Research report

How specialized are *writing-specific* brain regions? An fMRI study of writing, drawing and oral spelling

Samuel Planton [a,b,c], Marieke Longcamp [d], Patrice Péran [a], Jean-François Démonet [e] and Mélanie Jucla [b,*]

[a] *Toulouse NeuroImaging Center, ToNIC, Université de Toulouse, Inserm, UPS, France*
[b] *URI Octogone-Lordat (EA 4156), Université de Toulouse (UT2), Toulouse, France*
[c] *CNRS, Aix Marseille Université, Laboratoire Parole & Langage, UMR 7309, Aix-en-Provence, France*
[d] *CNRS, Aix Marseille Université, LNC, UMR 7291, FR 3C FR 3512, Marseille, France*
[e] *Centre Leenaards de la Mémoire, CHUV & Université de Lausanne, Lausanne, Switzerland*

ARTICLE INFO

ABSTRACT

Several brain imaging studies identified brain regions that are consistently involved in writing tasks; the left premotor and superior parietal cortices have been associated with the peripheral components of writing performance as opposed to other regions that support the central, orthographic components. Based on a meta-analysis by Planton, Jucla, Roux, and Demonet (2013), we focused on five such *writing areas* and questioned the task-specificity and hemispheric lateralization profile of the brain response in an functional magnetic resonance imaging (fMRI) experiment where 16 right-handed participants wrote down, spelled out orally object names, and drew shapes from object pictures. All writing-related areas were activated by drawing, and some of them by oral spelling, thus questioning their specialization for written production. The *graphemic/motor frontal area* (GMFA), a subpart of the superior premotor cortex close to Exner's area (Roux et al., 2009), was the only area with a *writing-specific* lateralization profile, that is, clear left lateralization during handwriting, and bilateral activity during drawing. Furthermore, the relative lateralization and levels of activation in the superior parietal cortex, ventral premotor cortex, ventral occipitotemporal cortex and right cerebellum across the three tasks brought out new evidence regarding their respective contributions to the writing processes.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Handwriting is an acquired composite ability involving visuospatial and motor skills that make it possible to map abstract orthographic representations to grapho-motor traces distributed in 2D space. Aside from classical neuropsychological studies, recent neuroimaging studies uncovered the different neural territories involved in this interfacing motor/linguistic network, i.e., regions that likely orchestrate the

---

interplay between the peripheral and the central components of written language production processes. A recent meta-analysis identified 12 distinct areas, some of which appeared consistently and significantly activated during writing relative to motor or linguistic control tasks; Planton, Jucla, Roux, and Demonet (2013). The posterior part of the left superior frontal sulcus, also known as the *graphemic/motor frontal area* (GMFA) and very close to the historically defined Exner's area (Roux, Draper, Kopke, & Démonet, 2010; Roux et al., 2009), and the left superior parietal cortex (superior parietal lobule − SPL, or anterior part of the intraparietal sulcus − IPS) have been repeatedly associated with writing, sometimes being referred to as "writing-specific" (Katanoda, Yoshikawa, & Sugishita, 2001; Menon & Desmond, 2001; Rapp & Dufor, 2011; Roux et al., 2009; Sugihara, Kaminaga, & Sugishita, 2006), based on their preferential response to writing relative to various motor or linguistic control tasks (see Kanwisher, 2010 for a definition of functional specificity).

Calling a brain region "specific of" is not uncommon in neurological or neuropsychological literature when a brain lesion is shown to affect a particular task but not other related tasks. The neuropsychological studies have indeed shown that left frontal superior or parietal superior lesions can lead to a writing-specific disorder or *pure agraphia syndrome* (Alexander, Fischer, & Friedman, 1992; Auerbach & Alexander, 1981; Otsuki, Soma, Arai, Otsuka, & Tsuji, 1999; Roeltgen, 2003). These findings have been extended by direct cortical stimulation studies (Lubrano, Roux, & Demonet, 2004; Magrassi, Bongetta, Bianchini, Berardesca, & Arienta, 2010; Roux et al., 2009). However, contrary to other language related functions such as letter identification (see C. Pernet, Schyns, & Demonet, 2007), writing is a more complex and composite process that relies on a variety of components (from visual control to hand control and orthographic/allographic interface) so that there is no straightforward strategy to address specificity issues vis a vis the neural substrates that likely orchestrate these various processes.

Nevertheless, the exact function of the GMFA and the IPS/SPL in the control of handwriting is still a matter of debate. In a meta-analysis of neuroimaging experiments, focusing on the distinction between central and peripheral processes, Purcell, Turkeltaub, Eden, and Rapp (2011) included these areas in a peripheral writing network, as they are only minimally active during orthographic tasks that do not require actual motor control (e.g., rhyme detection task). Rapp and Dufor (2011), however, have suggested that these areas play a central functional role in orthography-specific working memory (i.e., the graphemic buffer). These authors found that activity in these two regions was modulated by word length (for letters) − an effect that was especially significant in the GMFA. The IPS/SPL is often described as being involved in visuospatial or sensorimotor processing in writing, but a role in high-level motor control in connection with language areas has also been proposed (Segal & Petrides, 2012). In any case, the regularity with which these two areas are found to be activated in neuroimaging studies of writing leaves little doubt about their crucial role for writing. This core of evidence often leads to the conclusion that these brain regions display a relative specialization for writing. In skilled writers, these brain regions that

also support more general functions, such as motor control and orthographic processing, might have become, through learning and experience, finely tuned to the combination of processes necessary for writing to be achieved at expert level (or to writing-specific cognitive processes such as allographic selection, graphomotor planning for letters), leading to the "task-specific" consequences of a cerebral lesion.

Here our objective was to further understand the functional role of these so-called "writing-specific regions" by using an experimental design in which (i) we controlled for the peripheral and central contributions in the experimental tasks and (ii) we explored these effects in previously identified regions of interest that likely underpin writing-related cognitive components according to Planton et al. meta-analysis. Therefore, we designed an functional magnetic resonance imaging (fMRI) experiment where we compared handwritten picture naming with two closely-related cognitive tasks that also require the processing and recognition of visually presented objects and the production of a motor output, namely oral spelling (i.e., using speech instead of handwriting to produce the series of letters that form the name of the object), and object line drawing (i.e., reproducing the general shape of a visually presented object, as an analogical, rather than symbolic, manual outline of this object). We adopted a volume-of-interest (VOI) approach, focusing on three areas described as crucial for handwriting by Planton et al. (2013): the GMFA, the IPS/SPL and the posterior cerebellum (postCB), together with two other regions associated with handwriting and whose function remains unclear: the left ventral pre-motor area (vPM); a region reported to be involved in either phonological processing (Omura, Tsukamoto, Kotani, Ohgami, & Yoshikawa, 2004), orthographic lexical access (Rapp & Dufor, 2011; Rapp & Lipka, 2011), or the storage of motor representations of letters (Longcamp, Anton, Roth, & Velay, 2003, 2005); and the posterior inferior temporal cortex (or visual word form area − VWFA), thought to be involved in the storage or recovery of the *visual graphic images* of words (Beeson et al., 2003; Nakamura et al., 2000, 2002; Rapcsak & Beeson, 2004).

Oral spelling shares several processes with writing as the retrieval of orthographic representations and their transient storage in the graphemic buffer. It is the only language task that recruits the graphemic buffer independently of graphic output (Bonin, 2003; Hillis & Caramazza, 1989; Rapp, Epstein, & Tainturier, 2002; see Fig. 1). To our knowledge, oral spelling has not yet been addressed in neuroimaging experiments in healthy participants. Since the GMFA and IPS/SPL have been associated with the graphemic buffer during writing (Rapp & Dufor, 2011), the observation of joint activation in these areas during oral spelling and writing would lend support to the hypothesis that both tasks involve a common graphemic buffer. This would more generally demonstrate that activity in these regions is independent of motor output, thus support a *central* more than a *peripheral* process.

Like handwriting, drawing involves several visual motor components that are not related to language, such as fast and precise coordination of several fingers, wrist and arm movements to control the size and speed of strokes, plan sequential actions, and manage visual landmarks and hand placement in space. To the aim of controlling for the motor aspect of written
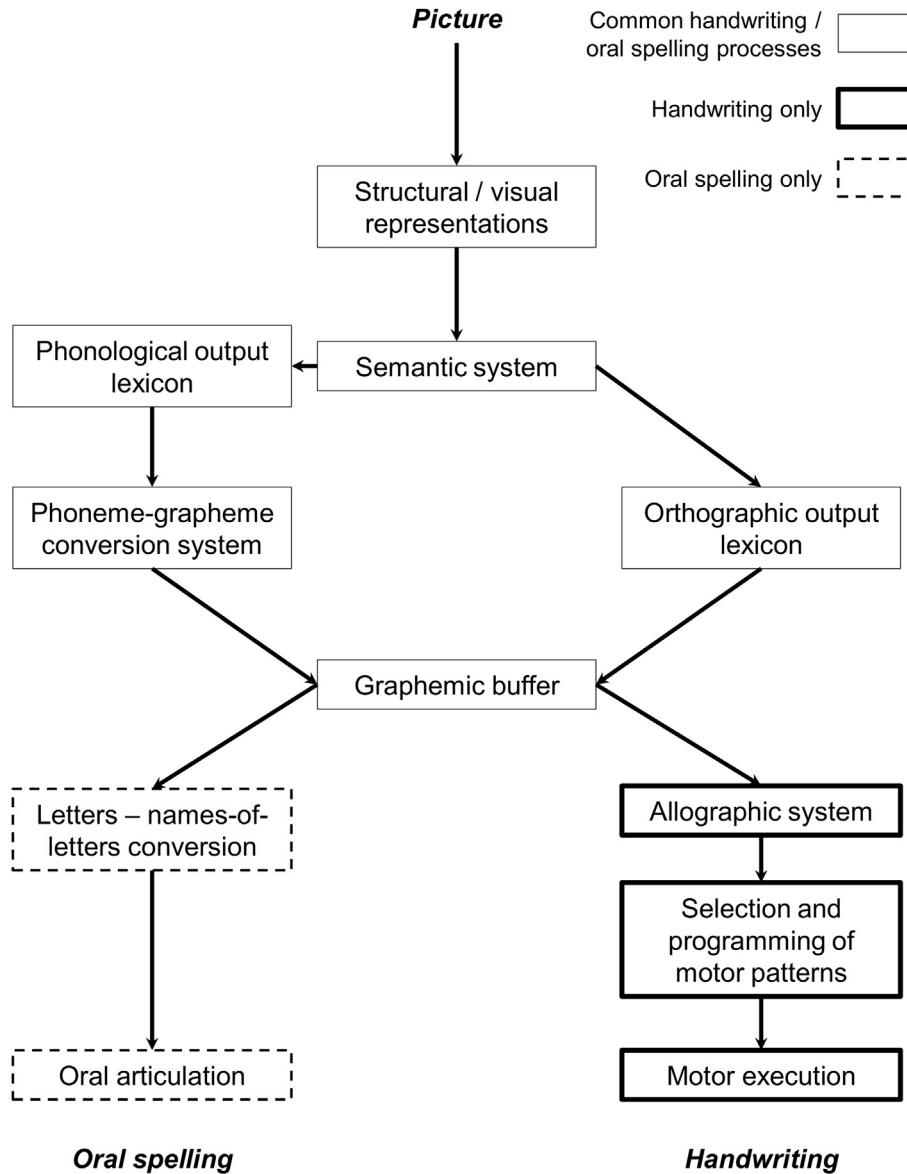
Fig. 1 — Cognitive processes involved in oral spelling and handwriting from a picture (adapted from Bonin, 2003).

production tasks, most of published neuroimaging studies of handwriting used motor (e.g., finger tapping) or graphomotor (e.g., repetitive drawing of circles) tasks that are very simple and/or rapidly automated. By contrast, drawing can be said to be just as complex as handwriting, in terms of motor control, although it does not result from as intensive and highly standardized learning and daily use as written production. Interestingly, the few studies to have focused on the brain substrates of nonlinguistic drawing tasks (e.g., clock drawing test, drawing of simple geometric shapes or objects) have revealed activation of frontoparietal networks similar to those that are activated during writing tasks, involving the superior parietal cortex, supplementary motor area, dorsal premotor and ventral premotor cortices, and cerebellum (Ferber, Mraz, Baker, & Graham, 2007; Gowen & Miall, 2006; Ino, Asada, Ito, Kimura, & Fukuyama, 2003; Makuuchi, Kaminaga, & Sugishita, 2003; Miall, Gowen, & Tchalenko, 2009). In the same way as the VWFA is activated by a number of higher-

order, vision-related processes other than reading (e.g., Mei et al., 2010; Price & Devlin, 2003), the above listed dorsal and action-related cortical regions may be recruited, though to a different extent, not only by handwriting but also by these nonlinguistic, higher-order motor tasks. Another important feature of parietofrontal brain activation during drawing is that it is mainly bilateral (Makuuchi et al., 2003). Unlike agraphia, which results from lesions in the left hemisphere in the vast majority of right-handed patients (Roeltgen, 2003), constructive apraxia (a motor and/or visuospatial deficit), involving disturbance of drawing (either after a model or spontaneously), can be caused by unilateral posterior lesions in one or other hemisphere (Gainotti, 1985; Laeng, 2006; Piercy, Hecaen, & De Ajuriaguerra, 1960). Here, in addition to directly comparing the task-related levels of activation in the selected VOIs, we therefore made the assumption that distinct, task-dependent asymmetries in handwriting areas during written naming versus the two comparison tasks would be an

indicator of the actual functional specificity of these areas. We expected to establish different task-related profiles of their lateralization, depending on the task being performed and their alleged role (i.e., central, peripheral or *writing-specific*).

2. Materials and method

2.1. Participants

Sixteen healthy native French speakers took part in the study (eight women, eight men; mean age: 25.3 ± 6.0 years). All participants were in good physical condition, exempt from brain damage, neurological or psychiatric disorders, had no major visual or hearing impairment, and no reading or writing deficits (e.g., dyslexia). All of them were right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971) mean score: +.84 ± .11. All participants gave their written informed consent before participating. The study was approved by the local ethics committee (CPP Sud-Ouest et Outre-Mer I, France).

2.2. Experimental design and tasks

The fMRI session consisted of two identical 15-min runs separated by a pause. Each one featured the same three tasks presented one after the other in a block design: a drawing task (reproduction of a visually presented picture), a written naming task and an oral spelling naming task. In all these tasks, each trial (70 trials per task) lasted 5000 msec (4000-msec picture display and 1000-msec fixation/intertrial interval). Each experimental block lasted 25 sec (5 trials) and was followed by a 20-sec rest block (passive fixation cross). Experimental blocks were preceded by a visual instruction (i.e., "DRAW", "WRITE" or "SPELL"). Stimulus presentation was synchronized with the acquisition of functional images using Presentation Software V. 14.8 (Neurobehavioral Systems).

In the written naming task, participants had to write the name of the object in the picture they were shown, using a pen on an MRI-compatible digitizing tablet, while fixating the picture (to avoid eye movements) and minimizing the movements of their upper arm and forearm. Their forearm rested on the edge of the tablet so that only the pen tip came into contact with the tablet. In order to minimize the biases associated with residual movements, head movement parameters were subsequently used as regressors in the data analysis model. Participants were instructed to write in their usual writing style, in lowercase cursive script. They did not receive any visual feedback on their production.

In the oral spelling task, participants were instructed simply to spell out loud the name of the object in the picture.

In the drawing task, participants had to roughly reproduce the picture shown on the screen using as few strokes as possible, while fixating the picture and minimizing upper arm and forearm movements.

Previous to the scanning session, participants underwent a training session to familiarize them with the procedure, namely, the visual stimuli, timings, and, in particular, handwriting or drawing while lying on their back and without looking at their hand. One important objective of the training session was to ensure that participants' productions had

similar durations across tasks (as we wished to limit the influence of the motor execution duration when interpreting the tasks-related effects on the BOLD signal). Each participant received systematic feed-back on performance timing from experimenters during training (e.g., "please put less details in your drawing", "you don't have to spell out so fast", etc.).

2.3. Stimuli

Stimuli were black-and-white line drawings, representing various easily identifiable everyday objects or animals, that had been selected from Alario and Ferrand (1999) database. For the written naming and oral spelling tasks, 70 pictures were selected for high naming agreement (i.e., degree to which individuals agree on the name of the picture: 96.3%) and according to the linguistic properties of the target word (mean number of letters: 5.7 ± 1.0, mean lexical frequency: 23.0 occurrences per hundred million). These stimuli (among others) had previously been used in a preliminary written naming test out of the scanner, in which a different group of 15 volunteers just had to quickly write the names of the objects in 100 drawings (displayed one after the other). The success rate for these drawings (which included the 70 pictures we selected for the current experiment) was 93.4% (i.e., correct choice of name and correct spelling). We therefore expected to find a similar result for the current experiment. Each participant had to write half of these 70 stimuli and orally spell out the other half in the first run of the scanning session, and vice versa in the second run. Several orders of presentation were constructed and counterbalanced across participants.

Stimuli for the drawing task were 35 line drawings taken from the same database (Alario and Ferrand, 1999).These were mainly selected for their low visual complexity (1.9 on a 5-point scale). Consequently, items from the drawing task and the written and oral tasks were not matched on visual complexity (which was higher for the latter two). The same stimuli had to be drawn in the first and second runs, but they were presented in a different pseudorandom order.

The full list of stimuli is provided in the Appendix.

2.4. MRI acquisition

Acquisition was performed with a Philips Achieva® (3T) MRI system equipped with a 32-channel SENSE head antenna. The visual stimuli were displayed via a Toshiba projector combined with a translucent screen. Noise-canceling headphones and earplugs were used as protection against the noise of the MRI acquisition. The digitizing tablet (Mag Design and Engineering) was placed obliquely above the waist of participants, allowing them to write with the pen provided. A high-resolution 3D anatomical scan was acquired for each participant at the beginning of the session, consisting of 170 T1-weighted images [TR = 8.2 msec, TE = 3.8 msec, flip angle = 8°, field of view (FOV) = 240 × 240 mm, voxel size = 1 mm³]. The functional images were then acquired with an echoplanar imaging (EPI) sequence (TR = 2500 msec, TE = 30 msec, flip angle = 90°, FOV = 224 × 236 mm). Each volume was composed of 44 axial slices covering the whole brain (slice thickness: 3 mm, slice dimensions: 76 × 79 pixels, voxel size: 2.95 × 2.95 × 3 mm).

2.5.   Data processing and contrasts

Data analysis was performed using SPM12b software (Wellcome Department of Imaging Neuroscience, London, UK, http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks, USA). Preprocessing of the EPI images included realignment, normalization to Montreal Neurological Institute (MNI) standard space, based on the deformation field resulting from the segmentation of the high-resolution structural image, coregistered onto the mean functional image, and smoothing with an 8-mm^3 full width at half maximum (FWHM) Gaussian kernel.

First- and second-level statistical analyses were performed using the general linear model (GLM) approach (Friston et al., 1994). The three conditions (drawing, written naming, oral spelling) were modeled at the first level with boxcar functions convolved with the canonical hemodynamic response function (HRF). The six motion parameters derived from the realignment step were included in the model as regressors of noninterest (to avoid artifacts due to participants moving in the scanner). A high-pass filter of 270 sec was used to filter the data (i.e., suppression of frequencies below ~3.7 MHz).

Contrasts corresponding to the activation for each of the three conditions (beta images) were created for each subject individually and then brought to the second level in a random effects group analysis in order to create the contrasts of interest (i.e., written naming vs drawing, written naming vs oral spelling and inverse contrasts). Whole-brain t-tests contrasts, comparing statistical maps between all three conditions, were conducted using a threshold of $p < .05$ voxel-wise corrected using Family Wise Error (FWE) correction. The anatomical location of significant clusters was determined using the xjView 8 toolbox for SPM (AAL atlas; Cui, Li, & Song, 2011). Group statistics maps were superimposed onto a standardized template for visualization with MRIcron (Rorden & Brett, 2000). Conjunction contrasts (method conjunction null) between written naming and drawing and between written naming and oral spelling were also conducted in order to locate regions with common activations.

2.6.   VOI analyses

In order to consider the activation of our regions of interest (i.e., writing areas) in each task, we extracted mean percent signal change for each participant and each task from five spherical (diameter: 8-mm) VOIs. Spheres were constructed according to coordinates originating from an earlier meta-analysis (Planton et al., 2013). The VOIs corresponded to the left IPS/SPL (MNI coordinates of center: −32, −38, 56), left GMFA (i.e., SFS, −22, −8, 54), left vPM (−50, 6, 26), left VWFA (−46, −62, −12) and right postCB (4, −66, −16). We conducted five repeated-measures analysis of variances (ANOVAs) on the task factor to compare the magnitude of activation (i.e., % signal change) of each VOI for each task (i.e., drawing vs written naming vs oral spelling). p Values were Bonferroni corrected. Tukey's HSD test was used for post hoc comparisons.

In the second step, to examine the lateralization of activation, we first extracted the mean percent signal change from five additional VOIs: right IPS/SPL (32, −38, 56), right GMFA (26, 0, 54), right vPM (50, 6, 26), right VWFA (−46, −62, −12) and left postCB (−4, −66, −16). While the coordinates for the right GMFA were directly obtained from a previous study (GMFA has been considered as a bilateral area; Planton et al., 2013; Roux et al., 2009), in the four other cases, the right (or left) counterpart was simply derived from the original writing area by multiplying the x coordinate by −1 (see Fig. 2). It should be noted that we decided to keep the whole sphere volumes for the right and left postCB VOIs even though they overlapped.

We then calculated a laterality index (LI) for each participant and each (pair of) VOIs for each task according to the following formula: $LI = 100 * \frac{LH - RH}{|LH| + |RH|}$, where LH represents the mean % signal change value for the left counterpart of each area and RH the mean % signal change value for the right counterpart. For each area and each task, a mean LI significantly above 20 was deemed to express left-sided dominance (t values were computed), while a LI significantly below −20 reflected right-sided dominance (such threshold is the most commonly used in the lateralization literature, see Seghier, 2008). In addition, when the mean LI was above 20 (or below −20), we used a T-test for single means to ensure that the observed mean was significantly above (or below) the value chosen as standard reference (i.e., 20 or −20). This procedure was applied as a way to take into account the between subjects variance rather than an effect at the group average level.

2.7.   Individual peaks

Since the first VOI analysis did not take into account potential inter-individual variability in the location of the writing areas
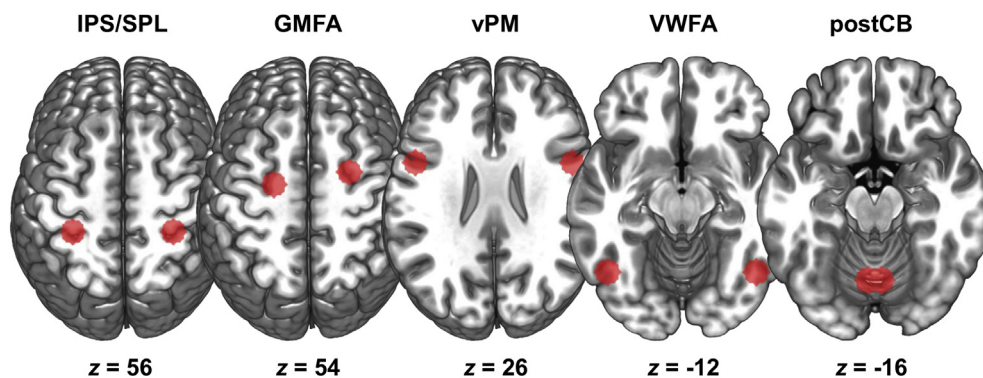

IPS/SPL   **GMFA**   **vPM**   **VWFA**   **postCB**

z = 56   *z = 54*   *z = 26*   *z = -12*   *z = -16*

Fig. 2 − Top view of the five spherical VOIs used to calculate laterality indices.

we conducted an additional analysis on a subject-by-subject basis. For each subject, we first identified the peaks corresponding to each of the five areas of interest by identifying the closest peak to the aforementioned coordinates within a "Written naming > Baseline" contrast, thresholded at $p < .05$ (FWE-corr). In order to simply determine whether these "writing peaks" were also activated during drawing and oral spelling, the activation of the considered voxel was then examined in the "Drawing > Baseline" and "Oral spelling > Baseline" contrasts, using the same threshold. We chose to restrict our investigations to a single voxel since averaging within a group of voxels may mask task-related differences when activations are close to each other (i.e., neighboring but non-overlapping cortical regions), which was another potential source of bias in the previous analysis.

3. Results

3.1. Behavioral results

Reaction times (RTs) and production durations (PDs) were collected from all trials in the written naming and drawing tasks thanks to a digitizing tablet. Since we did not use a voice recording device during the oral spelling task, behavioral data were not available for this task. Possible spelling errors were not taken into consideration for the writing task either since it was often difficult to establish their presence with certainty (due to the particular writing style of each participant in script mode and the lack of quality of the data provided by the tablet) and since only a low amount could be expected (see Section 2.3). For analyses of RTs and PDs we first rejected trials with RTs lower than 500 msec or higher than 2500 msec (5.69%), since abnormally short RTs could occur when the wrist of the subject unintentionally came into contact with the tablet, making both RT and PD invalid. For the analysis of PDs we additionally rejected PDs lower than 1000 msec (additional 1.09% of trials). Repeated-measures ANOVAs did not show any significant effect of task (written naming vs drawing), neither on RTs (written naming: 1240 msec, SD = 101 msec vs drawing: 1199 msec, SD = 117 msec); $F(1, 15) = 1.76$, $p = .204$, or on PDs (written naming: 2272 msec, SD = 202 msec vs drawing: 2184 msec, SD = 182 msec); $F(1, 15) = 2.79$, $p = .116$.

3.2. Neuroimaging contrasts and conjunctions

Fig. 3a shows the results for the contrast between writing the name of pictures and drawing pictures ($p < .05$, FWE). Activations were located in the cuneus/precuneus, middle temporal gyrus, and angular gyrus bilaterally, the right cerebellum and calcarine fissure. In order to determine whether these activities were consistent with the global writing network, the Written naming versus Drawing contrast was computed again using an inclusive Written naming versus Baseline ($p < .001$, uncorrected) mask. Only one small cluster survived the mask, located on the right calcarine fissure (BA 17, $x = 18$, $y = -93$, $z = -3$).

Results from the drawing versus written naming contrast are presented in Fig. 3b ($p < .05$, FWE). Activations were located in a bilateral network involving parietal superior and inferior,

occipitotemporal and frontal superior regions. Unilateral activations were also observed in the right ventral premotor cortex and the left cerebellum.

The conjunction between writing and drawing tasks (Fig. 4a) revealed a mainly left lateralized network involving the left primary motor and sensori-motor cortices, left superior parietal cortex, left supplementary motor area, left superior and ventral premotor cortex, right (and to a lesser extent left) cerebellum, bilateral occipital and ventral occipitotemporal cortex.

Fig. 3c and d shows results for the written naming versus oral spelling and oral spelling versus writing contrasts, revealing in the first case a likely hand motor network centered on the left postcentral gyrus (BA4) and involving right cerebellum and subcortical regions (thalamus, caudate nucleus), and in the second case a bilateral frontal inferior/temporal superior network.

In order to identify regions involved in the central processing of stimuli, followed by either a manual or an articulatory motor output (i.e., both perceptive and linguistic processes, including orthographic ones), we computed the conjunction between writing and oral spelling tasks (see Fig. 4b). Regions of common activation ($p < .05$, FWE) were located in the bilateral postCB, occipital cortex, and supplementary motor area. Smaller clusters were also present in the left middle/ventral premotor cortex. With a lower statistical threshold (voxel-wise $p < .001$ uncorrected), premotor activation extended to the most part of the precentral gyrus up to the pars opercularis of the inferior frontal gyrus, and another cluster emerged in the ventral occipitotemporal cortex, close to the VWFA ($x = -45$, $y = -57$, $z = -12$).

3.3. VOI and individual peaks analyses

3.3.1. Left-hemisphere and cerebellar writing areas VOIs
The main effect of task in the repeated-measures ANOVAs conducted on % signal change for each VOI was significant for the left IPS/SPL, $F(2, 30) = 89.3$, $p_{corr} < .0001$, left GMFA, $F(2, 30) = 20.94$, $p_{corr} < .0001$, and left VWFA, $F(2, 30) = 9.14$, $p_{corr} < .01$, but not for the left vPM, $F(2, 30) = 4.16$, $p_{corr} = .13$, and right postCB, $F(2, 30) = 2.72$, $p_{corr} = .41$ (see Fig. 5).

Post hoc analyses for the left IPS/SPL VOI revealed that the mean % signal change was lower during oral spelling than during both drawing ($p < .0001$) and written naming ($p < .0001$). Similarly, the % signal change in the left GMFA VOI was lower during oral spelling than during either drawing ($p < .0001$) or written naming ($p < .002$). In this region, the mean % signal change was also higher during drawing than during written naming ($p < .05$). Finally, for the left VWFA VOI, the mean % signal change was higher during drawing than during either oral spelling ($p < .002$) or written naming ($p < .005$).

3.3.2. Left-hemisphere individual peaks
We were able to identify a peak for each of our five regions of interest in the "Writing > Baseline" ($p < .05$, FWE-corr) for each of our participant (see axial slices on Fig. 6), with the exception of the subject 1, who did not show any significant activation in the VWFA (i.e., the peak closest to the coordinates of the VWFA was located in the cerebellum). As it can be seen on Fig. 6, for all five regions, the voxel identified in the writing
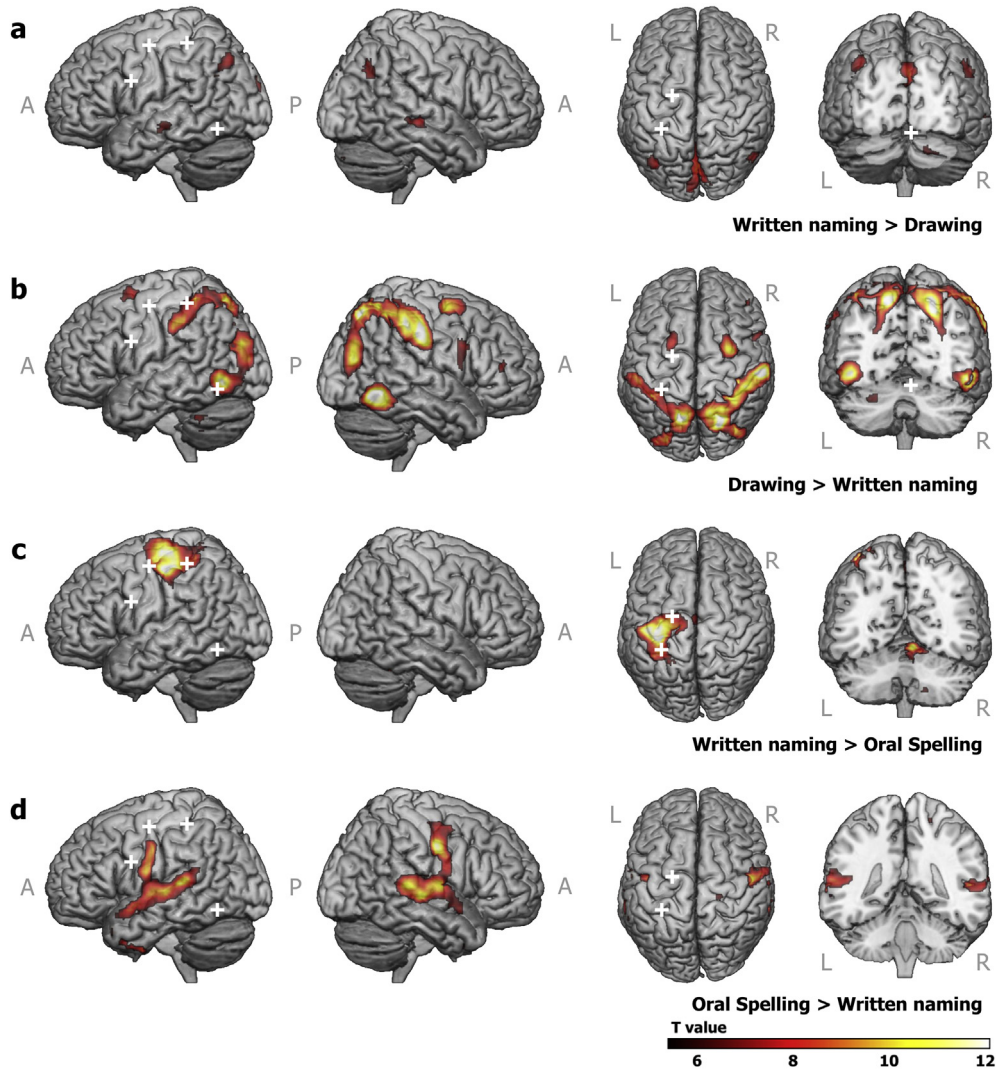
Fig. 3 – Activation maps for the main contrasts of interest (*p* < .05, FWE). Surface projections of the coordinates used to create the six VOIs are represented by white crosses when applicable.
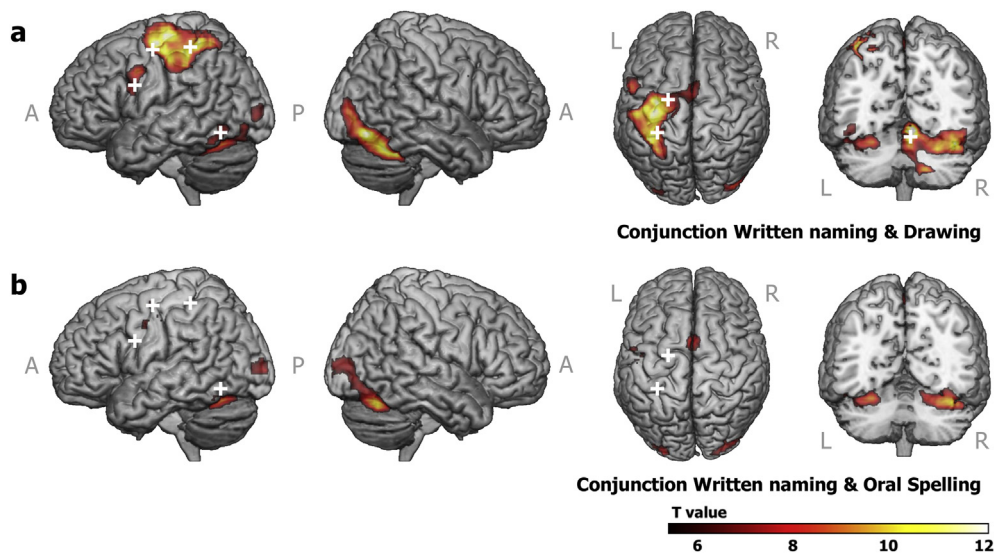

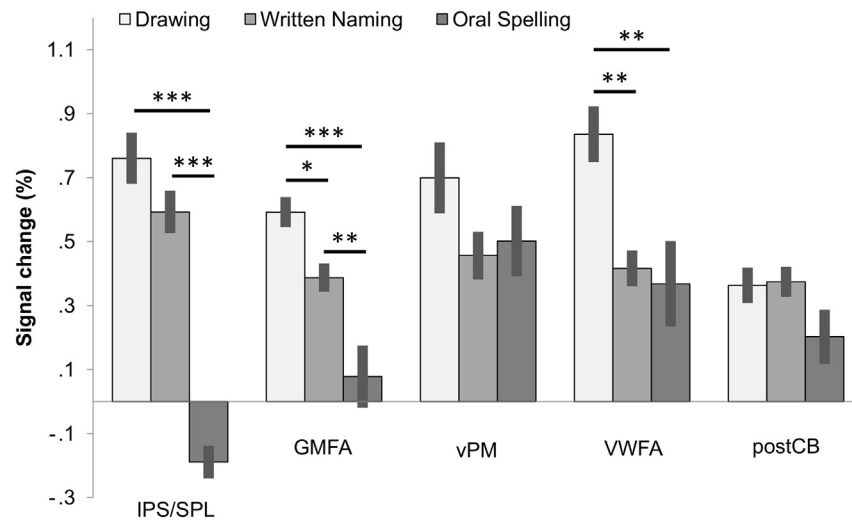Fig. 4 – Activation maps for the conjunction analyses (*p* < .05, FWE).

Fig. 5 — Mean activation (% signal change) within each unilateral VOI for each task. The error bars represent the standard errors of the mean. ***p < .001. **p < .01. *p < .05.

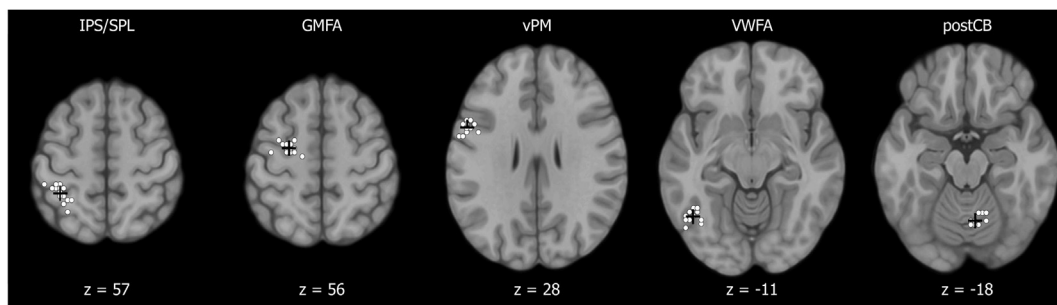| Written naming peak:	IPS/SPL		GMFA		vPM		VWFA		postCB	
Subject	Drawing	Oral Spelling	Drawing	Oral Spelling	Drawing	Oral Spelling	Drawing	Oral Spelling	Drawing	Oral Spelling
1	**	n.s.	**	n.s.	**	**	N.A.	N.A.	**	n.s.
2	**	**	**	*	**	**	**	n.s.	**	n.s.
3	**	n.s.	**	n.s.	n.s.	**	**	*	**	n.s.
4	**	*	**	*	**	*	**	*	**	n.s.
5	**	n.s.	**	**	**	**	**	**	**	**
6	**	n.s.	**	*	**	n.s.	**	n.s.	**	n.s.
7	**	n.s.	**	*	**	**	**	**	**	n.s.
8	**	n.s.	**	n.s.	**	*	**	n.s.	**	n.s.
9	**	n.s.	**	n.s.	**	*	**	**	**	**
10	**	**	**	n.s.	**	n.s.	**	**	**	n.s.
11	**	n.s.	**	n.s.	**	n.s.	**	n.s.	**	n.s.
12	**	n.s.	**	n.s.	**	n.s.	**	**	**	n.s.
13	**	*	**	*	**	**	**	**	**	n.s.
14	**	n.s.	**	n.s.	**	n.s.	**	*	**	n.s.
15	**	**	**	n.s.	**	**	**	**	**	**
16	**	n.s.	**	n.s.	**	n.s.	**	**	**	*

Fig. 6 — Activation of individual peaks from the written naming task during the drawing and the oral spelling task. White circles on axial slices represent individual peaks, black cross represents the centroid. *: voxel significant at p < .05 (FWE-corr); **: voxel significant at p < .001 (FWE-corr); n.s.: non significant; N.A.: not applicable (i.e., no significant activation peak was found for the written naming task).

task was also strongly activated during the drawing task in all subjects (except for the vPM in subject 3). It was not the case for the oral spelling tasks in which significant activations were more generally found for the VWFA (11 on 15 subjects) and the vPM (10 on 16) rather than for the GMFA (6 on 16), the IPS/SPL (5 on 16) or the postCB (4 on 16).

3.3.3. Laterality indices

Examination of the mean LI value showed that the BOLD response in the IPS/SPL was left-lateralized during written naming (LI = 79.6, t = 8.49, p < .0001) and during drawing (LI = 45.7, t = 4.09, p < .001), but bilateral during oral spelling (LI = −1.6) (see Fig. 7).
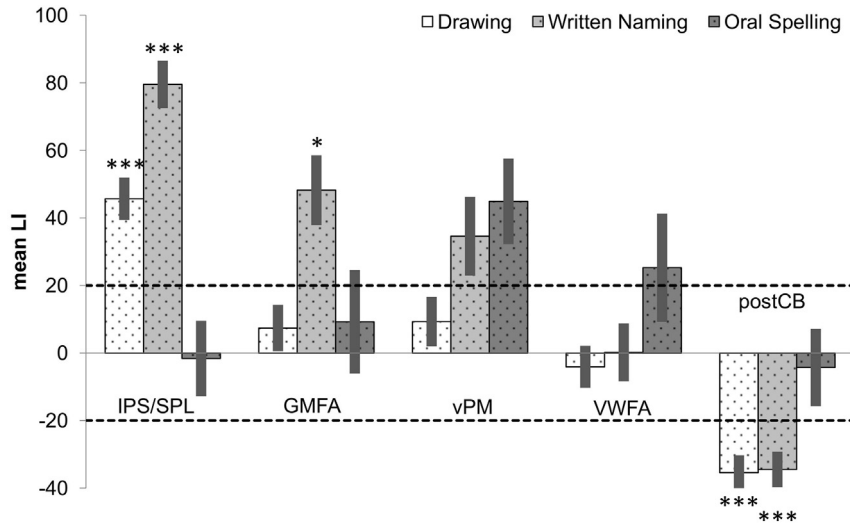
Fig. 7 – Mean LI in each bilateral VOI for each task. Means above 20 were compared with the standard value of 20, and means below −20 were compared with the standard value of −20. The error bars represent the standard errors of the mean. ***$p < .001$. *$p < .05$.

Activity in the GMFA was left-lateralized during written naming (LI = 48.2, $t = 2.73$, $p < .05$), but bilateral during drawing (LI = 7.4) and oral spelling (LI = 9.2).

Activity in the vPM was generally left-lateralized during written naming (LI = 34.6, $t = 1.25$, $p = .23$), but did not reach significance. The same pattern was observed in oral spelling, though with only a marginal effect (LI = 44.9, $t = 1.25$, $p = .07$). It was bilateral during drawing (LI = 9.3).

Activity in the VWFA was bilateral during drawing (LI = −4.1) and written naming (LI = .2), and left-lateralized during oral spelling (LI = 25.3, $t = .33$, $p = .74$), but without reaching significance.

Activity in the postCB was right-lateralized during written naming (LI = −34.5, $t = 6.51$, $p < .0001$), and during drawing (LI = −35.5, $t = 6.85$, $p < .0001$), but bilateral during oral spelling (LI = 9.2).

4.   Discussion

This study was designed to investigate whether the components of the brain network that subtends handwriting, particularly the so-called *writing-specific* areas, are also recruited during a nonlinguistic manual motor task (i.e., the drawing task; similar motor complexity and similar visual attentional coordination of movements) and during a linguistic but nonmanual task (i.e., the oral spelling task; similar orthographic processing). The comparison with the drawing task therefore served to investigate the *peripheral* (i.e., sensorimotor) functions of the handwriting areas, while the comparison with the oral spelling task served to investigate the *central* functions (i.e., lexical-semantic, orthographic processes, down to the graphemic buffer). We found that some of the five *writing VOIs* we selected displayed very similar levels of BOLD activity across tasks, questioning their specialization

to written production. However, such task specificity may relate to the hemispheric lateralization of changes in BOLD activation across VOIs.

4.1.   Common and task-related brain networks

We found first that the drawing and written naming of pictures recruited more or less the same network in our group of right-handed participants, involving the left primary motor and sensorimotor cortex, right cerebellum, left superior parietal cortex, left superior and ventral premotor cortex and bilateral occipital and occipitotemporal regions (see conjunction Fig. 4a). This network, identical to the *handwriting network* described in a previous study by (Planton et al., 2013), with the exception of the occipital activation resulting from the visual nature of the task, cannot therefore be defined as being strictly specific to written language production. Surprisingly, the written naming versus drawing comparison did not reveal the regions assumed to support central linguistic or orthographic processes as we expected (see Fig. 3a). Most of the observed activations, in the cuneus/precuneus and bilateral temporal cortex were outside the "writing network" (as evidenced by a masked contrast, see Section 3.2). They may reflect some degree of deactivation (of different amplitude) in the resting-state or default mode network (DMN; Fox et al., 2005; Raichle et al., 2001), the drawing task being presumably less automated and more costly, in terms of attentional resources, than the writing task in our subjects (decreases in activity of the DMN are assumed to occur during the more attention-demanding tasks). Furthermore, levels of activation in areas identified previously as being strongly specialized for handwriting (i.e., GMFA, IPS/SPL and postCB) were not higher for written naming than for drawing. The brain network for drawing was mainly bilateral (except for the primary motor cortex), whereas the activation for the written naming task

was predominantly left-lateralized. One may argue that these differences only reflect variations in low-level kinematic features. Longcamp et al. (2014), for example, reported substantial modulations in the BOLD signal that were related to variations in the duration of letter writing time. However, we did not observe such differences between tasks when examining the PDs. The latter tended to be actually longer for writing (i.e., 2272 msec vs 2284 msec). Between-subjects and within-subject variations were in addition very small in both tasks (standard deviations did not exceed 10% of the mean). Therefore we hypothesize that the more extensive and stronger activation for drawing relative to written naming (as seen on some of the VOI results) related to difference between tasks in terms of automatization and expertise. Handwriting, which most of us acquired through long-term training, probably generates a lower BOLD signal than does drawing a barely automated task (as recently illustrated, between individuals, with the activity in the foot motor cortex of a famous footballer during foot movements; Naito & Hirose, 2014). As stated above, degree of expertise to a task is also evidently related to the amount of attentional resources required to perform the task.

The topography of activation in the oral spelling task was quite different from that in the written naming task, as the former mainly activated bilateral temporal and inferior premotor regions together with the left pars opercularis-regions associated with word retrieval and speech production (Hickok & Poeppel, 2007; Price, 2012), while the latter was characterized by activations of manual motor and premotor regions of the left hemisphere (see Fig. 3c and d). The oral spelling task was chosen to highlight areas involved in orthographic production, including the graphemic buffer, independently of any manual gesture. Although we did not control for the duration of motor execution (since we did not have audio recordings for the oral task), which may limit the interpretations of variations of activation in motor-related regions, we assumed that linguistic processes prior to the motor response (i.e., retrieval of the orthographic representation from the same picture stimuli) would be broadly similar in both tasks. Joint activations for the handwriting and oral spelling tasks were found in the supplementary motor area, the left ventral premotor cortex and the left ventral occipito-temporal cortex. Interestingly, the two latter activations, although only emerging clearly when lowering the statistical threshold of the conjunction contrast, overlap well with the VWFA and vPM; two areas of the writing network usually associated with central spelling processes. However, these regions were also involved in drawing, thereby casting doubt on their specificity to such functional role.

4.2. The IPS/SPL

The left IPS/SPL or superior parietal cortex is the area most often associated with apraxic agraphia (Alexander et al., 1992; Auerbach & Alexander, 1981; Otsuki et al., 1999; Roeltgen, 2003), and is frequently described as being crucial for handwriting (Katanoda et al., 2001; Sugihara et al., 2006). It has consistently been found to be more strongly activated in handwriting than in simpler motor control tasks (finger tapping, drawing circles, etc.). We found here that the IPS/SPL VOI

we selected was, in fact, similarly activated, in all participants, and similarly left-lateralized during both the drawing of pictures (which we regarded as a nonlinguistic task that did not involve any phono-orthographic processing) and the written naming of words, although the lateralization appeared stronger for handwriting. In addition, it was not significantly activated in the oral spelling task, where hand movements were not required. Thus, contrary to recent studies suggesting a *writing-specific* role or a role of interface between central and peripheral writing processes (Magrassi et al., 2010; Segal & Petrides, 2012), we can only attribute a peripheral role to the IPS/SPL in handwriting (i.e., sensorimotor control of complex gestures; Creem-Regehr, 2009). We suggest that the involvement of this area in handwriting not only relates to written word production per se, but also extends to all sufficiently precise, complex, and non repetitive (i.e., a different word/drawing in each trial) manual tasks. The posterior parietal cortex, and particularly the IPS, has previously been associated with manual activities (e.g., grasping) that require online gesture control (Desmurget et al., 1999; Tunik, Frey, & Grafton, 2005). According to some authors, it may also encode higher-order representations of action goals (Tunik, Rice, Hamilton, & Grafton, 2007).

That said, activations of a broader region of posterior parietal cortex, posterior to the coordinates of the IPS/SPL we studied here (see white crosses on Fig. 3), appeared in fact differently lateralized in our two manual tasks: left-lateralized for written naming and bilateral for drawing (as it can be deduced from Fig. 3b and c). In contrast to handwriting, where the graphic forms of the letters are thought to be retrieved from long-term memory, copying drawings relies much more on visuospatial representations. In drawing, Ogawa and Inui (2009) identified greater bilateral activation in the IPS. This bilaterality may result from the demands of visuomotor co-ordination and visual-attentional control-functions that these regions are known to support (Connolly, Andersen, & Goodale, 2003; Corbetta & Shulman, 2002; Tunik, Ortigue, Adamovich, & Grafton, 2008). These functions are required even in simpler visually guided finger (e.g., Grafton, Mazziota, Woods, & Phelps, 1992) or arm (Buneo & Andersen, 2006) movement tasks. Our data however suggest that the bilateral parietal "drawing" area is rather located in the posterior than in the anterior part of the IPS.

4.3. The GMFA

The left GMFA, located in the posterior part of the superior frontal sulcus, may seem at first glance to have a similar profile of activity to the IPS/SPL: strongly activated during the two manual tasks (especially drawing) but not during the oral task, arguing for a peripheral/motor role rather than for the specific and oft-reported role in written production (Anderson, Damasio, & Damasio, 1990; Exner, 1881; Lubrano et al., 2004; Roux et al., 2009; Sugihara et al., 2006). As for most of our VOIs, the GMFA peak-voxel identified individually during the written naming task was also strongly significant in the drawing task for all participants. However, when we considered its right-sided counterpart, we observed an important difference, depending on the nature of the graphic production: left lateralization for written naming versus

bilateral activity for drawing. The left-sided lateralization of the neural responses to words versus other stimuli was frequently reported in the visual domain (Cohen et al., 2000; Kanwisher, McDermott, & Chun, 1997; Rossion, Joyce, Cottrell, & Tarr, 2003). Such functional lateralization in the ventral occipitotemporal cortex (left hemisphere advantage for visual words vs right sided advantage for faces or objects), is thought to take place progressively during learning and correlate with performance (Dehaene, Cohen, Morais, & Kolinsky, 2015; Dundas, Plaut, & Behrmann, 2013). A similar phenomenon may take place for written word production and, when its interhemispheric balance is considered, the GMFA profile of activation is suggestive of a *writing-specific* area. In our opinion, these results support the existence of a bilateral dorsal premotor area that is generally involved in the preparation or generation of highly coordinated and fine-grained motor commands (as in handwriting, drawing, musical performance or other high-expertise motoric repertoires), possibly serving as an interface between cognitive and motor networks (a role for the rostral premotor cortex asserted by Hanakawa, 2011). In addition, in line with previous findings (Roux et al., 2009), we submit that the left component of this territory has become specialized for generating the motor, allographic correlates of graphemes. The GMFA may also support the temporary storage of allographic schemes so that series of specific graphic motor patterns can be concatenated. This lateralization could arise through frequent interactions with the areas of the left hemisphere that support language processing when learning to write, at least in right-handed individuals. Van Galen (1991) psychomotor model of handwriting did regard the selection of allographs as the temporary activation of abstract motor programs corresponding to their graphemic representations (i.e., in a *motor output buffer*). Furthermore, this role would appear to be consistent with observations of patients with pure agraphia resulting from left frontal lesions, who display normal orthographic (e.g., oral spelling) and drawing skills (e.g., Anderson et al., 1990). In a recent attempt to clarify the neuropsychological dissociation between the writing of letters and the writing of digits (outlined by Anderson et al., 1990) through fMRI, Longcamp et al. (2014) identified the left superior premotor cortex as an area that is preferentially responsive to the writing of letters (as opposed to the writing of digits). This finding reinforces our view of a specialization of this region for graphic motor representations of language content, independently of the low-level features of the gesture that is actually performed. The alternative hypothesis, whereby the GMFA plays a critical role in the graphemic buffer (Rapp & Dufor, 2011), is not supported by our data, as we did not find any significant activation of this area during oral spelling-a task classically thought to require similar orthographic working memory processes (according to classical conceptions; e.g., Rapp et al., 2002). If we exclude the hypothesis of there being two different graphemic buffers (oral and manual) that rely on two different anatomical sites, we can infer that the cognitive function performed by the left GMFA in handwriting is clearly postorthographic, as we argued above, and possibly closer to the *motor output buffer* hypothesized by Van Galen (1991).

4.4. The vPM and VWFA

Of the five writing areas we studied here, the VOIs that exhibited similar levels of BOLD activity during written naming and oral spelling were the left vPM and left VWFA (and, to a lesser extent, the postCB). These two areas were also the ones where most participants showed a significant activation in oral spelling of a peak-voxel first localized in written naming (i.e., 10 participants for the vPM, 11 for the VWFA; see Fig. 6). These results are consistent with the hypothesis that these areas play a phono-orthographic role in central orthographic processes common to both tasks (Omura et al., 2004; Purcell, Napoliello, & Eden, 2011; Rapp & Dufor, 2011; Rapp & Lipka, 2011). However, they were also strongly activated during the non orthographic drawing task. Furthermore, the VWFA was significantly more strongly activated during drawing than during the other two tasks. In our view, the latter could result from the visual nature of the task, as the ventral occipitotemporal cortex, including the fusiform gyrus, has long been described as an extension of the visual system, devoted to identifying different perceptual categories such as faces, objects, colors and, of course, written words (Cohen et al., 2000; Dehaene, Cohen, Sigman, & Vinckier, 2005; Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002; Haxby et al., 2001; Kanwisher et al., 1997; Ungerleider & Haxby, 1994). The absence of any significant lateralization leads us to assume that the activity was vision-related, devoted to object recognition independently of the task, with greater attention being paid to the shape of the object to be reproduced by drawing. In addition, one might reasonably assume that in the writing and spelling tasks, unlike in the drawing task, the visual representations processes are only transiently involved, in the first hundreds of milliseconds, when the recovery of lexical semantic information is required. Interestingly, we only found a trend toward left lateralization, usually regarded as the sign of word processing (Rossion et al., 2003), for the oral spelling task (mean LI = 25.3). This could suggest that participants relied more on visual/orthographic word representations when they had to spell the word orally than when they had to write it down.

The vPM activation observed during drawing has previously been reported for drawing tasks (Harrington, Farias, Davis, & Buonocore, 2007; Ino et al., 2003; Makuuchi et al., 2003; Miall et al., 2009; Schaer, Jahn, & Lotze, 2012). Researchers have suggested that this structure plays a role in semantic access (Harrington et al., 2007), although non linguistic motor functions have also been tentatively attributed to the vPM (overlapping with Broca's area), namely associative sensorimotor learning and sensorimotor integration related to the execution of previously learned complex hand movements [acquired by imitation through the mirror neuron system in this region (e.g., Binkofski & Buccino, 2004; Binkofski & Buccino, 2006)]. The vPM is known to transmit sensorimotor information to the primary motor cortex during hand and finger movements (Chouinard & Paus, 2006), through interconnections with the intraparietal areas providing information for visually guiding the movement (Matelli & Luppino, 2000). However, the vPM activity observed while handling

objects or performing other manual motor tasks is more likely to be bilateral (Binkofski et al., 1999). Although the lack of significance suggests some interindividual variability, the overall tendency towards left lateralization during written naming (LI = 34.6) and oral spelling (LI = 44.9) may thus indicate that its role goes beyond the simple production of manual or articulatory movements, and also relates to the phono-orthographic processes that take place during handwriting. Its location in the left hemisphere, where the parietofrontal sensorimotor systems and language areas (superior temporal gyrus, Broca's area) converge, makes it a good candidate for mediating language-motor transformations in writing (e.g., phoneme-grapheme conversion). The same observation is actually valid for oral spelling, as the vPM has been described as forming part of an auditory(phonological)-motor coordination network in speech (Vigneau et al., 2006).

4.5. The postCB

At least two regions of the right cerebellum are known to be involved in handwriting. We focused on the one located in the central/posterior part, which is viewed to be the most specialized (Katanoda et al., 2001; Planton et al., 2013). As before, we expected that variations in the level of activity or the profile of lateralization across the different tasks would help clarify the nature of its contribution to handwriting. Right cerebellar activation in writing versus motor task contrasts has frequently been regarded as artefactual, arising from the lower motor complexity of the control task (e.g., Katanoda et al., 2001). Our results do not contradict this view, as we found identical levels of activation and laterality profiles in written naming and drawing: a strong signal clearly lateralized to the right, ipsilateral to the hand producing the movement (see conjunction Fig. 4a). Only the oral, non manual, task prompted non lateralized cerebellar activity, consistent with the fact that it is not a lateralized motor activity. Although more diverse cognitive (e.g., language, working memory) or metacognitive (acquiring abilities through automatization) functions cannot be excluded when considering the recent literature on the topic (Murdoch, 2010; Nicolson & Fawcett, 2011; C. R.; Pernet, Poline, Demonet, & Rousselet, 2009; Stoodley & Schmahmann, 2009), we found no evidence of the postCB fulfilling this role during handwriting.

5. Conclusion

The results of our analyses of the BOLD responses of five writing-related areas (i.e., GMFA, IPS/SPL, vPM, VWFA and postCB) during tasks closely related to handwriting (one graphomotor and one orthographic) challenge the assumption of their specialization for written production. The same frontoparietal networks were recruited by the picture drawing, and the specialization for handwriting only emerged through lateralization to the left hemisphere. While it may not be the case of the IPS/SPL and the postCB areas (respectively left- and right-lateralized for both manual tasks), this was much clearer for the GMFA, where left lateralization appears to be a distinguishing feature of word production as opposed to drawing. While additional studies are required to clarify the involvement of the two *central* writing areas, namely the left vPM and left VWFA (two areas also activated when copying a picture), the oral spelling task allowed us to rule out the hypothesis that the GMFA plays a crucial role as a graphemic buffer elicited both by oral spelling and by handwriting.

Appendix. List of items

Writing naming/Oral spelling		Drawing
abeille	aigle	ancre
avion	ampoule	bague
banc	balance	balai
botte	baleine	ballon
brosse	bureau	ballon_2
camion	cage	banana
canard	canon	bouton
carotte	cerveau	bras
chat	cigare	cerise
chemise	cloche	cintre
cheval	crabe	ciseau
clown	cravate	citron
corde	dauphin	clef
crayon	flipper	clou
fraise	gland	Coeur
gant	gorille	couteau
girafe	guitare	drapeau
lapin	hache	igloo
lion	hamac	jambe
loup	harpe	jupe
mouche	marteau	lampe
oiseau	montre	louche
panier	moto	moufle
peigne	moulin	nuage
piano	noeud	orange
poisson	palmier	pied
poule	pinceau	pipe
raisin	plume	poire
renard	prise	pomme
roue	raie	pouce
singe	selle	robe
souris	serpent	soleil
tambour	tableau	tasse
tortue	tigre	tomate
vache	valise	verre

REFERENCES

Alario, F. X., & Ferrand, L. (1999). A set of 400 pictures standardized for French: Norms for name agreement, image agreement, familiarity, visual complexity, image variability,

and age of acquisition. *Behavior Research Methods, Instruments, & Computers, 31*(3), 531–552.

Alexander, M. P., Fischer, R. S., & Friedman, R. (1992). Lesion localization in apractic agraphia. *Archives of Neurology, 49*(3), 246–251.

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, 113*(Pt 3), 749–766.

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., Rapcsak, S., Plante, E., Chargualaf, J., Chung, A., Johnson, S., et al. (2003). The neural substrates of writing: A functional magnetic resonance imaging study. *Aphasiology, 17*(6), 647–665. http://dx.doi.org/10.1080/02687030344000067.

Binkofski, F., & Buccino, G. (2004). Motor functions of the Broca's region. *Brain and Language, 89*(2), 362–369.

Binkofski, F., & Buccino, G. (2006). The role of ventral premotor cortex in action execution and action understanding. *Journal of Physiology-Paris, 99*(4), 396–405.

Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999). A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Experimental Brain Research, 128*(1–2), 210–213.

Bonin, P. (2003). *Production verbale de mots: approche cognitive.* De Boeck.

Buneo, C. A., & Andersen, R. A. (2006). The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia, 44*(13), 2594–2606.

Chouinard, P. A., & Paus, T. (2006). The primary motor and premotor areas of the human cerebral cortex. *The Neuroscientist, 12*(2), 143–152.

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M. A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain, 123*(Pt 2), 291–307.

Connolly, J. D., Andersen, R. A., & Goodale, M. A. (2003). FMRI evidence for a 'parietal reach region' in the human brain. *Experimental Brain Research, 153*(2), 140–145.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*(3), 201–215. http://dx.doi.org/10.1038/nrn755.

Creem-Regehr, S. H. (2009). Sensory-motor and cognitive functions of the human posterior parietal cortex involved in manual actions. *Neurobiology of Learning and Memory, 91*(2), 166–171.

Cui, X., Li, J., & Song, X. (2011). *xjview: a viewing program for SPM.* from http://www.alivelearn.net/xjview8/.

Dehaene, S., Cohen, L., Morais, J., & Kolinsky, R. (2015). Illiterate to literate: Behavioural and cerebral changes induced by reading acquisition. *Nature Reviews Neuroscience, 16*(4), 234–244.

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences, 9*(7), 335–341. http://dx.doi.org/10.1016/j.tics.2005.05.004.

Dehaene, S., Le Clec'H, G., Poline, J.-B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: A prelexical representation of visual words in the fusiform gyrus. *NeuroReport, 13*(3), 321–325.

Desmurget, M., Epstein, C., Turner, R., Prablanc, C., Alexander, G., & Grafton, S. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience, 2*(6), 563–567.

Dundas, E. M., Plaut, D. C., & Behrmann, M. (2013). The joint development of hemispheric lateralization for words and faces. *Journal of Experimental Psychology: General, 142*(2), 348.

Exner, S. (1881). *Untersuchungen über die Localisation der Functionen in der Grosshirnrinde des Menschen.* Braumüller.

Ferber, S., Mraz, R., Baker, N., & Graham, S. J. (2007). Shared and differential neural substrates of copying versus drawing: A functional magnetic resonance imaging study. *NeuroReport, 18*(11), 1089–1093. http://dx.doi.org/10.1097/Wnr.0b013e3281ac2143.

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences of the United States of America, 102*(27), 9673–9678.

Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. P., Frith, C. D., & Frackowiak, R. S. J. (1994). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping, 2*(4), 189–210. http://dx.doi.org/10.1002/hbm.460020402.

Gainotti, G. (1985). Constructional apraxia. *Handbook of Clinical Neurology, 1*(45), 491–506.

Gowen, E., & Miall, R. C. (2006). Eye-hand interactions in tracing and drawing tasks. *Human Movement Science, 25*(4–5), 568–585. http://dx.doi.org/10.1016/j.humov.2006.06.005.

Grafton, S. T., Mazziota, J. C., Woods, R. P., & Phelps, M. E. (1992). Human functional anatomy of visually guided finger movements. *Brain, 115*(2), 565–587.

Hanakawa, T. (2011). Rostral premotor cortex as a gateway between motor and cognitive networks. *Neuroscience Research, 70*(2), 144–154.

Harrington, G. S., Farias, D., Davis, C. H., & Buonocore, M. H. (2007). Comparison of the neural basis for imagined writing and drawing. *Human Brain Mapping, 28*(5), 450–459. http://dx.doi.org/10.1002/hbm.20286.

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science, 293*(5539), 2425–2430.

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience, 8*(5), 393–402. http://dx.doi.org/10.1038/nrn2113.

Hillis, A. E., & Caramazza, A. (1989). The graphemic buffer and attentional mechanisms. *Brain and Language, 36*(2), 208–235.

Ino, T., Asada, T., Ito, J., Kimura, T., & Fukuyama, H. (2003). Parieto-frontal networks for clock drawing revealed with fMRI. *Neuroscience Research, 45*(1), 71–77.

Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences of the United States of America, 107*(25), 11163–11170.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience, 17*(11), 4302–4311.

Katanoda, K., Yoshikawa, K., & Sugishita, M. (2001). A functional MRI study on the neural substrates for writing. *Human Brain Mapping, 13*(1), 34–42.

Laeng, B. (2006). Constructional apraxia after left or right unilateral stroke. *Neuropsychologia, 44*(9), 1595–1606.

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://dx.doi.org/10.1016/j.neuropsychologia.2005.01.020.

Longcamp, M., Lagarrigue, A., Nazarian, B., Roth, M., Anton, J.-L., Alario, F.-X., et al. (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.

Lubrano, V., Roux, F. E., & Demonet, J. F. (2004). Writing-specific sites in frontal areas: A cortical stimulation study. *Journal of Neurosurgery, 101*(5), 787–798. http://dx.doi.org/10.3171/jns.2004.101.5.0787.

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://dx.doi.org/10.1016/j.brainres.2010.05.046.

Makuuchi, M., Kaminaga, T., & Sugishita, M. (2003). Both parietal lobes are involved in drawing: A functional MRI study and implications for constructional apraxia. *Cognitive Brain Research, 16*(3), 338–347. http://dx.doi.org/10.1016/S0926-6410(02)00302-6.

Matelli, M., & Luppino, G. (2000). Parietofrontal circuits: Parallel channels for sensory-motor integrations. *Advances in Neurology, 84*, 51–61.

Mei, L., Xue, G., Chen, C., Xue, F., Zhang, M., & Dong, Q. (2010). The "visual word form area" is involved in successful memory encoding of both words and faces. *NeuroImage, 52*(1), 371–378.

Menon, V., & Desmond, J. E. (2001). Left superior parietal cortex involvement in writing: Integrating fMRI with lesion evidence. *Brain Research. Cognitive Brain Research, 12*(2), 337–340.

Miall, R. C., Gowen, E., & Tchalenko, J. (2009). Drawing cartoon faces—A functional imaging study of the cognitive neuroscience of drawing. *Cortex, 45*(3), 394–406.

Murdoch, B. E. (2010). The cerebellum and language: Historical perspective and review. *Cortex, 46*(7), 858–868. http://dx.doi.org/10.1016/j.cortex.2009.07.018.

Naito, E., & Hirose, S. (2014). Efficient foot motor control by Neymar's brain. *Frontiers in Human Neuroscience, 8*, 594.

Nakamura, K., Honda, M., Hirano, S., Oga, T., Sawamoto, N., Hanakawa, T., et al. (2002). Modulation of the visual word retrieval system in writing: A functional MRI study on the Japanese orthographies. *Journal of Cognitive Neuroscience, 14*(1), 104–115. http://dx.doi.org/10.1162/089892902317205366.

Nakamura, K., Honda, M., Okada, T., Hanakawa, T., Toma, K., Fukuyama, H., et al. (2000). Participation of the left posterior inferior temporal cortex in writing and mental recall of kanji orthography: A functional MRI study. *Brain, 123*(Pt 5), 954–967.

Nicolson, R. I., & Fawcett, A. J. (2011). Dyslexia, dysgraphia, procedural learning and the cerebellum. *Cortex, 47*(1), 117–127. http://dx.doi.org/10.1016/j.cortex.2009.08.016.

Ogawa, K., & Inui, T. (2009). The role of the posterior parietal cortex in drawing by copying. *Neuropsychologia, 47*(4), 1013–1022.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113.

Omura, K., Tsukamoto, T., Kotani, Y., Ohgami, Y., & Yoshikawa, K. (2004). Neural correlates of phoneme-to-grapheme conversion. *NeuroReport, 15*(6), 949–953.

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.

Pernet, C. R., Poline, J. B., Demonet, J. F., & Rousselet, G. A. (2009). Brain classification reveals the right cerebellum as the best biomarker of dyslexia. *BMC Neuroscience, 10*, 67. http://dx.doi.org/10.1186/1471-2202-10-67.

Pernet, C., Schyns, P. G., & Demonet, J.-F. (2007). Specific, selective or preferential: Comments on category specificity in neuroimaging. *NeuroImage, 35*(3), 991–997.

Piercy, M., Hecaen, H., & De Ajuriaguerra, J. (1960). Constructional apraxia associated with unilateral cerebral lesions: Left and right sided cases compared. *Brain, 83*, 225–242.

Planton, S., Jucla, M., Roux, F. E., & Demonet, J. F. (2013). The 'handwriting brain': A meta-analysis of neuroimaging studies of motor versus orthographic processes. *Cortex, 49*(10), 2772–2787. http://dx.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://dx.doi.org/10.1016/j.neuroimage.2012.04.062.

Price, C. J., & Devlin, J. T. (2003). The myth of the visual word form area. *NeuroImage, 19*(3), 473–481.

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://dx.doi.org/10.1016/j.neuroimage.2010.11.042.

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*. http://dx.doi.org/10.3389/fpsyg.2011.00239, 293–293.

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America, 98*(2), 676–682.

Rapcsak, S. Z., & Beeson, P. M. (2004). The role of left posterior inferior temporal cortex in spelling. *Neurology, 62*(12), 2221–2229.

Rapp, B., & Dufor, O. (2011). The neurotopography of written word production: An FMRI investigation of the distribution of sensitivity to length and frequency. *Journal of Cognitive Neuroscience, 23*(12), 4067–4081. http://dx.doi.org/10.1162/jocn_a_00109.

Rapp, B., Epstein, C., & Tainturier, M.-J. (2002). The integration of information across lexical and sublexical processes in spelling. *Cognitive Neuropsychology, 19*(1), 1–29. http://dx.doi.org/10.1080/0264329014300060.

Rapp, B., & Lipka, K. (2011). The literate brain: The relationship between spelling and reading. *Journal of Cognitive Neuroscience, 23*(5), 1180–1197. http://dx.doi.org/10.1162/jocn.2010.21507.

Roeltgen, D. P. (2003). Agraphia. In K. M. Heilman, & E. Valenstein (Eds.), *Clinical neuropsychology* (pp. 126–145). Oxford: Oxford University Press.

Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. *Behavioural Neurology, 12*(4), 191–200.

Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *NeuroImage, 20*(3), 1609–1624.

Roux, F.-E., Draper, L., Kopke, 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://dx.doi.org/10.1016/j.cortex.2010.03.001.

Roux, F.-E., Dufor, O., Giussani, C., Wamain, Y., Draper, L., Longcamp, M., et al. (2009). The graphemic/motor frontal area Exner's area revisited. *Annals of Neurology, 66*(4), 537–545. http://dx.doi.org/10.1002/ana.21804.

Schaer, K., Jahn, G., & Lotze, M. (2012). fMRI-activation during drawing a naturalistic or sketchy portrait. *Behavioural Brain Research, 233*(1), 209–216.

Segal, E., & Petrides, M. (2012). The anterior superior parietal lobule and its interactions with language and motor areas during writing. *The European Journal of Neuroscience, 35*(2), 309–322. http://dx.doi.org/10.1111/j.1460-9568.2011.07937.x.

Seghier, M. L. (2008). Laterality index in functional MRI: Methodological issues. *Magnetic Resonance Imaging, 26*(5), 594–601.

Stoodley, C. J., & Schmahmann, J. D. (2009). Functional topography in the human cerebellum: A meta-analysis of

neuroimaging studies. *NeuroImage, 44*(2), 489–501. http://dx.doi.org/10.1016/j.neuroimage.2008.08.039.

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://dx.doi.org/10.1016/j.neuroimage.2006.05.035.

Tunik, E., Frey, S. H., & Grafton, S. T. (2005). Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nature Neuroscience, 8*(4), 505–511.

Tunik, E., Ortigue, S., Adamovich, S. V., & Grafton, S. T. (2008). Differential recruitment of anterior intraparietal sulcus and superior parietal lobule during visually guided grasping revealed by electrical neuroimaging. *The Journal of Neuroscience, 28*(50), 13615–13620. http://dx.doi.org/10.1523/JNEUROSCI.3303-08.2008.

Tunik, E., Rice, N. J., Hamilton, A., & Grafton, S. T. (2007). Beyond grasping: Representation of action in human anterior intraparietal sulcus. *NeuroImage, 36*, T77–T86.

Ungerleider, L. G., & Haxby, J. V. (1994). 'What'and 'where'in the human brain. *Current Opinion in Neurobiology, 4*(2), 157–165.

Van Galen, G. P. (1991). Handwriting: Issues for a psychomotor theory. *Human Movement Science, 10*(2–3), 165–191. http://dx.doi.org/10.1016/0167-9457(91)90003-G.

Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., et al. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage, 30*(4), 1414–1432. http://dx.doi.org/10.1016/j.neuroimage.2005.11.002.