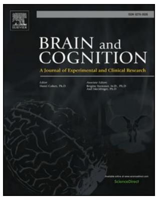
Brain and Cognition 184 (2025) 106272

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c



Neural correlates of lexical, sublexical and motor processes in word handwriting

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ARTICLE INFO

Keywords:
Spelling
Handwriting
Orthography
fMRI

ABSTRACT

Writing recruits a vast neural network underpinning both linguistic and motor processes. Previous studies have tried to identify which brain areas underpin both the linguistic and motor aspects of writing. However, little is known about the neural substrate of the lexical and sublexical "routes" for spelling. In this fMRI study, participants (n = 25) copied or saw/read symbols or words. Words varied in lexical frequency and phonology-to-orthography (P-O) consistency. Anterior parts of the inferior frontal gyrus were selectively recruited when copying P-O inconsistent words, while the right Heschl's gyrus was recruited only when copying consistent words. Non-specific motor and linguistic areas were also identified. Our results contribute to our knowledge of the neural substrate of the lexical and sublexical spelling routes and suggest that different brain areas might be involved in the lexical processing of input (reading) and output (writing) orthography.

1. Introduction

Handwriting words is a complex human ability that requires the integration of high-level linguistic processes such as spelling (i.e., central processes) and low-level motor processes associated with the execution of the written response (i.e., peripheral processes). Adding to this complexity, spelling itself is not a unitary process. It is widely agreed that known words can be spelled by retrieving word-level orthographic representations (following a *lexical* procedure), while unfamiliar words would be spelled by assembling individual phonemes to graphemes (following a *sublexical* procedure). Evidence from both neuropsychological and behavioural studies have confirmed this distinction (Purcell et al., 2011; Shallice, 1988) and a vast network of brain areas that might be recruited by the different components of the writing process has been identified. It is still unclear which areas in the extensive network identified during writing are associated to one or both spelling routes. In the present study, we aim to isolate the brain areas recruited by motor, lexical and sublexical processes during word copying, a very simple but scarcely studied writing task.

1.1. *Cognitive processes involved in word copying*

As in any other writing task, the processes involved in word copying can be categorised into those associated to the decoding of the stimuli, spelling processes, and execution of the motor response. As shown in Fig. 1, word copying is initiated with a visual analysis of the input, which is followed by decoding processes that lead to the identification of the word. This representation constitutes the input to initiate the spelling processes.

Words can be spelled resorting to two different sources of orthographic information or spelling routes. The lexical route (*a* in Fig. 1) would lead to the activation of whole-word (output) orthographic representations stored in long-term memory. In adult (skilled) readers, it is assumed that most familiar words visually presented will activate a semantic representation via this route. The sublexical route (*b* in Fig. 1) would activate graphemes from the phonemic representations activated during the decoding of the visual input. Although, in theory, words could be copied with minimal or null engagement of the spelling processes just by reproducing the model letter by letter, evidence from behavioural studies seems to confirm that adult writers consistently retrieve lexical and sublexical information during this task (Afonso & Álvarez, 2019; Afonso et al., 2015; Afonso et al., 2019; Cuetos, 1991;

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https://doi.org/10.1016/j.bandc.2025.106272
Received 1 November 2024; Received in revised form 29 January 2025; Accepted 30 January 2025

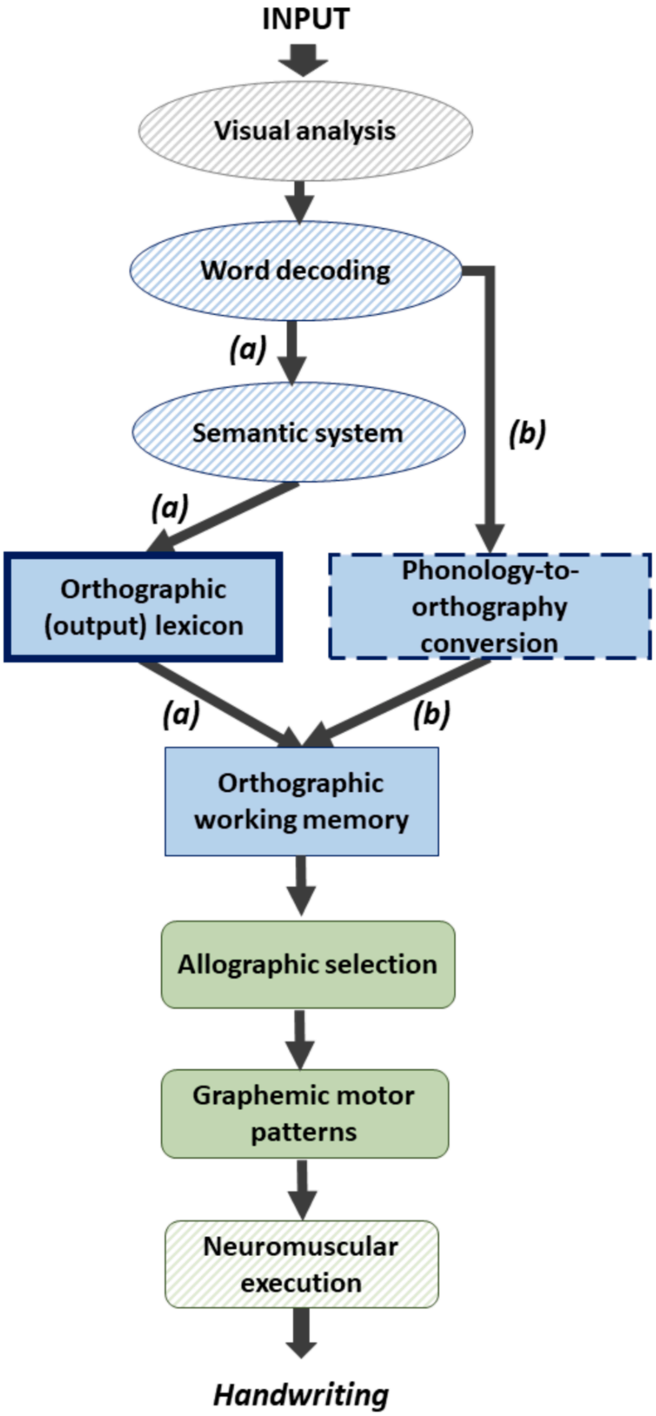

Fig. 1. *Cognitive model of word copying. See online version for colour image. Note.* In the figure, different shapes are used to represent different processing stages (i.e., ovals are used for input decoding processes, rectangles are used for spelling processes, and rounded rectangles are used for handwriting processes); colour is used to represent the nature of the units involved (grey is used for visual processes, blue for linguistic processes and green for motor processes); different fill patterns are used to represent the specificity of the process for writing (solid colours are used for writing-specific processes and line-pattern colours are used for domain-general processes).

Lambert et al., 2015). However, the relative impact of each route on the writing process will in part depend on the characteristics of the stimuli. The lexical route is mainly sensitive to word frequency. Thus, this route will quickly give access to the orthographic representation of high-frequency words, but it would be slower (or not available at all) for low-frequency words. The sublexical route would provide a reliable orthographic representation for words containing only consistent phoneme-to-grapheme (henceforth, P-G) correspondences (for example, the Spanish word /ˈma pa/ – *mapa* [map in English], in which each of the four phonemes have only one possible graphemic representation). Words containing phonemes with more than one potential graphemic representation (i.e., inconsistent correspondences such as *b* in /ˈka βo/ – *cabo* [cape in English], which could be spelt with letter *v* in Spanish) would activate several graphemic candidates. In these cases, lexical information would be required to ensure that an accurate spelling is produced.

Regardless of the route followed to retrieve orthographic representations, the sequence of graphemes must be stored in an orthographic working memory system during the unfolding of the handwriting movements (Rapp et al., 2016). Processes associated to the programming and execution of these movements (i.e., peripheral processes) include the selection of allographic forms (e.g., uppercase/lowercase), the retrieval of the appropriate graphemic motor patterns, as well as size control and muscular adjustment to produce the movement (Van Galen, 1991).

Recent *meta*-analyses seem to agree on the brain areas that are activated in the course of writing. Planton et al. (2013) found that handwriting consistently recruits a large network of fronto-parietal areas (including the middle frontal gyrus, the superior frontal sulcus, the primary motor cortex, the sensorimotor cortex, the inferior parietal lobule, the superior parietal lobule and the intraparietal sulcus), the fusiform gyrus, the cerebellum, the thalamus, and the putamen. In a previous *meta*-analysis, Purcell et al. (2011) had also identified most of these areas as relevant for writing, with the addition of the supramarginal gyrus (SMG), the insula and the superior temporal sulcus. However, clear links between specific regions and different levels of processing are still to be established. For example, some areas typically associated to handwriting might be linked to the activation of motor programmes for letters or might be more generally involved in hand movement. Thus, it remains unclear which brain areas can be considered part of a writing-specific neural network.

1.2. *Neural correlates of central processes of writing*

Until very recently, neuroimaging studies had not tried to determine if the activity found in different brain areas was associated to the lexical or the sublexical spelling procedures. Most of our knowledge on this issue comes from the neuropsychological study of patients suffering from dysgraphia or agraphia. Lesion studies have helped identify different behavioural profiles associated with impairment to the orthographic lexicon, the P-O conversion procedures, and the orthographic working memory system (Buchwald & Rapp, 2009; Rapp et al., 2016). Thanks to this work, it has been possible to establish links between the lost abilities and the location of the lesion.

In order to successfully isolate the central processes of writing in a neuroimaging study, the control (or baseline) task should, ideally, share all levels of processing with the studied writing task except for the spelling processes. In practice, previous studies have chosen control (or baseline) tasks sharing the perceptual-motor aspects of the response. These *motor control* tasks recruit similar peripheral processes but require little or no linguistic processing. Motor control tasks commonly used in previous studies include drawing simple shapes such as circles or loops (Beeson et al., 2003; Rapp & Dufor, 2011; Roux et al., 2009; Shah et al., 2013; Segal & Petrides, 2012), finger tapping (Katanoda et al., 2001), and symbol production or pseudoword writing (Omura et al., 2004; Segal & Petrides, 2012). Although the areas found to be selectively activated when writing words vary across studies, the fusiform gyrus, the left inferior frontal gyrus (IFG), the SMG, and the angular gyrus have been frequently associated to spelling processes. However, which areas might be associated to the use of the different spelling routes is less clear. Below, we summarise evidence from cognitive neuropsychology and neuroimaging studies that have shed some light on the neural substrate of the lexical and sublexical spelling processes.

Neural correlates of lexical processing.

When compared to healthy controls, patients suffering from disruption to the lexical route (i.e., lexical dysgraphia) are more sensitive to word frequency effects and perform worse in inconsistent/irregular[1] words than in consistent/regular words, reflecting an overreliance on the relatively spared P-G correspondences (Buchwald & Rapp, 2009). In these patients, lesions have been identified to affect mainly the left posterior inferior temporal cortex (Rapcsak & Beeson, 2004) and more precisely the left fusiform gyrus (Purcell et al., 2014; Tsapkini & Rapp, 2010; Tsapkini et al., 2011). However, this area is well known to be recruited in reading and visual word recognition tasks (Dehaene et al., 2002), and it is not thought to be writing specific. In fact, this area has been proposed to be the location of the so-called Visual Word Form Area (VWFA), a region thought to be fundamental for the processing of visually presented words (Cohen et al., 2000). Its precise function is still a matter of debate, but it has been proposed that the fusiform might store lexical orthographic representations underlying both reading and spelling (Rapp et al., 2016; Sakurai, 2004; Sakurai et al., 2008). In line with this idea, Purcell et al. (2014) found that patients with lesions to the left inferior temporal gyrus exhibited lexical deficits in both reading and spelling. Sakurai et al. (2008) described impaired kanji writing and reading in patients with lesions to the posterior parts of the middle and inferior temporal gyrus. As kanji reading and writing demand access to long-term memory orthographic representations for each word (differently from kanas, which represent syllables), these authors suggested that damage to these areas might interrupt the flow of information from and to the orthographic lexicon. Finally, it has been proposed that the left fusiform might be involved in other production tasks such as oral naming (Beeson et al., 2003). Altogether, the available evidence led Planton et al. (2013) to claim that the left inferior temporal cortex is part of an extended (domain-general) network for writing rather than a writing-specific area.

Damage to the angular gyrus has also been associated with a profile of lexical agraphia (Roeltgen & Heilman, 1984; Sakurai et al., 2008). This seems to suggest a role of this region in the lexical route for spelling. Sakurai et al. (2008) suggested that the lexical orthographic information stored in the posterior inferior temporal gyrus would be sent to the angular gyrus before reaching the areas responsible for motor planning. However, these authors claimed that the angular gyrus would also be part of the more ventral phonological route, connecting the phonological lexicon (located in the posterior superior temporal gyrus) with the motor areas in the frontal lobe via the arcuate fasciculus (Sakurai et al., 2008). They also suggested that this area would be involved as well in grapheme-to-phoneme decoding during reading. Thus, although the angular gyrus has often been considered a writing centre (Sugihara et al., 2006), its specificity for lexical orthographic processing has been questioned.

1.2.1. Neural correlates of sublexical processing

The left IFG and the SMG have been proposed to provide a neural substrate for the phoneme-to-grapheme conversion procedures. Lesions to these regions are associated to worse performance in pseudoword than in word spelling (Henry et al., 2007; Philipose et al., 2007; Rapcsak et al., 2009), consistently with a phonological dysgraphia profile (i.e., damage to the sublexical spelling route). Neuroimaging studies have confirmed greater activation in these two areas when writing to dictation kanas than symbols (Omura et al., 2004), and Palmis et al. (2019) found that the pars orbitalis of the IFG was more activated for irregular than regular words in French. However, there does not seem to be an agreement on the specific role of these areas during writing. Matsuo et al. (2000) failed to find differences in the activation of the SMG when writing kanjis and kanas, and a body of evidence seems to suggest that the IFG might not be exclusively involved in phonological processing. Rapp et al. (2016) found that lesions affecting the IFG produced orthographic long-term memory deficits, and that several patients with damage to this area exhibited spared pseudoword spelling. They concluded that the IFG might play a role in lexical access, perhaps in controlling the selection of a specific form among potential candidates that may have been activated in the lexicon.

In any case, previous studies suggest that neither the IFG nor the SMG are exclusively involved in word writing (Philipose et al., 2007; Purcell et al., 2011; Rapp & Duffor, 2011; Rapp & Lipka, 2011). The SMG has been found to be important also for orthography-to-phonology conversion in pseudoword reading (Pugh et al., 2001). Differences in the level of activation of the IFG are usually found between writing tasks and other motor tasks, but not between writing and other linguistic tasks such as naming (Beeson et al., 2003; Katanoda et al., 2001; Planton et al., 2013). Interestingly, Purcell et al. (2011) found that the pars orbitalis of the IFG was commonly activated in spelling and reading, but activation in more ventral portions of this area was not co-localised for reading and writing. This suggests task-specific localisation of the activation. The authors concluded that some portions of the IFG might be involved in task-independent phonological processing, while other portions might play a role in task-specific lexico-semantic processing or in the coordination of other task-specific brain areas. This intriguing possibility might explain the conflicting evidence reported in previous studies regarding the function of the IFG in writing. As we will discuss below, the IFG has even been claimed to be involved in peripheral aspects of writing production.

Other perisylvian area that has been proposed to be related to the application of P-O sublexical procedures is the insula. Lesions to the insula have been found to result in an inability to spell pseudowords with preserved capacity for spelling known words (Marien et al., 2001; Rapcsak & Beeson, 2004). In a functional neuroimaging study conducted in French, Palmis et al. (2019) reported greater activation in the insula for irregular than for regular words. However, it is unclear from these findings whether this activation is related to increased demands on the sublexical procedure due to the presence of a low probability P-G mapping, or, conversely, to the necessity to access lexical representations to correctly spell irregular words.

1.3. Neural correlates of peripheral processes in handwriting

As any other motor task, handwriting recruits brain areas related to movement planning and execution. Studies comparing handwriting to non-motor tasks have often reported activation in the left primary motor and sensorimotor cortices, the bilateral SPL and the cerebellum (Katanoda et al., 2001; Planton et al., 2013; 2017). However, these areas have also been found to be recruited when drawing (Raimo et al., 2021), which suggests that they are not writing specific. Among those areas more frequently proposed to be specifically associated to handwriting movements are a region in the left superior frontal gyrus (SFG) known as Exner's area (Exner, 1881; Longcamp et al., 2003; 2014; Purcell et al., 2011) and the inferior parietal sulcus (IPS; Segal & Petrides, 2012).

Exner's area has also been labelled as the Graphemic Motor Frontal Area by Longcamp et al. (2003), who suggested that it contains the motor programmes necessary to produce letters. This proposal seems to be supported by the fact that focal lesions to this area are associated with poor letter formation in the absence of a more general motor impairment (Anderson et al., 1990; Sakurai et al., 1997). The superior parietal lobe (SPL), as well as other regions around the IPS, has also been proposed to be involved in letter formation, with lesions to this area leading to pure agraphia (Alexander et al., 1992). Although Planton et al. (2013) found bilateral activation of the SPL while writing, comparisons with other tasks suggested that the left SPL might have specialised in visuospatial control for letter production as a consequence of handwriting learning;

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[1] P-G correspondences are considered irregular when they include an inconsistent segment that is not spelt with the most frequent grapheme.

in contrast, the right SPL would be part of a more general visuospatial or goal-oriented network.

It is important to note that some authors have claimed that the SFG, the SPL, and the IPS could be involved in higher-order processing during handwriting. Namely, these areas have been proposed to play a role in the integration of orthographic and motor representations (Planton et al., 2013; Roux et al., 2019). Alternatively, the SPL and the IPS might be part of the orthographic working memory network (Planton et al., 2013; Rapp & Dufor, 2011). Rapp and Lipka (2011) suggested that the SPL might be linked to the ability to select and produce letter shapes in the appropriate order. Conversely, areas typically associated to central processes have also been linked to peripheral activity. The opercular part of the IFG has been claimed to be part of the premotor hand area that would receive information from the SPL about the motor programmes to be transduced into specific hand movements (Sakurai et al., 2008). In line with this idea, previous evidence suggests that IFG might be specifically associated to letter production from memory (James & Gauthier, 2006). Thus, it remains uncertain which brain areas are purely motor and which areas are involved in higher-order integration of motor and linguistic processes.

1.4. *The present study*

The present study aims to identify the neural correlates of the linguistic and motor processes involved in the word-copying task. To successfully isolate linguistic processes, brain activity observed during word copying will be compared to the activity elicited during a covert word-reading task. Based on the cognitive model depicted in Fig. 1, it is assumed that all input decoding processes (visual analysis, letter identification, orthography-to-phonology conversion rules and access to the orthographic – input – lexicon) will be shared between these two tasks, while word copying will additionally activate areas associated to peripheral processes but also to writing-specific linguistic processes. A symbol-copying task was chosen to serve as the motor control task. In this task, participants were asked to copy strings of symbols (e.g., #%! *>&?). This task is assumed to share with copying the visual analysis processes and the non-writing-specific motor processes (muscular adjustment and size control). Thus, spelling processes (both orthographic – output – lexical access and P-O conversion) at the central level, and allographic selection and graphemic motor programme retrieval at the peripheral level would be exclusively recruited during word copying, and not during reading nor during symbol copying. To obtain more information about the neural correlates of the lexical and the sublexical routes for spelling, word frequency and P-O consistency were manipulated. As mentioned above, word frequency effects would reflect the use of the lexical route, while consistency effects would signal the influence of the sublexical route in the production process.

2. Method

2.1. *Participants*

Twenty-five participants took part in the study (21 female, 4 male; M_{age} = 20.30, SD = 3.60). According to the Edinburgh Handedness Inventory (EHI; Oldfield, 1971), they were all right-handed. They all self-reported to be free of any known psychiatric or neurological disorder. Participants were compensated with credits to fulfil a course requirement.

2.2. *Materials*

The experimental stimuli comprised 80 Spanish words (all nouns) and 40 symbol strings. For the words, lexical frequency and phoneme-to-grapheme consistency were orthogonally manipulated. Thus, 20 words were consistent, high-frequency words (e.g., *realidad*, reality in English), 20 were consistent, low-frequency words (*dilema*, dilemma), 20 were inconsistent, high frequency words (*cabeza*, head), and 20 were inconsistent, low-frequency words (*obelisco*, obelisk). Inconsistent words contained at least one phoneme with more than one possible graphemic representation. Namely, inconsistent words included the phoneme /b/ (that can be spelt *b* or v), /y/ (*ll* or *y*), or /j/, (*j* or g). The distribution of these graphemes in the Spanish lexicon is remarkably balanced, so none of these options could confidently be considered the dominant or regular spelling for the corresponding phoneme. According to the values provided by BuscaPalabras (Davis & Perea, 2005), all high-frequency words had a lexical frequency above 100 occurrences per million (M = 263.18; SD = 157.34), and low-frequency words had a lexical frequency below 7 occurrences per million (M = 5.22; SD = 1.35). Word length in number of letters (6–8 letters), phonemes (6–8 phonemes), and syllables (2–4 syllables), orthographic neighbourhood, mean token-positional bigram frequency, and mean token-absolute bigram frequency were controlled for across the four conditions. Across consistency conditions, lexical frequency was also controlled for. The full set of experimental words with the values for controlled variables is given in Table S1 [Supplementary material]. A total of 40 symbol strings were created by combining a set of symbols (#, %,!, *, >, &,?) in random order. Thus, all the strings were 7-symbol long. Experimental stimuli were presented in a white font on a black background. Sixteen additional words and 8 symbol strings were selected to serve as practice.

2.3. *Procedure*

Participants were presented with 60 blocks: 40 blocks of words and 20 words of symbols. Each block consisted of two trials, in which stimuli belonging to the same condition were presented (for example, two consistent high-frequency words). Thus, each participant performed a total of 120 trials (80 words and 40 symbol strings). In each trial, the stimulus was presented for 8,000 ms and followed by a 1,000-millisecond blank screen. Before each block, a cue presented for 1,000 ms on the centre of the screen indicated whether participants had to read or copy the stimuli within that block. A picture of an open book indicated that they had to silently read or look at the presented lowercase words or symbol strings. A picture of a hand holding a pencil indicated that they were required to produce each character of the target sequence (letter or symbol) with their right index finger on their right thigh. They were instructed to produce all the characters in the same spot on their thigh, rather than producing them in a left-to-right manner. Upper-case letters were required for words. After each block a new cue was presented signalling a change in the required response (reading or copying). Two different lists were created so the words and symbols that were read by half of the participants were copied by the other half. The experiment consisted of two runs, with a break after the first 36 blocks. The entire experimental session lasted around 45 min. The procedure of this experiment was approved by the Ethics Committee of the University of La Laguna.

2.4. *fMRI data acquisition*

The scanning was performed in a 3 T General Electric Signa Excite scan. Structural (T1-weighted MPRAGE: 256 × 256 matrix; FOV = 256 mm; 196 1-mm sagittal slices) and functional images were acquired (Gradient-Echo-EPI-sequence; TR = 2,000 ms; TE = 24 ms; FOV = 256 mm; flip angle = 80°; matrix = 64 × 64; interslice gap = 0.8 mm). During the first run, 384 volumes were acquired, and 270 were acquired during the second run.

2.5. *Data processing and analysis*

Data analysis was performed by using statistical parametric mapping (SPM12; Penny et al., 2011). Anatomical locations were obtained using the Automated Anatomical Labelling Atlas (Rolls, 2020) as implemented in the AtlasReader library (Notter et al., 2019) for Python. Echo-planar images were corrected for acquisition delay, realigned, segmented (with forward deformation fields), normalised (structural images with a 1 × 1 × 1 mm voxel size and functional images with 4 × 4 × 4 mm voxel size), and smoothed (Gaussian kernel: 8 × 8 × 8 mm). A high-pass filter (0.005 Hz) was applied to the data and model. The neural activity was modelled by a Glover (1999) canonical hemodynamic response function (HRF) function at stimulus onset. Three participants were excluded from further analysis due to excessive head motion, defined as translational or rotational movement exceeding 3 mm or 3 degrees in any direction. Ten separate predictors were included in a general linear model, one per each condition (reading consistent words, reading inconsistent words, reading high-frequency words, reading low-frequency words, seeing symbols, copying consistent words, copying inconsistent words, copying high-frequency words, copying low-frequency words, and copying symbols).

Parameter images for a series of contrasts were generated for each participant. Contrasts between reading and copying words were considered to isolate the peripheral aspects of writing. Due to the intrinsically more active nature of the copying conditions compared to the reading/seeing conditions, it is reasonable to expect strong differences between the tasks in attentional processes over time. Reading/seeing trials, in which participants were asked to passively look at the stimuli for 8 s, might have led to disengagement from the task after the initial processing of the stimulus. To reduce the potential differences in attentional processes between the copying and reading conditions, we first circumscribed these analyses to the first 2 s of each trial. In this analysis, we focused on the contrasts concerning the difference between producing the stimuli and just seeing the stimuli, regardless of the linguistic manipulations. These contrasts included: Copying Words > Reading Words, Reading Words > Copying Words, Copying Symbols > Seeing Symbols, Reading Symbols > Reading Words.

To isolate the areas involved in linguistic processing during writing, hemodynamic responses to copying symbol strings were subtracted from responses to copying words (Copying Words > Copying Symbols), and responses to copying words were subtracted from responses to copying symbol strings (Copying Symbols > Copying Words). To ensure that these effects were due to writing and not to stimulus decoding processes, they were compared to the results of the same contrasts for the trials under the Reading/seeing instruction (i.e., Reading Words > Seeing Symbols and Seeing Symbols > Reading Words, respectively). To investigate the neural correlates of P-G conversion processes, consistent and inconsistent words were compared during copying (Copying Consistent Words > Copying Inconsistent Words, Copying Inconsistent Words > Copying Consistent Words), and each type of word was compared to the motor control (Copying Consistent Words > Copying Symbols, Copying Symbols > Copying Consistent Words, Copying Inconsistent Words > Copying Symbols, Copying Symbols > Copying Inconsistent Words).

Similarly, to identify the neural correlates of lexical spelling, contrasts were considered for frequent and infrequent words (Copying HF > Copying LF, Copying LF > Copying HF, Copying HF > Copying Symbols, Copying Symbols > Copying HF, Copying LF > Copying Symbols, Copying Symbols > Copying LF). These contrasts were subjected to a second-level random-effects analysis.

Again, equivalent contrasts were conducted for Reading (Reading Consistent > Reading Inconsistent, Reading Inconsistent > Reading Consistent, Reading Consistent > Seeing Symbols, Seeing Symbols > Reading Consistent, Reading Inconsistent > Seeing Symbols, Seeing Symbols > Reading Inconsistent, Reading HF > Reading LF, Reading LF > Reading HF, Reading HF > Seeing Symbols, Seeing Symbols > Reading HF, Reading LF > Seeing Symbols, Seeing Symbols > Reading LF) to isolate writing-specific linguistic effects. The group contrast images were tested with a one-sample *t*-test against a null hypothesis of no effect. The threshold for statistical significance was set at a p-value of 0.001 voxel-wise (uncorrected) and a p-value of 0.001 (family-wise corrected) at the cluster level. All statistical analyses were conducted using the Nilearn library (Abraham et al., 2014) for Python.

3. Results

Peaks of activation for the contrasts conducted focusing on the differences between reading/seeing and copying (which considered only the first 2 s of each trial) can be seen in Table 1. Peaks of activation for the contrasts conducted considering the total duration of the trial (aim at comparing the actual production of different types of written words) are given in Table 2. A full list of the regions contributing to each significant cluster can be seen in Table S2 [Supplementary materials]. These contrasts allowed to isolate differences in brain activity associated to the production of words versus symbols (lexicality effect), consistent versus inconsistent words (consistency effect), and frequent versus infrequent words (word frequency effect). As processes involved in reading are not the focus of the present study, peaks for contrasts involving only reading conditions will not be discussed further, and results are mentioned only to clarify the nature of the effects found when copying (i.e., writing-specific or nonspecific).

3.1. *Copying versus reading*

Analyses focusing on the first 2 s after the presentation of each stimulus showed that copying words compared to reading words led to greater activation of an extensive network including the bilateral precentral gyrus, the left postcentral gyrus, the left SPL and the left SMG. Greater activation of the right cerebellum, the left putamen and the left thalamus was also observed. Similar areas showed increased activation when copying symbols compared to seeing symbols, with the exception of the putamen and the thalamus.

3.2. *Lexicality effect*

To isolate the areas specifically involved in producing words in opposition to producing any symbol, comparisons between copying words and copying symbols were conducted over the entire duration of the response. Overall, copying words was associated with greater activation in the right calcarine and in the bilateral middle temporal lobe compared to copying symbols. Copying words was also linked to decreased activation in the left cerebellum, the right fusiform, the superior parietal lobe, the bilateral superior frontal lobe and the left thalamus. To elucidate whether these areas are linked to lexical or sublexical processes, we explore contrasts involving specific types of words.

3.3. *Consistency effect*

No significant differences were found between copying consistent words and copying inconsistent words. Interestingly, contrasts between

Table 1
Peaks of activation in MNI coordinates for the copying versus reading/seeing contrasts.

Region of activation	x	y	z	z-score	Volume (mm)
Copying words > Reading words					
Left Precentral Gyrus	−24	−32	50	3.71	32,256
Right Cerebellum	24	−58	−26	3.84	11,984
Left Putamen	−34	0	14	3.38	9104
Right Precentral Gyrus	28	−12	48	3.91	4752
Left Thalamus	−10	−22	−8	3.68	4136
Copying symbols > Seeing symbols					
Left Precentral Gyrus	−24	−32	50	3.71	11,728
Right Cerebellum	12	−50	−22	3.74	7688
Left Postcentral Gyrus	−56	−10	32	4.59	4024

*$p < 0.05$ FWE at cluster level.

Table 2
Peaks of activation in MNI coordinates for the consistency and frequency contrasts.

Region of activation	x	y	z	z-score	Volume (mm)
Copying words > Copying symbols					
Right Calcarine	6	−88	12	3.80	5472
Left Middle Temporal	−60	−46	10	3.66	4016
Right Middle Temporal	62	−46	10	4.09	2488
Copying symbols > Copying words					
Left Cerebellum	−30	−66	6	5.10	49,960
Right Fusiform	28	−62	−16	4.84	26,296
Right Superior Parietal	30	−60	42	4.30	19,016
Left Superior Frontal	−24	−10	52	3.76	2384
Right Superior Frontal	28	−4	54	3.59*	2032
Left Thalamus	−18	−22	−2	3.36*	1848
Copying consistent > Copying symbols					
Left Middle Temporal	−56	−62	14	4.44	5648
Left Calcarine	0	−88	14	3.72	5016
Right Middle Temporal	58	−44	8	4.34	2928
Right Insula	38	−20	8	4.65*	1808
Copying symbols > Copying consistent					
Left Fusiform	−28	−70	0	5.46	50,824
Right Cerebellum	28	−60	−20	4.08	28,032
Right Angular	30	−62	40	4.27	17,656
Left Thalamus	−18	−22	−2	3.45	2848
Left Precentral Gyrus	−22	−12	52	3.59*	1696
Copying inconsistent > Copying symbols					
Left Calcarine	−4	−92	8	4.10	2584
Left Inferior Frontal (pars triangularis)	−50	26	4	3.48*	1760
Copying symbols > Copying inconsistent					
Left Fusiform	−28	−76	−14	4.58	26,872
Right Superior Occipital	28	−68	46	4.11	14,584
Right Cerebellum	24	−56	−22	4.22	10,752
Left Inferior Parietal	−26	−60	42	4.34	5032
Right Inferior Occipital	38	−80	−8	4.18	4320
Right Superior Frontal	28	−4	54	3.61*	2040
Left Superior Frontal	−24	−10	52	3.70*	1640
Copying HF > Copying LF					
Left Parietal Operculum	−28	−24	28	3.71	6104
Copying HF > Copying symbols					
Left Middle Temporal	−54	−56	12	3.83	6944
Left Calcarine	0	−88	10	3.73	6424
Right Middle Temporal	58	−46	8	4.36	3160
Right Middle Cingulate	8	−30	44	3.76	2656
Copying symbols > Copying HF					
Left Middle Occipital	−28	−78	2	4.50	36,144
Right Cerebellum	26	−60	−20	3.57	20,520
Right Superior Occipital	28	−64	42	4.23	12,056
Copying LF > Copying symbols					
Left Calcarine	−2	−92	6	4.42*	2336
Copying symbols > Copying LF					
Left Lateral Occipital	−30	−64	8	5.41	53,936
Right Calcarine	32	−60	8	5.22	46,472
Right Superior Frontal	28	−4	54	3.83	3056
Left Precentral	−22	−14	50	3.73	2864
Left Thalamus	−16	−26	−6	3.76	2448

*$p < 0.05$ FWE at cluster level.

each type of words and the motor conditions yielded different patterns of activation (see Fig. 2). Copying consistent words led to increased activity in the bilateral temporooccipital parts of the MTG, the left occipital cortex, the insula and the right Heschl's gyrus; they also showed reduced activity in the bilateral fusiform, the right cerebellum, the right SPL, the left thalamus, and the left precentral gyrus. Copying inconsistent words led to increased activation in the left occipital cortex and in the pars triangularis and orbitalis of the left IFG. Reduced activation was found in the left fusiform, the bilateral SPL, the right superior occipital, the angular gyrus, the bilateral cerebellum, the parietal inferior lobe, the middle and inferior areas of the occipital cortex, and the bilateral precentral gyrus. In sum, copying consistent –but not inconsistent– words led to increased activation of the insula and the Heschl's gyrus and decreased activity in the thalamus compared to copying non-linguistic stimuli. Copying inconsistent –but not consistent– words led to increased activation in the more anterior parts of the IFG and to reduced activation in the angular gyrus and the parietal inferior lobe.

3.4. *Word frequency effect*

A direct comparison of copying HF and LF words showed increased activation for HF words in the left parietal operculum. When compared with the copying symbols control, copying HF words led to increased activation of the temporooccipital part of the bilateral MTG, the bilateral occipital pole, and the posterior division of the right cingulate gyrus. Copying HF words was also associated to decreased activity in the bilateral fusiform. Copying LF words compared to symbols yielded increased activation in the left calcarine and decreased activation in the bilateral fusiform, the bilateral precentral and superior frontal gyri and the left thalamus (see Fig. 3).

4. Discussion

In the present study, brain activity observed with fMRI during a word copying task was compared to the activity obtained when the same stimuli were only read covertly and when symbol strings were copied. Including both a linguistic control task and a motor control task allowed us to identify brain areas involved in central and peripheral levels of processing during writing. More importantly, specific contrasts were conducted subtracting the brain activity observed for each type of words (i.e., high-frequency, low-frequency, consistent, and inconsistent words) from that observed for copying symbols. These contrasts allowed us to isolate the areas associated to the lexical and sublexical routes for spelling.

4.1. *Neural correlates of peripheral processing*

Domain-general and writing-specific peripheral processes were identified in this study. Overall, both copying words and symbols in comparison to reading/seeing blocks led to the selective activation of several areas known to be associated with hand movements and sensations. The activation found in the left precentral gyrus (primary motor cortex) is unsurprising given the motor component present only in the copying tasks. The same can be said of the activation in the postcentral gyrus, which is the location of the sense of touch (Lloyd et al., 2015). This is in line with the demands of the copying blocks, as participants were requested to write on their thigh, producing touch sensations absent in the silent reading/seeing tasks. Additionally, the increased activity observed in the cerebellum confirms previous findings that this area is involved in letter/hand movement sequencing (Lupo et al., 2019). In sum, our findings confirm that these areas are related to hand movement more generally. The fact that the cerebellum has been previously reported to be writing-specific might arise from the fact that motor control tasks typically used rarely demand the production of sequenced movements. In that regard, the motor control task used in the present study is more similar to those involved in the production of letter strings.

Other areas previously proposed to be writing-specific were also found to be more active when copying words, but also when copying symbols, in comparison to reading/seeing blocks. These areas included the SPL and the SMG. The left SPL has been considered a main area of motor-language integration (Planton et al., 2013; Segal & Petrides, 2012). More specifically, it has been suggested to be the location of the motor programmes for letters and words (Menon & Desmond, 2001). Planton et al. (2013) proposed that the right SPL could play a role in

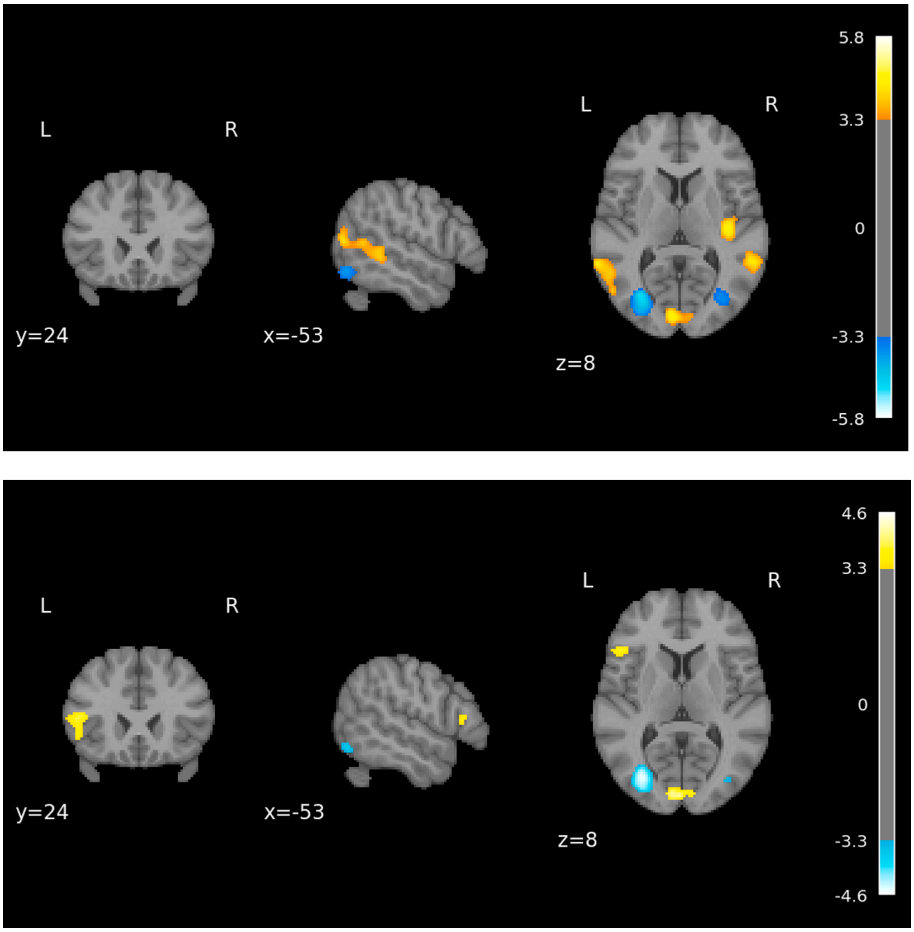

Fig. 2. *Significant peak activations for the contrast Copying Words > Copying Symbols (yellow) and Copying Symbols > Copying Words (blue) for Consistent Words (top panel) and for Inconsistent Words (bottom panel). See online version for colour image.* (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

visuospatial control more generally, while the left SPL would have specialised for visuospatial control for writing as a consequence of exposure to handwriting. However, in our study the left SPL showed increased activation when copying both words and symbols. Moreover, there were no difference in this area when word copying was compared to symbol copying. Similarly, the increased activity observed in the SMG in the copying versus the non-copying blocks suggests that it might not be a writing-specific area. Interestingly, levels of activation in the SMG were found to be sensitive to the lexical properties of the stimuli. This pattern suggests that the SMG might be linked to motor processes that are affected by linguistic processes. This possibility is discussed in more depth below. More research is necessary to ascertain the contribution of these areas to writing, but our results confirm their involvement in producing sequences of letters and other similar symbols.

Copying words (but not copying symbols) was associated to increased activation in the putamen and the thalamus. These areas are known to be involved in both motor and linguistic processes. The putamen has been linked to the ability to automatically produce previously learned movements (Griffiths et al., 1994), and the thalamus has been suggested to play a role during response execution in language production tasks (Klostermann et al., 2013). Our results suggest that these areas might be involved specifically in word written production (or at least to a larger extent than in other similar motor tasks). The higher level of automatization of the patterns for letters compared to those for symbols might be responsible for this difference. More research is needed to ascertain whether a similar involvement of the thalamus and the putamen can be observed in the production of other highly practised symbols.

4.2. Neural correlates of lexical processing

In terms of linguistic processes, our results showed decreased activation in the fusiform gyrus for words compared to symbols in all conditions, confirming the involvement of this area during writing regardless of the type of word being produced. This difference was also present in the contrasts comparing reading words with seeing symbols. This finding extends the well-documented role of this area in orthographic processing to the copying task. Decreased activation in the fusiform when exposed to words of increasing frequency and in words compared to nonwords have been previously reported (Kronbichler et al., 2004; Wang et al., 2011; Yang et al., 2018). The fact that we found a similar pattern for symbols might indicate that symbols that are graphically similar to letters are processed in the posterior fusiform gyrus in the same manner as letters. Differences in activation on this area between words and nonwords have been interpreted to reflect the involvement of this area in orthographic processing, with many authors proposing the fusiform gyrus to be the storage location of orthographic long-term representations underlying both reading and writing. Sakurai et al. (2008) characterised the posterior inferior temporal cortex (where the fusiform can be found) as the location of the orthographic lexicon. In their model of writing, lexical representations are accessed here before the information is passed downstream to the angular gyrus. Although we did not find evidence of greater activation of the fusiform for low- than for high-frequency words, we did nonetheless replicate the pattern of reduced activity in the fusiform for words than for nonwords (in our case, symbols) previously obtained in reading (Kronbichler et al., 2007; Bruno et al., 2008). It is possible that the frequency of use of our low-

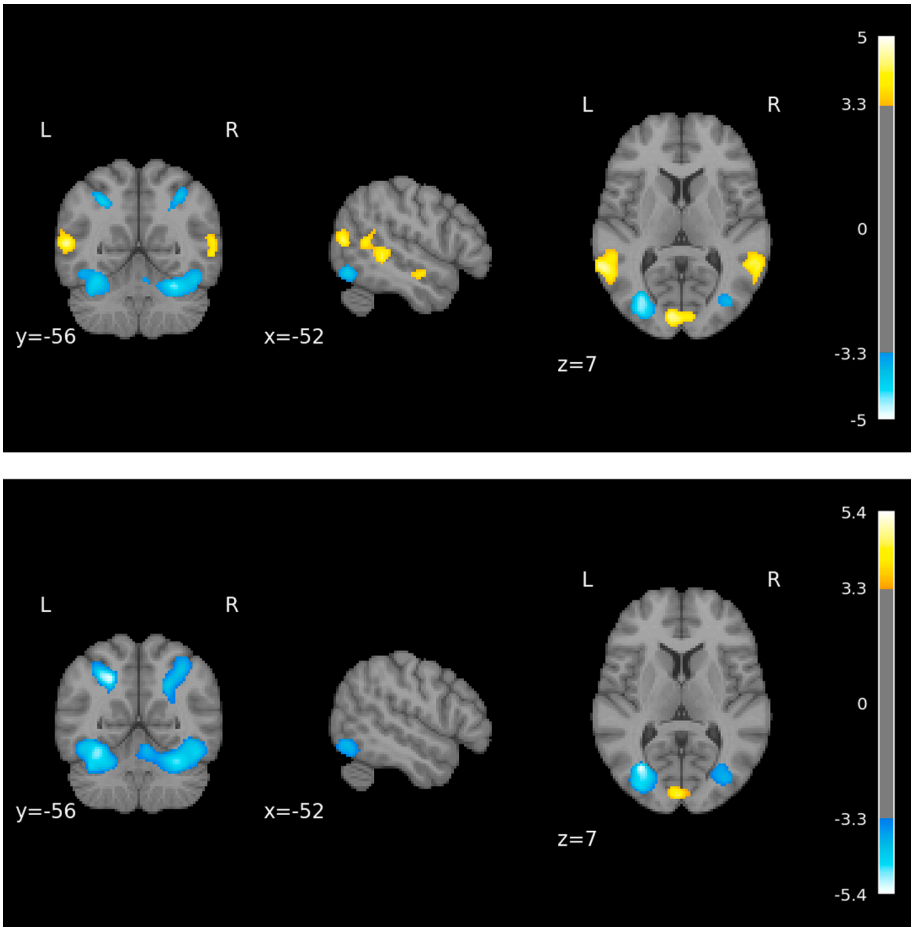

Fig. 3. *Significant peak activations for the contrast Copying Words > Copying Symbols (yellow) and Copying Symbols > Copying Words (blue) for high-frequency words (top panel) and for low-frequency words (bottom panel). See online version for colour image.* (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

frequency words was not sufficiently low as to make these words unavailable in the lexicon. If this interpretation is correct, our findings may suggest that low-frequency words, if they are known, are not exclusively processed resorting to phoneme-to-grapheme conversion procedures in Spanish. They are also accessed in the lexicon, at least in a copying task.

It may be argued that the involvement of the fusiform gyrus might be purely due to the necessity to read the stimulus word in the copying task. According to this interpretation, the changes in activity detected in the fusiform would be exclusively linked to the reading process. As mentioned above, the evidence for a role of the fusiform in visual word recognition is extensive (Cohen et al., 2000; Cohen & Dehaene, 2004; Nobre et al., 1994). However, previous research investigating writing with non-visual stimuli has provided support for the involvement of this area also during writing (Planton et al., 2013; Purcell et al., 2011; Sugihara et al., 2006; Tsapkini & Rapp, 2010). In sum, functional imaging evidence reported here and in previous studies seems to suggest that the fusiform might be the location for orthographic lexical representations used both in reading and in writing (Purcell et al., 2014; Rapp et al., 2016; Sakurai, 2004; Sakurai et al., 2008).

Differences were also found in the pattern of activation found for HF and LF words in comparison to symbols during copying. HF words led to greater activation of the parietal operculum (which includes the SMG) than LF words. As discussed above, the SMG showed increased activation during productive than receptive blocks (both for words and symbols), suggesting an involvement in motor processes. If the SMG is involved in the translation of a visual/phonological representation into a motor pattern, increased engagement in the case of HF words might be reflecting the widely agreed cascading of information from linguistic to motor processes during handwriting. Although the specific mechanism by which information flows from central to peripheral processes is still unclear, facilitatory effects of word frequency on the speed of the hand movements involved in the production of written words has been previously reported (Afonso et al., 2018; Kandel & Perret, 2015; Roux et al., 2013). Additionally, HF but not LF words led to increased activation of the middle temporal gyrus in comparison to symbols. As discussed, damage to the left middle temporal gyrus has been associated to agraphia for kanjis (Sakurai et al., 2008), which requires access to the whole-word representation. However, bilateral activation of the posterior middle temporal gyrus has also been found to be associated to semantic processing (Jung-Beeman, 2005; Jung-Beeman, 2005; Pugh et al., 2001) and semantic integration (Kircher et al., 2009). The fact that most word conditions elicited a difference with symbols in this area (but not LF words) is in line with the interpretation of this effect in terms of semantic processing of most words. This difference with symbols was also present in reading blocks, so it is unlikely to be specific to writing processes.

4.3. *Neural correlates of sublexical processing*

We also found differences in the neural activation associated to the production of inconsistent and consistent words, confirming the use of two different routes when copying. Consistent words showed increased activation in the Heschl's gyrus compared to copying symbols. On the other hand, copying inconsistent (but not consistent) words led to the activation of the pars triangularis and orbitalis of the left IFG. These results are in line with previous claims about the role of these areas during writing production. Sakurai et al. (2008) proposed that the phonological route for writing might start in the Helsch's gyri, with information then sent to the angular gyrus and SMG before reaching premotor hand areas in the frontal cortex. Meanwhile, anterior regions of the IFG have been associated to lexical and semantic processing (Friederici et al., 2000; Hagoort et al., 2004; Rapp et al., 2016). Rapp and Dufor (2011) provided evidence supporting the role of the IFG in the access to and/or storage of orthographic long-term representations in writing. Rapp et al. (2016) proposed that although the posterior parts of the inferior temporal cortex might store long-term word level orthographic representations, the IFG might be the location of a different component of the orthographic long-term memory responsible for selecting among different orthographic candidates. Another possibility is that the fusiform might be the site for the orthographic input lexicon while the IFG would be additionally engaged when orthographic *output* representations are required. In any case, our results suggest that our participants might have engaged in a phonologically mediated route (involving the Heschl's gyrus) when spelling consistent words, but not when spelling inconsistent words. For inconsistent words, the lexical route via the anterior parts of the IFG would be dominant, presumably to ensure the accurate spelling of the inconsistent segment. These effects were not found when words were just read, reinforcing the notion that these areas are specifically recruited by spelling processes.

4.4. Conclusion

Based on the pattern of results obtained here and in previous studies—and using the model of copying introduced in Fig. 1 as a framework for interpretation—we tentatively propose an anatomically constrained model of the word copying task in Fig. 4. Words (differently from non-linguistic stimuli) would activate long-term orthographic representations stored in the fusiform gyrus, as it would happen during reading. Differently from reading, in the copying task these orthographic representations would send information directly upwards initiating a lexical spelling route (a), and activate associated phonological forms stored in the Heschl's gyrus initiating the sublexical route (b). If the retrieved phonological representations contain inconsistent patterns, this might signal in the anterior parts of the IFG the presence of competition between alternative orthographic forms that needs to be resolved. The output of these central processes would travel then to the SMG, which seems to play a role in motor-language integration. Finally, brain areas involved in sensory motor integration and motor control more generally (SPL, pre- and post-central gyrus) would be recruited, leading to the execution of the required hand movements.

This model is similar in several points to that suggested by Sakurai and colleagues (2008) based on the evidence obtained with agraphic patients. However, our findings allow us to add a proposal of when and where precisely spelling inconsistencies would trigger a mechanism for conflict resolution in the IFG. Moreover, it makes explicit claims about which areas would be activated by other similar linguistic and motor tasks and which would be specific to writing. Although some aspects of our proposal are, inevitably, tentative in nature, we hope that it will contribute to generate hypotheses to be tested in future confirmatory research. For example, future studies might explore differences in brain activity during a task that might rely more on spelling processes than the copying task. Additionally, studies using a language with a less transparent orthography than Spanish would help identify more precisely the networks specifically involved in the lexical and sublexical routes for spelling.

CRediT authorship contribution statement

Olivia Afonso: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Conceptualization. **Alberto Avilés:** Writing – review & editing, Visualization, Validation, Software, Formal analysis, Data curation. **Carlos J. Álvarez:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

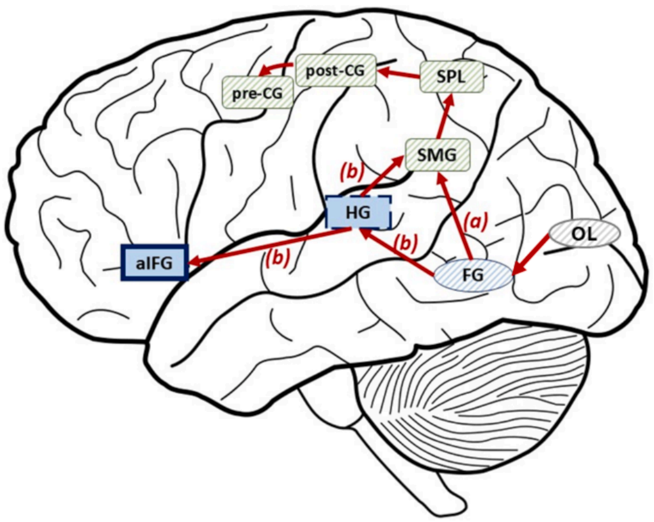

Fig. 4. *Anatomically constrained model of word copying. See online version for colour image. Note.* As in Fig. 1, in Fig. 4 different shapes are used to represent different processing stages (i.e., ovals are used for input decoding processes, rectangles are used for processes, and rounded rectangles are used for handwriting processes); colour is used to represent the nature of the units involved (grey is used for visual processes, blue for linguistic processes and green for motor processes); different fill patterns are used to represent the specificity of the process for writing (solid colours are used for writing-specific processes and line-pattern colours are used for domain-general processes). Post-CG = postcentral gyrus; pre-CG = precentral gyrus; FG = fusiform gyrus; HG = Heschl's gyrus; aIFG = anterior inferior frontal gyrus; SMG = supramarginal gyrus; SPL = superior parietal lobule); OL = occipital lobe. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This study was funded by grant PID2020-114246GB-I00 from the Ministry of Economy and Competitiveness, Spanish Government to Carlos J. Álvarez and by the Collaborative Research and Travel Award, granted to Olivia Afonso by Oxford Brookes University.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandc.2025.106272.

Data availability

The authors do not have permission to share data.

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