

The Neurotopography of Written Word Production: An fMRI Investigation of the Distribution of Sensitivity to Length and Frequency

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Abstract

■ This research is directed at charting the neurotopography of the component processes of the spelling system by using fMRI to identify the neural substrates that are sensitive to the factors of lexical frequency and word length. In spelling, word frequency effects index orthographic long-term memory whereas length effects, as measured by the number of letters, index orthographic working memory (grapheme buffering). Using the task of spelling to dictation in the scanner, we found a highly differentiated neural distribution of sensitivity to the factors of length and lexical frequency, with areas exhibiting sensitivity to length but not fre-

quency and vice versa. In addition, a direct comparison with the results of a previous study [Rapp, B., & Lipka, K. The literate brain: The relationship between spelling and reading. *Journal of Cognitive Neuroscience*, 23, 1180–1197, 2011] that used a very different spelling task yielded a converging pattern of findings regarding the neural substrates of the central components of spelling. Also, with regard to relationship between reading and spelling, we replicated previous functional neuroimaging studies that have shown overlapping regions of activation in the left posterior inferior frontal gyrus and midfusiform gyrus for word reading and spelling. ■

INTRODUCTION

Written language production plays an important role in daily routines, such as typing e-mail, taking notes, filling out applications, writing checks, etc. Furthermore, as electronic communication increases, the time some people spend in written communication, through activities such as e-mailing, texting, chatting, instant messaging, tweeting, etc., may come close to or even surpass the time spent speaking. However, compared with spoken language and written language comprehension (reading), very little research has been dedicated to investigating the neural substrates of written language production (spelling). Although there have been a small number of neuroimaging studies that have investigated the overall neural substrates of the spelling process, these have not, for the most part, directly investigated the neural underpinnings of specific cognitive components of spelling. In this article, we report on research directed at identifying the neural substrates of the cognitive components of word spelling that are specifically sensitive to lexical frequency and/or letter length.

who have acquired written language production impairments as a consequence of a neural injury (typically due to stroke or tumor). In this section, we summarize the findings that have emerged, largely from this research, regarding the cognitive organization of the spelling process.

The literature on acquired dysgraphia has revealed that individual processing components may be selectively disrupted, thus providing a wealth of information regarding the internal operation of the spelling system (for reviews, see Tainturier & Rapp, 2001; Roeltgen, 1993). This work has shown that learned word spellings are stored in a long-term memory (LTM) system often referred to as the orthographic lexicon. These lexical orthographic representations are stored in an abstract, modality-independent format (S-U-G-A-R), and, as depicted in Figure 1, can be accessed from a word's meaning (granular substance used for sweetening) in tasks such as writing from meaning, written picture naming, etc. It may also be possible, in tasks such as writing to dictation, to by-pass meaning and recover word spellings from orthographic LTM directly from a word's sound (Patterson, 1986). In addition to lexical retrieval, spellings (especially for unfamiliar words) may be assembled sublexically, through a phonology-to-orthography conversion process that applies information that has been learned regarding the sublexical relationships between sounds and their spellings. Such a system will generate plausible spellings for phoneme strings, in this case generating spellings such as SHUGER, SHOUGUR, and so forth. Orthographic information that is either retrieved from orthographic LTM or assembled thru phonology-to-orthography

Cognitive Components of the Spelling Process: Evidence from Acquired Dysgraphia

Much of the evidence to date regarding the cognitive processes of spelling comes from the study of individuals

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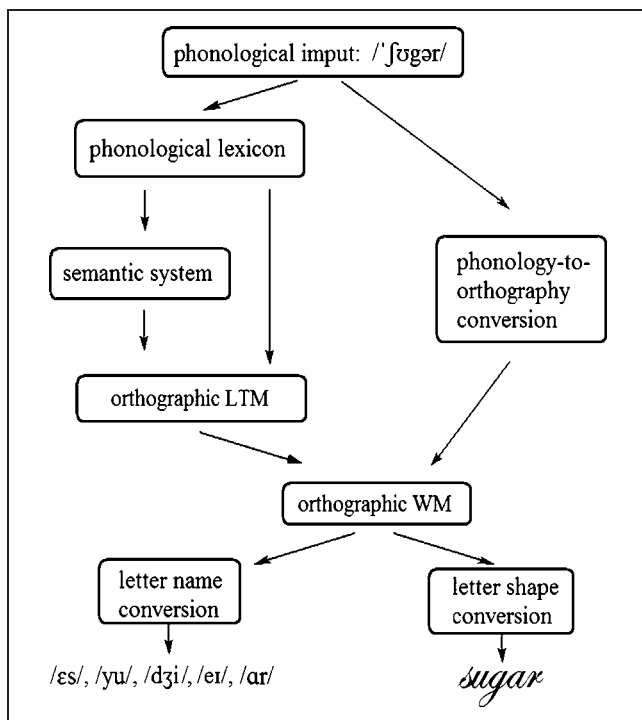


Figure 1. A schematic representation of a functional architecture of the spelling process.

conversion must be maintained active in orthographic working memory (WM; typically referred to as the graphemic buffer) while each letter is serially selected for production. Letter production involves assigning each letter a specific form: letter names for oral spelling and letter shapes (upper/lower case and font) for written spelling. Finally, motor plans that specify the movements and the effectors involved in producing the letter forms (e.g., saying letter names, writing letter shapes, or typing) are retrieved, assembled, and executed. The evidence indicates that this basic architecture applies in a similar manner across alphabetic languages regardless of the transparency of the orthography (see Raman & Weekes, 2005, for a review), although there may be some significant differences for logographically based scripts such as Chinese and Japanese Kanji (e.g., see Sakurai, Mimura, & Mannen, 2008; Sakurai, Terao, et al., 2008; Lee, 2004; Tan et al., 2001; Tan & Perfetti, 1997; Sakurai, Sakai, Sakuta, & Iwata, 1994; Iwata, 1984, for relevant neuroimaging evidence regarding reading and writing).

The neuropsychological work not only reveals that cognitive components may be disrupted with considerable selectivity but also that disruption to each component has characteristic consequences for spelling behavior. In this article, we will be specifically concerned with the orthographic LTM and WM components and, therefore, will focus our discussion and review on these. Research indicates that disruptions to orthographic LTM and WM are each characterized by a specific pattern of spelling errors and by differential sensitivity to the factors of lexical

frequency and length. In deficits affecting orthographic LTM, words that are more frequent are less likely to be disrupted than less frequent words, with frequency indexing the robustness of the LTM representations under conditions of damage (e.g., Goodman & Caramazza, 1986). Orthographic WM deficits result in greater probability of error for letters in longer than shorter words, where length is measured by the number of letters rather than the number of sounds. For example, “though” has only two phonemes but six letters, whereas “sew” also has two phonemes but only three letters. Under circumstances of disruption to orthographic WM, the likelihood that a letter will be produced incorrectly is higher for the former than for the latter. This sensitivity to letter length is, presumably, a consequence of the fact that damage further reduces the normally limited capacity of this WM system. Interestingly, orthographic LTM deficits have typically been shown to be insensitive to letter length, whereas orthographic WM deficits are largely insensitive to lexical frequency (e.g., for more detailed discussion, see Buchwald & Rapp, 2009; Sage & Ellis, 2004).

The Neural Substrates of Written Language Production

Lesion/deficit correlation studies (in chronic and acute stroke) and, more recently, fMRI studies have provided information regarding the neural substrates of the spelling process. It is an interesting question if these three approaches (functional neuroimaging and chronic and acute lesions) reveal similar or different aspects of the neural underpinnings of cognitive processes. Certainly, the lesion methods provide more direct information about the necessary substrates, whereas the neuroimaging methods may reveal both necessary and concomitant activations; furthermore, chronic and acute lesions may be differentially sensitive to consequences of functional reorganization and neurophysiological factors related to the time post-lesion. Nonetheless, for the purposes of this very brief review, we will assume that the results from these approaches are largely convergent, particularly in the context of considerable variability across studies (e.g., in terms of tasks and lesion volumes, etc.).

Lesion/deficit correlation studies have traditionally emphasized the role of the superior parietal cortex, superior premotor region (also known as the Exner’s area; Exner, 1881), and the angular gyrus. More recent work, including evidence from acute stroke (e.g., Hillis et al., 2002) has included the left inferior frontal gyrus and the inferior temporal lobe including the midfusiform gyrus (for reviews, see Tsapkini & Rapp, 2010; Philipose et al., 2007; Hillis & Rapp, 2004; Rapcsak & Beeson, 2002; Friedman, Ween, & Albert, 1993; Roeltgen, 1993).

Functional neuroimaging evidence from neurologically intact individuals has confirmed these loci, with fMRI studies (involving a range of different spelling tasks) identifying spelling-based activation in these same regions in

both alphabetic (Purcell, Napoliello, & Eden, 2011; Rapp & Lipka, 2011; Beeson et al., 2003; Booth et al., 2002) and nonalphabetic scripts when phonograms are used (Sugihara, Kaminaga, & Sugishita, 2006; Katanoda, Yoshikawa, & Sugashita, 2001; Sugishita, Takayama, Shiono, Yoshikawa, & Takahashi, 1996). We would like to note at this point that, although there is a substantial functional neuroimaging literature on written language production in various nonalphabetic scripts (particularly Chinese and Japanese), we will limit our discussion in this article to research on alphabetic scripts because space limitations make it difficult to review both script types while addressing the various differences between them.

With regard to the neural localization of specific functional components of the spelling process (such as those depicted in Figure 1), the evidence is less clear. In the lesion/deficit literature, this is because lesions are typically large and individuals often suffer from multiple deficits. Furthermore, functional neuroimaging studies have not, for the most part, investigated the neural substrates of specific spelling components, instead they have either considered the spelling network more generally or have limited themselves to distinguishing central spelling operations from peripheral ones involved in motor planning and execution (e.g., Purcell et al., 2011; Norton, Kovelman, & Petitto, 2007; Beeson et al., 2003).

The more peripheral production-related components of the writing process have been most typically associated, both through lesion and neuroimaging research, with the following areas: left intraparietal sulcus, left superior parietal lobule, left premotor area, and bilateral SMAs (for a review, see Beeson et al., 2003). In terms of central components, the focus has largely concerned orthographic LTM with few studies considering the neural substrates of orthographic WM.

With regard to orthographic LTM, evidence from chronic stroke has linked disruption to these processes with damage to the left angular gyrus (BA 39) and the inferior temporal lobe, including the inferior temporal gyrus and the fusiform gyrus (BA 37; for a review, see Rapcsak & Beeson, 2002). In addition, there is evidence from acute stroke (see Hillis et al., 2002), implicating the left inferior frontal gyrus (IFG) (BA 44) in orthographic LTM. In the fMRI literature, Rapp and Lipka (2011) specifically examined lexical orthographic processes by identifying neural regions sensitive to the difference between high- and low-frequency words (matched for length and other factors) using experimental and control tasks designed to isolate the central components of the spelling process. They found significant sensitivity to lexical frequency in the left fusiform gyrus, STS, the right cingulate gyrus, and the left inferior frontal junction (IFJ); the posterior portion of the inferior frontal gyrus that abuts the descending precentral sulcus; see Derrfuss, Brass, & von Cramon, 2004).

Chronic lesions producing disruptions to orthographic WM have primarily involved left frontal and parietal lobes and, less often, temporal or occipital cortex (for a review,

Rapcsak & Beeson, 2002). In addition, Cloutman et al. (2009) carried out a study of individuals in the first 48 hours after left hemisphere stroke onset, with one group showing clear signs of impairment to orthographic WM while the other had sparing of orthographic WM. Perfusion and diffusion weighted imaging revealed that the following areas were reliably associated with damage to orthographic WM compared with the cases with sparing of orthographic WM: precentral and premotor cortex (BA 4 and BA 6), postcentral gyrus (BA 2 and BA 3), white matter underlying pFC (BA 48), the caudate nucleus and, less reliably, posterior IFG (BA 45 and BA 47), and lateral occipital cortex (BA 19).

The Relationship between Spelling and Other Skills

Given the focus of this investigation on orthographic LTM and WM in spelling, it is worth considering whether these components of the spelling process are specific to spelling or are shared with other language components. The most natural set of potentially related skills to consider are spoken word production, reading, and verbal or spatial WM.

Writing and Speaking

There have been a number of case reports of individuals with lexically based spoken naming deficits (rather than postlexical or articulatory) who can, nonetheless, write the names of the words they cannot say (e.g., they might say “lion” in naming a picture of tiger but write TIGER). This pattern of orthographic autonomy of written from spoken lexical retrieval has been reported both for opaque scripts such as English (Rapp, Benzing, & Caramazza, 1997; Caramazza & Hillis, 1990) and highly transparent ones such as Italian (Miceli, Benvegnù, Capasso, & Caramazza, 1997) or Spanish (Cuetos & Labos, 2001). These data indicate that, even at the lexical level, the neural substrates of spoken and written word production are, in important ways, distinct. A direct comparison of written and spoken word production has not, however, been undertaken in functional neuroimaging research.

Writing and Reading

There has been considerable interest in understanding the relationship between reading and spelling. This question has been investigated in behavioral studies with neurologically intact adults and children, with individuals with acquired deficits as well as in a small number of neuroimaging studies. The basic approach in these studies has been to examine if specific aspects of reading and spelling performance (or activation patterns) are highly similar or different in relevant respects. Most attention has been paid to the possibility of shared LTM representations, with only a small amount of work considering the possibility of shared orthographic WM and with even less attention directed at the relationship between letter recognition and

production (e.g., Longcamp, Anton, Roth, & Velay, 2003; Rapp & Caramazza, 1997).

The weight of the behavioral evidence favors shared orthographic LTM representations, on the basis of findings from both neurologically intact individuals (Burt & Tate, 2002; Holmes & Carruthers, 1998; Monsell, 1987) and individuals with acquired deficits (Tsapkini & Rapp, 2010; Philipose et al., 2007; Rapcsak & Beeson, 2004; Behrmann & Bub, 1992; Friedman & Hadley, 1992; Coltheart & Funnell, 1987). However, these conclusions have not been uncontroversial, and alternative interpretations have been offered (for reviews, see Rapp & Lipka, 2011; Hillis & Rapp, 2004; Tainturier & Rapp, 2001). Recent functional neuroimaging evidence has added strong support to the shared components position, with Rapp and Lipka (2011), Purcell et al. (2011), and Cho, Rapcsak, and Beeson (2009) reporting coactivation for reading and spelling in the left midfusiform gyrus and in the left inferior frontal gyrus/junction. In addition, Rapp and Lipka (2011) reported sensitivity to lexical frequency in these two regions, strengthening the argument that the shared substrates between reading and spelling are specifically involved in lexical (orthographic) processing (Roux et al., 2009; Lubrano, Roux, & Démonet, 2004).

In terms of the role of orthographic WM in spelling and reading, there have been a handful of studies of acquired impairments that have concluded that there is a shared orthographic WM system (Tainturier & Rapp, 2003; Caramazza, Capasso, & Miceli, 1996; Hillis & Caramazza, 1995). In these articles, it is argued that spelling words and pseudowords places roughly comparable demands on the orthographic WM system whereas reading words (but not pseudowords) places minimal demands on the system because of the fact that words are largely read in parallel.

Spelling and WM Systems

There are no studies that have specifically examined if orthographic WM shares mechanisms and/or resources with other types of WM. In published reports of individuals with impairments to orthographic WM, there is either no data on performance on other WM tasks or the data are inconclusive. If we consider the neural substrates of the lesions in individuals with impairments to orthographic WM, many of these locations are generally consistent with the frontal-parietal localizations of verbal and spatial/object WM systems (Yee, Roe, & Courtney, 2010; D'Esposito, Postle, & Rypma, 2000; Postle, Berger, Taich, & D'Esposito, 2000; Postle, Stern, Rosen, & Corkin, 2000; Courtney, Ungerleider, Keil, & Haxby, 1996). However, findings at this level of generality are also consistent with domain-specific WM systems recruiting distinct, albeit adjacent, substrates. A better understanding of this question will require research examining behavioral and/or activation patterns for multiple WM tasks in the same individuals.

Revealing the Neurotopography of Spelling: Identifying Frequency and Length-sensitive Cortex

The fact that the brain can be damaged and result in behavioral deficits that are quite selectively sensitive to word frequency (orthographic LTM) or length (orthographic WM) indicates that the cognitive processes that give rise to these effects are instantiated in the brain with considerable independence of one another. However, as our review also indicates, there is very little data from functional neuroimaging identifying the neural substrates of the frequency and length-sensitive regions that are involved in spelling. In the research we report on in this article, we directly address this gap by identifying neural activation patterns associated with these factors.

Sensitivity to word frequency is reflected in behavioral measures (RTs or accuracy) or in neural activation in terms of increased RTs, errors, and neural response to low-frequency compared with high-frequency words. These effects are considered to index some aspect of word processing both in written and spoken word comprehension and production. These effects are typically attributed to the processing of LTM word form representations or to the processes involved in their selection. In terms of fMRI research, lexical effects have been observed across domains in written input processing (Kronbichler et al., 2004), written production (Rapp & Lipka, 2011), spoken perception (Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006), and spoken production (Wilson, Isenberg, & Hickok, 2009; Graves, Grabowski, Mehta, & Gordon, 2007). Given the pervasiveness of lexical frequency effects, their interpretation requires careful consideration of tasks and conditions to identify the particular lexical source of the effects in any given study.

Sensitivity to word length is also expected from various components of the language processing system. Whereas for written stimuli, length is typically measured in terms of number of letters, for spoken stimuli, it is measured in terms of number of phonemes and/or syllables. Sensitivity to letter length is certainly expected from components that have a WM function such as orthographic WM but may also arise from other processes involved in written word production, making it important to control for differences in motor demands for words of different lengths (see Methods section, for further discussion). In terms of functional neuroimaging, length effects have been examined less often than have frequency effects and have never been considered in spelling; nonetheless, length effects have been reported for pseudoword reading (Valdois et al., 2006) and also in spoken production (Graves et al., 2007).

In this article we report on an fMRI study designed to examine the distribution of neural responsivity to manipulations of lexical frequency (high and low) and length (long and short). The challenge of this type of research is to isolate the frequency and length-sensitive substrates that specifically reflect the activity of the spelling system.

We do so through the manipulation of stimulus properties and careful design of control tasks. Understanding the neural distribution of these effects will provide key information for charting out the neural instantiation of major components of the spelling system. In addition to this primary focus of the article, we also take the opportunity to attempt to replicate previous findings indicating that word reading and spelling share specific neural substrates (Purcell et al., 2011; Rapp & Lipka, 2011; Cho et al., 2009). Furthermore, we evaluate the degree to which there is convergence of findings across different types of spelling tasks, comparing the findings of the study reported in this article, which used the task of writing to dictation, with the results of Rapp and Lipka (2011), which used a letter probe task. The theory of spelling described above and schematized in Figure 1 assumes that a range of spelling tasks (despite their differences) all make use of the central components of the spelling process (including orthographic LTM and WM). On this basis, convergence of findings across studies would be predicted, and confirmation of these predictions would further strengthen the theoretical claims.

METHODS

We report on three analyses, the first is concerned with charting out the overall substrates involved in spelling to dictation and, in addition, includes a comparison of the spelling network to the network observed in passive reading (a task in which written words are viewed with no overt response or decision required). In the second analysis, we compare the spelling activations from this study, which required handwriting output, to those reported by Rapp and Lipka (2011), who used a letter probe spelling task with a button-press response. This comparison allows us to consider convergence of findings across tasks, as well as to achieve differentiation between the central and production-related components of spelling. Finally, the third analysis is the focus of the article, as it investigates substrates within the spelling network that are specifically sensitive to the effects of lexical frequency and/or length.

Participants

Eight neurologically intact, right-handed, native English speakers participated to this study (five men, three women). All were college students at Johns Hopkins University with no known history of reading or spelling disabilities. They self-rated their spelling ability at least 7 on a 10-point scale and scored at least 75% on a spelling screening test. All were paid for their participation in the research.

Imaging Parameters

MRI data were acquired with a 1.5T Philips Gyroscan ACS-NT scanner (Best, The Netherlands) at the F.M. Kirby

Research Center for Functional Brain Imaging at the Kennedy Krieger Institute (Baltimore, MD). Whole-brain, T2-weighted, gradient-echo EPIs were acquired in 18 transverse slices using a Philips six-channel receive-only SENSE coil (repetition time = 1500 msec, echo time = 40 msec, flip angle = 70°, field of view = 230 × 230 mm, matrix = 64 × 64, slice thickness = 5 mm with 1-mm gap). Structural images were acquired using an MP-RAGE T1-weighted sequence, which yielded images with a 1-mm isotropic voxel resolution (matrix = 256 × 256, repetition time = 8.16 msec, echo time = 3.8 msec, flip angle = 8°).

Tasks and Stimuli

Spelling and passive reading were evaluated using different experimental and control tasks presented in different runs, for a total of 6 runs (4 for spelling, 2 for reading) administered in one scanning session. All subjects completed a practice run of the spelling and reading tasks at least one day before the scanning session. Tasks were presented using E-Prime software (Schneider, Eschman, & Zuccolotto, 2002). A notepad attached to a Velcro strap was secured around each participant's right thigh and served as the written response surface. A longer Velcro strap was wrapped above the elbow to minimize arm and hand movements. A video camera recorded participants' hand movements while in the scanner for later analysis. Auditory stimuli were presented via electrostatic headphones.

Spelling

Spelling was evaluated using three tasks: the experimental task of spelling-to-dictation and the two control tasks of circle drawing and alphabet writing (modeled after Beeson et al., 2003). Each run contained eight blocks of trials (four blocks of spelling-to-dictation and two each of circle drawing and alphabet writing). The alphabet writing task was determined to be a nonoptimal control task, as it requires a number of skills, including alphabet recall, that are irrelevant for spelling and which complicate the interpretation of findings. For this reason, the results of this task will not be reported.

Each of the three spelling-related tasks was presented in blocks of six trials, with block order randomized within runs, across subjects. Trials for all three tasks had the same event structure: (1) a 500-msec fixation period during which a crosshair appeared in the center of the screen, (2) a 1000-msec instruction period during which the word SPELL, ALPHABET, or CIRCLES appeared in the center of the screen indicating the task type, (3) an auditory stimulus presentation period that included both a silent period and an auditory stimulus, such that the silent period plus the auditory stimulus combined to 1500 msec, (4) a 6000-msec response period with a blank screen and a brief auditory beep instructing participants to begin their written responses; participants were instructed to write for the entire

response period until the crosshair appeared on the screen indicating the start of the next trial. Participants used a pencil to produce their written responses, and they were instructed to write alphabetic stimuli in uppercase print (approximately 1 in. in height), one letter on top of the other. Trial-specific instructions were as follows: In SPELL trials, participants were to write the heard word as often as possible within the response period; in CIRCLES trials, participants were to ignore the heard word and draw continuous circles throughout the response period; in ALPHABET trials, participants were also to ignore the heard word and to write as much of the alphabet as possible within the response period, beginning with the letter A on each trial. Regardless of task, the trials were designed to be equivalent in terms of visual and auditory stimulus events and the period of motor response. The critical difference was that the SPELL task had the additional cognitive requirements of retrieving the spelling representation of the heard word from orthographic LTM, processing it through orthographic WM and then retrieving and producing the corresponding letter forms and motor plans.

The auditorily presented word stimuli for the SPELL and CIRCLES tasks were monomorphemic words (nouns and adjectives) consisting of equal numbers of high- and low-frequency, four- and eight-letter words. For each task, there were four 48-word sets, corresponding to a low-frequency four-letter word set, a high-frequency four-letter word set, a low frequency eight-letter word set, and a high-frequency eight-letter word set. Low-frequency words had frequencies between 1 and 3 (occurrences per million; Kucera & Francis, 1967), and high-frequency words had a written frequency of 50 or more. Stimuli were matched across tasks, such that comparisons of length and frequency yielded nonsignificant *p* values; furthermore, high- and low-frequency words were matched for number of phonological syllables as well as proportion of nouns and adjectives in the word sets.

Passive Reading Localizer Task

The reading localizer task was modeled after Cohen et al. (2002) and consisted of passive viewing of written stimuli (high- and low-frequency words, pseudowords, and consonant strings) and checkerboards without an overt response or decision. Stimuli were presented in two runs, each consisting of 20 blocks of 10 trials each with four blocks per stimulus type. Block order was randomized within blocks, across subjects. Each run began with a 6-sec fixation period and ended with a 12-sec fixation period. Each trial began with a 500-msec fixation period, followed by a 200-msec display of a visual stimulus (word, pseudoword, consonant string, or checkerboard, depending on the block type), and each stimulus was followed by an 800-msec blank screen. Word stimuli consisted of 160 words with equal numbers of high- and low-frequency, long (seven-letter) and short (four-letter) words. Pseudoword stimuli consisted of 80 orthographically legal nonword strings, half of which

were four letters in length, half seven letters in length. There were 80 consonant strings that consisted of equal numbers of four- and seven-letter strings. The black and white checkerboard stimuli matched the alphabetic stimuli in spatial extent. Because the purpose of the reading task was for comparison with the spelling task and because the latter included only word stimuli, only the results for word reading will be reported.

Data Analysis

All analyses were carried out using Brain Voyager QX [1.10.4] (Brain Innovation, Maastricht, the Netherlands; Goebel, Esposito, & Formisano, 2006). In terms of preprocessing, functional images were slice-time and motion corrected and a temporal high-pass filter was applied to remove components occurring fewer than three cycles over the course of a run. The images were normalized to Talairach space (Talairach & Tournoux, 1988), resampled to 3-mm isotropic voxels, and spatially smoothed (8-mm FWHM Gaussian kernel). Functional analyses were carried out within a gray matter mask, which was created by combining all participants' individual gray matter masks. The mask excluded from analysis areas corresponding skull, ventricles, and much of the white matter while preserving all the subcortical central structures. Throughout, locations are reported in Talairach coordinates (Lancaster et al., 2000; Talairach & Tournoux, 1988) unless otherwise indicated. Clusters smaller than 55 voxels are not reported.

Two general linear models separately modeled the spelling and passive reading tasks (Friston et al., 1995); for the spelling tasks, an event-related design was used, whereas for the reading task, a block design was used. Spelling was modeled with eight regressors: one corresponding to the combined initial fixation and written instruction period of every trial, another corresponding to the auditory word stimulus period of every trial, one corresponding to the response period for the ALPHABET trials (these will not be discussed further), four corresponding to the four different types of word trials in the SPELL condition: high-frequency/long, high-frequency/short, low-frequency/long, low-frequency/short and one corresponding to run number. All time points corresponding to the response period of the CIRCLES trials served as baseline for the spelling task. Reading was modeled with regressors corresponding to the following stimulus types: consonant strings, pseudowords, fixation, and high- and low-frequency words and one corresponding to run number. All time points corresponding to checkerboard trials served as baseline for the reading task.

RESULTS

Analysis 1. Identifying the Spelling Network

A brain-wide evaluation of word spelling (all four word types) compared with the circle drawing baseline was

carried out using a cluster-size threshold to correct for multiple comparisons (voxel-wise $p = .005$, cluster level $p = .05$). This contrast revealed a network for WORDS > CIRCLES that was largely within the left hemisphere (see Figure 2) and specifically consisted of six clusters with peaks in the following neuroanatomical regions: left hemisphere precentral and fusiform gyri, right hemisphere supramarginal gyrus and precuneus, as well as clusters in the left and right hemispheres of the cerebellum (see bolded clusters in Table 1). In addition, there were several clusters that were more active for CIRCLES than WORDS, which were somewhat more bilaterally distributed in the right and left cuneus, precuneus, middle and superior occipital gyri, and the superior/middle temporal gyri (also see Table 1).

The cluster with its peak in the precentral gyrus was extremely large (75,724 voxels). To identify any secondary peaks that fell within this (or any other) clusters, an additional analysis was carried out, in which activation peaks were identified in a stepwise fashion, beginning with a very stringent uncorrected threshold ($p < .0000001$) and decreasing the p value in eight steps until reaching the p value used in the original cluster thresholded analysis ($p = .005$). This procedure revealed that the large left precentral gyrus cluster contained 20 additional peaks located in both left and right cortices as well as subcortically. These are listed in Table 1, under the bolded precentral gyrus cluster. None of the other bolded clusters contained additional peaks.

To situate these spelling activations in the context of reading, the contrast of WORDS > CHECKERBOARDS from the passive reading task was carried out (voxel-wise $p = .0005$, cluster level $p = .05$). This analysis revealed large areas of activation predominantly in the left hemisphere frontal, parietal, and temporal regions, consistent

with activations typically reported in previous studies using this task (Figure 2 in Cohen et al., 2002). To specifically examine the relationship between the substrates recruited for spelling and reading, we examined the intersection of spelling (SPELL > CIRCLES) and reading (WORDS > CHECKERBOARDS). This analysis revealed the following shared activation regions for spelling and reading in the left hemisphere [IFJ ($-42, -2, 27$; 3605 voxels), fusiform gyrus ($-43, -54, -7$; 403 voxels), superior frontal sulcus (SFS; $-25, -8, 43$; 349 voxels), inferior parietal lobule ($-31, -45, 41$; 1224 voxels), left superior frontal gyrus (medial aspect; $-12, 6, 49$; 149 voxels), the caudate ($-23, -21, 21$; 111 voxels), and putamen ($-28, -13, 1$; 846 voxels)] and in the right hemisphere [the middle frontal gyrus (medial aspect; $11, 27, 33$; 64 voxels), the insula ($43, -8, 18$; 61 voxels), and the caudate ($18, -27, 22$; 342 voxels)]. The coactivation of the left IFJ and the midfusiform for reading and spelling was also found by Purcell et al. (2011) and Rapp and Lipka (2011).

Analysis 2. Convergence/Divergence across Spelling Tasks: A Comparison with Rapp and Lipka (2011)

To examine similarities and differences in neural substrates recruited across different spelling tasks, we compared the results reported just above in Analysis 1 with the results reported in Rapp and Lipka (2011). Rapp and Lipka used a spelling probe task in which participants heard a word, saw a letter, and then responded with a button press to indicate whether the letter was in the spelling of the heard word. The control task used was a case verification task in which participants heard a word (which they were told they could ignore), saw a letter, and responded with a button press to indicate if the letter was

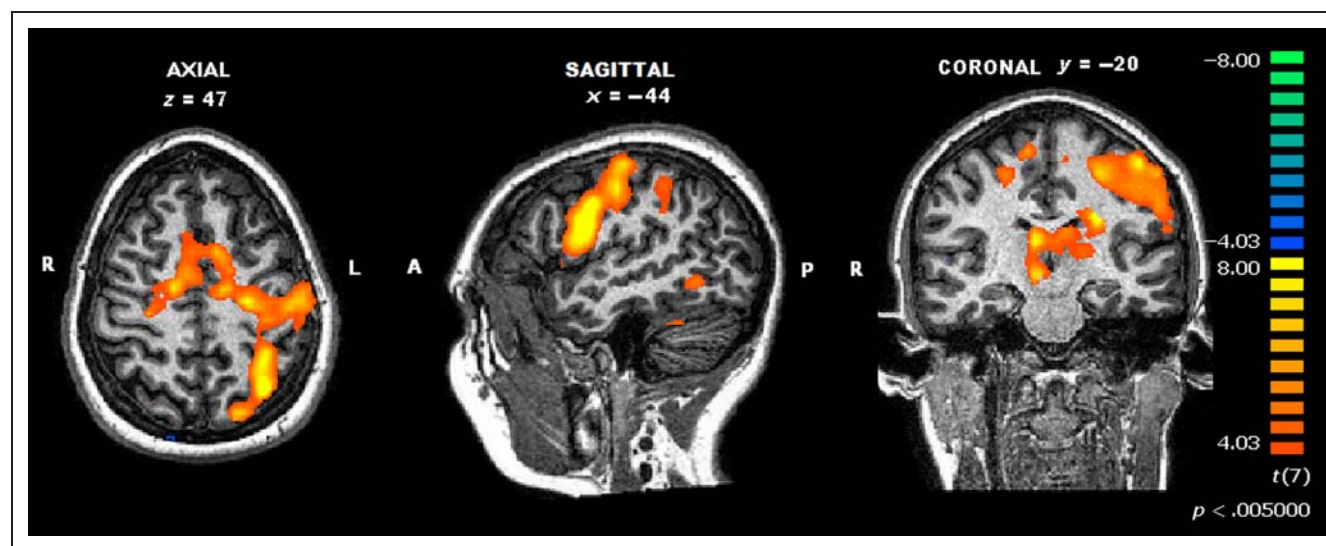


Figure 2. Results from the whole-brain contrast comparing spelling to dictation to circle drawing (WORDS > CIRCLES) using a cluster size correction for multiple comparisons (voxel-wise, $p = .005$, cluster level $p = .05$). See Table 1 for information regarding location of activation peaks. The results of this contrast were used as the mask for Analysis 3.

Table 1. Results from Two Contrasts: SPELL > CIRCLES and CIRCLES > SPELL

	Peak X	Peak Y	Peak Z	Cluster Size (Voxelwise $p = .005$, Cluster $p = .05$)	t Value at the Peak	p Value at the Peak
<i>SPELL > CIRCLES</i>						
Precentral gyrus (BA 6)	-22	-17	51	75724	10.6	.000015
Superior frontal gyrus (medial aspect; BA 6)	-10	-14	51		10.152	.000019
IFJ (BA 6)	-43	-5	30		11.723	.000007
Inferior frontal gyrus (BA 9)	-46	1	21		25.805	<0
Cingulate gyrus (BA 24)	-13	-8	36		8.167	.00008
Inferior parietal lobule (BA 40)	-52	-26	33		8.0178	.00009
Precuneus (BA 7)	-25	-68	33		7.815	.000106
Precuneus (BA 7)	-31	-44	45		11.147	.00001
Superior parietal lobule (BA 7)	-31	-59	48		13.319	.000003
Postcentral gyrus (BA 3)	-49	-17	45		11.314	.000009
Precentral gyrus (BA 6)	44	-5	30		9.66	.000027
Superior frontal gyrus (medial aspect; BA 6)	14	-11	48		8.459	.000064
Thalamus (ventral lateral nucleus)	-16	-14	12		7.478	.00014
Thalamus (medial dorsal nucleus)	8	-20	12		9.127	.000039
Putamen	-25	7	0		7.05	.000202
Putamen	-31	-8	3		8.042	.000088
Caudate body	-16	16	12		8.573	.000058
Caudate body	-22	-20	24		11.806	.000007
Caudate body	-4	4	21		15.603	.000001
Caudate body	14	1	15		9.211	.000037
Caudate body	11	13	12		15.701	.000001
Fusiform gyrus (BA 37)	-37	-59	-6	455	6.571	.000312
Inferior parietal lobule (BA 40)	32	-41	36	362	5.168	.001298
Precuneus (BA 7)	20	-65	51	313	5.681	.00075
Left cerebellum	-19	-59	-21	1895	8.105	.000084
Right cerebellum	2	-68	-18	747	5.787	.000672
<i>CIRCLES > SPELL</i>						
Middle occipital gyrus (BA 19)	-25	-86	9	797	-7.588	.000127
Superior temporal gyrus (BA 22)	-52	-14	0	323	-7.533	.000134
Superior occipital gyrus (BA 19)	41	-83	24	662	-6.601	.000304
Superior temporal gyrus (BA 22)	50	-17	3	1064	-7.377	.000152
Cuneus (BA 19)	-4	-89	21	383	-4.942	.00167
Precuneus (BA 7)	-4	-74	36	2271	-7.111	.000192
Precuneus (BA 19)	17	-83	42	894	-6.0167	.000533

In **bold** are the clusters identified using the cluster-size threshold correction (voxel-wise $p = .005$, cluster level $p = .05$). All nonbolded clusters were identified as located within the large precentral cluster (see text for details). Peak locations are in Talairach coordinates.

Table 2. Clusters Resulting from the Intersection of Activations From the Task of Spelling to Dictation (WORDS > CASE; Reported in Table 1) and the Activations Reported in Rapp and Lipka (2011) for the Spelling Probe Task (SPELL > CASE)

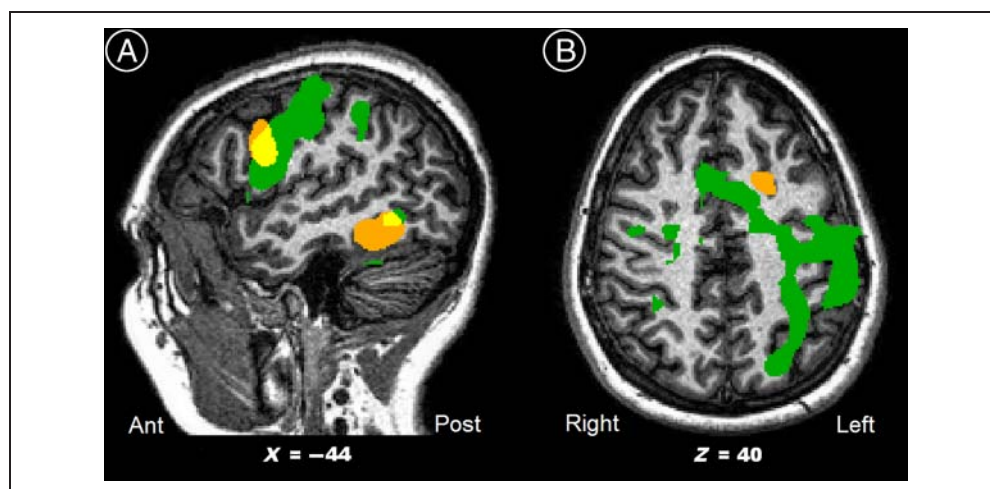
<i>Intersection of WORDS > CIRCLES and SPELL > CASE</i>	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>Cluster Size (Number of Voxels)</i>
Left IFJ (BA 6/BA 9)	-42	2.9	24	1992
Left fusiform gyrus (BA 37)	-43	-53	-7.9	188
Left cingulate gyrus (BA 24)	-12	9	30	255
Left caudate	-24	-21	21	108
Right caudate (tail)	20	-28	23	126

Contrasts from both tasks were corrected for multiple comparisons at the same level (voxel-wise, $p = .005$, cluster level $p = .05$). Talairach coordinates correspond to the geometric center of each intersection cluster.

in upper or lower case. In this way, the two tasks were matched in terms of stimulus input and motor response, but the letter probe task additionally required retrieval of a word's spelling from LTM and maintenance and inspection in WM while a decision was made regarding the status of the target letter. Therefore, in terms of the spelling theory depicted in Figure 1, the experimental versus control tasks in both studies should identify orthographic LTM and WM components, whereas the contrast of SPELL > CIRCLES should additionally recruit processes involved in letter shape selection and motor planning that are specific to the requirement, in writing-to-dictation, of producing a series of letters in the handwriting format. It is also worth noting that, although this accurately characterizes the similarities and differences between the two sets of tasks in terms of cognitive components recruited, we cannot exclude the possibility of more subtle differences between the tasks in terms of the demands they place on the same components.

To compare the results of the two studies, we examined the intersection of the contrast SPELL > CIRCLES (Analysis 1, above) with the contrast SPELL > CASE from Rapp and Lipka (2011). Both sets of results were generated from data that were cluster-size thresholded at the same level (voxelwise $p = .005$, cluster level $p = .05$). As indicated in Table 2, this intersection analysis revealed the following left hemisphere clusters, IFJ (BA 6/BA 9), fusiform gyrus (BA 37), cingulate gyrus (BA 24), and caudate nucleus, as well as a cluster in the tail of the right hemisphere caudate nucleus. Figure 3A depicts the intersection clusters for the IFJ and fusiform regions. With regard to the region of the SFS, as depicted in Figure 3B, both studies produced significant activity in this neuro-anatomical region, although the activation from the SPELL > CASE contrast was somewhat more anterior and inferior (-15, 11, 37) to that produced by the SPELL > CIRCLES contrast (-22, -17, 51), and the latter was also more extensive (see Figure 3).

Figure 3. Comparison of activations resulting from different spelling tasks. Depicted are clusters resulting from the intersection of the contrast between spelling to dictation (WORDS > CASE) reported in Table 1, and the results reported in Rapp and Lipka (2011) for the contrast between a spelling probe task and control task (SPELL > CASE). Both contrasts were corrected for multiple comparisons at the same level (voxel-wise, $p = .005$, cluster level $p = .05$). Green = voxels significant for WORDS > CIRCLES, orange = voxels significant for SPELL > CASE, yellow = intersection between the two tasks. (A) A sagittal view depicting the IFJ and fusiform intersection clusters. (B) An axial view depicting the activations from the two studies that involve the SFS. Note that the activation from the current study that includes the SFS is more posterior and extensive than the one from the Rapp and Lipka (2011) study, extending into the parietal lobe. Further information regarding these intersection clusters is reported in Table 2.



The nonoverlapping areas across the two studies are of interest as well. These were almost entirely areas that were significant for SPELL > CIRCLES but not for SPELL > CASE, making them good candidates for processes involved in the representation, serial selection, and production of letter shapes. These areas consisted of activations located almost entirely in the superior parietal lobe (see Figure 3B) as well as in subcortical regions.

Analysis 3. The Distribution of Sensitivity to Length and Frequency in Spelling

To examine the distribution of neural sensitivities to lexical frequency and word length, we examined the contrast LONG > SHORT words (with the two word sets matched for the number of high- and low-frequency words) and also the contrast LOW FREQUENCY > HIGH FREQUENCY (with the two word sets matched for the numbers of long and short words). It should be noted that, with regard to the length comparison, to have a “pure” contrast of the letter-length demands placed on orthographic WM, the written responses should be equated in terms of handwriting activity. Otherwise activation differences associated with length effects may be due to the increased motor planning and execution associated with writing more letters. To equate long and short words for the number of letters produced, participants were instructed to write each word repeatedly during the response period. In this way, participants produced motor responses during comparable periods, regardless of letter length, while still allowing a manipulation of WM demands. In fact, this is the first study in which length effects in spelling

have been examined in a manner that specifically controls for the number of letters produced.

Video taping of the written responses during scanning allowed for the observation of the number of letters actually written on each trial. Analysis of the video tapes revealed that the mean numbers of letters produced per condition were as follows: Hifreq/Long = 9.4 letters, Hifreq/short = 8.6 letters, Lofreq/long = 9.2 letters, and Lofreq/short = 8.8 letters. This indicates that per trial, on average, participants produced 9.3 letters for the eight-letter stimuli and 8.7 letters for the four-letter stimuli; that is, there was about half a letter difference in the number of letters actually written for long compared with short words. With four-letter stimuli, participants typically wrote each word twice and then often produced the first letter of the third repetition, whereas with eight-letter words, they typically wrote each word once and then frequently produced the first or the two first letters of the second repetition. Although long and short words were quite well matched in terms of letters actually produced, the overall difference between them was statistically significant ($t = 5.12$, $p = .0037$), although it was only significant for high-frequency words ($t = 5.64$, $p = .0024$) and not for low-frequency words ($t = 1.72$, $p = .14$).

For the analysis of the fMRI data, the spelling network identified in Analysis 1 (through the brain-wide, contrast of WORDS > CIRCLES) was used as a mask within which to examine the contrasts LOW FREQUENCY > HIGH FREQUENCY and LONG > SHORT (voxel-wise $p = .005$, cluster level $p = .05$). Interestingly, this analysis yielded clusters that were sensitive to either frequency or length, but not both. Frequency-sensitive clusters were observed in the left IFJ ($-49, 1, 33; 312$) and anterior cingulate

Table 3. Characteristics of the Significant Frequency and Length Sensitive Clusters Revealed in Analysis 3, which Compared Activations for High- versus. Low-Frequency Words (LOW > HIGH) and Long versus Short Words (LONG > SHORT)

	Peak X	Peak Y	Peak Z	Cluster Size	T	p
<i>LOW > HIGH FREQUENCY</i>						
Left IFJ (BA 6)	-49	1	33	312	6.45	.0003
Anterior cingulate (BA 32)	-1	13	39	168	5.07	.0014
Bilateral thalami	1	-17	0	767	10.76	.0000
Putamen	-25	-8	3	701	9.67	.0000
<i>LOW > HIGH FREQUENCY (VOI Analysis)</i>						
Left fusiform gyrus (BA 37)	-37	-59	-6	455	2.753	.0059
<i>LONG > SHORT</i>						
SFS (BA 6)	-13	-11	51	629	5.84	.0006
Superior parietal lobule (BA 7)	-28	-50	52	289	7.46	.0001

The analysis was carried out within the SPELL > CIRCLES mask depicted in Figure 2. Correction for multiple comparisons was applied (cluster-wise $p = .005$, cluster level $p = .05$) and Talairach coordinates for the peak voxels are reported. Also reported is the cluster in the left fusiform gyrus that was used in a VOI analysis and was shown to be sensitive to frequency but not to length.

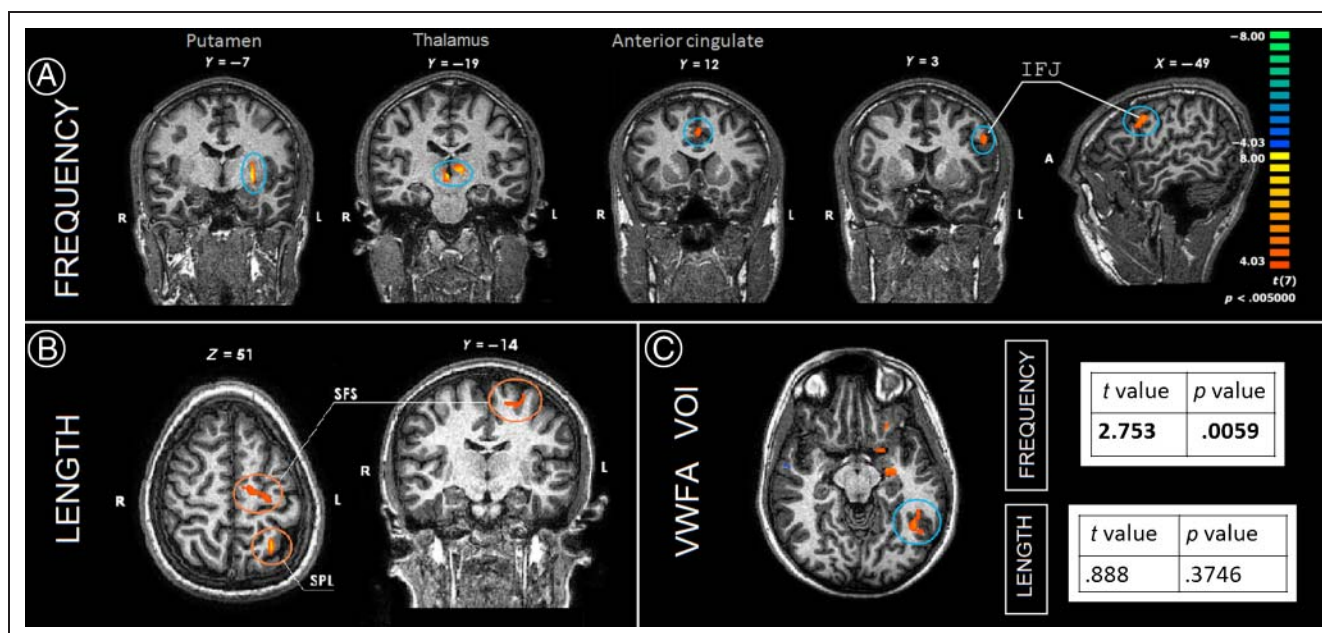


Figure 4. The results of Analysis 3 comparing high- versus low-frequency words (LOW > HIGH) and also long versus short words (LONG > SHORT) for the task of spelling words to dictation. A and B depict the results of an analysis carried out within the SPELL > CIRCLES mask depicted in Figure 2; correction for multiple comparisons was applied (cluster-wise $p = .005$, cluster level $p = .05$). (A) Axial views of the four significant clusters resulting from the frequency comparison and an additional sagittal view of the IFJ cluster. (B) A horizontal view of the two length-sensitive clusters, one in the SFS, and the other in the superior parietal lobule; also depicted is an additional coronal view of the SFS cluster. (C) The cluster in the left fusiform gyrus (reported in Table 1) that served as a VOI for the comparison of LOW > HIGH and LONG > SHORT. Reported also are the t and p values indicating a significant effect of frequency and a nonsignificant effect of length within this VOI. Additional details are available in Table 3.

(-1, 13, 39), as well as subcortically in the left putamen and bilaterally in the thalamus (see Table 3, for details). The frequency-sensitive areas are depicted in Figure 4A. Length effects were observed in only two left hemisphere clusters: in the superior frontal sulcus (SFS) (-13, -11, 51) and the superior parietal lobule (-28, -50, 52). These are depicted in Figure 4B. As indicated just above, participants produced significantly more letters for long compared with short words (when both low- and high-frequency words are combined). Given the small, yet significant difference, between the number of letters produced for long compared with short words, we carried out the same analysis using only low-frequency words because for this word set the long and short words did not differ in terms of the number of letters actually produced. The contrast LONG > SHORT carried out with just low-frequency words yielded the same significant cluster in the SFS, whereas the parietal cluster was no longer significant for length. These results indicate that the SFS cluster is more robustly sensitive to letter length, independent of any possible production-related factors, whereas the parietal cluster's function may be closely linked to letter production itself. Finally, given the consistency with which the left fusiform (BA 37) region has emerged in neuroimaging and deficit/lesion studies of spelling, we also carried out a VOI analysis on the left fusiform cluster (-37, -59, -6) reported in Analysis 1 (Table 1). When both frequency (LOW > HIGH) and length (LONG > SHORT) contrasts were examined within this VOI, there was

a significant effect of word frequency ($t = 2.75, p = .006$), but not of letter length ($t = 0.89, p = .38$; see Figure 4C and Table 3). In this way, the left midfusiform gyrus joins the group of clusters exhibiting sensitivity to lexical frequency.

DISCUSSION

The objectives of this research were to begin to chart the neurotopography of the component processes of the spelling system by identifying the neural substrates that are sensitive to the factors of lexical frequency and letter length. In behavioral, neuropsychological and neuroimaging research, word frequency effects are typically associated with lexical LTM processes, whereas word-length effects are associated with orthographic WM. The principal finding of the study reported in this article is that, using tasks designed to isolate spelling processes, we found a highly differentiated neural distribution of sensitivity to the factors of length and lexical frequency, with specific areas exhibiting sensitivity to length but not frequency and vice versa. In addition, a direct comparison of the results from this study and Rapp and Lipka (2011), although the two studies involved very different spelling tasks, yielded a pattern of converging and diverging activations that support previous findings regarding the neural substrates of the central components of spelling and those involved in motor planning and production. Finally, with regard to relationship between reading and spelling, we also replicated previous

functional neuroimaging studies (Purcell et al., 2011; Rapp & Lipka, 2011) that have shown overlapping regions of activation in the left IFG/IFJ and midfusiform for word reading and spelling in the same participants (also see Cho et al., 2009).

Frequency Effects and Orthographic LTM

The finding of frequency-sensitive cortex in the IFJ and the midfusiform gyrus replicates the findings of Rapp and Lipka (2011), the only other functional neuroimaging study that has specifically examined frequency effects in spelling. As indicated in the Introduction, there is evidence from the lesion literature associating damage to these two areas with the constellation of behavioral markers that index disruption to the orthographic LTM. In combination, these sets of findings make the processing and/or storage of orthographic lexical representations strong candidates for the functions supported by these two cortical areas. It must be mentioned, however, that in the broader literature, both regions have been associated with a wide range of different cognitive operations (regarding the left fusiform, see Price & Devlin, 2003, but see Tsapkini & Rapp, 2010; Cohen & Dehaene, 2004, for responses). Nonetheless, the experimental and control tasks and the stimulus characteristics that were used in this study (as well as Rapp & Lipka, 2011) were designed to manipulate lexical frequency while controlling for phonological (syllable length), grammatical category, as well as response and decision variables. Thus, although alternative interpretations cannot be ruled out, a strong case can be made for the role of these areas in some aspect of lexical orthographic representation and processing.

This naturally leads to the question of the specific characterization of the cognitive functions supported by the two topographically quite distant cortical areas. Although both exhibit frequency sensitivity, it does not follow that they support precisely the same frequency-sensitive operations. In this regard, it is interesting to note that the IFJ/IFG region has been associated with lexical selection in a number of studies (Thompson-Schill et al., 1998; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995), a function not generally ascribed to the fusiform. This raises the possibility that IFJ region may be responsible for the control processes involved in selection among multiple orthographic word forms, although the word forms themselves may be stored elsewhere, such as in the fusiform gyrus. Although this is speculative and nothing in our results specifically argues for this particular account, it is a hypothesis that is consistent with the literature and merits further investigation in future neuroimaging and cognitive neuropsychological research. For example, it would be informative to study cases of acquired lexical dysgraphia with frontal versus fusiform lesions to determine if the functional deficits, although similar in many respects, differ in ways that might be predicted by a hypothesis that distinguishes between lexical selection and storage.

Another question raised by the findings of this study concerns the role of the other frequency-sensitive regions that were identified, namely the left cingulate and subcortical structures such as the putamen and thalamus. One would want to see greater replication of these findings and more detailed testing before developing a specific hypothesis regarding their roles. Nonetheless, it is worth noting that Rapp and Lipka (2011) also reported frequency sensitivity in the cingulate, although in that case, it was the right posterior cingulate. Furthermore, Purcell et al. (2011) and Beeson et al. (2003) also reported spelling activity in the left and bilateral cingulate although in these studies the activations cannot be specifically associated with lexical effects. Also, if we consider orthographic processing more broadly, there have been a number of neuroimaging studies of reading that have reported larger responses for low frequency words or pseudowords relative to high frequency words in the cingulate as well as in subcortical structures such as the thalamus and putamen (Fiebach, Friederici, Müller, & von Cramon, 2002).

Length Effects and Orthographic WM

To our knowledge, this is the first neuroimaging study to examine length-sensitive neural substrates in spelling. The results identify the SFS as the strongest, although not necessarily the only, candidate for orthographic WM processes. This premotor region has long been associated with spelling, and its location is generally consistent with the region referred to as Exner's area (Roux, Draper, Köpke, & Démonet, 2010; Roux et al., 2009; Exner, 1881). Although this region has traditionally been associated with a role in the generation of motor commands for handwritten letters, there are a number of reasons that support the more specific hypothesis that at least some substrates within this region may be involved in orthographic WM.

First, there is the finding from this study that this region is sensitive to letter length even when motor planning and production demands are matched across short and long words. Recall that this was accomplished (for low-frequency words) by ensuring that, on average, comparable numbers of letters were produced for long and short words. This approach is certainly not without its limitations, in particular, it does not control for the fact that shorter words are "placed into" orthographic WM more often than longer words. Nonetheless, this kind of control provides the cleanest test to date of sensitivity to WM demands. Second, it is important to note that the SFS was not active in the reading task (also replicating Purcell et al., 2011; Rapp & Lipka, 2011). As reviewed in the Introduction, it has been proposed (e.g., Caramazza et al., 1996) that orthographic WM is critical in the spelling of both words and pseudowords, whereas in reading, it is primarily engaged by pseudowords (Ans, Carbonnel, & Valdois, 1998).¹ Thus, for theoretical reasons, length sensitivity is predicted for word spelling but not word reading, consistent with the observed pattern of presence/absence of activation in the SFS in spelling

compared with reading in this and the earlier fMRI studies. In addition, there are several sources of evidence indicating that the SFS area, although clearly involved in written language production, has a role that is independent of the particular format of letters or the effectors used in production. Effector and format independence are also key characteristics of orthographic WM. In this regard, it is relevant that Roux et al. (2009) found that left SFS is recruited regardless of the hand individuals were writing with. These researchers also found that direct cortical stimulation of left SFS disrupted writing although it did not disrupt hand movement themselves (this was the case even for a left-handed individual). Furthermore, Purcell et al. (2011) and Longcamp et al. (2008) found that typing significantly activated this region, providing evidence that production of letter forms is not a prerequisite for its recruitment. Finally, there are findings from both chronic and acute stroke indicating, as reviewed in the Introduction, that deficits to orthographic WM have been often associated with frontal (premotor) and parietal lobe lesions (see Cloutman et al., 2009, for a review). In summary, there are various lines of evidence that support the hypothesis that at least some portion of the SFS is involved in some aspect of orthographic WM. For the moment the conclusion can only be tentative and in future work, it will be important to delineate the relationship between orthographic WM and WM in other domains (verbal, spatial, or object WM).

It is also important to point out that there are cases in the lesion literature in which clear orthographic WM deficits occur in individuals with lesions confined to the parietal lobe (e.g., Buchwald & Rapp, 2009). This raises the question of the proper interpretation of the finding, in the current study, of length sensitivity in the superior parietal lobule. Recall that the length sensitivity in the parietal lobe was not significant when long and short words were matched for number of letters produced (in the analysis involving only low-frequency words). Although this weakens the argument that the parietal activation reflects orthographic WM processes, it is also premature to reject this possibility given the relatively weak statistical power provided by the number of participants included in this study. Another possibility to consider, however, is that orthographic WM is undoubtedly a multicomponent process (as are other WM systems), and therefore, there may be aspects of orthographic WM that are more closely tied to production and which, therefore, may be sensitive to the production factors, such as the number of elements produced. Also relevant to understanding the parietal activation is the finding that parietal regions (along with subcortical ones) were not significantly active in Rapp and Lipka (2011). Given the different output modes of the two tasks (written vs. button press), a natural inference is that the areas of nonoverlap represent processes involved in the production aspects of written output. In this context, the length sensitivity observed in the superior parietal lobule would be consistent with what other research has considered to be its role in spatial and motor

planning (Menon & Desmond, 2001). However, any conclusions on the basis of differences observed between the current study and Rapp and Lipka (2011) can only be tentative given that, as we have indicated earlier, in addition to the different output modes, there may be other subtle differences between the two sets of tasks used in these studies. Again, this is an area that is very much in need of replication studies using similar and different tasks that will allow for clearer patterns of convergence and divergence to be documented.

Convergence and Divergence across Tasks and Studies

We directly compared the findings of the current study with those of Rapp and Lipka (2011) and found striking convergence across studies in terms of their joint activation of the left hemisphere midfusiform and IFJ. We also found, in both studies, significant activation in the SFS, although these activations did not overlap. As indicated above, the first two areas are strong candidates for orthographic LTM processes, whereas the third is a candidate for orthographic WM. Furthermore, these findings are confirmed in the existing functional neuroimaging studies of spelling. Thus, Purcell et al. (2011) and Beeson et al. (2003) all report activations in these three regions, and Roux et al. (2009) report activation in the SFS region. With regard to the SFS region and its possible orthographic WM function, it is important to consider that differences in the precise activation locations in this general region across studies may not only reflect the different subcomponents of orthographic WM but may also be due to the many closely related processes involved in motor planning and production.

In conclusion, we have identified brain areas that are reliably active in spelling across a number of studies, tasks, and spelling output modalities. This convergence of evidence provides a solid basis for moving forward in developing not only a more detailed understanding of the neural substrates of spelling but also of the relationships between spelling functions and similar functions in other cognitive domains.

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Note

1. Unless word presentation format is manipulated to decrease parallel access, for example, Tainturier and Rapp (2003).

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