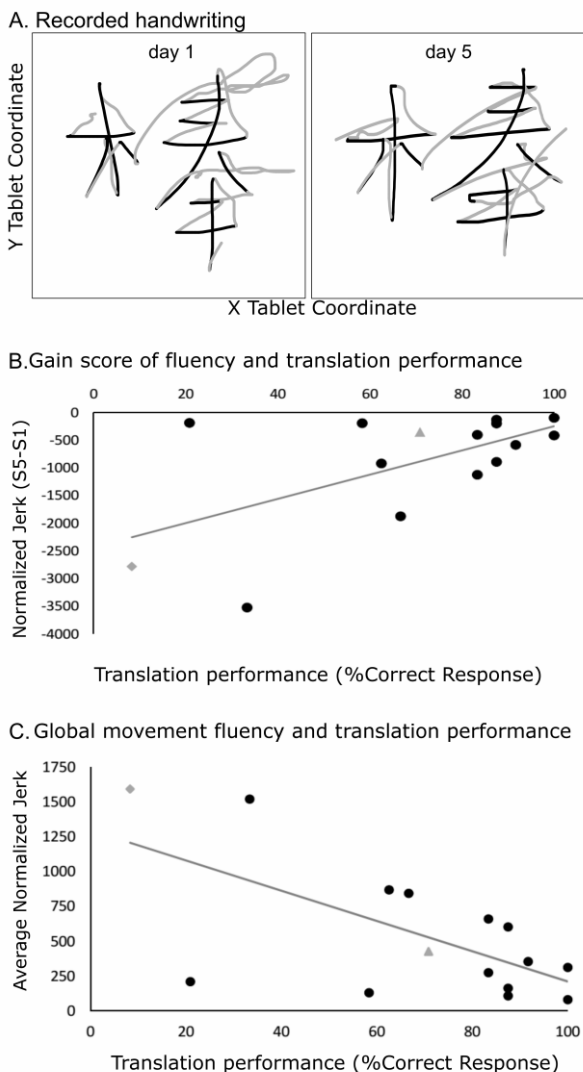


Figure 2. Kinematic data. A. Handwriting sample for the character 棒 “stick” traced by a participant at the day 1 and 5 of training. Black lines correspond to the pen down trajectory (i.e., writing trace) and the grey lines correspond to the pen up trajectory (i.e., movement in the air between each writing strokes). B. Scatterplot showing the relationship between the gain score of fluency (Normalized Jerk in session 5 minus session 1) and the translation performance in percentage of correct response on the trained writing characters at the end of training (day 5). C. Correlation between global movement fluency (Normalized Jerk) per participant (average between session1 & 5) and final translation performance in percentage of correct response. A high Jerk score corresponds to a non-fluent movement. For B & C, grey marks represent participants who were excluded from the final group for the fMRI data analysis due to poor behavioral performance (grey diamond) and head movements inside the scanner (grey triangle). Seven participants, that were included in the fMRI analyses, are not represented in the graphs due to technical difficulties in recording their kinematic data.

3.1.3 Response to catch trials in the fMRI task

Behavioral data in the 2-alternative choice catch trials during the fMRI scanning were analyzed using a four-way ANOVA (Repeated Measures ANOVAs) to compare response accuracy across Catch-trials (translation vs. pinyin), Training condition (writing vs. pronunciation), Radical (phonological vs. semantic) and Generalization (learned vs. novel).

The analysis showed a main effect of Generalization ($F(1,20) = 8.26, p < 0.01$) and Radical ($F(1, 20) = 6.45, p < 0.05$). Accuracy was higher for learned than for novel characters (88.75% vs. 66.96% respectively) and for phonological than for semantic radicals (80.73% vs. 74.99% respectively). Both the effect of Generalization and of Radical were modified by the interaction with Catch-trial ($F(1,20) = 9.18, p < 0.01$; and $F(1,20) = 35.34, p < 0.0001$, respectively). The two-way interaction between Catch-trial, Generalization and Radical was also significant ($F(1,20) = 24.99 ; p < 0.0001$). No effect of Training modality or any interactions of Training modality with other factors were observed. Results are summarized in Figure 3. In general, participants responded more accurately to the translation question for characters bearing semantic radicals, and to the pinyin question for characters bearing phonological radicals. This was especially true for novel characters.

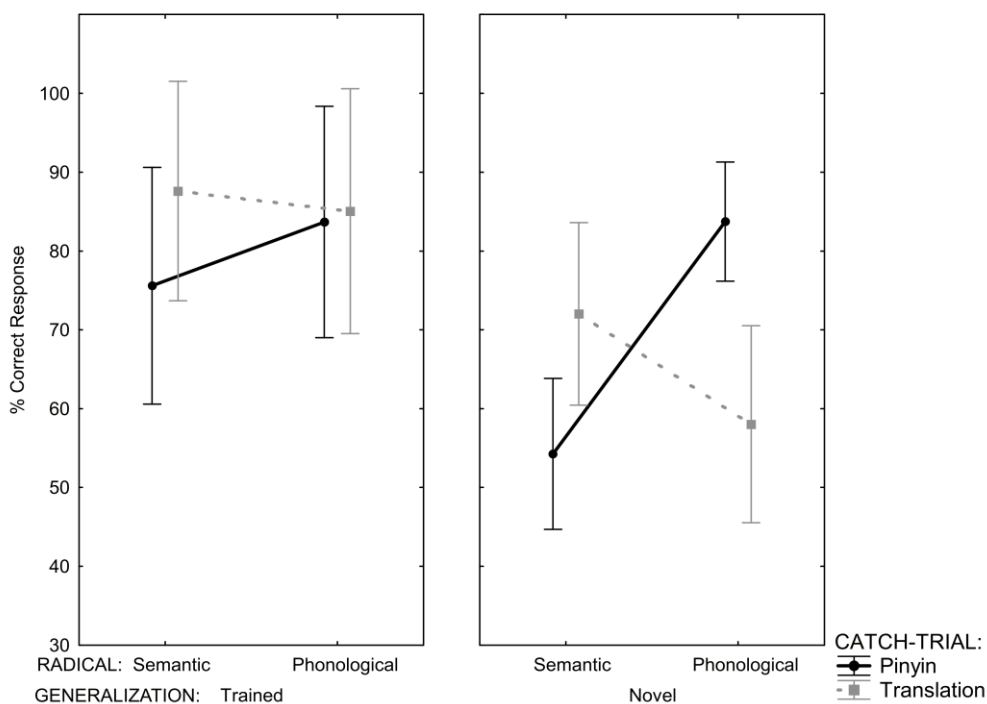


Figure 3. Percentage of correct responses across the type of Catch-trials (translation, grey dashed line, vs. pinyin, black solid line) over the fMRI session for learned and novel characters depending on character's radical (semantic vs phonologic). The error bars are 95% confidence intervals centered on the mean.

3.2 fMRI results

To examine the effects of Training modality, Radical and Generalization, we conducted 5 analyses. The first analysis, which was a whole brain analysis, allowed us to delineate the networks underlying writing and oral pronunciation, respectively. The second analysis used the activation peaks we found in the whole brain analysis to determine the overlap with reading network. In the third analysis we used SVC analyzes to look more precisely at the training-related effects in the reading task. The fourth analysis used behavioral performance on the post-scanning translation task as a covariate, to establish the BOLD response to characters trained by hand vs. via pronunciation in the reading task. In the fifth analysis, we specifically examined the activation of the left fusiform area as a ROI.

3.2.1 Writing and Pronunciation network : whole brain analysis

The writing vs. pronunciation localizer contrast revealed a network formed of dorsal parieto-frontal regions mostly lateralized in the left hemisphere (with a global maximum slightly posterior to the central sulcus, at the level of the hand knob of the primary somatosensory/motor cortex), the right cerebellar vermis, the left thalamus and several other subcortical structures, notably the left putamen (see Table I.A and Figure 4.A(red)).

Table I. Activation peaks in the Writing Localizer and the overlap with the reading network.

For (A), only the activations reaching a threshold of $p < 0.05$, FWE-corrected for multiple comparisons at the whole brain level are shown. For (B) the activation peaks in the reading task as assessed by SVC correction, $p < 0.05$, FWE-corrected for multiple comparisons in a 10 mm radius sphere centered on the activation peaks of the localizer.

		A. Writing Localizer				B. Overlap of main reading network and Localizer				
Lobe	Hemisphere	region	MNI coordinates			peak Z-value	MNI coordinates			peak Z-value
			x	y	z		x	y	z	
Frontal										
Left		Central sulcus	-36	-24	54	6.84	-42	-30	51	3.34
		Precentral gyrus	-36	-12	57	6.45	-39	-6	60	5.10
		Superior frontal sulcus	-24	-9	57	6.29	-27	-3	54	4.91
Right		Medial frontal gyrus	-3	-9	51	5.49				
		Superior frontal gyrus	27	0	57	6.11				
		Superior frontal sulcus	30	-6	51	5.87	33	-3	51	3.81
Parietal										
Left		Postcentral gyrus	-36	-33	54	7.06				
		Superior postcentral sulcus	-24	-51	60	6.74				
		Inferior parietal gyrus	-54	-27	39	6.54				
		Superior Parietal Lobule /IPS	-18	-63	57	6.49	-21	-63	42	Inf
		Intra-Parietal sulcus	-36	-42	57	6.47	-39	-39	39	6.48
Right		superior parietal gyrus	27	-51	63	6.93	30	-54	57	7.22
		superior parietal gyrus	21	-69	45	6.75	27	-66	48	Inf
		Intraparietal sulcus	51	-24	39	5.62	39	-36	51	5.01
		Precunueus	15	-57	45	5.52				
Occipital										
Right		Intra-occipital sulcus	27	-66	24	6.37	30	-69	27	Inf
		Middle occipital gyrus	51	-60	-6	5.36				
Temporal										
Left		Fusiform gyrus	-27	-42	-15	5.21	-27	-45	-18	Inf
Right		Middle Temporal gyrus	51	-60	-6	5.36	51	-60	-9	Inf
		Fusiform gyrus					33	-45	-21	Inf
Cerebellum										
Right		Vermis 4 5	6	-57	-15	7.01	3	-54	-12	3,56
		Cerebellum 4 5	24	-48	-21	5.96				
Sub-cortical										
Left		Thalamus (pulvinar)	-9	-24	6	6.07	-12	-24	0	4,8
		Insula	-42	-3	3	5.47				
		Putamen	-30	-18	9	5.21				

The pronunciation vs. writing contrast revealed a network formed of bilateral inferior precentral and temporal regions, and of a large cluster in the left inferior frontal gyrus (see Table II.A and Figure 4.A(green)).

Table II. Activation peaks in the Pronunciation Localizer and the overlap with in the reading network.

For (A), only the activations reaching a threshold of $p < 0.05$, FWE-corrected for multiple comparisons at the whole brain level are shown. For (B) the activation peaks in the reading task as assessed by SVC correction, $p < 0.05$, FWE-corrected for multiple comparisons in a 10 mm radius sphere centered on the activation peaks of the localizer.

Lobe		A. Pronunciation Localizer				B.Overlap of main reading network and Localizer			
		MNI coordinates			peak Z-value	MNI coordinates			peak Z-value
Hemisphere	region	x	y	z		x	y	z	
Frontal									
Medial	Superior frontal gyrus	-3	12	60	5.48	-6	12	57	7,1
Left	Precentral gyrus	-60	-6	18	6.36				
	Precentral gyrus	-45	-9	33	6.17	-51	9,00	39	3,5
	Inferior frontal gyrus, pars triangularis	-51	24	12	5.69				
	Inferior frontal gyrus, pars opercularis	-45	15	24	5.52	-42	12	27	Inf
	Inferior frontal gyrus, pars orbitalis	-33	33	-3	5.64				
	Inferior frontal gyrus, pars triangularis	-51	30	21	4.85				
	Inferior frontal gyrus, pars orbitalis	-36	39	0	4.79				
Right	Precentral gyrus	45	-12	33	6.20	48	-6	39	3,5
Temporal									
Left	Superior temporal gyrus	-60	-30	6	5.36				
Right	Middle temporal gyrus	57	-33	3	6.26				
	Transverse temporal gyrus	60	-12	9	6.09				

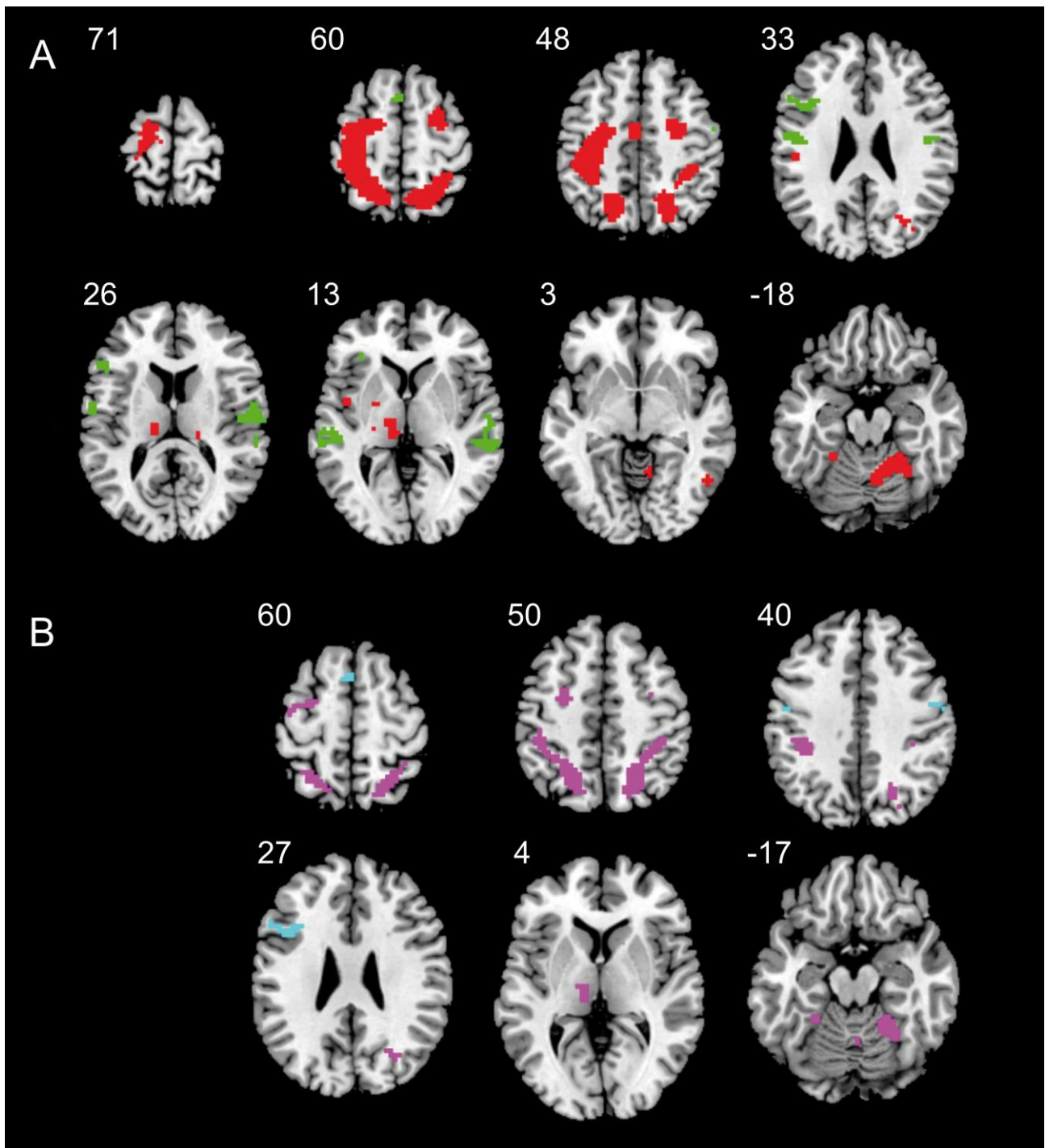


Figure 4. A- Brain network delineated by the writing – pronunciation localizer (red) and the pronunciation – writing localizer contrast (green). Brain regions are identified at a threshold of $p < 0.05$, FWE-corrected for multiple comparisons. B- Overlap between the writing and reading networks (pink) and the pronunciation and reading networks (cyan). This overlap is shown here for descriptive purposes. The reading activations were thresholded at $p < 0.001$, uncorrected for multiple comparisons. The illustration was created with mricron, . <https://www.nitrc.org/projects/mricron>.

3.2.2 Main reading network and spatial correspondence with the peaks of the writing and pronunciation localizers (whole brain analysis)

Compared to fixation, the reading task activated a broad network, described in Table III. Several regions within this network (bilaterally in the parietal cortex and in the anterior fusiform gyri) were in close spatial proximity to the peaks defined by the writing localizer (see Figure 5.B(pink)). The left SFS, the left central sulcus at the level of the hand knob of the primary motor cortex and the right cerebellum were also significantly activated during reading (see Table I.B). Furthermore, several parts of the frontal cortex, bilaterally in the precentral gyrus, in the medial superior frontal gyrus and pars opercularis of the left inferior frontal gyrus corresponded to the peaks defined by the pronunciation localizer (see Figure 5.B(cyan) and Table II.B).

Table III. Regions activated in the passive reading Chinese Characters vs fixation point.

Only the activations reaching a threshold of $p < 0.05$ FWE-corrected at the voxel level are shown. For a global overview of the activations see Figure 6.

Lobes		MNI coordinates			peak
hemisphere	region	x	y	z	Z-value
Frontal Lobe					
Left	Inferior precentral sulcus	-42	6	30	Inf
	Superior frontal gyrus	-6	9	51	Inf
	Middle frontal gyrus	-45	0	54	7.65
	Inferior frontal gyrus	-42	27	21	6.33
	Frontomarginal gyrus	-30	60	0	5.77
Right	Middle frontal gyrus	57	3	42	7.31
	Middle frontal gyrus	48	0	54	6.54
	Precentral gyrus	39	-18	66	6.56
	Superior precentral sulcus	36	0	63	6.51
	Superior precentral sulcus	27	-15	72	4.93
	Precentral gyrus	48	3	30	5.89
	Precentral gyrus	54	-9	51	4.98
Parietal Lobe					
Left	Intraparietal sulcus	-24	-66	36	Inf
	Superior Parietal Lobule	-27	-60	51	Inf
Right	Postcentral gyrus	45	-24	60	5.78
Occipital Lobe					
Left	Superior occipital gyrus	-15	-96	-6	Inf
	Middle occipital gyrus	-27	-87	0	Inf
	Inferior occipital gyrus	-36	-69	-15	Inf
Right	Superior occipital gyrus	24	-87	-6	Inf
	Middle occipital gyrus	36	-84	6	Inf
	Inferior lingual gyrus/Fusiform	33	-60	-12	Inf
Limbic Lobe					
Left	Parahippocampal Gyrus	-21	-30	-3	Inf
Right	Parahippocampal Gyrus	21	-30	-3	Inf

3.2.3 *Training-related effects in the reading task (small volume correction)*

When the effects in the reading task were referred to the writing network (SVC-correction on the peaks of the writing localizer; see Table IV), a main effect of Training modality, with stronger activation when reading characters trained by hand, was found in the left IPS/ SPL (-18 -66 54; $z = 3.23$; Figure 5.C) and the *left thalamus/putamen* (-12 -27 15; $z = 3.69$; Figure 5.D). The left SFS displayed no effect of Training modality or Generalization. However, there was a significant interaction between Training modality and Generalization in the precentral gyrus (-36 -9 57; $z = 3.78$; Figure 5.A), very close to the SFS. The same interaction was observed in the left central sulcus, at the level of the hand knob of the primary motor cortex (-36 -30 63; $z = 3.44$; Figure 5.B). For characters trained via pronunciation, activation dropped sharply for novel characters in comparison to learned characters. In contrast, characters trained via handwriting showed no such decrease in activation for novel, generalized characters.

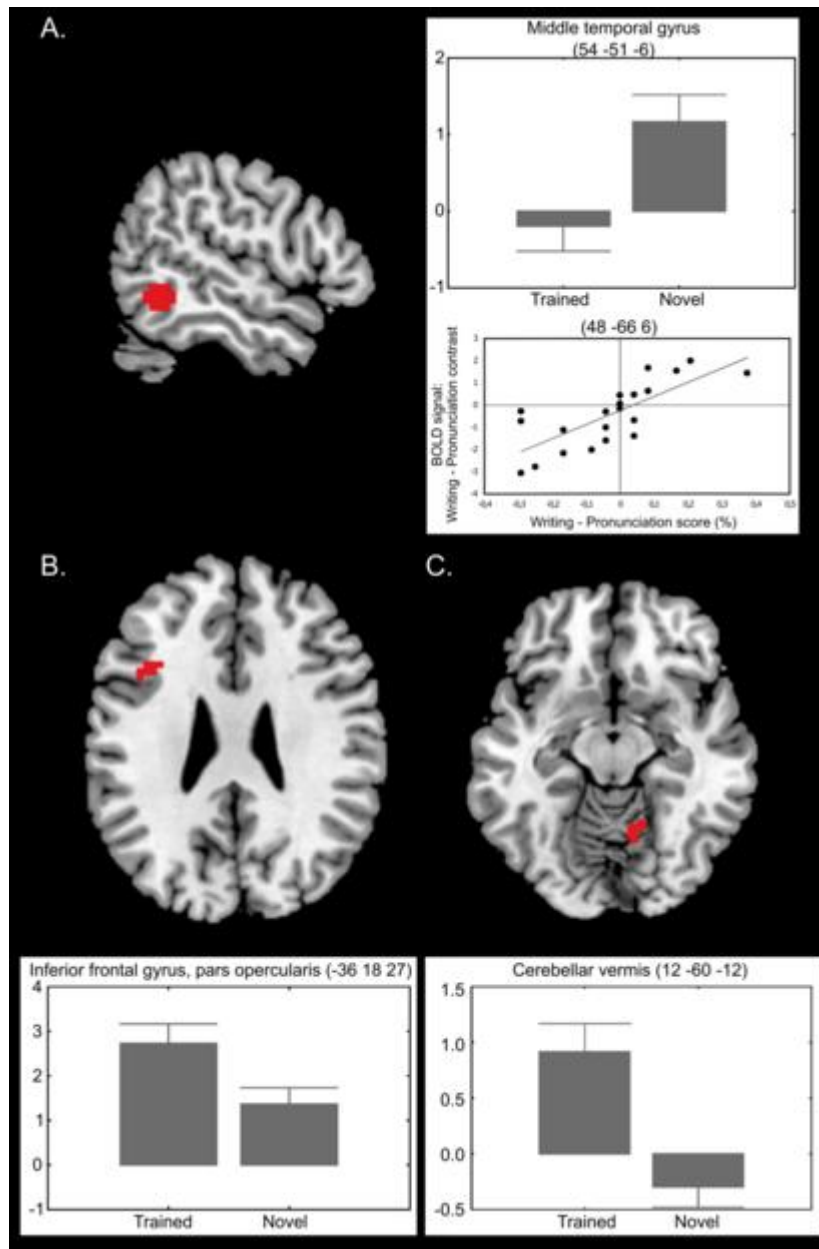


Figure 6. Generalization effects in the reading task. The graphs represent the contrast values as a function of the condition, and the scatterplot depict the effect of behavioral differences between training modalities on the corresponding brain differences.

In addition, a main effect of Generalization was found in the right cerebellar vermis (12 -60 -12; $z = 3.47$; Figure 6.C) and in the medial part of the superior frontal gyrus (-9 -9 54; $z=3.10$), with stronger activation when reading trained characters than novel ones. A Generalization effect was also found in the right middle temporal gyrus (54 -51 -6; $z = 4.72$; Figure 6.A), with greater activation for novel than trained characters. In addition, when the effects in the reading task were referred to the pronunciation network (SVC-correction on the peaks of pronunciation localizer; see Table IV), we found that Generalization affected the signal in the left inferior frontal gyrus, pars opercularis, which responded more strongly to trained than novel characters (-

36 18 27; $z = 3.47$; Figure 6.B). The medial frontal gyrus (-3 12 63; $z = 3.34$) displayed an effect of Radical, with greater activation for semantic than phonetic radicals.

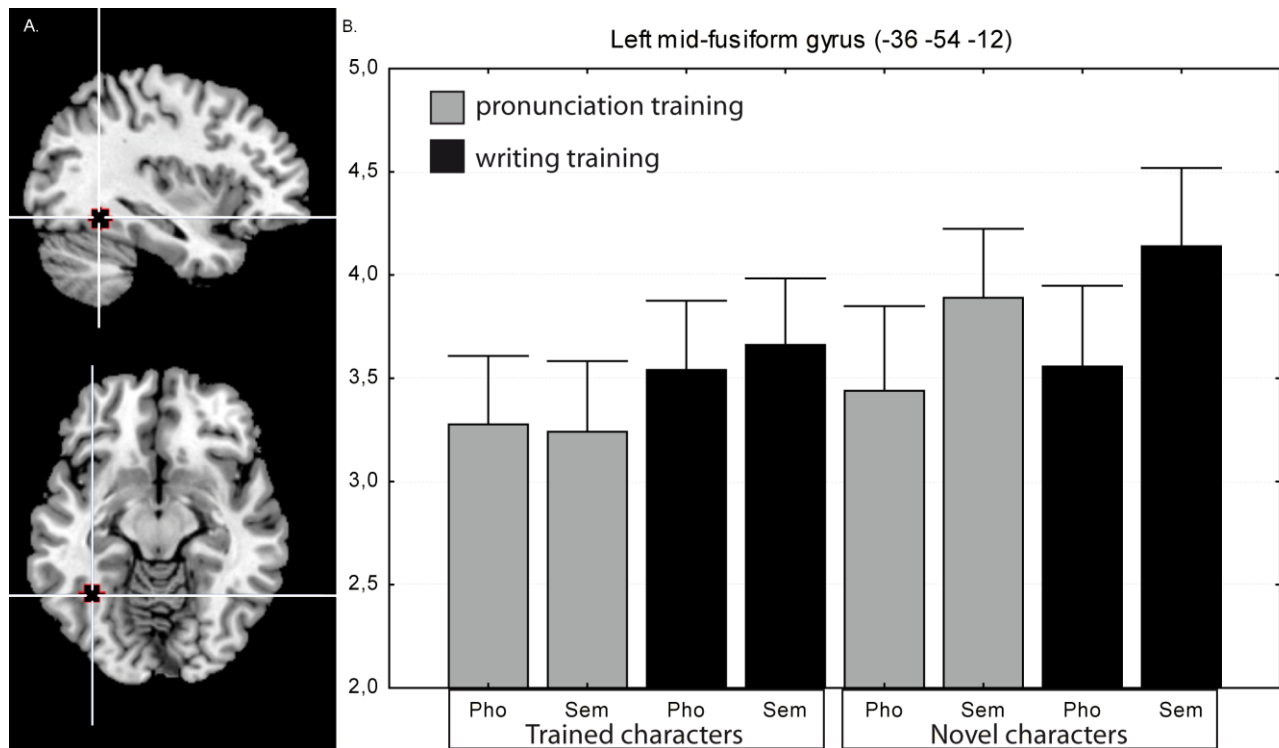


Figure 7. A. Region of interest (ROI) for the group in the left mid-fusiform gyrus (MNI coordinates: -36 -54 -12; sphere of 6 mm radius around this point). **B.** The graph represents the result of the brain activation in this region for training modality (writing vs pronounce), generalization (learned vs novel) and radical (phonological vs semantic).

Table IV. Effects of experimental factors in the reading task occurring in the vicinity of the activation peaks in localizers.

The activation peaks in the reading task as assessed by SVC correction, $p < 0.05$, FWE-corrected for multiple comparisons in a 10 mm radius sphere centered on the activation peaks of the localizer.

Experimental factors	Lobe	Hemisphere	Region	MNI coordinates			peak Z-value	Localizer
				x	y	z		
Modality	Parietal	Left	Superior Parietal Lobule /IPS	-18	-66	54	3.23	Writing
Modality	Sub-cortical	Left	Thalamus (pulvinar)	-12	-27	15	3.69	Writing
Radical	Frontal	Medial	Superior frontal gyrus	-3	12	63	3.34	Pronunciation
Generalization	Frontal	Left	Medial frontal gyrus	-9	-9	54	3.10	
Generalization	Temporal	Right	Middle Temporal gyrus	54	-51	-6	4.72	Writing
Generalization	Cerebellum	Right	Vermis 4 5	12	-60	-12	3.47	Writing
Generalization	Frontal	Left	Inferior frontal gyrus, pars opercularis	-36	18	27	3.47	Pronunciation
Modality x Generalization Interaction	Frontal	Left	Central sulcus	-36	-30	63	3.44	Writing
Modality x Generalization Interaction	Frontal	Left	Precentral gyrus	-36	-9	57	3.78	Writing

3.2.4 Behavioral data as a covariate in the reading task for trained characters

To further examine the effects of training modality, we calculated the difference in performance on the post fMRI translation task for characters trained by handwriting and those trained via pronunciation, and used the score as a covariate in the analysis of the contrast between training modalities. This analysis revealed several regions in the left parietal cortex (including the intraparietal sulcus, $r = 0.70$; $p < 0.05$; Figure 5.C) and in the right middle temporal gyrus ($r = 0.76$; $p < 0.05$; Figure 6.A) were in close spatial proximity to the peaks defined by the writing localizer (see Table V). The left SFS ($r = 0.72$; $p < .05$; Figure 5.A) and the left precentral gyrus ($r = 0.72$; $p < .05$) were also significantly activated during reading. Moreover, the right precentral gyrus was spatially close to the peaks defined by the pronunciation localizer (see Table V). For each of this region the contrast between writing-trained and pronunciation-trained characters was positively correlate to the translation performance (writing – pronunciation, trained characters) in the final test.

Table V. Behavioral performance on the post-scanning translation task as a covariate in the reading task to characters trained by handwriting vs. pronunciation, occurring in the vicinity in the localizers peaks.

The activation peaks in the reading task as assessed by SVC correction, $p < 0.05$, FWE-corrected for multiple comparisons in a 10 mm radius sphere centered on the activation peaks of the localizer.

Lobe	Hemisphere	region	MNI coordinates			peak Z-value	correlation	Localizer
			x	y	z			
Frontal								
Left		Precentral gyrus	-36	-6	57	3.52	0.72	Writing
		Superior frontal sulcus	-27	-3	63	3.58	0.70	Writing
Right		Precentral gyrus	48	-21	36	3.46	0.72	Pronunciation
Parietal								
Left		Inferior parietal gyrus	-57	-21	33	3.66	0.72	Writing
		Superior Parietal Lobule /IPS	-15	-66	54	3.34	0.70	Writing
Right		Intraparietal sulcus	51	-21	36	3.90	0.72	Writing
Temporal								
Right		Middle Temporal gyrus	48	-63	3	3.5	0.76	Writing

3.2.5 ROI analysis of the left mid-fusiform gyrus:

The ROI analysis of the activation of the left mid-fusiform (Figure 7) revealed a main effect of Training modality ($t = 2.73$; $p < 0.004$) with a greater response to characters trained by hand than pronunciation. The effect of Radical was significant ($t = 3.10$; $p < 0.002$), with a greater response to characters that contained learned semantic as opposed to phonetic radicals. This effect was modified by the interaction between Radical and Generalization ($t = 2.55$, $p < 0.006$), with a greater response to novel characters with shared semantic radicals than to the 3 other types.

4 Discussion

The present study investigated the implication of the neural substrates of writing in a reading task that involved processing of single, newly learned Chinese words. In this aim, we first delimited the network sustaining writing using a functional localizer. Then, we examined brain activation during the reading of trained Chinese characters in a group of French speakers who were studying Chinese at university level. We tested the effects of training modality (handwriting vs. pronunciation) and type of radical (semantic or phonetic), and examined the transfer of knowledge (generalization) to novel characters sharing radicals with the trained characters. We found that the reading and writing networks displayed similar activation peaks in several parieto-frontal brain regions and in several occipito-temporal areas. In addition, some regions identified in the literature as writing-specific, together with the left mid-fusiform gyrus and the right middle temporal gyrus, also showed a variable response as a function of the experimental factors, and as a function of participants' behavioral performance on a translation task carried out outside the scanner. We discuss our results in light of current findings on the relationship between reading and writing in the brain.

4.1 Behavioral findings

Our behavioral data, both in the pen and paper tests carried out in the course of training and in the scanner, revealed no specific effect of training Modality or Radical. Nevertheless, when we considered the quality of participants' handwriting we observed that with training participants became more fluent to write the characters. In addition, the fluency of their handwriting and their improvement in writing with training were both correlated with their subsequent translation performance (at the final post-fMRI test). This is consistent with the developmental approach of Tan, Spinks, Eden, Perfetti, & Siok (2005), who showed that the ability to read Chinese is strongly related to writing performance skills. A parallel finding has been reported in alphabetic languages, various studies have demonstrated that handwriting quality can predict reading level for the next grade (Berninger, Whitaker, & Feng, 1996; Molfese, Beswick, Molnar, & Jacobi-Vessels, 2006) as in Chinese language (Tan et al., 2003; even with dyslexic children Chan, Ho, Tsang, Lee, & Chung, 2006). In adult learners of Chinese, Guan et al. (2011, 2015) showed greater accuracy for characters that were handwritten compared to characters trained via pinyin on behavioral tasks that tapped into lexical processing. Moreover, the quality of the handwritten productions predicted learning. In the present data, handwriting training did not impact the integration of semantic information more strongly than pronunciation training did. However, handwriting quality at the end of the training was related to high-level linguistic information, namely

the acquired semantic knowledge of the characters (see Guan et al., 2015, for similar effects of handwriting quality and linguistic processing).

4.2 Overlapping neural substrates in reading and writing

We measured the brain signal evoked by reading lexical entries, i.e. words as opposed to simple characters, and by finger movements in the course of writing in the same participants. Although previous authors have already investigated the question of common neural substrates of perception and production of written language (Purcell, Napoliello, & Eden, 2011; Rapp & Lipka, 2011), those studies were interested in the central aspects of spelling skills, not in the neural substrates of motor control of writing. In addition, a growing number of studies have indicated that handwriting knowledge is important in the visuospatial processing of single characters (James & Atwood, 2009; James & Gauthier, 2006, 2009; James, 2010; Longcamp et al., 2008, 2003, 2005, 2011), but these studies did not investigate processing of the characters in a linguistic context. As such, ours is one of the first studies to investigate the implication of the writing network in the process of actual reading.

The reading task gave rise to activations in the typical regions of the left occipito-temporal and inferior frontal cortices (Bolger, Perfetti, & Schneider, 2005; Jobard et al., 2003). The writing localizer task aimed at isolating the neural substrates of orthographic and graphomotor processing of characters by comparing the actual copying of characters to their oral pronunciation (reading outloud). It should be noted, first, that the activations observed in the writing vs. pronunciation contrast, determined in a localizer run, encompass both writing-specific brain regions and sensorimotor regions controlling the hand and finger. As such, the activations cannot be assumed to be selective to handwriting alone but indeed also encompass handwriting movements. Our results revealed high spatial correspondence between some of the clusters found in this contrast and brain regions previously identified as specific to writing in the neuroimaging literature, in the left superior parietal, and superior frontal cortices, and in the cerebellum (Planton et al., 2013; Purcell, Turkeltaub, et al., 2011). The coordinates of activation peaks within the left parietal, central and precentral cortices, and in the cerebellum and thalamus directly match with the coordinates reported by the meta-analysis of Planton et al. (2013). Importantly, we found that the reading task evoked significant activation in the same regions, usually considered crucial for the control of writing.

Our results showed that the pronunciation localizer revealed a less extended network, possibly because the task of pronouncing the name of characters aloud is less demanding than copying them for non-experienced readers and writers. Nonetheless, the reading task also revealed activation peaks localized in close proximity to the motor and inferior frontal activation clusters defined by the pronunciation localizer. This

is an indication that phonological and articulatory speech representations are strongly intertwined with the neural substrates of reading in the literate brain (Dehaene et al., 2010). In addition, the common activation of the inferior frontal gyrus in spelling outloud and reading was already reported by Rapp & Lipka (2011), and by Purcell & Rapp (2013).

The significant activation of left SFS in the reading task, without concurrent overt movement (aside from the response in the catch trials, which were not included in the contrasts of interest), is in line with previous reports of premotor activations in the course of visual processing of single characters (James & Gauthier, 2006; Longcamp et al., 2003, 2005). The left SFS is consistently described as an important writing center (Katanoda, Yoshikawa, & Sugishita, 2001; Longcamp et al., 2014, 2003; Menon & Desmond, 2001; Planton et al., 2013; Sugihara et al., 2006) and is considered the equivalent of the clinically-defined Exner's area. Damage to Exner's area leads to agraphia characterized by ill-formed graphemes (Anderson et al., 1990; Roeltgen, 2003; Roux, Draper, Köpke, & Démonet, 2010). This region has therefore long been considered important for the coding of graphic movements in memory. Roux and colleagues (2009) proposed the label graphemic/motor frontal area (GMFA), because it is assumed to play a role in "transforming the orthographic code into graphic traces". Longcamp et al. (2014) observed stronger activation of the left SFS for letters than for digits, which suggests that this area is crucial for graphic movements but specifically in relation to linguistic units. The present results, showing activation of the left SFS during reading, is in agreement with those reported by James et al. (2006), who described a preferential response of this region for letters than control stimuli both in a reading and in a writing task, and by Nakamura et al. (2012), who found that a very similar location of the dorsal premotor cortex was sensitive to repetition priming in reading, as was the left fusiform gyrus. Nakamura and colleagues (2012) argued that reading universally relies on both visual and gestural systems. Our study confirms the gestural coding interpretation in reading by demonstrating the overlap of activation peaks in the reading task and in the writing localizer.

The SFS activation observed during reading was located in the dorsal most part of an extended left frontal cluster encompassing the middle frontal gyrus (MFG). Middle frontal activation is a typical feature of reading in Chinese (Li, Legault, & Litcofsky, 2014; Siok, Perfetti, Jin, & Tan, 2004; Tan et al., 2001, 2003; Wu, Ho, & Chen, 2012) and has sometimes been interpreted as being related to the reactivation of motor patterns for writing (Perfetti, Cao, & Booth, 2013). Yet, the pattern we observed suggests that the reactivation of motor patterns for writing in the course of reading is likely distinct from the processes leading to left middle frontal gyrus activation. Indeed, although we observed a large activation of the MFG, only a very posterior and dorsal fraction of it overlapped with the writing localizer. As such, the overlap between reading and writing corresponded to what has often been termed as the classical Exner's area, but the

majority of the activation observed in reading in the middle frontal gyrus was outside of this area. It is thus questionable whether the MFG activation we observed is specifically linked to reading. Note that Cao et al. (2010, 2011) found that the activation of the left MFG increased with age and reading skill in Chinese native speakers when engaged in tasks that required selecting amongst orthographic and/or phonological competitors. They suggested that this effect revealed an increase in top-down control of lexical processing.

In addition, a massive overlap between activations for reading and writing was found in extended bilateral parietal regions. Although superior parietal activations are not typically reported in brain imaging studies of reading (Jobard et al., 2003; Price, 2012), they have nonetheless been evidenced when attentional demands on the reading task are high (Ihnen, Petersen, & Schlaggar, 2015) or when stimuli are spatially distorted (Nakamura et al., 2012). They are classically reported and often associated with Inferior Parietal Lobule (IPL) activation in relation to increased visuospatial demands in reading Chinese (Kuo et al., 2001; Tan et al., 2001). In Nakamura et al. (2012), these regions were also found to be sensitive to repetition-suppression priming, together with the left fusiform gyrus and the SFS, when word primes were briefly flashed, both in Chinese and French. Such a result supports the hypothesis that a “distributed set of brain regions represents a fast and invariant network underlying fluent reading across different cultures” (Nakamura et al., 2012, p 4). Our data, showing overlap of bilateral posterior parietal activations between reading and handwriting, suggest that these areas probably reflect processes that are general in written language processing. In handwriting, a bilateral increase of the signal in the posterior parietal region has been shown during the production of over-trained characters compared to the early learning of new characters (Seitz et al., 1997). As such, it is most likely related to the stability of the kinematic representation in memory. Although the parietal overlap was widespread, it included, in its left dorsal and medial part, the region that has been identified as specific to the motor control of writing, i.e. the left SPL / IPS (Planton et al., 2013; Purcell, Turkeltaub, et al., 2011). The functional importance of this activation and its sensitivity to training modality is discussed below.

4.3 Effect of training modality, and its interaction with other factors

The left SPL/IPS responded differentially as a function of training modality, with greater activation for characters learned via handwriting. The involvement of the SPL in visual processing of characters learned by hand was first documented in an fMRI study by Longcamp et al. (2008) for unknown alphabetic characters trained by hand as compared to via typing. Cao, Vu, et al. (2013) also reported activation of the SPL for Chinese characters learned by writing vs. typing pinyin. Deng, Booth, Chou, Ding, & Peng (2008) found that SPL activation was correlated with increases in accuracy for trained characters across learning sessions

(activation decreased from early to late scans). They suggested that this area is involved in the processing of sub-lexical units (i.e. radicals) linked to the visuo-spatial features of Chinese characters. Our results support this hypothesis and suggest that this process is enhanced by learning words by hand.

The above interpretation is supported by data from neuropsychological studies on writing disorders showing that damage to the left SPL can cause pure apraxic agraphia (English: Alexander et al., 1992; Auerbach & Alexander, 1981; Japanese: Otsuki, Soma, Arai, Otsuka, & Tsuji, 1999; Sakurai et al., 2007-patients 3 & 4), a selective impairment of the order of writing strokes in the absence of sensorimotor or linguistic deficits. A lesion of the SPL therefore translates to a sequence motor programming problem (Otsuki et al., 1999; Sakurai et al., 2007; Scarone et al., 2009). The crucial involvement of the left SPL in writing is supported by fMRI studies (Beeson et al., 2010; Brownsett & Wise, 2010; Katanoda et al., 2001; Menon & Desmond, 2001; Nakamura et al., 2000; Segal & Petrides, 2012; Sugihara et al., 2006), and two meta-analyses identified a left anterior SPL/IPS cluster as specific to the motor control process of writing (Planton et al., 2013; Purcell, Turkeltaub, et al., 2011). Its relation to linguistic processing in the course of writing is supported by the finding that direct cortical stimulation of a limited area of the left superior parietal gyrus performed during awake surgery can cause spelling errors (Magrassi, Bongetta, Bianchini, Berardesca, & Arienta, 2010). The SPL could therefore be involved in a more general process of translating language into writing, and has been considered “as an area of high-level motor control which is in an ideal position to interact with different language and motor areas during the act of writing” (Segal & Petrides, 2012, p.320). The left SPL is also one of the three principal regions (with the left middle frontal gyrus and the left mid-fusiform gyrus) commonly activated across different levels of processing in Chinese: orthographic, semantic and phonological (Booth et al., 2006; Kuo et al., 2001; Lee et al., 2004; Siok et al., 2004; Wu et al., 2012). Its significant involvement in the present reading task, and in the writing localizer, together with its sensitivity to the training modality is clearly compatible with a greater reactivation of motor knowledge in the course of reading when the words were trained via writing.

The response of the left SFS, the other major brain center for the coding of writing movements, varied as a function of the generalization factor, but differently for characters trained by hand than by pronunciation. When characters were produced by hand, the activation of this region remained stable across trained and novel characters. In contrast, for characters learned through pronunciation, activation of the SFS dropped sharply for novel characters. The peak coordinates of this effect are strikingly close to the peak coordinates of both the writing localizer and previously reported activations of this region in handwriting (Katanoda et al., 2001; Longcamp et al., 2014, 2003; Menon & Desmond, 2001; Planton et al., 2013;

Sugihara et al., 2006), or viewing of characters trained by hand (Longcamp et al., 2008). The analysis of catch trials revealed opposite effects of radical type for novel words, i.e., participants were better at identifying the correct translation for novel words containing a learned semantic than phonetic radical and, conversely, were better at identifying the correct syllable for novel words containing a learned phonetic than semantic radical. This is a strong indication that participants were actively processing the structure of the characters to identify their putative pronunciation or meaning. Hence, learning by hand preferentially activated the left SFS during generalization, possibly in relation to this active encoding mechanism. The level of activation of the left SFS did not vary as a function of training modality in and of itself. This may be due to the linguistic context, which may have promoted a specific activation of this region for all trained characters (indeed, as reported above, the SFS was among the areas of overlap between the reading task and the writing localizer, independently of the experimental manipulations). However, when faced with novel characters, participants apparently relied on their writing experience to facilitate processing and transfer knowledge via the reactivation of graphic movements supported by this region.

The same interaction, between training modality and generalization was also observed in the left primary motor cortex, at the level of the hand knob. The involvement of the primary motor cortex in the present reading task, indicating an actual simulation of hand movements, was not expected but is nonetheless in line with Cao, Vu, et al. (2013).

4.4 Response of the left mid-fusiform gyrus

Interestingly, when we compared the writing and pronunciation localizer tasks, we found that despite equivalent visual stimulation, the writing task led to stronger activation of the left fusiform gyrus. An activation peak was also present at a comparable location in the reading task. This finding is in line with the hypothesis of overlapping neural correlates of orthographic processing in reading and writing (Purcell & Rapp, 2013; Rapp & Lipka, 2011). However, the neuroanatomical position of this activation remains clearly distinct from the classically reported occipito-temporal brain center for reading in the mid-fusiform gyrus, that is much more lateral (Devlin et al., 2006; Jobard et al., 2003; McCandliss, Cohen, & Dehaene, 2003; Nakamura et al., 2012; Price, 2012; Rapp & Lipka, 2011). In addition, we found no significant effect of the experimental variables in the reading task in close proximity to this region. Conversely, when a region of interest was defined in the mid-fusiform gyrus according to the reading literature, we found that it displayed a greater response to characters trained by hand than to characters trained through pronunciation. This supports the idea that reading newly learned characters draws upon specific writing knowledge, and confirms the results of James and Atwood (2009) in adults, and James

(2010) in children who showed that the fusiform response to newly learned single characters is influenced by the associated motor knowledge. According to Li and James (2016), handwriting enhances the link between the visual and motor systems by providing the visual system variable instances of a given character, a process that could reinforce the representation of the characters. In similar fashion, Yu, Gong, Qiu, & Zhou (2011) showed that the order of presentation of the sequence of strokes of Chinese characters affects the left fusiform response. This area may therefore be sensitive to the dynamic information encoding of Chinese, implicitly present in written characters (see also Qiu & Zhou, 2010, in an ERP protocol). This finding, combined with ours, suggests a top-down influence of motor reactivation on mid-fusiform activity (Price, 2012). Previous studies, showing increased activation in this region (Cao, Vu, et al., 2013), have also suggested that handwriting learning might increase the quality of orthographic representations.

In addition to the main effect of training modality, the left mid-fusiform cortex displayed sensitivity to the interaction between linguistic properties and novelty. Activation was greater for novel than trained characters that contained learned semantic radicals but did not vary as a function of novelty for words that contained learned phonetic radicals. This result, showing an effect of linguistic properties of stimuli clearly questions the hypothesis that the fusiform area is solely linked to “visual” processing. Rather, the fusiform may play a far more complex role in linguistic processing than feedforward orthographic processing (Devlin et al., 2006; Tsapkini & Rapp, 2010). A generalization effect in this region was previously described by Deng et al. (2008), who also observed greater activation in the left mid-fusiform when subjects read characters with semantically related radicals. They compared their findings to those of Xue, Chen, Jin, & Dong (2006), who found stronger activation for an artificial logographic language than for Chinese in the left fusiform gyrus. They proposed that such was due to a familiarity effect: the left fusiform gyrus could be preferentially activated for less familiar (difficult) characters. Indeed, many studies have suggested that this area may act as an interface between visual form information and higher-order stimulus properties (Devlin et al., 2006; Tsapkini & Rapp, 2010). Our data clearly supports this view, and indicates that the left mid-fusiform could be a point of convergence between stored visual, motor and linguistic information linked to words during reading.

4.5 Brain activation differences between learned and novel characters

Overall, trained characters' led to greater activation of a part of the left inferior frontal gyrus (pars opercularis) that belongs to the pronunciation network, and in the right cerebellum, which belongs to the handwriting network. The left IFG is among the regions that are consistently activated in various reading tasks (Jobard et al., 2003). Recent work suggests that this activation reflects rapid access to articulatory codes triggered by word presentation (Klein et al., 2015), but only when the task requires explicit naming of

the words. This interpretation is consistent with the fact that, given the uncertainty associated with the occurrence and nature of the catch trials, participants systematically accessed the phonological (and semantic) content of the characters. However, this process was not enhanced when characters were trained by pronunciation.

Concerning the activation of the right cerebellum that overlaps with the writing localizer, the very same region is regularly reported as specifically involved in the motor control of writing (Planton et al., 2013; Purcell, Turkeltaub, et al., 2011) for dominant right handed individuals. Traditionally, the cerebellum has been associated with the planning and coordinating movements, as well as with the visuospatial control of gestures (Horowitz, Gallea, Najee-ullah, & Hallett, 2013). Research on motor learning has long underlined its role in motor memory consolidation (Shadmehr & Holcomb, 1997). Our finding of stronger activation of the cerebellum for trained than for novel characters could be an indication of possible simulation of hand movements in the course of memory consolidation of trained characters. However, the processes underlain by the cerebellar activation did not depend on the type of training experience with the characters. In fact, a growing number of observations suggest that higher level language tasks, both verbal and written, engage the right lateral posterior cerebellum (Mariën et al., 2014), and its role in reading has already been discussed following the findings of abnormal cerebellar involvement in dyslexic adults (Nicolson et al., 1999; Nicolson & Fawcett, 2011). The present result supports the idea that the right cerebellum is involved in learning to read (Mariën et al., 2014), perhaps through its broader role in language processing, including writing.

Finally, the data also revealed the involvement of the right middle temporal gyrus, which showed overlapping activation in the writing localizer and the reading task, which was more strongly activated for novel than for trained characters. This region has been associated with visuospatial processing of logographic systems in both reading (Buchweitz, Mason, Hasegawa, & Just, 2009; Kuo et al., 2001; Matsuo et al., 2003; Nakamura et al., 2000; Tan, Laird, et al., 2005) and writing (Katanoda et al., 2001). Katanoda et al. (2001) found, for instance, activation of the right temporal gyrus in handwriting. This was reported when writing was compared to tapping, but not when it was compared to naming. Katanoda et al. (2001) proposed that this structure is “associated with various visual processes required for the identification” of characters. Rao and Singh (2015), observed a similar pattern when subjects read Hindi/Devanagari, and more so for visually complex than for simple words. This also agrees with the finding of stronger activation of the right middle temporal gyrus during visual processing of handwritten letters, the latter posing a greater challenge to identify compared to standard printed letters (Longcamp et al., 2011). In addition, as stated by Longcamp et al. (2011), this activation can also be interpreted as corresponding to MT/V5, which in primates contains neurons that are sensitive to the direction and velocity of visual-motion (Albright, Desimone, & Gross, 1984).

Some studies indicate that V5/MT activation can be triggered in the absence of actual visual motion if the static stimulus implies motion (Dumoulin et al., 2000; Watson et al., 1993). In Longcamp et al. (2014), the right middle temporal gyrus was among the regions that responded as a function of writing duration. Activation increased with movement duration, most likely because of the longer online visual processing of the dynamical visual feedback of the writing gesture. Our finding that the activation of the right temporal gyrus was stronger for novel than for trained characters may be related to the difficulty in visually processing the novel characters and/or the lack of expertise of our native French speakers as concerns reading Chinese. The right hemisphere is more involved in reading for younger and less skilled readers, and lower accuracy is correlated with greater activation in the right middle temporal gyrus (Chou et al., 2006; see also Shaywitz et al., 2002).

5 Conclusion

We measured the brain signal evoked by reading words and by handwriting in the same participants, and we evidenced overlapping neural substrates between reading and motor processing involved in writing in the air with the index finger. Our study also points towards several regions comprised in the writing network whose fine-grained response to the experimental manipulations reveals that the neural substrates of writing are differentially involved in reading depending on the stored knowledge for words. Stored knowledge also impacts the response of the left mid-fusiform, confirming its involvement as the brain region where linguistic, visual and sensorimotor information converge during orthographic processing, and of the left inferior frontal gyrus, whose activation is stronger for learned words relative to novel words, in a location common with the activation triggered by pronouncing words.

ACKNOWLEDGMENTS

This research, carried out within the Labex BLRI (ANR-11-LABX-0036), has benefited from support from the French government, managed by the French National Agency for Research (ANR), under the project title Investments of the Future A*MIDEX (ANR-11-IDEX-0001-02). We thank Justine Romolacci-Velay for help in the training sessions.

REFERENCES

- Albright, T. D., Desimone, R., & Gross, C. G. (1984). Columnar organization of directionally selective cells in visual area MT of the macaque. *Journal of Neurophysiology*, *51*(1), 16-31.
- Alexander, M. P., Friedman, R. B., Loverso, F., & Fischer, R. S. (1992). Lesion localization of phonological agraphia. *Brain and Language*, *43*(1), 83-95.
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32-46. <http://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Anderson, S. W., Damasio, A. R., & Damasio, H. (1990). Troubled letters but not numbers. Domain specific cognitive impairments following focal damage in frontal cortex. *Brain: A Journal of Neurology*, *113* (Pt 3), 749-766. <http://doi.org/http://dx.doi.org/10.1093/brain/113.3.749>
- Auerbach, S. H., & Alexander, M. P. (1981). Pure agraphia and unilateral optic ataxia associated with a left superior parietal lobule lesion. *Journal of Neurology, Neurosurgery, and Psychiatry*, *44*(5), 430-432.
- Beeson, P. M., Rapcsak, S., Plante, E., Chargualaf, J., Chung, A., Johnson, S., & Trouard, T. (2010). The neural substrates of writing: A functional magnetic resonance imaging study. *Aphasiology*, *17*(6-7), 647-665. <http://doi.org/10.1080/02687030344000067>
- Berninger, V., Whitaker, D., & Feng, Y. (1996). Assessment of planning, translating, and revising in junior high writers, *34*(1), 23-52.
- Bolger, D. J., Perfetti, C. A., & Schneider, W. (2005). Cross-cultural effect on the brain revisited: Universal structures plus writing system variation. *Human Brain Mapping*, *25*(1), 92-104. <http://doi.org/10.1002/hbm.20124>
- Booth, J. R., Lu, D., Burman, D. D., Chou, T.-L., Jin, Z., Peng, D.-L., ... Liu, L. (2006). Specialization of phonological and semantic processing in Chinese word reading. *Brain Research*, *1071*(1), 197-207. <http://doi.org/10.1016/j.brainres.2005.11.097>
- Brownsett, S. L. E., & Wise, R. J. S. (2010). The Contribution of the Parietal Lobes to Speaking and Writing. *Cerebral Cortex*, *20*(3), 517-523. <http://doi.org/10.1093/cercor/bhp120>
- Buchweitz, A., Mason, R. A., Hasegawa, M., & Just, M. A. (2009). Japanese and English sentence reading comprehension and writing systems: An fMRI study of first and second language effects on brain activation. *Bilingualism: Language and Cognition*, *12*(2), 141_151. <http://doi.org/10.1017/S1366728908003970>
- Cao, F., Khalid, K., Lee, R., Brennan, C., Yang, Y., Li, K., ... Booth, J. R. (2011). Development of brain networks involved in spoken word processing of Mandarin Chinese. *NeuroImage*, *57*(3), 750-759. <http://doi.org/10.1016/j.neuroimage.2010.09.047>
- Cao, F., Khalid, K., Zaveri, R., Bolger, D. J., Bitan, T., & Booth, J. R. (2010). Neural correlates of priming effects in children during spoken word processing with orthographic demands. *Brain and Language*, *114*(2), 80-89. <http://doi.org/10.1016/j.bandl.2009.07.005>
- Cao, F., Rickles, B., Vu, M., Zhu, Z., Chan, D. H. L., Harris, L. N., ... Perfetti, C. A. (2013). Early stage visual-orthographic processes predict long-term retention of word form and meaning: a visual encoding training study. *Journal of Neurolinguistics*, *26*(4), 440-461. <http://doi.org/10.1016/j.jneuroling.2013.01.003>
- Cao, F., Vu, M., Chan, D. H. L., Lawrence, J. M., Harris, L. N., Guan, Q., ... Perfetti, C. A. (2013). Writing affects the brain network of reading in Chinese: a functional magnetic resonance imaging study. *Human Brain Mapping*, *34*(7), 1670-1684. <http://doi.org/10.1002/hbm.22017>

- Chan, D. W., Ho, C. S.-H., Tsang, S.-M., Lee, S.-H., & Chung, K. K. (2006). Exploring the reading–writing connection in Chinese children with dyslexia in Hong Kong - Springer. *Reading and Writing*, 19(6), 543-561.
- Chou, T.-L., Booth, J. R., Bitan, T., Burman, D. D., Bigio, J. D., Cone, N. E., ... Cao, F. (2006). Developmental and skill effects on the neural correlates of semantic processing to visually presented words. *Human Brain Mapping*, 27(11), 915-924. <http://doi.org/10.1002/hbm.20231>
- Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Filho, G. N., Jobert, A., ... Cohen, L. (2010). How Learning to Read Changes the Cortical Networks for Vision and Language. *Science*, 330(6009), 1359-1364. <http://doi.org/10.1126/science.1194140>
- Deng, Y., Booth, J. R., Chou, T.-L., Ding, G.-S., & Peng, D.-L. (2008). Item-specific and generalization effects on brain activation when learning Chinese characters. *Neuropsychologia*, 46(7), 1864-1876. <http://doi.org/10.1016/j.neuropsychologia.2007.09.010>
- Devlin, J. T., Jamison, H. L., Gonnerman, L. M., & Matthews, P. M. (2006). The role of the posterior fusiform gyrus in reading. *Journal of Cognitive Neuroscience*, 18(6), 911-922. <http://doi.org/10.1162/jocn.2006.18.6.911>
- Dumoulin, S. O., Bittar, R. G., Kabani, N. J., Baker, C. L., Goualher, G. L., Pike, G. B., & Evans, A. C. (2000). A New Anatomical Landmark for Reliable Identification of Human Area V5/MT: a Quantitative Analysis of Sulcal Patterning. *Cerebral Cortex*, 10(5), 454-463. <http://doi.org/10.1093/cercor/10.5.454>
- Duvernoy, H. M., & Bourgouin, P. (1999). *The Human Brain: Surface, Three-dimensional Sectional Anatomy with MRI, and Vascularization*. Springer Science & Business Media.
- Flores d'Arcais. (1994). Order of strokes writing as a cue for retrieval in reading chinese characters. *European Journal of Cognitive Psychology*, 6(4), 337-355. <http://doi.org/10.1080/09541449408406519>
- Friston, K. J., Holmes, A. P., Poline, J.-B., Grasby, P. J., Williams, S. C. R., Frackowiak, R. S. J., & Turner, R. (1995). Analysis of fMRI Time-Series Revisited. *NeuroImage*, 2(1), 45-53. <http://doi.org/10.1006/nimg.1995.1007>
- Guan, C. Q., Liu, Y., Chan, D. H. L., Ye, F., & Perfetti, C. A. (2011). Writing strengthens orthography and alphabetic-coding strengthens phonology in learning to read Chinese. *Journal of Educational Psychology*, 103(3), 509-522. <http://doi.org/10.1037/a0023730>
- Guan, C. Q., Perfetti, C. A., & Meng, W. (2015). Writing quality predicts Chinese learning. *Reading and Writing*, 28(6), 763-795. <http://doi.org/10.1007/s11145-015-9549-0>
- Han, Z., & Bi, Y. (2009). Oral spelling and writing in a logographic language: insights from a Chinese dysgraphic individual. *Brain and Language*, 110(1), 23-28. <http://doi.org/10.1016/j.bandl.2008.12.002>
- Horowitz, S. G., Gallea, C., Najee-ullah, M. 'Ali, & Hallett, M. (2013). Functional Anatomy of Writing with the Dominant Hand. *PLoS ONE*, 8(7). <http://doi.org/10.1371/journal.pone.0067931>
- Hutton, C., Bork, A., Josephs, O., Deichmann, R., Ashburner, J., & Turner, R. (2002). Image Distortion Correction in fMRI: A Quantitative Evaluation. *NeuroImage*, 16(1), 217-240. <http://doi.org/10.1006/nimg.2001.1054>
- Ihnen, S. K. Z., Petersen, S. E., & Schlaggar, B. L. (2015). Separable Roles for Attentional Control Sub-Systems in Reading Tasks: A Combined Behavioral and fMRI Study. *Cerebral Cortex*, 25(5), 1198-1218. <http://doi.org/10.1093/cercor/bht313>
- Ishihara, K., Ichikawa, H., Suzuki, Y., Shiota, J. 'ichi, Nakano, I., & Kawamura, M. (2010). Is lesion of Exner's area linked to progressive agraphia in amyotrophic lateral sclerosis with dementia? An autopsy case

- report. *Behavioural Neurology*, 23(3), 153-158. <http://doi.org/10.3233/BEN-2010-0276>
- James, K. H. (2010). Sensori-motor experience leads to changes in visual processing in the developing brain. *Developmental Science*, 13(2), 279-288. <http://doi.org/10.1111/j.1467-7687.2009.00883.x>
- James, K. H., & Atwood, Thea, 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(1). Consulté à l'adresse <http://www.tandfonline.com/doi/abs/10.1080/02643290802425914>
- James, K. H., & Engelhardt, L. (2012). The effects of handwriting experience on functional brain development in pre-literate children. *Trends in Neuroscience and Education*, 1(1), 32-42. <http://doi.org/10.1016/j.tine.2012.08.001>
- James, K. H., & Gauthier, I. (2006). Letter processing automatically recruits a sensory-motor brain network. *Neuropsychologia*, 44(14), 2937-2949. <http://doi.org/10.1016/j.neuropsychologia.2006.06.026>
- James, K. H., & Gauthier, I. (2009). When writing impairs reading: Letter perception's susceptibility to motor interference. *Journal of Experimental Psychology: General*, 138(3), 416-431. <http://doi.org/10.1037/a0015836>
- Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: a meta-analysis of 35 neuroimaging studies. *NeuroImage*, 20(2), 693-712. [http://doi.org/10.1016/S1053-8119\(03\)00343-4](http://doi.org/10.1016/S1053-8119(03)00343-4)
- Katanoda, K., Yoshikawa, K., & Sugishita, M. (2001). A functional MRI study on the neural substrates for writing. *Human Brain Mapping*, 13(1), 34-42. <http://doi.org/10.1002/hbm.1023>
- Kato, C., Isoda, H., Takehara, Y., Matsuo, K., Moriya, T., & Nakai, T. (1999). Involvement of motor cortices in retrieval of kanji studied by functional MRI. *Neuroreport*, 10(6), 1335-1339.
- Kersey, A. J., & James, K. H. (2013). Brain activation patterns resulting from learning letter forms through active self-production and passive observation in young children. *Frontiers in Psychology*, 4. <http://doi.org/10.3389/fpsyg.2013.00567>
- Klein, M., Grainger, J., Wheat, K. L., Millman, R. E., Simpson, M. I. G., Hansen, P. C., & Cornelissen, P. L. (2015). Early Activity in Broca's Area During Reading Reflects Fast Access to Articulatory Codes From Print. *Cerebral Cortex (New York, N.Y.: 1991)*, 25(7), 1715-1723. <http://doi.org/10.1093/cercor/bht350>
- Kuo, W.-J., Yeh, T.-C., Duann, J.-R., Wu, Y.-T., Ho, L.-T., Hung, D. L., ... Hsieh, J.-C. (2001). A left-lateralized network for reading Chinese words: a 3 T fMRI study. *NeuroReport*, 12(18), 3997-4001. <http://doi.org/10.1.1.10.6160>
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., ... Fox, P. T. (2000). Automated Talairach Atlas labels for functional brain mapping. *Human Brain Mapping*, 10(3), 120-131. [http://doi.org/10.1002/1097-0193\(200007\)10:3<120::AID-HBM30>3.0.CO;2-8](http://doi.org/10.1002/1097-0193(200007)10:3<120::AID-HBM30>3.0.CO;2-8)
- Lee, C.-Y., Tsai, J.-L., Kuo, W.-J., Yeh, T.-C., Wu, Y.-T., Ho, L.-T., ... Hsieh, J.-C. (2004). Neuronal correlates of consistency and frequency effects on Chinese character naming: an event-related fMRI study. *NeuroImage*, 23(4), 1235-1245. <http://doi.org/10.1016/j.neuroimage.2004.07.064>
- Li, J. X., & James, K. H. (2016). Handwriting generates variable visual output to facilitate symbol learning. *Journal of Experimental Psychology: General*, 145(3), 298-313. <http://doi.org/10.1037/xge0000134>
- Li, P., Legault, J., & Litcofsky, K. A. (2014). Neuroplasticity as a function of second language learning: Anatomical changes in the human brain. *Cortex*, 58, 301-324. <http://doi.org/10.1016/j.cortex.2014.05.001>
- 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(4), 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(12), 1801-1809. <http://doi.org/10.1016/j.neuropsychologia.2005.01.020>
- Longcamp, M., Boucard, C., Gilhodes, J.-C., Anton, J.-L., Roth, M., Nazarian, B., & Velay, J.-L. (2008). Learning through hand- or typewriting influences visual recognition of new graphic shapes: behavioral and functional imaging evidence. *Journal of Cognitive Neuroscience*, 20(5), 802-815. <http://doi.org/10.1162/jocn.2008.20504>
- Longcamp, M., Boucard, C., Gilhodes, J.-C., & Velay, J.-L. (2006). Remembering the orientation of newly learned characters depends on the associated writing knowledge: a comparison between handwriting and typing. *Human Movement Science*, 25(4-5), 646-656. <http://doi.org/10.1016/j.humov.2006.07.007>
- Longcamp, M., Hlushchuk, Y., & Hari, R. (2011). What differs in visual recognition of handwritten vs. printed letters? An fMRI study. *Human Brain Mapping*, 32(8), 1250-1259. <http://doi.org/10.1002/hbm.21105>
- Longcamp, M., Lagarrigue, A., Nazarian, B., Roth, M., Anton, J.-L., Alario, F.-X., & Velay, J.-L. (2014). Functional specificity in the motor system: Evidence from coupled fMRI and kinematic recordings during letter and digit writing. *Human Brain Mapping*, 35(12), 6077-6087. <http://doi.org/10.1002/hbm.22606>
- Magrassi, L., Bongetta, D., Bianchini, S., Berardesca, M., & Arienta, C. (2010). Central and peripheral components of writing critically depend on a defined area of the dominant superior parietal gyrus. *Brain Research*, 1346, 145-154. <http://doi.org/10.1016/j.brainres.2010.05.046>
- Mariën, P., Ackermann, H., Adamaszek, M., Barwood, C. H. S., Beaton, A., Desmond, J., ... Ziegler, W. (2014). Consensus Paper: Language and the Cerebellum: an Ongoing Enigma. *Cerebellum (London, England)*, 13(3), 386-410. <http://doi.org/10.1007/s12311-013-0540-5>
- Matsuo, K., Kato, C., Okada, T., Moriya, T., Glover, G. H., & Nakai, T. (2003). Finger movements lighten neural loads in the recognition of ideographic characters. *Brain Research. Cognitive Brain Research*, 17(2), 263-272. [http://doi.org/10.1016/S0926-6410\(03\)00114-9](http://doi.org/10.1016/S0926-6410(03)00114-9)
- McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, 7(7), 293-299. [http://doi.org/10.1016/S1364-6613\(03\)00134-7](http://doi.org/10.1016/S1364-6613(03)00134-7)
- Menon, V., & Desmond, J. E. (2001). Left superior parietal cortex involvement in writing: integrating fMRI with lesion evidence. *Cognitive Brain Research*, 12(2), 337-340. [http://doi.org/10.1016/S0926-6410\(01\)00063-5](http://doi.org/10.1016/S0926-6410(01)00063-5)
- Molfese, V. J., Beswick, J., Molnar, A., & Jacobi-Vessels, J. (2006). Alphabetic Skills in Preschool: A Preliminary Study of Letter Naming and Letter Writing. *Developmental Neuropsychology*, 29(1), 5-19. http://doi.org/10.1207/s15326942dn2901_2
- Nakamura, K., Honda, M., Okada, T., Hanakawa, T., Toma, K., Fukuyama, H., ... Shibasaki, H. (2000). Participation of the left posterior inferior temporal cortex in writing and mental recall of kanji orthography. *Brain*, 123(5), 954-967. <http://doi.org/10.1093/brain/123.5.954>
- Nakamura, K., Kuo, W.-J., Pegado, F., Cohen, L., Tzeng, O. J. L., & Dehaene, S. (2012). Universal brain systems for recognizing word shapes and handwriting gestures during reading. *Proceedings of the National Academy of Sciences*, 109(50), 20762-20767. <http://doi.org/10.1073/pnas.1217749109>
- Nicolson, R. I., & Fawcett, A. J. (2011). Dyslexia, dysgraphia, procedural learning and the cerebellum. *Cortex*, 47(1), 117-127. <http://doi.org/10.1016/j.cortex.2009.08.016>
- Nicolson, R. I., Fawcett, A. J., Berry, E. L., Jenkins, I. H., Dean, P., & Brooks, D. J. (1999). Association of abnormal cerebellar activation with motor learning difficulties in dyslexic adults. *The Lancet*,

353(9165), 1662-1667. [http://doi.org/10.1016/S0140-6736\(98\)09165-X](http://doi.org/10.1016/S0140-6736(98)09165-X)

- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97-113.
- Otsuki, M., Soma, Y., Arai, T., Otsuka, A., & Tsuji, S. (1999). Pure apraxic agraphia with abnormal writing stroke sequences: report of a Japanese patient with a left superior parietal haemorrhage. *Journal of Neurology, Neurosurgery, and Psychiatry*, 66(2), 233-237.
- Perfetti, C. A., & Tan, L.-H. (2013). Write to read: the brain's universal reading and writing network. *Trends in Cognitive Sciences*, 17(2), 56-57. <http://doi.org/10.1016/j.tics.2012.12.008>
- Perfetti, C., Cao, F., & Booth, J. (2013). Specialization and Universals in the Development of Reading Skill: How Chinese Research Informs a Universal. *Scientific studies of reading : the official journal of the Society for the Scientific Study of Reading*, 17(1), 5-21. <http://doi.org/10.1080/10888438.2012.689786>
- Planton, S., Jucla, M., Roux, F.-E., & Démonet, J.-F. (2013). The « handwriting brain »: a meta-analysis of neuroimaging studies of motor versus orthographic processes. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, 49(10), 2772-2787. <http://doi.org/10.1016/j.cortex.2013.05.011>
- Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage*, 62(2), 816-847. <http://doi.org/10.1016/j.neuroimage.2012.04.062>
- Purcell, J. J., Napoliello, E. M., & Eden, G. F. (2011). A combined fMRI study of typed spelling and reading. *NeuroImage*, 55(2), 750-762. <http://doi.org/10.1016/j.neuroimage.2010.11.042>
- Purcell, J. J., & Rapp, B. (2013). Identifying functional reorganization of spelling networks: an individual peak probability comparison approach. *Frontiers in Psychology*, 4. <http://doi.org/10.3389/fpsyg.2013.00964>
- Purcell, J. J., Turkeltaub, P. E., Eden, G. F., & Rapp, B. (2011). Examining the central and peripheral processes of written word production through meta-analysis. *Frontiers in Psychology*, 2, 239. <http://doi.org/10.3389/fpsyg.2011.00239>
- Qiu, Y., & Zhou, X. (2010). Perceiving the writing sequence of Chinese characters: An ERP investigation. *NeuroImage*, 50(2), 782-795. <http://doi.org/10.1016/j.neuroimage.2009.12.003>
- Rao, C., & Singh, N. C. (2015). Visuospatial complexity modulates reading in the brain. *Brain and Language*, 141, 50-61. <http://doi.org/10.1016/j.bandl.2014.11.010>
- Rapp, B., & Lipka, K. (2011). The Literate Brain: The Relationship between Spelling and Reading. *Journal of Cognitive Neuroscience*, 23(5), 1180-1197. <http://doi.org/10.1162/jocn.2010.21507>
- Roeltgen, D. P. (2003). *Agraphia* (Oxford University Press, USA, Vol. Fourth Edition). Kenneth M. Heilman, M.D.; Edward Valenstein, M.D.
- Roux, F.-E., Draper, L., Köpke, B., & Démonet, J.-F. (2010). Who actually read Exner? Returning to the source of the frontal « writing centre » hypothesis. *Cortex*, 46(9), 1204-1210. <http://doi.org/10.1016/j.cortex.2010.03.001>
- Sakurai, Y., Onuma, Y., Nakazawa, G., Ugawa, Y., Momose, T., Tsuji, S., & Mannen, T. (2007). Parietal Dysgraphia: Characterization of Abnormal Writing Stroke Sequences, Character Formation and Character Recall. *Behavioural Neurology*, 18(2), 99-114. <http://doi.org/10.1155/2007/906417>
- Scarone, P., Gatignol, P., Guillaume, S., Denvil, D., Capelle, L., & Duffau, H. (2009). Agraphia after awake surgery for brain tumor: new insights into the anatomo-functional network of writing. *Surgical Neurology*, 72(3), 223-241; discussion 241. <http://doi.org/10.1016/j.surneu.2008.10.074>

- Segal, E., & Petrides, M. (2012). The anterior superior parietal lobule and its interactions with language and motor areas during writing. *European Journal of Neuroscience*, *35*(2), 309-322. <http://doi.org/10.1111/j.1460-9568.2011.07937.x>
- Seitz, R. J., Canavan, A. G. M., Yágüez, L., Herzog, H., Tellmann, L., Knorr, U., ... Hömberg, V. (1997). Representations of Graphomotor Trajectories in the Human Parietal Cortex: Evidence for Controlled Processing and Automatic Performance. *European Journal of Neuroscience*, *9*(2), 378-389. <http://doi.org/10.1111/j.1460-9568.1997.tb01407.x>
- Shadmehr, R., & Holcomb, H. H. (1997). Neural Correlates of Motor Memory Consolidation. *Science*, *277*(5327), 821-825. <http://doi.org/10.1126/science.277.5327.821>
- Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Mencl, W. E., Fulbright, R. K., Skudlarski, P., ... Gore, J. C. (2002). Disruption of posterior brain systems for reading in children with developmental dyslexia. *Biological Psychiatry*, *52*(2), 101-110. [http://doi.org/10.1016/S0006-3223\(02\)01365-3](http://doi.org/10.1016/S0006-3223(02)01365-3)
- Siok, W. T., Perfetti, C. A., Jin, Z., & Tan, L. H. (2004). Biological abnormality of impaired reading is constrained by culture. *Nature*, *431*, 71-76. <http://doi.org/10.1038/nature02865>
- Sugihara, G., Kaminaga, T., & Sugishita, M. (2006). Interindividual uniformity and variety of the « Writing center »: a functional MRI study. *NeuroImage*, *32*(4), 1837-1849. <http://doi.org/10.1016/j.neuroimage.2006.05.035>
- Tan, L. H., Laird, A. R., Li, K., & Fox, P. T. (2005). Neuroanatomical correlates of phonological processing of Chinese characters and alphabetic words: A meta-analysis. *Human Brain Mapping*, *25*(1), 83-91. <http://doi.org/10.1002/hbm.20134>
- Tan, L. H., Liu, H.-L., Perfetti, C. A., Spinks, J. A., Fox, P. T., & Gao, J.-H. (2001). The Neural System Underlying Chinese Logograph Reading. *NeuroImage*, *13*, 836-846. <http://doi.org/10.1006/nimg.2001.074>
- Tan, L. H., Spinks, J. A., Eden, G. F., Perfetti, C. A., & Siok, W. T. (2005). Reading depends on writing, in Chinese. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(24), 8781-8785. <http://doi.org/10.1073/pnas.0503523102>
- Tan, L. H., Spinks, J. A., Feng, C.-M., Siok, W. T., Perfetti, C. A., Xiong, J., ... Gao, J.-H. (2003). Neural systems of second language reading are shaped by native language. *Human Brain Mapping*, *18*(3), 158-166. <http://doi.org/10.1002/hbm.10089>
- Teulings, H.-L., Contreras-Vidal, J. L., Stelmach, G. E., & Adler, C. H. (1997). Parkinsonism Reduces Coordination of Fingers, Wrist, and Arm in Fine Motor Control. *Experimental Neurology*, *146*(1), 159-170. <http://doi.org/10.1006/exnr.1997.6507>
- Tsapkini, K., & Rapp, B. (2010). The orthography-specific functions of the left fusiform gyrus: Evidence of modality and category specificity. *Cortex*, *46*(2), 185-205. <http://doi.org/10.1016/j.cortex.2009.02.025>
- Watson, J. D. G., Myers, R., Frackowiak, R. S. J., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., ... Zeki, S. (1993). Area V5 of the Human Brain: Evidence from a Combined Study Using Positron Emission Tomography and Magnetic Resonance Imaging. *Cerebral Cortex*, *3*(2), 79-94. <http://doi.org/10.1093/cercor/3.2.79>
- Wu, C.-Y., Ho, M.-H. R., & Chen, S.-H. A. (2012). A meta-analysis of fMRI studies on Chinese orthographic, phonological, and semantic processing. *NeuroImage*, *63*(1), 381-391. <http://doi.org/10.1016/j.neuroimage.2012.06.047>
- 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*(3), 1315-1326. <http://doi.org/10.1016/j.neuroimage.2005.11.055>
- Yu, H., Gong, L., Qiu, Y., & Zhou, X. (2011). Seeing Chinese characters in action: an fMRI study of the

Corresponding author : Aurelie Lagarrigue

perception of writing sequences. *Brain and Language*, 119(2), 60-67.
<http://doi.org/10.1016/j.bandl.2010.11.007>