Shared premotor activity in spoken and written communication

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ABSTRACT

The aim of the present study was to uncover a possible common neural organizing principle in spoken and written communication, through the coupling of perceptual and motor representations. In order to identify possible shared neural substrates for processing the basic units of spoken and written language, a sparse sampling fMRI acquisition protocol was performed on the same subjects in two experimental sessions with similar sets of letters being read and written and of phonemes being heard and orally produced. We found evidence of common premotor regions activated in spoken and written language, both in perception and in production. The location of those brain regions was confined to the left lateral and medial frontal cortices, at locations corresponding to the premotor cortex, inferior frontal cortex and supplementary motor area. Interestingly, the speaking and writing tasks also appeared to be controlled by largely overlapping networks, possibly indicating some domain general cognitive processing. Finally, the spatial distribution of individual activation peaks further showed more dorsal and more left-lateralized premotor activations in written than in spoken language.

1. Introduction

Spoken language is one of the defining characteristics of humans that spontaneously develops without formal teaching in the first years of life. Its neural organization is the product of millenaries of evolution, with premises of its sensorimotor organization investigated in non-human primates (Aboitiz & Garcia, 1997; Aboitiz, 2012; Jürgens, 2002; MacNeilage, 1998; Rauschecker & Scott, 2009; Rilling, 2014; Scott & Johnsrude, 2003). Through dedicated pathways, this specialized neural machinery is exquisitely tuned to allow discrimination and categorization of highly complex sounds, and production of those same sounds through precise coordination of the speech articulators, leading to nearly perfectly accurate perceptual and motor skills (Guenther & Vladusich, 2012; Guenther, 2006; Hickok & Poeppel, 2000, 2004, 2007; Hickok, Houde, & Rong, 2011; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Rauschecker & Scott, 2009; Rauschecker, 2011; Scott & Johnsrude, 2003; Skipper, Van Wassenhove, Nusbaum, & Small, 2007; Tourville & Guenther, 2011). Neurobiological models argue that speech motor control and auditory speech processing partly operate through a cortical dorsal stream that mediates a mapping between auditory, somatosensory and articulatory-motor speech representations. During speech production, modulation of neural responses observed within the auditory and somatosensory cortices are thought to

reflect feedback control mechanisms in which sensory consequences of the speech-motor act are evaluated with actual sensory inputs in order to evaluate accurate production (Guenther & Vladusich, 2012; Guenther, 2006; Hickok et al., 2011; Houde et al., 2002; Tourville & Guenther, 2011). Conversely, motor activity observed during speech perception has been proposed to partly constrain phonetic interpretation of the sensory inputs through the internal generation of candidate articulatory categorizations (Hickok & Poeppel, 2000, 2004, 2007; Liberman & Mattingly, 1985; Rauschecker, 2011; Rauschecker & Scott, 2009; Scott & Johnsrude, 2003; Skipper, Van Wassenhove, Nusbaum, & Small, 2007).

Contrary to spoken language, mastering written language requires several years of intense training, and is thought to induce plasticity in brain regions and brain networks initially devoted to other functions (Dehaene & Cohen, 2007; Dehaene et al., 2010). Processing graphemes for reading or writing is well known to engage a hierarchy of occipital and ventral temporal brain regions that code increasingly complex visual features. Ultimately, some regions acquire a certain degree of functional specificity to basic units of written language (Jobard, Crivello, & Tzourio-Mazoyer, 2003; Planton, Jucla, Roux, & Démonet, 2013). This is the case of the highly investigated fusiform gyrus (also called ventral occipito-temporal area), identified in word-reading tasks (Cohen et al., 2000), in single letters perception (Polk et al., 2002) and

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in writing (Dufor & Rapp, 2013). For some researchers, this region hosts "abstract letter identities", that is amodal representations of single letters that can be mobilized in various contexts (Rothlein & Rapp, 2014). In the motor system as well, both neuropsychological descriptions of brain damaged patients, brain imaging studies and meta analyses, support the view that the functioning of restricted regions of the left dorsal premotor and left superior parietal cortex, whose localization is remarkably similar across studies, is mandatory for the production of graphemes through handwriting (Planton et al., 2013)).

Although spoken and written languages engage very different perceptual and motor processes, several lines of evidence however suggest that they are partly intertwined. Letters are not only visual objects or writing movements: they are also strongly associated to sounds, especially through their names. Letters name is considered a component of the neural representation of letters (Rothlein & Rapp, 2014). Behaviorally, phonological information can efficiently prime letter recognition (Arguin & Bub, 1995; Bowers, Vigliocco, & Haan, 1998; Ziegler, Ferrand, Jacobs, Rey, & Grainger, 2000) and modulate the brain's response to visually presented letters (Dietz, Jones, Gareau, Zeffiro, & Eden, 2005; Madec et al., 2016; Xue, Chen, Jin, & Dong, 2006). Reciprocally, when contrasting literate with illiterate adults, literacy was found to modulate activity in the planum temporale in response to spoken inputs (Dehaene et al., 2010), and more generally, in the networks involved in speech processing (Castro-Caldas, Petersson, Reis, Stone-Elander, & Ingvar, 1998).

Based on these studies, the working hypothesis of the present functional magnetic resonance imaging (fMRI) study relies on the theoretical proposal that written and spoken modalities are partly intertwined. In order to identify possible shared neural substrates for processing the basic units of spoken and written language, a sparse sampling fMRI acquisition protocol was performed on the same group of literate adults, in two experimental sessions with similar sets of letters being read and written and of phonemes being heard and orally produced. Importantly, the two sessions were organized exactly in the same way, with the same experimental design, similar items (the phonemes /p/, /b/, /t/, and /d/ in the listening and speaking tasks, and the letters p, b, t and d in the reading and writing tasks) and the same imaging parameters (sparse sampling). Compared to the baseline, the average BOLD activity in the listening, speaking, reading and writing tasks was first calculated. Several conjunction analyses were then performed on these contrasts in order to determine common neural activity across tasks (listening ∩ speaking, reading ∩ writing, listening ∩ reading, speaking ∩ writing, listening ∩ speaking ∩ reading ∩ writing). Interestingly, previous studies provided evidence for auditory activity during reading (Jancke & Shah, 2004; Perrone-Bertolotti et al., 2012; van Atteveldt, Roebroeck, & Goebel, 2009). Regions of interest (ROIs) analyses were carried out in order to further determine possible crossmodal activity in primary and associative auditory and visual brain areas (i.e., auditory activity for written language and visual activity for spoken language).

In this framework, one strong hypothesis is that of a possible common organizing principle for processing units of written and spoken language, through the coupling of perceptual and motor representations during perception. In both cases, this organizing principle emerges spontaneously in the course of learning. When learning speech sounds, a perceptuo-motor coupling sets up in human infants, based on a combination of auditory and somatosensory information with motor commands, through babbling and imitation (Guenther & Vladusich, 2012; Schwartz, Basirat, Ménard, & Sato, 2012; Tourville & Guenther, 2011). In written language, repeated writing of the individual letters is assumed to stabilize the visuospatial representations of single letters (Longcamp, Zerbato-Poudou, & Velay, 2005) and to provide the child with variable instances that subsequently help assigning a given identity to an encountered shape with more flexibility (James, 2010; Li & James, 2016). Based on these early perceptuo-motor associations, sensorimotor interactions are also thought to play a key role in adults. A

On the one hand, a matching between motor and sensory representations is indirectly supported by an impressive number of neurophysiological studies showing activity in the motor system during both speech perception and visual processing of single letters (e.g., Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Longcamp, Anton, Roth, & Velay, 2003; Watkins, Strafella, & Paus, 2003; Papathanasiou, Filipović, Whurr, Rothwell, & Jahanshahi, 2004; Wilson, Saygun, Sereno, & Iacoboni, 2004; James & Gauthier, 2006; Pulvermüller et al., 2006; Skipper et al., 2007; Tremblay & Small, 2011; Nakamura et al., 2012; Nakatsuka et al., 2012; Schomers, Kirilina, Weigand, Bajbouj, & Pulvermüller, 2015; for reviews, see Longcamp, Hlushchuk, & Hari, 2011; Skipper, Devlin, & Lametti, 2017). On the other hand, several lines of evidence suggest that motor reactivation during perception is not an epiphenomenon, or ancillary to understanding (Hickok & Poeppel, 2007), but has a functional relevance. In speech, this is attested by the findings that activation of motor and premotor cortices during speech perception is stronger when the speech signal is noisy (Du, Buchsbaum, Grady, & Alain, 2014; Osnes, Hugdahl, & Specht, 2011), that sensorimotor activity within the cortical dorsal stream correlates with auditory phonemic categorization (Alho et al., 2012; Chevillet, Jiang, Rauschecker, & Riesenhuber, 2013; Alho et al., 2014), and by transcranial magnetic stimulation (TMS) studies showing that premotor regions partly mediate phonemic discrimination in noise (d'Ausilio et al., 2009; Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007) and speech segmentation under normal listening conditions (Möttönen & Watkins, 2012; Murakami, Kell, Restle, Ugawa, & Ziemann, 2015; Sato, Tremblay, & Gracco, 2009). In written language, this is attested by neuropsychological (Anderson, Damasio, & Damasio, 1990), behavioral (James & Gauthier, 2009) and TMS (Pattamadilok, Ponz, Planton, & Bonnard, 2016) studies showing that reading is disturbed when cortical motor regions are made unavailable. Based on this body of research, and in addition to identifying the shared neural substrates of written and spoken language, the present study also aimed at comparing the coupling of perceptual and motor representations in spoken versus written language. Since previous studies suggested a dorsal vs. ventral distribution of precentral activity during writing and speaking (e.g., Longcamp et al., 2014; Grabski, Lamalle, Vilain, et al., 2012), the spatial distribution of individual activation peaks common between perception and production in motor regions was determined to compare the extent and position of motor brain activation shared between perception and production of the units of spoken versus written language, while qualitatively accounting for possible inter-individual variability.

2. Methods

2.1. Participants

Twenty-six healthy, literate adults (14 females and 12 males, with a mean age of 26 years (± 4 SD), ranging from 18 to 34 years) participated in the study after giving their informed consent. All participants were recruited via e-mails sent to Toulouse University. They were right-handed according to standard handedness inventory (Oldfield, 1971; mean score of 95/100), were native French speakers, except one French participant who was native Arabic speaker but Arabic-French bilingual and perfectly fluent in French (three other participants also declared they were French-English or French-Spanish bilinguals), with a mean age of education of 15 (± 2 SD) years from the elementary school. They all had normal or corrected-to-normal vision and no self-reported history of auditory, motor, speaking, hearing, reading, writing and language disorders. Participants were screened for medical problems and contraindications to MRI, and they were compensated for the time spent in the study. The protocol was approved by the Ethical Committee of Toulouse (ID RCB: 2013-A01740-45) and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki. Data sets from three participants were excluded from the analyses, one

because of technical problems during MRI acquisition, and the two others because of problems in the experimental procedure. Overall, data sets from 23 participants were therefore analyzed in the whole-brain group and motor clustering analyses. In the ROI analysis, one subject was removed because of missing activity according to our ROI criteria (see below).

2.2. Stimuli

In order to investigate and to compare the functional neuroanatomy of listening, speaking, reading and writing, the four p, b, t and d consonants in the reading and writing tasks and corresponding syllables in the listening and speaking tasks were selected. The stimuli were selected in order to provide a gradient of phonological parameters, they differed according to their place of articulation (labial vs. coronal) and/or voicing (voiced vs. unvoiced). Note that in addition to representing the names of the corresponding letters, all four syllables (and the corresponding letters) had meaning in French depending on northern/southern accent (/be/: "baie"/"bay", /de/: "dé"/"dice", /pe/: "pet"/"fart", /te/: "thé"/"tea"). However, given the instructions, the tasks and the limited set of stimuli, the impact of possible lexical processes were minimal. As for the distinction between letters and syllables, consonants in French cannot be produced outside a monosyllabic context (e.g., the letter /t/ is produced /te/).

Acoustic stimuli. Multiple utterances of /pe/, /be/, /te/, /de/ syllables, pronounced in French as p, b, t, d consonants, were individually recorded by six native French speakers in a soundproof room (three female and males speakers; sampling rate of 44.1 kHz with 16-bit quantization recording). None of the speakers participated in the fMRI study. Five clearly articulated tokens were edited and selected per syllable and per speaker. Using Praat software (Boersma & Weenink, 2013), each syllable was manually cut, at zero crossing points, from the consonantal onset for unvoiced /pe/ and /te/ syllables or from the voicing onset for voiced /be/ and /de/ syllables to the vocalic offset. With this procedure, one hundred-twenty distinct syllables were therefore selected for the listening and speaking tasks, with the stimuli matched for global acoustic duration (mean value ± SD: 237 ms ± 6) and normalized for intensity (mean value ± SD: 79 dB ± 0).

Visual stimuli. Multiple occurrences of p, b, t, d consonant letters were individually produced by three native French writers with a thin black felt pen on smooth white cardstock, at a size approximately 3 to 4 times the normal writing size. None of the writers participated in the fMRI study. The cardstock was then scanned, providing high definition images from which five representative exemplars of each letter were chosen, extracted and processed using an image manipulation software. In addition, three word processing fonts with or without serif were chosen. Letters p, b, t, d were isolated for each font and manipulated (slightly tilted, shrinked or size of up- or downstrokes modified) in order to create five distinct exemplars of each. The resulting letters were processed the same way as the handwritten letters, and the same gray level was applied to the strokes. With this procedure, one hundred-twenty distinct consonant letters images (5 exemplars × 4 letters × 6 fonts) in grayscale were therefore selected for the reading and writing tasks (see Fig. S1 in Supplemental Data for examples).

2.3. Procedure

Each participant performed two distinct fMRI sessions, done with the same acquisition parameters, and related to either one listening and one speaking tasks, or to one reading and one writing tasks (see Fig. 1). One important aspect of the present study is that consonants were presented or produced in isolation in a single trial during a silent interval between subsequent volume scans (see Data Acquisition). This sparse sampling procedure minimized the effects of scanner noise during speech perception and production as well as movement artifacts due to speech production. Each scanning session lasted approximately

one hour and their order was counterbalanced across participants.

The listening-speaking fMRI session consisted of ten functional runs and one anatomical scan. The sequence of stimuli was the same in the listening and speaking tasks, except that three catch trials were added pseudorandomly to the listening task in order to ensure a constant degree of attention (see below). In both tasks, the trials (the same consonant never occurring twice in succession), were pseudorandomly presented in each run. Participants were asked to keep their eyes open in all functional runs. A fixation cross was displayed at the middle of the screen in all trials. To minimize possible covert motor simulation, the listening task was performed in the first five functional runs. Each of these runs consisted of thirty-three trials and each trial was 8 s in length. In twenty-four trials, participants were asked to passively listen to p, b, t or d consonant. In the catch trials, the symbol "?" replaced the fixation cross, and participants listened to a single consonant and had to manually decide with their left hand if it was identical or not to the consonant presented in the previous trial (one-back task). Finally, a baseline condition, without any movement or sensory stimulation, occurred in six trials. Participant's left manual responses in the catch trials were recorded through a two-button fiber-optic button response pad (2 * 2 Forp button). After an anatomical scan, the five last runs involved the speaking task, using exactly the same acquisition parameters. The experimental procedure and sequence was the same, except that participants had to repeat the perceived consonant. Each of these runs consisted of thirty trials and each trial was 8 s in length. In twenty-four trials, participants were asked to overtly produce p, b, t, or d consonant, with an auditory target indicating the consonant to be produced. As in the listening task, a baseline condition, without any movement or auditory stimulation, was also added. In the listening-speaking fMRI session, participants wore MRI-compatible headphones with noise-reducing passive material through which auditory stimuli were delivered (MR-Confon audio system, www.mr-confon.de) and their speech productions were monitored using an MRI-compatible microphone (CONFON Dual-Channel-MIC-DCHS 02, MR Confon, Magdeburg, Germany).

The reading-writing fMRI session also consisted of ten functional runs and one anatomical scan. Except the visual nature of stimuli, in the reading task and the writing tasks, the experimental procedure and acquisition parameters were exactly identical to those used in the listening-reading fMRI session. Each visual stimulus was displayed on the center of the screen for 1000 ms on a black background. In the writing task, the response was monitored using an MRI compatible graphic tablet (Digitizing tablet DT01, Mag Design and Engineering, California, USA). Participants wrote with their dominant right hand with their elbow resting on a cushion. They were instructed to use their wrist and fingers to produce the single letters, to start writing once they had identified the letter, and to rest their hand on the edge of the tablet between trials. The onset and offset of the pen-tip were recorded for each trial.

From the above-mentioned procedure, it is worthwhile noting that the overt speaking task induced auditory feedback, while no visual feedback of their writing trace was available because the digitizer had a correct temporal but a low spatial accuracy. Also note that the speaking and writing tasks included a perceptual stage related to the acoustic or visual target presentation.

Altogether, each fMRI session therefore consisted of 315 functional scans (perception task: 5 runs × (((4 stimuli + 1 baseline) × 6 trials) + 3 catch trials); production task: 5 runs × ((4 stimuli + 1 baseline) × 6 trials). In addition, three 'dummy' scans at the beginning of each run were added to allow for equilibration of the MRI signal and were removed from the analyses.

2.4. MRI data acquisition

Magnetic resonance images were acquired with a 3T whole-body MR scanner (Philips Achieva, UMR 1214 ToNIC, INSERM, Toulouse).
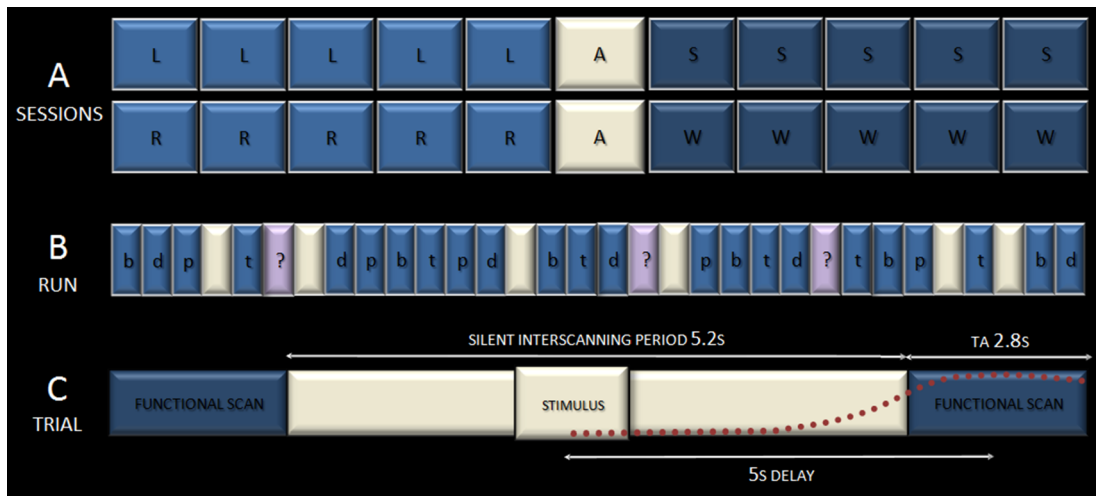
Fig. 1. Experimental design. A) All participants performed two distinct one-hour sparse sampling scanning sessions, done with the same acquisition parameters, and related to either one listening (L) and one speaking (S) tasks or to one reading (R) and one writing (W) tasks. Each scanning session consisted of ten runs, each lasting approximately five minutes, and one anatomical scan (A). B) Each run consisted of twenty-four trials in which participants were asked to listen to, speak, read or write either p, b, t or d consonant and six baseline trials. In addition, three catch trials were added in the listening and speaking tasks. C) For each trial, the time interval between the perceived or produced consonant and the midpoint of the following functional scan acquisition was of 5 s (the predicted hemodynamic response function is indicated in red; TA: Time of Acquisition). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Participants were laid in the scanner with head movements minimized with a SENS-head 32 channel and foam cushions. The display of the visual and auditory stimuli, and the recordings of the button presses in the catch trials and of the pen tip onset and offset in the writing task were controlled using Presentation software (Neurobehavioral Systems, Albany, USA). Visual instructions and visual stimuli were and displayed on a screen situated behind the scanner via a mirror placed above the subject's eyes.

In both sessions, functional images were obtained using a T2*-weighted, echo-planar imaging (EPI) sequence with whole-brain coverage (TR = 8 s, acquisition time = 2.8 s, TE = 30 ms, flip angle = 90°). The long TR is necessary to allow the sparse-sampling procedure (see below). Each functional scan comprised fifty-three axial slices parallel to the anteroposterior commissural plane acquired in non-interleaved order (80×80 matrix; field of view: 240 mm; $3 \times 3 \, mm^2$ in plane resolution with a slice thickness of 3 mm without
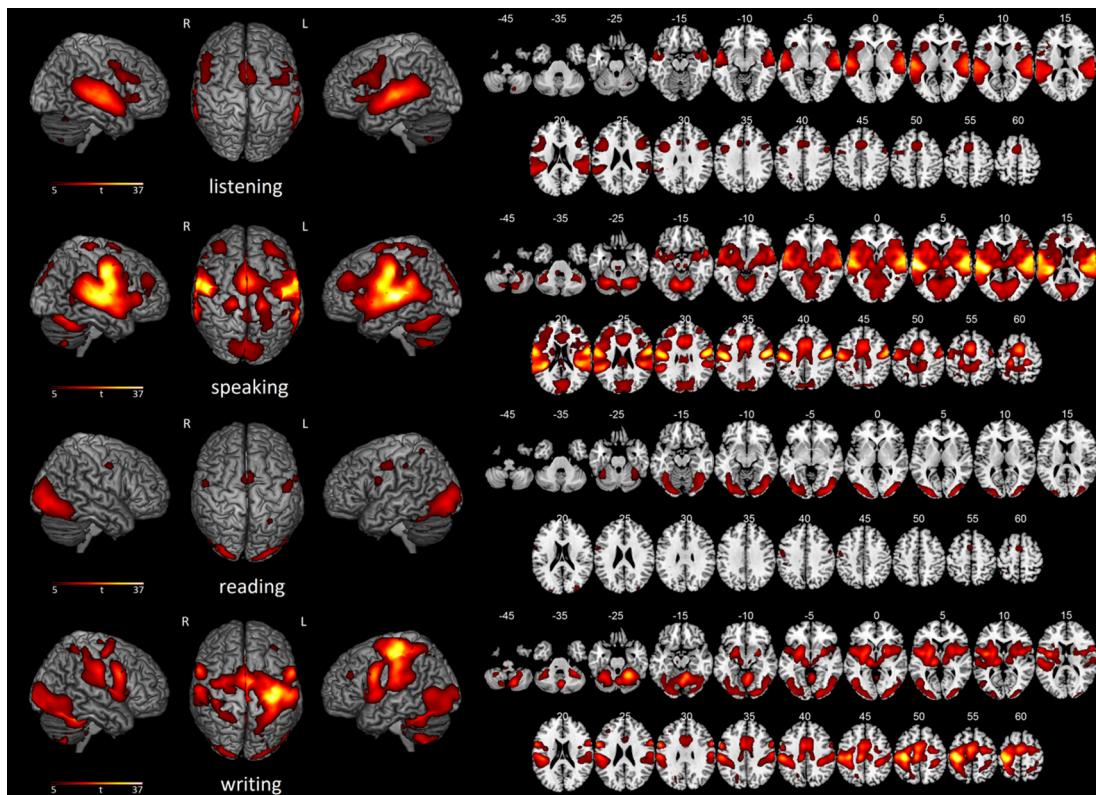
Fig. 2. Brain activity in the listening, speaking, reading and writing tasks compared to the baseline (unidirectional t-contrasts, p < .05 FWE corrected at the voxel level, cluster extent threshold of 20 voxels, see Table S1 in Supplemental Data for details).

gap). A high-resolution T1-weighted whole-brain structural image was acquired for each participant after the last functional run (sagittal volume of $256 \times 256 \times 170$ mm^3 with a 1 mm isotropic resolution, inversion delay: 900 ms, sense 2.2, slices 170, TR/TE = 8.3/3.8 in ms, flip angle = 8).

In the listening-speaking session, a sparse sampling acquisition paradigm was used in order to avoid movement artifacts due to speech and writing production and to minimize scanner noise during both speech perception and production (e.g., Birn, Bandettini, Cox, & Shaker, 1999; Hall et al., 1999; Gracco, Tremblay, & Pike, 2005). Functional scanning therefore occurred only during a fraction of the TR, alternating with silent interscanning periods, where participants listened to or produced a single consonant. Since the rising hemodynamic response is estimated to occur with a 4–6 s delay in case of speech perception and production (Grabski, Lamalle, Vilain, et al., 2012, Grabski, Lamalle, et al., 2012; Grabski et al., 2013), the time interval between the acoustic consonantal onset and the midpoint of the following functional scan acquisition was set at 5 s. In order to compare the four tasks, the same acquisition parameters were used in the reading-writing fMRI session, with the time interval between the visual consonant letter and the midpoint of the following functional scan acquisition being of 5 s.

2.5. Data analyses

Data were analyzed using the SPM8 software package (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK) running on Matlab (Mathworks, Natick, MA, USA). Activated brain regions were first labeled using the probabilistic cytoarchitectonic atlas Anatomy toolbox (Eickhoff et al., 2005) and, if a brain region was not assigned or not specified in the Anatomy toolbox, using the Talairach Daemon software (Lancaster et al., 2000). For tables, the maximum activation peak provided by the Anatomy toolbox within each distinct anatomical region of each cluster of activity was reported (note that the maximum number of peaks per cluster provided by Anatomy and SPM is thirteen; in case of very large clusters, brain regions not reported are described in the text). For visualization, activation maps were superimposed on a standard brain template using the MRICRON software (http://www.sph.sc.edu/comd/rorden/mricron/).

Data preprocessing. In each fMRI session, data pre-processing steps for each participant included rigid realignment of functional images within each run and on a trial-by-trial basis by estimating the six movement parameters of a rigid-body transformation, coregistration of the structural image to the mean functional image, segmentation and normalization of the structural image to common subject space using the group-wise DARTEL registration method implemented in SPM8, warping of all realigned functional images using deformation flow fields generated from the normalization step, transformation into the MNI space and spatial smoothing using a 8 mm full-width at half maximum Gaussian kernel.

Individual analyses. For each fMRI session and each participant, BOLD activity was analyzed using the General Linear Model, including for each run four regressors of interest (one for each consonant), as well as one regressor of no interest related to the catch trials and the six realignment parameters as nuisance regressors in order to control for head movements, with the baseline trials forming an implicit baseline. The BOLD response for each event was modeled using a single-bin finite impulse response (FIR) basis function spanning the time of acquisition (2.8 s). Before estimation, a high-pass filtering with a cutoff period of 128 s was applied. Beta weights associated with the modeled FIR responses were then computed to fit the observed BOLD signal time course in each voxel for each condition. Individual statistical maps were calculated for each condition with the related baseline and subsequently used for group statistics.

Whole-Brain group analyses. In order to draw population-based inferences, a second-level random effect group analysis was carried-out. A full factorial design was used, with the language type (2 levels: oral,

written), the language mode (2 levels: perception, production) and the stimulus (4 levels: p, b, t, d) as within-subject factors and the subjects treated as a random factor (Glascher & Gitelman, 2008). First, given the $2 \times 2 \times 4$ factorial design (language type × language mode × stimulus), BOLD activity changes for each experimental factor was calculated independently of the others: i.e., possible activity changes between the listening and speaking tasks compared to the reading and writing tasks (main effect of language type, bidirectional F-contrast), in the listening and reading tasks compared to the speaking and writing tasks (main effect of language mode, bidirectional F-contrast) and between the four stimuli (main effect of stimulus, bidirectional F-contrast). All interactions between the three experimental factors were also computed (language type × language mode, language type × stimulus, language mode × stimulus, language type × language mode × stimulus, bidirectional F-contrasts). For concision, since these results appeared in line with the literature, they are presented in Supplemental Data (see Fig. S3 and Table S3). Second, four t-contrasts were calculated to determine the average BOLD activity in the listening, speaking, reading and writing tasks, compared to their respective baseline. Several conjunction analyses were then performed on these contrasts in order to determine common neural activity across tasks (listening ∩ speaking, reading ∩ writing, listening ∩ reading, speaking ∩ writing, listening ∩ speaking ∩ reading ∩ writing). In addition, for each task, four t-contrasts were calculated to determine possible differences in BOLD activity between voiced vs. unvoiced stimuli as well as between labial vs. coronal stimuli (See Fig. S4 and Table S6 in Supplemental Data for results).

All contrasts were calculated with a Family-Wise-Error (FWE, Worsley, Evans, Marrett, & Neelin, 1992) corrected level of $p < .05$ at the voxel level with a cluster extent of at least 20 voxels. This conservative thresholding procedure was used because the activations in each task were compared to the activation in the baseline. To avoid interpretation biases, we also provide a representation of the results of the conjunctions according to the method used by Allen, Erhardt, and Calhoun (2012) in Supplemental Data (see Fig. S2).

ROI Analysis – Heteromodal or cross-modal activity in perceptual regions. ROI analyses were carried out in order to further determine whether perceptual brain regions specific to a given language-type (oral, written) induced BOLD changes in the other type (heteromodal or cross-modal activity). To this end, individual ROIs in primary and associative auditory regions were defined on the basis of normalized individual data. For the oral type, we defined ROIs in the left and right primary auditory cortices, and in the left and right planum temporale. For the written type, we defined regions in the primary visual cortex, and in the left and right fusiform gyri. For each participant and each sensory brain area, we determined the maximum activation peak at the closest vicinity of a predefined reference peak. For the auditory mode, the reference peaks were defined as the maximum activation peaks observed in the group analysis during speech perception in BA41 (Posterior Auditory Cortex, combined cytoarchitectonic maps of areas Te 1.0, Te 1.1 and Te 1.2; see Morosan et al., 2001, Rademacher et al., 2001, coordinates for the group −48–18 4 and 51–11 1 resp. for left and right hemispheres) and in BA42 and BA22 (planum temporale, coordinates for the group −64–20 5 and 66–13 2 resp. for left and right hemispheres) according to the SPM anatomy toolbox (Eickhoff et al., 2005). For the visual mode, we searched the local maxima at the closest vicinity of the point 0–90 −10 (calcarine sulcus, primary visual cortex) and in the left and right fusiform gyri. For the fusiform gyri, given the spatial extent of the anatomical region and the fact that visual perception usually leads to several ventral activation clusters, we restricted the search to the local maxima near the coordinates of the visual word form area (as defined by Jobard et al. (2003) at −44–58 −15) and of the counterpart of this region in the right hemisphere (44–58 −15). Individual ROIs in each sensory areas were then defined by a 6 mm-radius sphere centered on the selected maximum activation peak". One subject, for whom we were not able to define any ROI in the visual

modality (primary visual cortex and fusiform gyri) was discarded from the analysis. The time-series were then extracted and averaged between all voxels within a given ROI for each subject, and converted to both zscore and percent change (after detrending) within each run. Both normalization measures give similar results, with less variation between ROIs with zscore normalization. We show the percent change results because they are easier to interpret. For each subject, we first computed the median of the percentage of BOLD signal across all runs in the absence and in the presence of a stimulus (for the hearing and reading tasks, catch trials were ignored; there was no catch trial in the speaking and writing tasks). Then we computed and displayed the difference of medians for each individual. We also display the group mean and the confidence intervals across subjects (95% CI for the increase due to the presence of a stimulus). Those measures are considered an indication of the reliability of the activation of a given ROI compared to a situation where no stimulus is present: we considered that we observed significant BOLD changes when the CIs did not include zero, because the CIs represent the possible range of the population mean. In that case, we report the range of population mean (effect size) compatible with our data. For visualization purposes, we also displayed the difference of medians for each individual, as they are more reliable measures at the individual level.

Individual spatial analyses of frontal activations - motor clustering. Since inter-subject variability in brain anatomy limits the spatial accuracy of group maps, individual analyses were carried out to qualitatively determine the spatial distribution and organization of common motor activations observed during listening and speaking (listening ∩ speaking) as well as during as reading and writing (reading ∩ writing). For both left and right hemispheres, four specific search spaces related to the pars triangularis (BA45, IFG-PT) and pars opercularis (BA44, IFG-PO) of the inferior frontal gyrus and to the premotor (BA6, PMC) and primary motor (BA4, M1, combined cytoarchitectonic maps of areas 4a and 4p) cortices were first created using the Anatomy toolbox (Eickhoff et al., 2005). Note that the pars triangularis of the inferior frontal gyrus is not a motor area but it is classically involved in spoken and written tasks. For each participant, analyses restricted to the search spaces were then performed on individual GLMs using the Anatomy toolbox on the two contrasts 'listening ∩ speaking' and 'reading ∩ writing', with small volume correction applied on each search space at a threshold of P < 0.001 uncorrected for multiple comparisons with an extend threshold of k ≥ 20 voxels. MNI coordinates of the center of gravity (COG) of each cluster of activity within each search space were determined in both hemispheres.

3. Results

3.1. Behavioral scores.

Responses to catch trials. Participant responses in catch trials in the listening and reading tasks were analyzed offline. Mean percentage of correct responses was of 91% (± 2%) in the listening task and of 95% (± 2%) in the reading task.

Acoustic recordings. All vocal responses in the speaking task were analyzed using Praat software (Boersma & Weenink, 2013). A semi-automatic procedure was first devised for segmenting participants' recorded syllables. For each participant, the procedure involved the segmentation of each syllable based on an intensity and duration algorithm detection. Based on minimal duration and low intensity energy parameters, the algorithm automatically identified pauses between each syllable and set the syllable's boundaries on that basis. All boundaries were then hand-corrected, based on waveform and spectrogram information. Wrong productions were then identified with on average 93% of correct productions (± 5% SD). Because of technical problems during acoustic recordings, one male participant was removed from this analysis.

Digitizer recordings. The onset and offset of the pen tip were analyzed for each trial. The data from 3 participants could not be recorded accurately. The data for the remaining 20 participants indicated that participants gave a response in the vast majority of the trials (23 non-responses out of the 2400 trials analyzed). The timing of the response was in a normal range for all participants (mean response time = 0. 99 s; sd = 0. 16 s and mean response duration = 1.19 s; sd = 0.36 s).

3.2. Neural correlates of listening, speaking, reading and writing (Fig. 2 and Table S1)

Listening. Compared to the baseline condition, the listening task induced large bilateral auditory activations, ranging from the primary and secondary auditory cortices in the transverse temporal gyrus (TTG), to the superior part of the temporal gyrus/sulcus (STG/STS) and temporopolar area rostrally, and to the planum temporale in posterior STG/STS and temporo-parietal junction caudally. Auditory activation extended medially to the insular cortex, dorsally to the ventral part of the supramarginal gyrus and parietal operculum, and ventrally to the posterior middle temporal gyrus (MTG). Bilateral frontal activations were also observed in the pars opercularis and pars triangularis of the inferior frontal gyrus (IFG), extending to the adjacent middle frontal gyrus and ventral premotor cortex. Further activity was observed in the supplementary motor area and adjacent middle cingulate cortex, the left intraparietal sulcus and adjacent superior parietal lobule, the cerebellum (lobules VI, VII and VIII) and the thalamus.

Speaking. Compared to the baseline condition, the speaking task induced large bilateral activations of the primary sensorimotor and premotor cortices, the pars opercularis and pars triangularis of IFG, extending rostrally to the adjacent middle frontal gyrus and dorsolateral prefrontal cortex. Large bilateral auditory activations were also observed in TTG, STG/STS and MTG. Additional activity was found in the supplementary motor area, extending to the anterior, middle and posterior cingulate cortices, the inferior and superior parietal lobule, the rolandic and parietal operculum, the thalamus, the anterior insular cortex, the basal ganglia, and the cerebellum (lobules V, VI, VII, VIII, X) extending to ventral regions of the primary and secondary visual cortex.

Reading. Compared to the baseline condition, the reading task induced large bilateral visual activations, ranging from the primary and secondary visual cortices to the fusiform gyrus. Additional clusters of activity were observed in the left ventral premotor cortex, extending to the pars opercularis of the left IFG, a more dorsal region of the ventral premotor cortex and adjacent primary motor cortex, the supplementary motor area, the dorsal part of the left supramarginal gyrus and the left superior parietal lobule.

Writing. Compared to the baseline condition, the writing task induced large bilateral activations of the primary sensorimotor and ventral/dorsal premotor cortices, extending rostrally to the pars opercularis of left IFG and caudally to the supramarginal gyrus, intraparietal sulcus and superior parietal lobule. In accordance with the writing task and right-handedness of the participants, the dorsal premotor and adjacent motor activations appeared predominant in the left hemisphere. Large bilateral visual activations were also observed in primary, secondary and associative visual areas, the fusiform gyrus extending to dorsal parts of the cerebellum (lobules VI). Additional activity was found in the supplementary motor area, extending to the anterior and middle cingulate cortices, the left dorsolateral prefrontal cortex, the rolandic and parietal operculum, the thalamus, the anterior insular cortex, the basal ganglia and the cerebellum (lobules V, VI, VII, VIII).

In sum, activations observed in each individual task appear fully consistent with previous brain-imaging studies, with large auditory activity in the listening and speaking tasks, visual activity in the reading and writing tasks, as well as specific brain areas classically involved in motor preparation, execution and coordination in the speaking and writing tasks (see Table 1).

Table 1

Maximum activation peak summary of brain regions showing overlapping activity across the listening, speaking, reading and writing tasks (conjunction analysis, unidirectional t-contrasts, p < .05 FWE corrected at the voxel level, cluster extent threshold of 20 voxels).

Clusters & Regions	BA	MNI coordinates			T
		X	Y	Z	
Cluster 1 (477 voxels)					
Supplementary motor area	6	−5	2	60	6.88
Cluster 2 (62 voxels)					
Inferior frontal gyrus – pars opercularis	44	−57	5	22	5.97
Premotor cortex	6	−62	2	21	5.56
Cluster 3 (30 voxels)					
Premotor cortex	6	−50	−4	40	5.77

3.3. Conjunctions analyses (Fig. 3,4 & S2 and Tables 1 & S2[1])

Listening ∩ Speaking. Overlapping activity in the listening and speaking tasks was observed in the bilateral auditory cortices, ranging from the primary and secondary auditory cortices in the transverse temporal gyrus (TTG), to the superior part of the temporal gyrus/sulcus (STG/STS) and temporopolar area rostrally, and to the planum temporale in posterior STG/STS and temporo-parietal junction caudally. Auditory activation extended medially to the insular cortex, dorsally to the ventral part of the supramarginal gyrus and parietal operculum, and ventrally to the posterior middle temporal gyrus (MTG). Bilateral frontal activations were also observed in the pars opercularis and pars triangularis of the inferior frontal gyrus (IFG), extending to the adjacent middle frontal gyrus and ventral premotor cortex. Further activity was observed in the supplementary motor area and adjacent middle cingulate cortex, the cerebellum (lobules VI, VII and VIII) and the thalamus (see Fig. 3).

Reading ∩ Writing. Conjunction of the reading and writing task induced large bilateral visual activations, ranging from the primary and secondary visual cortices to the fusiform gyrus. Additional clusters of activity were observed in the left ventral premotor cortex, extending to the pars opercularis of the left IFG, a more dorsal region of the ventral premotor cortex and adjacent primary motor cortex, the supplementary motor area, the dorsal part of the left supramarginal gyrus and the left superior parietal lobule.

Listening ∩ Reading. Overlapping activity in the listening and reading tasks was observed in the supplementary motor area and in two ventral premotor clusters in the left hemisphere, the most ventral one (z = 21) extending to the dorso-caudal part of the pars opercularis of IFG, the other being located 2 cm dorsally (z = 40) at the boundary of the ventral and dorsal premotor cortices.

Speaking ∩ Writing. Large overlapping activity in the speaking and writing tasks was observed in the lateral dorsal and ventral premotor cortices, extending rostrally to the pars opercularis of IFG and medially to the insular cortex, basal ganglia and thalamus. In addition, some activation of the dorsal primary motor cortex was found in the left hemisphere. Common parietal activities were found in the supramarginal gyrus, extending rostrally to the parietal operculum and rostro-dorsally to the primary somatosensory cortex (areas 1 and 3 in the left hemisphere and area 3 in the right hemisphere), and in the left superior parietal lobule. Additional auditory activity was observed in the left hemisphere in TTG and pSTG. Other common activations were observed in the supplementary motor area, extending to the middle

cingulate cortex, the bilateral dorsal (lobules V-VI) and ventral (lobules VII-VIII) parts of the cerebellum, at the boundary between the ventro-caudal part of the left angular gyrus and the posterior part of the middle temporal gyrus, the left dorsolateral prefrontal cortex, and the right primary and secondary visual areas.

Listening ∩ Speaking ∩ Reading ∩ Writing. Overlapping activity in the four tasks were identical to that observed in the conjunction analysis between the listening and reading tasks (see above). As previously noted, these activations were observed in the supplementary motor area and in two ventral premotor clusters in the left hemisphere, the most ventral one extending in to the most dorso-caudal part of the pars opercularis of IFG, the other being located 2 cm dorsally.

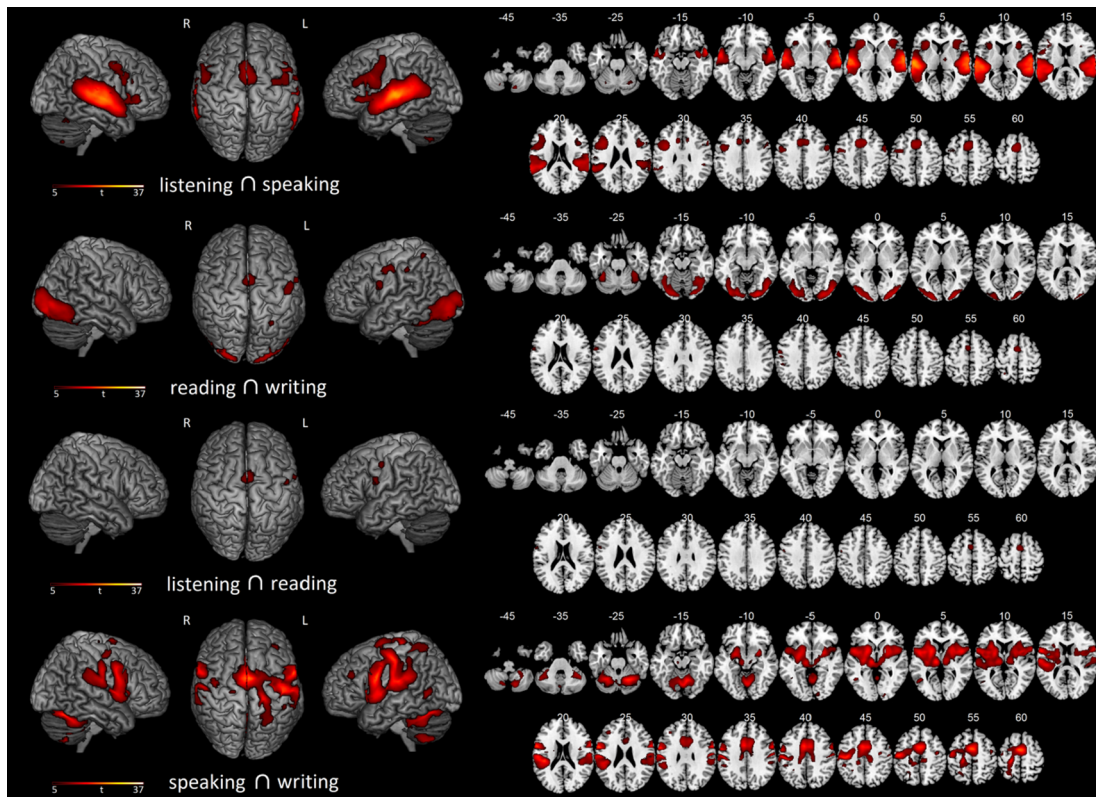*3.4. Main effects and interactions (Fig. S3, Table S3)*

Main Effect of Language Type. Irrespective of the stimuli, stronger activity was found for the oral type in bilateral auditory cortices, extending dorsally to the temporo-parietal junction, the ventral part of the supramarginal gyrus and the parietal operculum, and medially to the insular cortex, the ventral premotor and primary sensorimotor cortex bilaterally, the the left pars opercularis of IFG and adjacent middle frontal gyrus, the right pars orbitalis of IFG, the dorsolateral prefrontal cortex and adjacent middle frontal gyrus, and in the anterior part of the supplementary motor area. Conversely, activity only observed for the written type was found in the left dorsal premotor and sensorimotor cortices, in in visual areas, as well as in the fusiform gyrus, dorsal region (lobule VI) and ventral region (lobule VIII) of the right cerebellum, in the right dorsal premotor cortex, in a posterior part of the supplementary motor area, and in regions in the left insular cortex and supramarginal gyri.

Main Effect of Language Mode. Activity was found to be stronger or only present in the production mode in the bilateral primary motor and premotor cortices, especially in the left hemisphere with an additional dorsal activation. These stronger activations in the production mode extended dorsally to the supplementary motor area and adjacent middle and anterior cingulate cortex, medially to the insular cortex, basal ganglia and thalamus, rostrally to the pars opercularis of IFG, caudally to the parietal operculum and suparmarginal gyrus, and ventrally to TTG and STG. No regions showed stronger activity in the perception compared to the production mode.

Language Type × Language Mode Interaction. Activity changes between the oral and written types that varied according to the perception and production modes were found in several clusters. First, stronger activity in the writing task compared to all other tasks was found in the left dorsal part of the primary motor cortex, extending rostrally to the adjacent dorsal premotor cortex and caudally to the primary somatosensory cortex and supramarginal gyrus. Another cluster in the right hemisphere showed similar pattern of activity but was restricted to the primary somatosensory cortex and adjacent supramarginal gyrus and intraparietal sulcus. Other clusters showing stronger activity in the writing task were found in the right dorsal premotor cortex, the right cerebellum, the posterior part of the supplementary motor area, the left insular cortex and the left parietal operculum. Conversely, stronger activity in the speaking task was observed bilaterally in the ventral part of the primary motor cortex, extending rostrally to the adjacent left ventral premotor cortex, caudally to the primary somatosensory cortex, and ventrally to the right parietal operculum, and the auditory cortex (TTG and STG). Other clusters showing stronger activity in the speaking task were found in two small regions located in the left and right dorsal part of the premotor and/or primary motor cortices.

3.5. ROI analysis – Cross-modal activity (Fig. 5, and Table S4)

The individual coordinates for the seven ROIs analyzed are given in Table S4. The writing task, but not the reading task, led to BOLD

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[1] In order to provide the readers with a sense of the extent of the effects, and to limit interpretation biases, we also provide a representation of the results of the conjunctions according to the method used by Allen, Erhardt and Calhoun et al. (2012) in Figure S2 in Supplemental Data.

Fig. 3. Overlapping brain activity across the listening and speaking tasks, the reading and writing tasks, the listening and reading tasks and the speaking and writing tasks (unidirectional t-contrasts, p < .05 FWE corrected at the voxel level, cluster extent threshold of 20 voxels (see Table S2 in Supplemental Data for details). Note that on the 3D views from the top, the left of the brain is on the right of the images, while the left of the brain is on the left of the image on the axial sections.
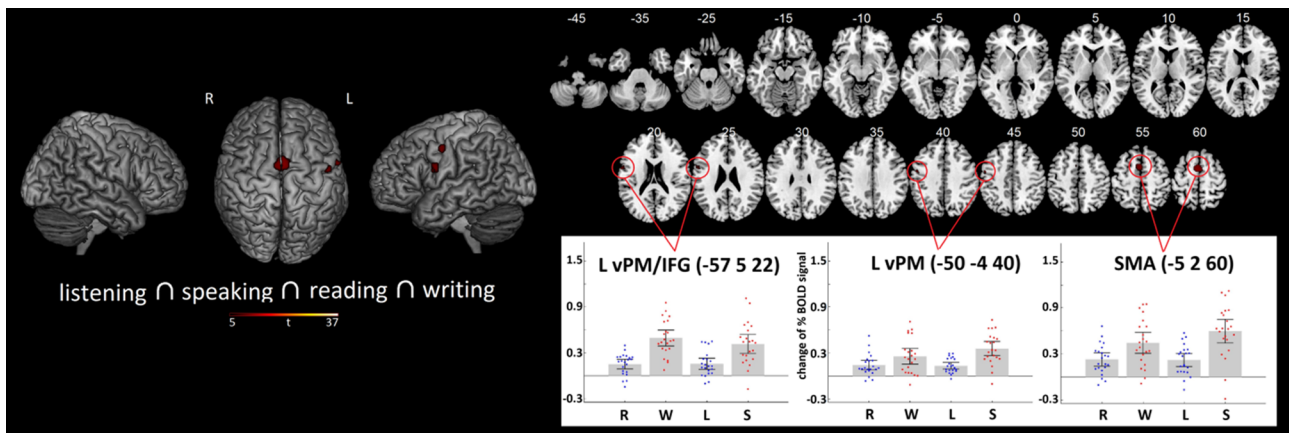
Fig. 4. Overlapping brain activity across the listening, speaking, reading and writing tasks (conjunction analysis, unidirectional t-contrast, p < .05 FWE corrected at the voxel level, cluster extent threshold of 20 voxels, see Table S2 in Supplemental Data for details). The BOLD percent signal changes for the 4 tasks compared to rest in the supplementary motor area (SMA), left ventral premotor cortex vPM) and left ventral premotor/inferior frontal gyrus (vPM/IFG) are indicated. The error bars represent confidence intervals across subjects (95% CI).

changes in the left primary auditory cortex and in the left planum temporale (the effect size estimated by the 95% CI was 0.1 to 0.2% change). The listening and speaking tasks led to changes in the primary visual cortex (0.05 to 0.2% for listening and 0.1 to 0.3% for speaking).

3.6. Individual spatial analyses of frontal activations - motor clustering (Fig. 6 and Table S5)

Individual variability for the listening ∩ speaking compared to the reading ∩ writing conjunctions is revealed by individual motor clustering analyses (see Fig. 6).

Overall, in the left and right hemispheres and in the listening ∩ speaking and reading ∩ writing conjunctions, the total number of centers of gravity of the motor activation peaks differed between the four ROIs ($\chi 2 = 32.76$, p < .00001) and were mostly confined in the premotor cortex (n = 57) and in the pars opercularis of IFG (n = 42), with a lower number of activation peaks observed in the primary motor cortex (n = 23) and in the pars triangularis of IFG (n = 14). In addition, a higher number of activation peaks was observed in the listening ∩ speaking conjunction compared to the reading ∩ writing conjunction (listening ∩ speaking: n = 93, reading ∩ writing: n = 43; $\chi 2 = 18.38$, p < .00002). This partly results from the fact that, while
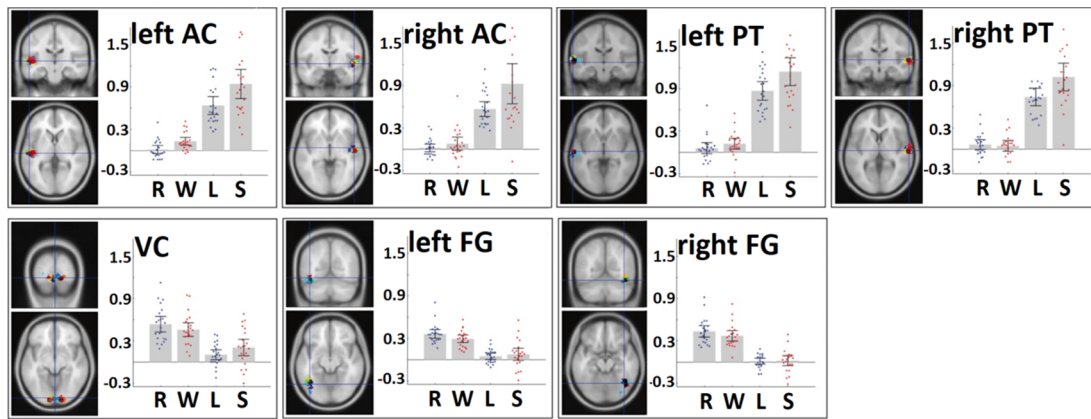
Fig. 5. Percent signal change per task as a function of the ROI. The values represent the difference of the medians in the absence and in the presence of the stimulus, for each individual (points) and averaged for the whole group (bars). The error bars represent the 95% confidence intervals of the difference between the medians in the presence and in the absence of the stimulus. The coronal and axial slices represent the position of the individual ROIs (each color corresponds to the ROI of one participant, see Table S4 for individual coordinates). For the auditory mode, the reference coordinates were defined in BA41 (Primary Auditory Cortex, coordinates -48 -18 4 and 51 -11 1 resp. for left and right hemispheres) and in BA42 and BA22 (planum temporale, coordinates -64 -20 5 and 66 -13 2 resp. for left and right hemispheres). For the visual mode, the reference coordinates were at 0 -90 -10 (calcarine sulcus, primary visual cortex) and in the fusiform gyri, at the coordinates of the visual word form area (left hemisphere, -44 -58 -15) and of the counterpart of this region in the right hemisphere (44 -58 -15). The ROIs were defined as the volume resulting from the combination of the individual cluster whose local maximum was the closest from the reference coordinates, and a 6 mm-radius sphere centered on the coordinates of this local maximum.

bilateral activity was observed in the listening ∩ speaking conjunction (left hemisphere: n = 51, right hemisphere: n = 42; $\chi 2 = 0.87$, p = .35), motor activity appeared predominantly in the left hemisphere in the reading ∩ writing conjunction (left hemisphere: n = 42, right hemisphere: n = 11; $\chi 2 = 18.13$, p < .00003). Importantly, the location of activation peaks in the left hemisphere was confined in the ventral part of the premotor cortex for the listening ∩ speaking conjunction, while several activation peaks were located in the dorsal premotor cortex in the reading ∩ writing conjunction. For other comparisons, small numbers preclude making strong conclusions. We simply note that in the pars opercularis of IFG, the number of activation peaks was higher in the listening ∩ speaking conjunction than in the reading ∩ writing conjunction, especially in the right hemisphere (listening ∩ speaking, left hemisphere: n = 18, reading ∩ writing, left hemisphere: n = 8; listening ∩ speaking, right hemisphere: n = 14, reading ∩ writing, left hemisphere: n = 2). A similar tendency was observed in the right primary motor cortices (listening ∩ speaking, left hemisphere: n = 10, reading ∩ writing, left hemisphere: n = 7; listening ∩ speaking, right hemisphere: n = 6, reading ∩ writing, right hemisphere: n = 0). Finally, activity in the right pars triangularis almost only appeared during the listening ∩ speaking conjunction (listening ∩ speaking, left hemisphere: n = 5, reading ∩ writing, left hemisphere: n = 1; listening ∩ speaking, right hemisphere: n = 7, reading ∩ writing, right hemisphere: n = 1).

4. Discussion

This study aimed at testing the existence of common neural substrates and common mechanisms of perceptual-motor coupling when processing the basic units of spoken and written language. Several important results can be emphasized.

4.1. Shared neural substrates in the left and medial frontal cortices

First, we found evidence of neural substrates shared between spoken and written language. The brain regions where the overlap between the four conditions was maximal were found in the left lateral and medial frontal cortices, at locations corresponding to the inferior frontal gyrus, the ventral premotor cortex and the SMA.

The implication of the left inferior frontal and ventral premotor regions in speech motor control, and more specifically in the planning of articulatory and speech movements, is well acknowledged (Bohland & Guenther, 2006; Grabski, Lamalle, Vilain, et al., 2012, Grabski, Lamalle, et al., 2012; Grabski et al., 2013; Guenther & Vladusich, 2012; Guenther, 2006; Riecker et al., 2005; Sörös et al., 2006; Tourville & Guenther, 2011). It has also been suggested that these regions represent a "speech sound map" that provides a link between the motor program and sensory representation of a speech sound (Guenther & Vladusich, 2012; Guenther, 2006). Their involvement has also consistently been
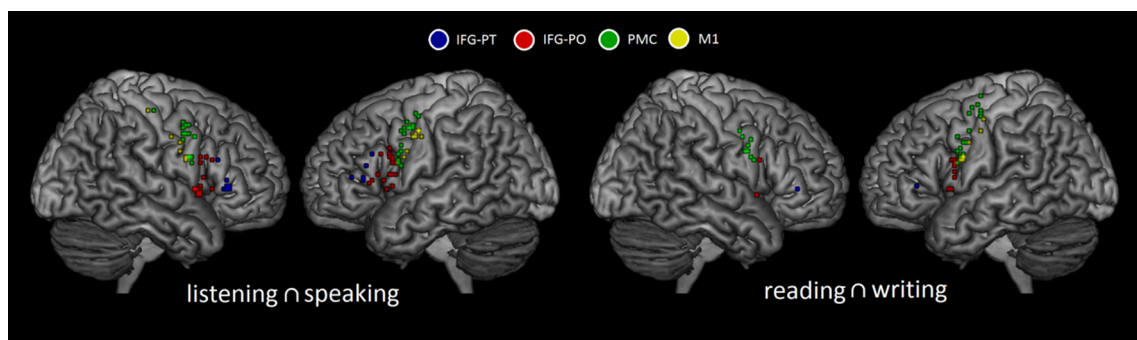
Fig. 6. Individual centers of gravity (COG) related to common motor activity in the listening ∩ speaking and in the reading ∩ writing conjunctions within the pars triangularis (BA45, IFG-PT) and pars opercularis (BA44, IFG-PO) of the inferior frontal gyrus and to the premotor (BA6, PMC) and primary motor (BA4, M1) cortices. See Table S5 in Supplemental Data for details.

demonstrated in the course of speech perception and appears in line with neurobiological models (Hickok & Poeppel, 2000, 2004, 2007; Rauschecker & Scott, 2009; Rauschecker, 2011; Scott & Johnsrude, 2003; Skipper et al., 2007). These models postulate that speech processing is partly mediated by a simulation process from the inferior frontal gyrus and ventral premotor cortex that partly constrain phonetic interpretation of the sensory inputs through the internal generation of candidate articulatory categorizations. Further, the same two lateral ventral premotor/inferior frontal regions have already been shown to participate in single letter perception (Flowers et al., 2004; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006) and production (Planton et al., 2013), and to be conjointly activated by the two tasks (James & Gauthier, 2006; Longcamp et al., 2003). From these studies, it is therefore tempting to interpret the activations common to the four tasks as an indication of articulatory motor reactivation in listening, reading and writing, possibly through inner speech, subvocal rehearsal or verbal motor imagery (Sato, Vilain, Lamalle, & Grabski, 2015) or more automatic perceptual-motor 'resonance' (Fadiga et al., 2002), even if the tasks do not explicitly require access to the letters' names (note that although possible vocal outputs were not recorded in the perception tasks, it is unlikely that participants overtly produced the perceived letter/consonant since they were only instructed to passively listen to or read each presented stimulus). From that view, the fact that premotor activity was found to be equal in the speaking and writing tasks, and to also be equal but lower in the listening and reading tasks (see Fig. 4), might suggest similar articulatory planning processing in the two first motor tasks, together with reduced motor reactivation in the two perceptual tasks. Note that, if this interpretation is correct, the degree of association between the letters and sounds specific to a given language might affect the results (see Madec et al., 2016). French is a non-transparent language where a letter can correspond to several sounds. In fact, in a study where convergence between speech and reading was tested with fMRI in 4 languages of variable opacity (Rueckl et al., 2015), it was shown that the two modalities converge in a set of regions including the premotor regions found in the present study. This convergence remained the same for the 4 languages, although the degree of activation of the premotor regions varied slightly as a function of the transparency. For the authors, this convergence occurs because the organization of the speech network universally constrains the written language network.

Alternatively, if common premotor activations are actually related to articulatory planning and/or reactivation for single letters, one might nonetheless expect the signal level stronger for the spoken than written type. Given the observed heteromodal activity in these regions, they might therefore not be primarily speech related but rather subserve more general functions. For some authors, those regions lying anterior to the central sulcus belong to a sensorimotor brain system that subserves more domain-general cognitive and attentional functions, and is engaged when a task is demanding in terms of cognitive resources (Brass, Derrfuss, Forstmann, & Cramon, 2005; Duncan & Owen, 2000; Fedorenko, Duncan, & Kanwisher, 2013). This interpretation may hold because general cognitive processes such as response selection were at play in both the speaking and writing tasks, and due to the presence of catch trials to a less extent in the listening and reading tasks. Although this hypothesis cannot be discarded here, response selection processes appeared to be limited in the speaking and writing tasks since the same (simple) stimuli were used repeatedly and were externally triggered. This hypothesis is also hardly compatible with previous findings of specific involvement of similar ventral precentral regions in reading where letters were compared to control stimuli well-matched in terms of their difficulty (Anderson et al., 1990; James & Gauthier, 2006; Longcamp et al., 2003).

Another possible interpretation comes from the possibility that premotor cortices possess superordinate properties (Schubotz & von Cramon, 2001; Schubotz, Anwander, Knösche, von Cramon, & Tittgemeyer, 2010; Schubotz, von Cramon, & Lohmann, 2003). In Shubotz and colleagues' studies, the premotor activations were found to systematically represent information in different domains (time, space, objects) in various non-motor visual (Schubotz & von Cramon, 2001) and auditory (Schubotz et al., 2003) tasks, according to a ventral-to-dorsal organization. The lowest ventral / inferior frontal regions would represent timing information (in relation to the planning and execution of articulatory and arm/manual sequences during speaking and writing), the intermediate ventral regions would represent information on object properties, and the most dorsal regions would represent information on object's location. It is possible that object- and time-related properties are relevant in the present four tasks, and triggered activation in the parts of the premotor cortex that possess the corresponding superordinate properties.

The SMA is involved in both speech perception and production (Hertrich, Dietrich, & Ackermann, 2016; Lima, Krishnan, & Scott, 2016), and in reading and writing (Longcamp et al., 2014; Planton et al., 2013; Price, 2010), and appears to be connected to the lateral inferior frontal gyrus through the Frontal Aslant Tract (Dick, Garic, Graziano, & Tremblay, 2019). During speaking, it is usually thought to participate in the initiation of speech motor programs, internally specified action selection, inhibition and in higher superordinate planning functions (Alario, Chinay, Lehericy, & Cohen, 2006; Peeva et al., 2010; Tourville & Guenther, 2011; Tremblay & Gracco, 2006). There is however no clear consensus about the exact functional contribution of this region to language (for a review, see Hertrich et al., 2016). Further, its recruitment during auditory speech processing, even during listening, also suggests its contribution to auditory imagery and higher order sensorimotor control and predictive functions (for a review, see Lima et al., 2016). In the course of writing, SMA is rather thought to compute general features of the movement, in particular its sequential structure (Roland, Larsen, Lassen, & Skinhoj, 1980; Tanji & Shima, 1994). In writing, the SMA's contribution is however considered non-specific, because it is no longer present when handwriting tasks are compared to matched graphomotor control tasks (e.g., drawing non-linguistic stimuli such as circles, abstract symbols or pseudo-letters; Planton et al., 2013).

Finally, it is worthwhile noting that, due to the 1-back procedure involved in the catch trials, the perception tasks may have involved limited verbal working memory, executive and comparison/decision processes in other trials. Since no catch trials and related processes were required in the production tasks, the observed overlap BOLD activity in the inferior frontal gyrus, the ventral premotor cortex and the SMA is however unlikely due to these processes. It should also be noted that the activations in the writing task could be influenced by the absence of visual feedback, although writing in expert adults is generally considered completely proactive (van Galen, 1991).

4.2. Motor-perceptual resonance in written and spoken language

Interestingly, the motor nature of the precentral activations in both listening and speaking and in reading and writing is further confirmed at the individual level by motor clustering analyses and the conjoint activation of both the premotor and the primary motor cortex in the majority of the participants (see Fig. 6). Strikingly, the extent of the observed common premotor activation was qualitatively more important during listening and speaking than during reading and writing. Aside from methodological differences, this difference might relate to ontogenetic factors, with motor-perceptual coupling in speech occurring earlier in development and therefore being subsequently stronger. It might also relate to phylogenetic factors, because speech relies more strongly on "pre-wired" brain circuits being the result of evolution (Aboitiz & Garcia, 1997; Aboitiz, 2012; Jürgens, 2002; MacNeilage, 1998; Rauschecker & Scott, 2009; Rilling, 2014; Scott & Johnsrude, 2003), while written language is built upon the "recycling" of brain regions initially devoted to other functions (Dehaene & Cohen, 2007; Dehaene et al., 2010). It could also stem from greater reliance on motor

representations when processing auditory speech, possibly because the discrimination of phonemes is more demanding (due to important timing constraints; Du et al., 2014). Finally, this difference might be a by-product of more variable inter-individual patterns for written than for spoken language. In general, the pattern of precentral activations is highly variable between individuals, in terms of activation strength, extent and position. However, while the position of individual activations along the z-axis varies from very ventral to very dorsal locations in the case of letters perception, it is more homogeneously located in a single ventral premotor/inferior frontal cluster in the case of phonemes perception.

The lateralization and distribution of precentral activations is also qualitatively different in the spoken and written types. First, whereas the precentral activations in the spoken type are bilateral, they remain distributed in the left hemisphere in the written type for a majority of participants. This is visible on the distribution of the individual activation peaks. The lateralization of precentral activations during the perception of single letters has indeed been shown to depend on the manual laterality of the participants (Longcamp, Anton, Roth, & Velay, 2005) and fits well with the use of manual motor simulation or "resonance". The spatial distribution of the individual precentral peaks was more dorsal and caudal, following the precentral gyrus in the written type, whereas in the spoken type the individual clusters tended to extend rostrally and ventrally onto the inferior frontal gyrus. This is compatible with the typically described distribution of precentral activations in the production of writing movements (Dufor & Rapp, 2013; Longcamp et al., 2014; Pattamadilok et al., 2016; Planton, Longcamp, Péran, Démonet, & Jucla, 2017; Sugihara, Kaminaga, & Sugishita, 2006) and articulation (Brown, Ngan, & Liotti, 2008; Grabski, Lamalle, Vilain, et al., 2012; Terumitsu, Fujii, Suzuki, Kwee, & Nakada, 2006), and with the acknowledged implication of the inferior frontal gyrus in the processing of spoken language (Price, 2010). The distinct distribution and lateralization of the precentral activations common to perception and production in the two language types is therefore a good indication of motor reactivation during perception occurring according to a somatotopic organization (activations following the somatotopy of the involved effectors has been demonstrated in other domains of action-perception coupling; see Buccino et al., 2001; Jastorff, Begliomini, Fabbri-Destro, Rizzolatti, & Orban, 2010).

4.3. Cross-modal sensory activations

The ROI analysis showed that the early sensory areas were activated by the other modality, because the confidence intervals were located above zero. The left primary auditory cortex responded relatively weakly but significantly in the writing task but not in the reading task. The response of the left planum temporale was even weaker but also significant in the writing task. In the primary visual cortex, the response was also significant for the two speech tasks, but the response of the left fusiform gyrus at the level of the visual word form area did not differ from zero. This pattern of results was unexpected, as the early sensory areas were initially included in the ROI analysis as controls of the associative areas that compute language-specific representations. It is inconsistent with the results of previous investigations of conjoint auditory and visual letters perception (Raij, Uutela, & Hari, 2000; van Atteveldt, Formisano, Goebel, & Blomert, 2004), most likely because those studies did not compare unimodal letter processing to a resting baseline.

It is now well acknowledged that sensory input of one modality can lead to significant responses to modulations of the activity in sensory areas of another modality. This has been shown in a wide range of sensory modalities where one modality is usually tightly coupled with another: vision and audition (Calvert et al., 1997), touch and vision (Sathian & Zangaladze, 2002; Zangaladze, Epstein, Grafton, & Sathian, 1999), vision and vestibular sense (Indovina et al., 2005). In the case of speech, there is a very strong coupling of auditory vocal processing with

visual processing of the speaker's articulatory movements (Calvert et al., 1997; Campbell, 2008; von Kriegstein, 2012), that could explain the present results. In visual letter processing, the coupling between script and speech has also been studied (Jancke & Shah, 2004; Perrone-Bertolotti et al., 2012; van Atteveldt et al., 2009), but the reason why the auditory cortex responds to writing but not to reading letters is difficult to explain in this context. In an ecological situation, writing is nonetheless usually associated with auditory friction and scrapping sounds (Danna & Velay, 2015), so that the auditory cortex is possibly automatically preactivated even in the absence of auditory feedback. Contrary to Raij et al. (2000) and van van Atteveldt et al. (2004), we found no reliable heteromodal activation of the superior temporal gyrus/superior temporal sulcus when unimodal visual letters and speech sounds were presented. In addition, although in some cases (most likely when the task demands access to the letter name), the level of activation of the fusiform gyrus is modulated by inputs from upstream regions coding for phonological processing (Dietz et al., 2005; Madec et al., 2016; Xue et al., 2006), our results confirm that speech itself is not sufficient to lead to significant activation of the fusiform gyrus at the level of the visual word form area.

4.4. Extended overlap between the two production tasks

The last main result is that speaking and writing are controlled by largely overlapping networks, as attested by the overlap observed in the production tasks (see Fig. 3 and S3). This indicates that while some activations remain specific to a given language type, other regions are probably engaged in domain general cognitive processing (Brass et al., 2005; Duncan & Owen, 2000; Fedorenko et al., 2013). Neural networks encompassing frontal regions involved in cognitive control have been shown to be engaged during spoken language production (Bourguignon, 2014; Geranmayeh, Wise, Mehta, & Leech, 2014). Those networks are likely to be active also during writing. In addition, massive involvement of overlapping bilateral basal ganglia and cerebellum in the two production tasks is consistent with the existence of effector-independent representations of motor sequences in cortico-subcortical circuits (Hikosaka, Nakamura, Sakai, & Nakahara, 2002). It is however worthwhile noting that the left dorsal premotor cortex, at the level of the superior frontal gyrus, remained strongly implicated in the control of handwriting movements, and much less so in the other three tasks, supporting previous studies who used various types of control tasks (Longcamp et al., 2014; Roux et al., 2009; Sugihara et al., 2006). Similarly, the right ventral premotor cortex displays a much stronger activation in the speaking task than in the other three tasks, with this region being identified as crucial for the integration of somatosensory feedback during speech production (Golfinopoulos et al., 2011; Guenther & Vladusich, 2012).

5. Conclusions

To conclude, our study shows that across perception and production modes, three left frontal brain regions are shared between spoken and written language. In addition, motor-perceptual resonance appears to be a general mechanism in communication, which occurs in both spoken and written language with an extent, lateralization and spatial distribution that differ between the two language types. It is more variable between individuals in written than in spoken language, possibly due to variable learning strategies relying either more on manual or more on verbal coding. Until recently, spoken communication was clearly dominant in human language, but recent digital tools increase the amount of written communication dramatically (Kiefer & Velay, 2016). Our results thus call for the opening of new integrative approaches focusing on the relationships between the two facets of human communication, in particular on how they are coded in common and distinct subregions of the frontal cortex.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandl.2019.104694.

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