CORTEX 50 (2014) 64–75

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

The neural basis for writing from dictation in the temporoparietal cortex

Franck-Emmanuel Roux [a,b,*], *Jean-Baptiste Durand* [c], *Emilie Réhault* [a], *Samuel Planton* [a], *Louisa Draper* [a] *and Jean-François Démonet* [d]

[a] *INSERM, Imagerie Cérébrale et Handicaps Neurologiques; Université de Toulouse, UPS, Imagerie Cérébrale et Handicaps Neurologiques UMR 825, Centres Hospitalo-Universitaires, Toulouse, France*

[b] *Pôle NeuroSciences, Centres Hospitalo-Universitaires, Toulouse, France*

[c] *Centre de Recherche Cerveau et Cognition, Centres Hospitalo-Universitaires, Toulouse, France*

[d] *Leenaards Memory Center, Departement of Clinical Neurosciences CHUV & University of Lausanne, Switzerland*

ARTICLE INFO

Article history:
Received 13 February 2013
Reviewed 11 April 2013
Revised 24 June 2013
Accepted 19 September 2013
Action editor Rhonda Friedman
Published online 19 October 2013

Keywords:
Pure agraphia
Writing
Word deafness
Electrostimulation
Brain mapping

ABSTRACT

Cortical electrical stimulation mapping was used to study neural substrates of the function of writing in the temporoparietal cortex. We identified the sites involved in oral language (sentence reading and naming) and writing from dictation, in order to spare these areas during removal of brain tumours in 30 patients (23 in the left, and 7 in the right hemisphere). Electrostimulation of the cortex impaired writing ability in 62 restricted cortical areas (.25 cm^2). These were found in left temporoparietal lobes and were mostly located along the superior temporal gyrus (Brodmann's areas 22 and 42). Stimulation of right temporoparietal lobes in right-handed patients produced no writing impairments. However there was a high variability of location between individuals. Stimulation resulted in combined symptoms (affecting oral language and writing) in fourteen patients, whereas in eight other patients, stimulation-induced pure agraphia symptoms with no oral language disturbance in twelve of the identified areas. Each detected area affected writing in a different way. We detected the various different stages of the auditory-to-motor pathway of writing from dictation: either through comprehension of the dictated sentences (word deafness areas), lexico-semantic retrieval, or phonologic processing. In group analysis, barycentres of all different types of writing interferences reveal a hierarchical functional organization along the superior temporal gyrus from initial word recognition to lexico-semantic and phonologic processes along the ventral and the dorsal comprehension pathways, supporting the previously described auditory-to-motor process. The left posterior Sylvian region supports different aspects of writing function that are extremely specialized and localized, sometimes being segregated in a way that could account for the occurrence of pure agraphia that has long-been described in cases of damage to this region.

---

[*] *Corresponding author*. INSERM 825 et Service de Neurochirurgie, Hôpital Purpan, F-31059 Toulouse, France.
E-mail address: franck_emmanuel.roux@yahoo.fr (F.-E. Roux).

http://dx.doi.org/10.1016/j.cortex.2013.09.012

1. Introduction

Writing by hand is an acquired language function involving several brain regions (Benson, 1979). The origin of the written words comes from three main modalities, i.e., either spontaneous production, copying a text or writing from dictation. Neurolinguistics models offer a framework upon which to formulate hypotheses on the neural and anatomical underpinnings of many psycholinguistics processes involved in writing (Hickok & Poeppel, 2007; Roeltgen & Heilman, 1984). For instance, it can be hypothesized that the first stage in the pathway of writing under dictation would involve both superior temporal gyri, known to be crucial for speech perception and comprehension (Buchman, Garron, Trost-Cardamone, Wichter, & Schwartz, 1986; Binder, Swanson, Hammeke, & Sabsevitz, 2008; Creutzfeldt, Ojemann, & Lettich, 1989; Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004; Friederici, 2011; Lichtheim, 1885). The next stage, decoding the dictated message from initial prelexical processing (Scott & Wise, 2004) to the top-down semantic and syntactic processes (Hickok & Poeppel, 2007) is supported by the speech perception ventral pathway that spreads along the left superior temporal gyrus (see DeWitt and Rauschecker, 2012 for review). The dorsal comprehension pathway from posterior temporal to frontal premotor regions, via parts of the arcuate and superior longitudinal fasciculi, could support auditory motor integrations (Hickok & Poeppel, 2007; see Friederici, 2012 for review) supposed to be important in handwriting processes. Indeed, studies of patients with brain injuries (Henry, Beeson, Stark, & Rapcsak, 2007; Kim, Chu, Lee, Kim, & Park, 2002; Sakurai, Mimura, & Mannen, 2008), or using brain imaging (Sugihara, Kaminaga, & Sugishita, 2006), have shown that some retrosylvian regions are likely to support lexico-semantic and phonological writing processes. Within these regions, it is possible that writing function could share the same neuronal resources as other language functions (Beeson et al., 2003; Katanoda, Yoshikawa, & Sugishita, 2001; Purcell, Napoliello, & Eden, 2011). However, from the founding observations of Jules Déjerine (Déjerine, 1891), the existence of neural substrates specifically for writing in the temporal lobe has been hypothesized, based on patients with pure agraphia (Auerbach & Alexander, 1981), a rare condition in which a patient with a brain lesion loses only the ability to write, without any other disturbance of either oral language or motor function (Benson, 1979; Roux et al., 2009).

Cortical electrostimulation was combined with mapping of language functions during brain tumour removal to study the anatomical bases of the process of handwriting under dictation. The study specifically looked at the posterior Sylvian neural structures and examined writing-specific effects during electrostimulation. During the removal of brain tumours that lie in areas of the brain related to language function, it is standard clinical practice to wake the patient in order to identify and spare functional areas (Roux, Boetto, Sacko, Chollet, & Trémoulet, 2003, 2009). This is achieved using electrostimulation of areas of the brain, whilst the patient performs a task relating to the function being studied, e.g., picture naming, reading, or writing. Stimulation-induced impairment of the task indicates that the area beneath the electrode carries out that function. The main advantages of this brain mapping technique are its high level of accuracy, its simplicity for trained teams and lack of adverse affects for the patient (Lesser, Lueders, Dinner, Hahn, & Cohen, 1984; Ojemann, Ojemann, Lettich, & Berger, 1989). Using this technique, we studied 30 patients who needed brain mapping in temporoparietal areas for accurate and safe tumour removal (23 for tumors in their left hemisphere and 7 in their right hemisphere – Table 1 and 2).

2. Material and methods

2.1. Patients

The study involved French-speaking patients with the following inclusion criteria: (i) underwent tumour resection in our Neurosurgery Department, (ii) had no or minor language deficit pre-operatively, and (iii) had a lesion (brain tumour) located in the temporoparietal lobe. All patients underwent "awake surgery" (Roux et al.., 2003) combined with electrostimulation and naming, reading and writing tasks, in order to directly map these functional language areas. All patients and their families gave informed consent to the study of their language areas by direct brain mapping. The consultative committee of INSERM (Institut National de la Santé et de la Recherche Médicale) gave approval for the storage of patients'

Table 1 – Demographics and topography of explored brain regions – all patients but one with left hemispheric tumors.

Patient	Gender/age/occupation/handedness (Edinburgh score)
1	M/75/medical doctor/RH (+80)
2	F/32/secretary/RH (+90)
3	M/33/computer engineer/RH (+90)
4	M/60/technician/RH (+80)
5	M/62/retired social worker/RH (+90)
6	F/52/secretary/RH (+85)
7	M/52/restaurant manager/RH (+90)
8	M/64/retired computer engineer/RH (+80)
9	M/51/sport manager (rugby)/RH (+90)
10	M/27/student/RH (+70)
11	M/59/retired sports teacher/RH (+70)
12	F/19/student/RH (+90)
13	F/28/teacher/RH (+90)
14	M/48/engineer/RH (+85)
15	M/46/craftsman: painter/RH (+90)
16	F/32/housewife/RH (+80)
17	M/36/computer engineer/RH (+90)
18	M/74/retired postman/RH (+80)
19	M/64/architect/LH (−50)
20	M/42/school teacher/LH (−90)[a]
21	M/63/retired postman/RH (+90)
22	M/70/retired craftsman/RH (+100)
23	M/57/architect/RH (+90)
24	F/35/computer engineer/LH (−40)

LH: Left-handed; RH: Right-handed.
M: male, F: female.
[a] Left-handed patient (with a left-handed family) with a right temporal tumor who had his right hemisphere studied.

Table 2 – Demographics and topography of explored brain regions – 6 right-handed patients studied in right hemisphere.

Patient	Gender/age/occupation/handedness (Edinburgh score)
1	F/28/craftsman/RH (+100)
2	F/46/shop manager/RH (+90)
3	M/50/violonist/RH (+90)
4	M/23/computer engineer/RH (+80)
5	M/56/engineer/RH (+100)
6	F/43/secretary/RH (+80)

data and preservation of their anonymity. Data from successive brain mappings were prospectively collected by the same team using the same protocol throughout the 6 years of the study.

All patients underwent an assessment of handedness (Oldfield, 1971) and pre- and postoperative language standardized tests of visual naming (Deloche, Metz-Lutz, & Kremin, 1997), written and oral understanding, oral fluency, reading, dictation, repetition, written transcription, and object handling (Nespoulous et al., 1992). Although debatable, hemisphere dominance was only determined by handedness. Writing was specifically evaluated by the assessment of copying (isolated letters, words and numbers) and short sentence dictation tasks. Numbers of errors and handwriting form were scored and compared pre- and postoperatively.

2.2. *Cortical mapping procedures*

The level of electrostimulation was kept below that expected to cause electrical diffusion and afterdischarges to ensure that the stimulated area remained accurately localized to the area of cortex under study. Prior to stimulation of the subjects during the study, the afterdischarge threshold was determined by electrocorticography. The cortex was directly stimulated using the bipolar electrode of the "Nimbus" cortical stimulator (1 mm wide electrodes separated by 6 mm – Newmedic®, Toulouse, France). The current amplitude started at 2 mA and was progressively increased by 1 mA. Stimulation with biphasic square wave pulses of 1 msec at 60 Hz was guided by a neuronavigational system with 3D reconstructions of the brain (Stealth Station, Sofamor Danek, Surgical navigation technologies, Broomfield, CO, USA). Intensity of stimulation varied from 4.5 to 5.8 mA in all patients (mean: 5.15 mA; Standard Deviation: .29).

The whole stimulation-mapping procedure was systematically video-recorded. The number of cortical stimulation sites varied from one patient to another depending on the size of craniotomy, with sites of cortical stimulation approximately .5 cm from each other. The patients were initially asked to perform two oral language tasks: a visual naming task using various drawn objects, and a reading task (using various regular and irregular French words). Then the patients were asked to write down unrelated and unrehearsed simple sentences (Roux et al., 2009), dictated to them, with their preferred hand (see in Appendix A examples of sentences). Each stimulation site was tested systematically with the naming, reading and writing tasks. For the writing task, at each site, dictation of a sentence was commenced, and then

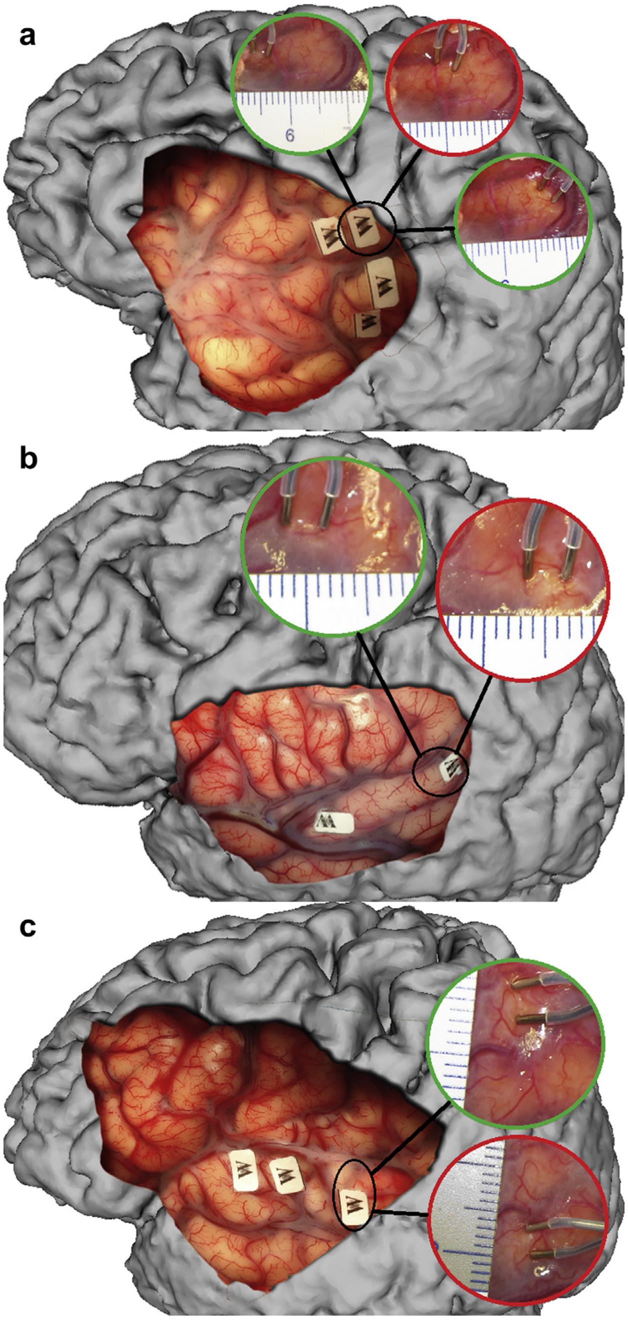

Fig. 1 – Example of results from three direct brain mapping procedures in 3 patients: operative pictures were superimposed onto 3D reconstructions of the patients' brains. Writing interference sites were discretely located in small sites of cortex (red circles). Stimulation of the closest sites located in the immediate vicinity (5 mm) of these areas led no writing interference (green circles). In 1a, Patient 4, four writing interference sites (semantic paragraphia) were found; two in the superior temporal gyrus, and two just above the Sylvian fissure. In 1b, Patient 12 had an area of word deafness in the superior temporal gyrus, and also an area of semantic paragraphia more caudally. In 1c, Patient 21 had three writing interference sites in the superior temporal gyrus (word deafness areas), where stimulation prevented him from understanding the dictated sentences.

Table 3 – Electrostimulation-induced interference sites: Intra-operative coordinates and type of interference on electrostimulation in the 22 patients with response to stimulation.

Patient	Task interference			TALAIRACH			Gyrus localization	Brodmann	Type of interference
	Writing	Reading	Naming	nx	nY	nZ			
1	W	R	0	−57.8871	−3.4260	1.0572	Superior temporal gyrus	BA 22	Semantic paragraphia
2	W	0	N	−61.0714	−10.0917	−.2374	Superior temporal gyrus	BA 22	Phonemic paragraphia
3	W	0	0	−64.9505	−29.9217	11.1875	Superior temporal gyrus	BA 42	Word deafness
3	W	R	N	−64.8028	−19.3417	18.5521	Postcentral gyrus	BA 40	Word deafness
4	W	R	N	−62.9234	−13.3291	20.3258	Postcentral gyrus	BA 43	Semantic paragraphia
4	W	R	N	−62.6341	−22.6663	23.0166	Inferior parietal lobule	BA 40	Semantic paragraphia
4	W	0	0	−65.8093	−26.1859	11.7516	Superior temporal gyrus	BA 42	Semantic paragraphia
4	W	0	0	−64.9483	−19.2385	3.5840	Superior temporal gyrus	BA 22	Semantic paragraphia
5	W	R	0	−63.1794	−30.7802	24.7235	Inferior parietal lobule	BA 40	Word deafness
5	W	0	0	−64.8399	−37.7358	16.3092	Superior temporal gyrus	BA 22	Semantic paragraphia
6	W	R	N	−64.2282	−32.2025	21.8625	Superior temporal gyrus	BA 42	Phonemic paragraphia
6	W	R	N	−58.8201	−57.8074	25.0577	Superior temporal gyrus	BA 39	Phonemic paragraphia
7	W	0	0	−64.4375	−9.7976	−9.1811	Middle temporal gyrus	BA 21	Phonemic paragraphia
7	W	0	0	−65.8914	−23.8675	−1.6588	Superior temporal gyrus	BA 21	Phonemic paragraphia
8	W	0	0	−65.4944	−38.9825	9.0617	Superior temporal gyrus	BA 22	Word deafness
8	W	R	N	−65.7560	−36.0039	15.7371	Superior temporal gyrus	BA 22	Phonemic paragraphia
8	W	R	N	−64.5990	−47.1652	18.0244	Superior temporal gyrus	BA 22	Phonemic paragraphia
8	W	R	N	−58.6203	−62.6915	17.0462	Superior temporal gyrus	BA 39	Phonemic paragraphia
8	W	R	N	−63.4143	−51.7178	11.9542	Superior temporal gyrus	BA 22	Phonemic paragraphia
8	W	R	N	−66.9328	−44.4890	−.4751	Middle temporal gyrus	BA 22	Phonemic paragraphia
8	W	R	N	−62.7684	−68.5712	3.8907	Middle temporal gyrus	BA 37	Phonemic paragraphia
9	W	R	0	−62.5788	−6.6594	1.8724	Superior temporal gyrus	BA 22	Phonemic paragraphia
9	W	R	0	−64.3816	−20.5314	10.3465	Superior temporal gyrus	BA 42	Phonemic paragraphia
9	W	R	0	−64.6827	−25.3499	23.0360	Inferior parietal lobule	BA 40	Phonemic paragraphia
10	W	R	N	−65.3636	−35.8005	20.9606	Superior temporal gyrus	BA 22	Phonemic paragraphia
10	W	0	N	−66.8849	−30.7193	10.5569	Superior temporal gyrus	BA 42	Semantic paragraphia
10	W	0	0	−64.4785	−43.9244	10.0049	Superior temporal gyrus	BA 22	Semantic paragraphia
11	W	R	N	−63.1722	−38.1445	28.3748	Inferior parietal lobule	BA 40	Phonemic paragraphia
11	W	R	N	−61.4721	−44.7553	15.5915	Superior temporal gyrus	BA 22	Semantic paragraphia
11	W	R	N	−65.2337	−35.6388	14.4032	Superior temporal gyrus	BA 22	Semantic paragraphia
11	W	R	N	−64.5520	−25.1958	8.9153	Superior temporal gyrus	BA 42	Semantic paragraphia
12	W	0	0	−64.3023	−19.2928	1.5645	Superior temporal gyrus	BA 22	Word deafness
12	W	R	0	−65.1756	−32.3056	12.8596	Superior temporal gyrus	BA 42	Semantic paragraphia
13	W	R	0	−64.0114	−35.7311	30.5147	Inferior parietal lobule	BA 40	Phonemic paragraphia
14	W	0	0	−65.4289	−31.1104	13.8596	Superior temporal gyrus	BA 42	Word deafness
15	W	R	N	−65.2020	−42.4342	24.2874	Inferior parietal lobule	BA 40	Phonemic paragraphia
15	W	0	0	−59.6170	−53.5436	32.1003	Supramarginal gyrus	BA 40	Phonemic paragraphia
16	W	R	N	−65.1366	−17.3126	5.8361	Superior temporal gyrus	BA 22	Semantic paragraphia
16	W	R	N	−65.8675	−24.8921	−.4816	Superior temporal gyrus	BA 22	Semantic paragraphia
16	W	R	N	−66.1800	−26.3276	21.6202	Postcentral gyrus	BA 40	Phonemic paragraphia
16	W	R	N	−68.1427	−31.5337	9.5386	Superior temporal gyrus	BA 22	Semantic paragraphia
16	W	R	N	−66.5496	−37.0802	4.0002	Middle temporal gyrus	BA 22	Semantic paragraphia
16	W	R	N	−65.5585	−38.1843	19.4481	Superior temporal gyrus	BA 22	Semantic paragraphia
17	W	0	0	−63.4226	−30.2223	11.7121	Superior temporal gyrus	BA 42	Semantic paragraphia
17	W	R	N	−64.3316	−24.1881	20.7499	Postcentral gyrus	BA 40	Phonemic paragraphia
18	W	R	N	−65.6772	−36.5414	19.4889	Superior temporal gyrus	BA 22	Phonemic paragraphia
18	W	R	N	−66.4372	−35.7578	10.3953	Superior temporal gyrus	BA 22	Phonemic paragraphia
18	W	R	N	−65.8827	−24.9331	10.9332	Superior temporal gyrus	BA 42	Phonemic paragraphia
18	W	0	0	−66.9100	−33.7572	−7.0217	Middle temporal gyrus	BA 21	Phonemic paragraphia
19	W	R	0	−56.1568	−65.8131	2.8173	Inferior temporal gyrus	BA 37	Phonemic paragraphia
19	W	R	0	−65.8355	−31.5824	14.6324	Superior temporal gyrus	BA 22	Phonemic paragraphia
19	W	0	0	−67.1071	−38.1741	11.7288	Superior temporal gyrus	BA 22	Word deafness
19	W	R	N	−66.6751	−32.2573	21.8307	Superior temporal gyrus	BA 42	Phonemic paragraphia
19	W	R	N	−64.7405	−36.1318	30.3001	Inferior parietal lobule	BA 40	Phonemic paragraphia
19	W	R	N	−65.1186	−27.5733	30.5878	Inferior parietal lobule	BA 40	Phonemic paragraphia
20	W	0	0	−65.6654	−18.7547	25.0339	Postcentral gyrus	BA 1	Phonemic paragraphia
20	W	0	0	−65.4540	−27.9815	26.3554	Inferior parietal lobule	BA 40	Phonemic paragraphia
20	W	0	0	−63.9147	−20.0653	30.1709	Postcentral gyrus	BA 2	Phonemic paragraphia
21	W	R	N	−58.1582	4.5804	−.8018	Superior temporal gyrus	BA 22	Word deafness
21	W	0	0	−60.9765	−4.5798	3.3571	Superior temporal gyrus	BA 22	Word deafness
21	W	0	0	−65.3731	−21.6617	4.4615	Superior temporal gyrus	BA 22	Word deafness
22	W	R	N	−61.4801	−8.4670	2.8254	Superior temporal gyrus	BA 22	Word deafness

direct stimulation was applied while the patients were writing. An assistant alerted the surgeon of any stimulation-induced performance impairments.

In the rare cases where difficulties to understand the dictation were detected in one site, we also tested other comprehension abilities using a few other tasks; i.e., word repetition tasks, basic orders tasks “show me your nose?”, or confrontation naming tasks when the patient is shown four different images (for instance a flower, a boat, a dog, a hammer) and asked “show me where is the boat?” Our goal was to know whether the interferences in comprehension of the dictation were isolated or could be more related to “word deafness” symptoms. We studied speech comprehension/repetition deficits only in sites where the dictation was impaired by a comprehension mechanism. Brain mapping in awake surgery can be rather time consuming and some patients can obviously be tired (with some loss of attention) after several tasks. Thus we focused in this series of 30 patients on 3 main tasks and added some comprehension tasks in selected sites.

To be verified as a cortical “language” location in each task, each stimulated site was meticulously tested at least three times and sites showing no reproducible language interference were not included in the study. “Pure agraphia” was defined as a phonologic or semantic writing disturbance within the same cortical area with no naming and no reading interference *and* otherwise no understanding problems. Difficulties in understanding the dictation were not considered as “pure agraphia”.

When a functional site was found, it was marked with a sterile paper ticket of .25 cm^2. Intra-operative photographs of the brain were taken showing the validated sites according to this procedure. Although the aim of this mapping procedure is to spare language areas during tumour removal, occasionally it was not possible to spare these functional sites in the resection for oncological reasons.

3. Results

Electrostimulation during writing, naming and reading tasks provoked either isolated interferences of just one task i.e., pure agraphia symptoms, or combined interferences in two or all the three of the language tasks used in 22 patients. In two patients (patients 23 and 24), writing, reading, and naming were unaffected during the whole stimulation session. For the purpose of this study into writing function, only those sites provoking writing interferences (either isolated or associated with naming and reading interferences) are discussed here. Isolated naming and reading interferences are not reported. During the electrostimulation process, no motor hand contractions or ocular movements that could have been perceived as a reason for writing disturbance, were seen during stimulation of the sites that induced these writing interferences. No electrical diffusion was detected with electrocorticography.

3.1. *Writing interferences: number and localization*

Overall, 467 cortical sites were stimulated in 23 patients who had their left hemisphere studied and in the sole left-handed patient (patient 20) who had his right hemisphere studied.

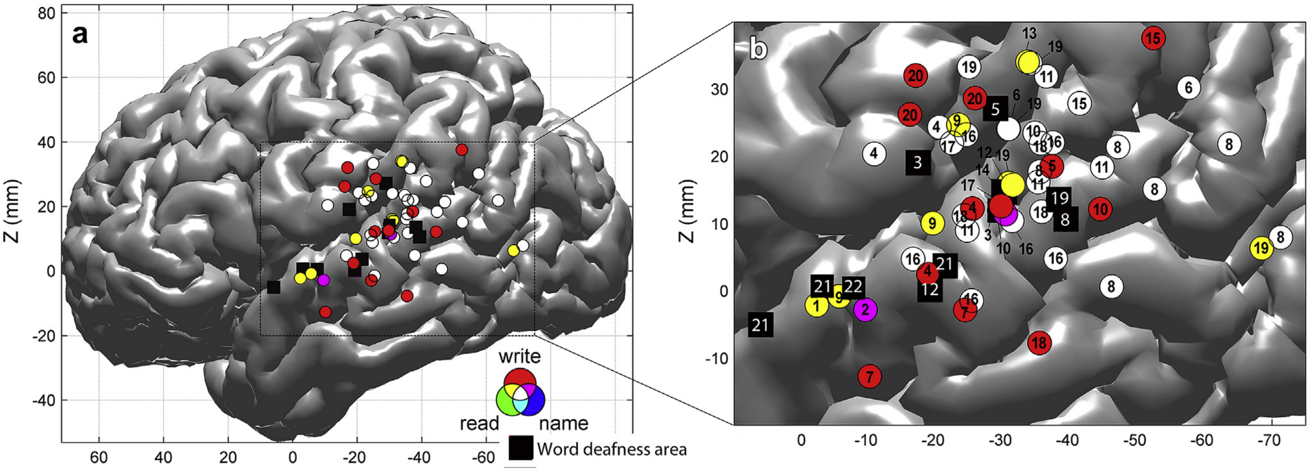

Fig. 2 – Direct brain mapping findings: localization of agraphia areas. 3D brain views showing stimulation sites positioned in the standard normalized Montreal Neurological Institute (MNI) space. Each patient had her/his 3D brain volume normalized in the MNI space and parameters were used to obtain normalized coordinates from stimulation site location which were per-operatively visualized and positioned on 3D original images provided by a neuronavigation software (Medtronic®). Afterward, these data are translated into Talairach Daemon space (http://www.talairach.org). In 2a, Sites with pure agraphia symptoms during stimulation are represented by red dots (12 sites). Black squares represent sites of writing and other comprehension task difficulties (word deafness symptoms). White dots represent common sites for naming, reading and lexico-semantic or phonemic writing interferences. Yellow dots represent sites where stimulation elicited writing and reading interference (no naming interference). Purple dots represent sites where stimulation elicited writing and naming interference (no reading interference). Two patients had no positive stimulation sites. Please note that stimulation sites from 22 patients are grouped together on the left hemisphere. Patient 20, who is left-handed, was operated on the right hemisphere (see details of coordinates of normalized stimulated sites in Table 3). He had 3 pure agraphia interference sites. In 2b, sites were labeled with the corresponding number of the patient as detailed in Table 3.

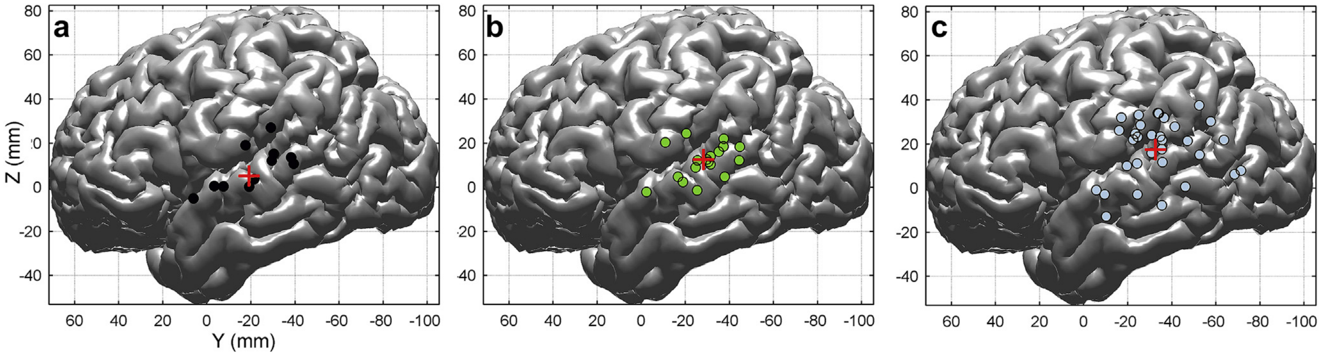

Fig. 3 – Direct brain mapping findings: localization of the types of interferences. As for Fig. 2, 3D brain views showing stimulation sites finally positioned in the standard Talairach space. In 3a, black dots represent sites where patients did not understand the dictated sentences, mostly in the superior temporal gyrus. Electrostimulation of these areas led to word deafness symptoms (dictation and other basic comprehension functions were impaired). In group analysis, barycentre [$X = -67; Y = -20; Z = 8$ (red cross); superior temporal gyrus; BA42] of these word deafness areas was located antero-laterally from Heschl's gyrus; in 3b, green dots represent semantic interferences [Barycenter, $X = -68; Y = -28; Z = 11$ (red cross); superior temporal gyrus; BA42], and in 3c sky blue dots represent phonologic interferences [Barycenter, $X = -67; Y = -34; Z = 18$ (red cross); superior temporal gyrus; BA22]. Phonologic interferences were more distributed than semantic ones.

Writing interference areas found in these cases were rare (62 writing interferences in these 24 patients – from 0 to 6 interferences – mean: 2.58) and located in discrete cortical sites. Each interference area was localized to an area 5 mm wide. These interference sites had distinct margins, whereby a small displacement of the electrode into an adjacent cortical area located in the same gyrus 5 mm away made the interference disappear. (See Fig. 1 for examples of brain mapping and the extremely localized pattern of these interferences). The number and the localization of the writing interferences found was variable within a certain range among patients as detailed in Table 3. On this group, 15 patients had high grade tumors, and 9 low-grade tumors; within the temporoparietal region the localization of the tumors varied a lot although no tumor was located in the posterior T1 gyrus. Overall, 41 writing interferences were found in the high grade group and 21 in the low-grade group (this difference was not significant; $p > .05$).

No writing interferences were detected testing the right middle, superior temporal and supramarginal gyri in 6 right-handed patients. As would be expected, no postoperative agraphia symptoms were noted in these patients.

3.2. *Pure agraphia symptoms*

The localization of the isolated or combined writing interferences is illustrated in Fig. 2. Overall, eight patients (patients 4, 5, 7, 10, 15, 17, 18, 20) showed pure agraphia symptoms (no disturbance in the other two language tests) due to semantic or phonemic interferences in the 12 different areas. Agraphia symptoms due to a global comprehension deficit were not considered as pure agraphia symptoms and were labeled as "word deafness" symptoms. The remaining 14 patients showed a combination of interference in either 2 or 3 tasks; in the same cortical areas, electrostimulation provoked writing and naming and/or reading interferences.

3.3. *Failure to understand the dictated sentences*

Failure to understand the dictated sentences (e.g., the patient said: "I don't understand the sentences you dictated" or "please repeat the sentence") was detected in some sites (Fig. 3a). In these 11 cortical sites, the deficit was of global speech comprehension (word deafness symptoms); impaired word repetitions, difficulties in follow basic orders were observed suggesting a global deficit of speech comprehension as in word deafness syndrome. Once stimulation was removed and the sentence dictated again, patients resumed writing correctly after a few seconds.

3.4. *Writing interferences: type*

Two different types of writing disorders were found during stimulation on a given cortical area (Fig. 3b and c shows the localization of these sites):

1. Semantic or verbal paragraphias, sometimes with perseveration phenomenon (18 sites). Patients missed the target word and wrote words that were orthographically correct but inappropriate to the sentence dictated.
2. Phonological paragraphias, such as repetition or omissions of vowels or consonants, transpositions of letters or syllables, use of jargon (33 sites). We did not find clear distinction between the types of phonological paragraphias (vowel/consonant transpositions, syllable level transpositions, or jargon production) in different regions of the cortex. For instance, we found voxel/consonant transpositions in an area and a few minutes later stimulation of the same area at the same current intensity led to jargon production.

In 8 cases, we were able to document various perturbations of the different stages of writing processing within the same patient. For example, in patients 5, 8, 12, and 19, we observed

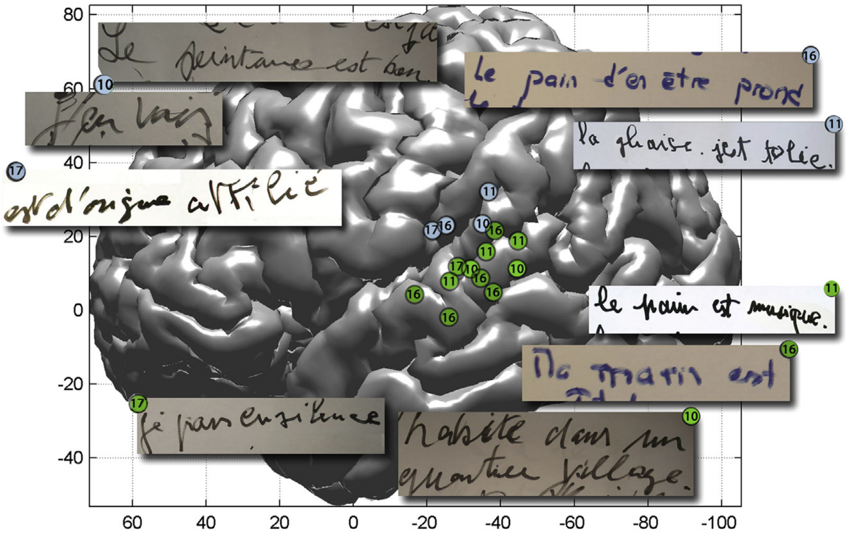

Fig. 4 – Localization of semantic and phonemic agraphia sites in a sub-group of 4 patients. In each of these 4 patients (cases 10, 11, 16, and 17) we found both phonemic (sky blue dots) and semantic or verbal paragraphia (green dots) sites. See some examples of handwriting during electrostimulation: phonemic paragraphias are noted "*attilié*" for "*italienne*"- Italian [17], "*jeintanes*" for "*pain tendre*" – wheat bread [10], "*j'en vais*" for "*j'aime*" – I like [10], "*d'en être prond*" for "*tendre est bon*" – tender is good [16], "*ghaise jest tolie*" for "*chaise est jolie*" – chair is nice [11]. Semantic or verbal paraphasia are seen elsewhere, "*musique*" for "*tendre*" – music for tender [11], "*marin*" for "*mère*" – sailor for mother [16], "*quartier*" for "*petit*" – district for small [10] and "*silence*" for "*vacances*" – silent for holidays [17]. Electrostimulation temporary inhibited in each of them a ventral, lexical pathway (superior temporal gyrus) where patients had semantic paragraphias and a more dorsal, sub-lexical pathway (supramarginal gyrus) where patients had phonemic paragraphias.

interference sites affecting speech comprehension while others affected written production, with either semantic or phonological paragraphias depending on the case. In patients 10, 11, 16, and 17, we observed agraphia symptoms that were semantic or phonological depending on the stimulated area in each of these patients (Fig. 4).

Analysis of the patient's level of awareness of the electrostimulation-induced deficit in the writing process revealed marked differences between patients. When electrostimulation-induced word deafness, patients were aware of their difficulty in all cases, and asked for repetition of the dictated sentence or orders. When electrostimulation-induced paragraphias, patients were not aware of their writing errors. Once the sentence had been dictated, they wrote without hesitation and without awareness of their phonemic or semantic paragraphias. They only became aware of their writing errors once the stimulation had stopped, when they were asked to read what they had just written.

3.5. *Postoperative writing analysis*

Writing sites found in hemispheres were spared where possible during surgery. Although 10 patients had some dysphasic symptoms one month after surgery, none of these patients had postoperative pure agraphia symptoms.

4. Discussion

In this study, we found that the process of writing from dictation involves extremely localized areas of the left temporal-parietal cortex. Although most electrostimulation-induced writing interferences remained centered along the superior temporal gyrus, high individual variability was observed. These cortical areas were either task-specific, involving only writing (pure agraphia areas) or also affected other language processes such as picture naming or sentence reading. Further, we were able to isolate the disturbance of different parts of the pathway involved in dictation tasks, from auditory word recognition to semantic and phonological processes as described in dual stream models of language comprehension processing (Friederici, 2011; Hickok & Poeppel, 2007; Rauschecker, 2011).

4.1. *Individual variability and mosaic organization*

Inter-subject differences in cortical functional locations are universal in electrostimulation experiments (Ojemann et al., 1989; Penfield & Robert, 1959) and also very frequently recognized in brain imaging for various cognitive functions (Allen, Erhardt, Wei, Eichele, & Calhoun, 2012; Brett, Johnsrude, & Owen, 2002; Uylings, Rajkowska, Sanz-Arigita, Amunts, & Zilles, 2005). It is precisely this uncertainty and variability across subjects that underpins the importance of performing neurosurgical mapping procedures to establish the exact localization of language functions a specific patient. However, in spite of this variability, reproducible patterns in localizing brain functions can be observed.

By virtue of its spatial accuracy (i.e., precision of location), electrostimulation allows one to distinguish the cognitive function supported by small neighboring patches of cortex even in very specific cognition or language domains. This "mosaic", patchy pattern is a standard finding in many electrostimulation studies (Boatman, 2004; Lüders et al., 1991; Matsumoto et al., 2011; Ojemann et al., 1989; Penfield & Robert, 1959; Roux, Lubrano, Lauwers-Cances, Giussani, & Demonet, 2008; Simos et al., 2002; Usui et al., 2003). With regards to the first step of writing from dictation, i.e., speech comprehension, a certain degree of variability in the localization of the functional areas involved in this process has been described in some previous electrostimulation studies (Boatman, 2004). Localizing the neural bases of the subsequent linguistic steps downstream from this in the writing from dictation process, many previous brain activation studies (Katanoda et al., 2001; Menon & Desmond, 2001; Sugihara et al., 2006) and electrostimulation studies (Lesser et al., 1984; Lubrano, Roux, & Démonet, 2004; Roux et al., 2003, 2009) have also described a relative but substantial degree of individual variability. For instance, using functional MRI (fMRI), Sugihara et al. found an inconsistency in the involvement of the left supramarginal gyrus and intraparietal fissure between volunteers during writing tasks (Sugihara et al., 2006). In the present study, interindividual variability was also observed; for instance pure agraphia areas were not localized in a definitive brain area but rather were found amid a relatively extended territory along the middle part of the superior temporal gyrus. For example, on the Y axis along the superior temporal and supramarginal gyri, the most rostral pure agraphia area (found in patient 7) was located 44 mm away from the most caudal one (found in patient 15).

Many reasons can account for the relative variability between individuals observed in the localization of speech comprehension areas or other areas inducing phonological or semantic interferences. In primates, it has been shown that the auditory system could occupy large portions of cortex, including the entire superior temporal gyrus and large portions of the parietal regions (Poremba et al., 2003). Variability of the human cytoarchitectonic structures in some primary (Morosan et al., 2001; Uylings et al., 2005) or heteromodal areas of the human brain (Casper et al., 2006; Uylings et al., 2005) could explain the composite and highly individual specific maps generated in our study. More technical factors, such as the limitation of stimulation to gyral structures only (while the depth of the sulci were not explored), the influence of epileptic activity, as well as the influence of some slow-growing tumors on the spatial organization of functional cortical representation, could also account for cross-subject inconsistency (Lubrano, Draper, & Roux, 2010).

Finally, we found in 5 individuals (patients 1, 9, 12, 13, and 19) shared writing and reading neural structures (i.e., yellow dots in our Fig. 2). It is interesting because only two areas, the left inferior frontal gyrus and the fusiform gyrus, were previously identified to be shared across spelling and reading within the same subjects in the study of Purcell et al. (Purcell et al., 2011) as well as in a similar study carried out by Rapp and Lipka (Rapp & Lipka, 2011). To date, no fMRI study examining reading and spelling within the same subjects (Purcell et al., 2011; Rapp & Lipka, 2011) has demonstrated selective overlap of reading and spelling within the left temporoparietal cortex. Our results showed that shared reading and spelling neuronal structures could also be detected along the left superior temporal and supramarginal gyri.

4.2. *Pure agraphia symptoms*

The correlation of pure agraphia symptoms (loss of the ability of writing, without any oral language or motor disturbances) with discrete anatomical areas has long-been debated (Déjerine, 1891; Auerbach & Alexander, 1981; Lesser et al., 1984; Roux et al., 2009). Using fMRI in a group of volunteers, Purcell et al. appear to find many overlap in locations studying reading and writing (Purcell et al., 2011). We also found many shared areas between naming, reading and writing. But pure lexico-semantic or phonological dysgraphia symptoms (i.e., dissociated from oral language tasks) were detected in 8 of our patients while stimulating small patches of perisylvian cortex. Lexico-semantic errors were mainly elicited by stimulation of the temporal cortex (BA 22 and BA 42) while phonological errors were associated more with sites distributed around the posterior part of the middle and superior temporal gyri and the anterior part of the supramarginal gyrus. One of the reasons why this electrostimulation study occasionally found dissociations between writing tasks and other tasks might be the extreme accuracy of this technique of brain mapping. The demonstration of stimulation-induced dissociated writing symptoms (as opposed to those associated with speech symptoms) in this study is in accordance with the cases of similar symptoms of pure agraphia that have long-been described in some patients with lesions in this region (Rosati & De Bastiani, 1979; Yokota, Ishiai, Furukawa, & Tsukagoshi, 1990). For instance, Rosati and De Bastiani described a case with paragraphic errors, transpositions, omission of letters or syllables and perseverations (Rosati & De Bastiani, 1979) and Yokota described pure agraphia for Kanji (Japanese script) in a Japanese patient with a small lesion of the posterior Sylvian fissure (Yokota et al., 1990). We hypothesize that cases of pure agraphia associated with posterior Sylvian lesions are exceedingly rare, as they would only occur in the case of a small, critically-located lesion affecting writing-related cortical areas only, without encroaching on those related to speech.

Finally, bias factors in the definition of pure agraphia symptoms should be acknowledged. The "specificity" pattern of a cortical area (for instance pure agraphia symptoms) could depend on the number or type of tasks used in a given study. We cannot exclude the possibility that other functions (other than writing, naming, reading) not tested in this study could be revealed in these cortical areas by electrostimulation if specifically tested. Nevertheless, the same type of limitation can also apply to brain imaging experiments or neurophysiological studies of brain-damaged patients, both of which would usually involve a limited number of experimental tasks or conditions that cannot practically test for all possible cognitive functions.

4.3. *Speech comprehension stage of writing from a dictation*

The neural underpinnings of speech comprehension are thought to be hierarchically organized with increasing coding complexity from phoneme to sentence comprehension along the superior temporal gyrus (DeWitt & Rauschecker, 2012; Friederici, 2012). Thus, the processing of auditory word forms is related to the middle part of the left superior temporal gyrus (Binder, Liebenthal, Possing, Medler, & Ward, 2004; DeWitt & Rauschecker, 2012; Friederici, 2011, 2012). The present study, performed on 30 patients, showed that the speech comprehension area is generally located in the middle part of the left superior temporal gyrus, lateral and anterior to the primary auditory cortex in the parabelt region of the auditory cortex (BA 22 or 42). Indeed, word deafness has been previously described in patients with brain lesions located in this region (Buchman et al., 1986; Kirshner, Webb, & Duncan, 1981); and convergent results from electrostimulation and brain activation studies have also been reported (Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Boatman, 2004; Matsumoto et al., 2011; Rapp & Dufor, 2011). Matsumoto studied speech perception in 2 patients by electrostimulation during neurosurgical procedures and found impairment of auditory sentence comprehension in restricted areas of the middle part of left superior temporal gyrus (Matsumoto et al., 2011). Reviewing some electrostimulation studies, Boatman localized syllable discrimination deficits within the middle-posterior region of the superior temporal gyrus (Boatman, 2004), sometimes with bilateral representation (Boatman et al., 1998). Other neurosurgical (Creutzfeldt et al., 1989) or fMRI (Just et al., 1996) studies also found bilateral involvement of the superior temporal gyrus in speech recognition.

Contrary to some previous word deafness studies or case reports (Buchman et al., 1986; Creutzfeldt et al., 1989; Just et al., 1996), all speech comprehension deficit areas in the current study were detected in the left hemispheres (unless those detected in the left-handed patient in his right temporoparietal region), with none found in the right hemisphere of right-handed patients. Electrostimulation in these areas did not cause “hearing suppression” (Fenoy, Severson, Volkov, Brugge, & Howard, 2006) in that the patients could still hear; rather that despite being able to hear, they did not understand the dictation. In our patients, stimulation of these word deafness areas led to impairments in comprehension (dictation, repetition, basic orders) and occasionally naming and reading impairments. Thus, dictation was not specifically impaired by electrostimulation in these areas. Nevertheless, one could hypothesize the existence of a specific neuronal population in the left superior temporal gyrus involved in the early stage of writing from dictation i.e., comprehension of the dictated words. Anyway, the results suggest that after the earliest processing stages in the right and left primary auditory region (Griffiths & Warren, 2002), word and sentence recognition necessary for writing transposition was strongly related to the left superior temporal gyrus. When the left superior temporal gyrus is intact, the right auditory cortex is probably not engaged in dictation comprehension processing, since electrostimulation in this region never impaired word recognition, contrary to the left. This left-sided dominance for speech perception has also been put forward by other studies (Boatman, 2004; Scott & Wise, 2004). However, this may not be universally true in all patients, especially in left-handed patients or in atypical cases, but does agree with studies showing early auditory analysis of the speech signal in bilateral primary auditory areas followed by later stage processing concentrated in the left hemisphere (Binder et al., 2004).

4.4. *Lexico-semantic and phonologic stages of writing from a dictation*

Upon stimulation of specific sites, dissociation was observed between lexical-semantic and phonological processing stages, in a subset of 4 of our patients. When stimulating these cortical sites, these patients while not complaining about auditory perception of sentence stimuli, wrote the whole sentence with major language deviations, consisting in either lexical-semantic or phonological errors, depending on whether the stimulation was applied to the temporal or the inferior parietal cortex, respectively. Crucially the patients were not aware of such errors (as described by other authors in stimulation experiments in this region; Schönwiesner et al, 2007). Patients acknowledged their errors upon post hoc reading their own scripts. This is rather different from patients with agraphia from chronic brain lesions in who some brain plasticity mechanisms allow them sometimes to be aware of their trouble. While stunning, these findings were compelling and reproduced both within and across patients. From these observations, one can infer that the electrical stimulation of the temporal or parietal neural circuits disturbed information processing involved in the dictation task upstream of more peripheral stages that are under conscious control. According to the current psycholinguistic models of spelling (Roeltgen & Heilman, 1984), the neural circuits which were challenged in our 4 patients, would represent, at least in part, the cortical underpinnings of the central orthographic processes involved either in the direct lexical pathway or the indirect sub-lexical one. Our findings indicate that the former is supported by the left superior temporal cortex while some neural substrates of the latter likely lie in the left supramarginal gyrus.

As suggested by neurocognitive models of reading, the sub-lexical and lexical reading processes are segregated in the left posterior perisylvian cortex (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Levy et al., 2009; Price, 2012). Using the electrical stimulation method, we showed recently the anatomical segregation of the two reading processes in the very same cortical regions as those explored in the present work, with a specific deficit of pseudoword reading upon stimulation of the left supramarginal gyrus, and a specific irregular word reading disorder when stimulating the left superior temporal gyrus (Roux et al., 2012). While obtained in two independent series of patients studied either with reading tasks or with dictation tasks, our observations all concur in strikingly convergent findings with double dissociation effects in the same patients. Disregarding whether reading or writing were tested, we observed that the stimulation of a restricted cortical area in the inferior part of the left supramarginal gyrus disturbed specifically the sub-lexical processing while performance related to the lexical processing were unaffected. On the opposite, when the same patients were stimulated in the left superior temporal gyrus, performance showed a specific impairment of the lexical orthographic procedure that consisted in either failures to read irregular words in the reading experiment or lexical-semantic deviations in the dictation experiment whereas the sub-lexical procedure remained unaffected (either normal reading of pseudowords or absence of letter-level paragraphias).

Our convergent findings that stimulation of the left supramarginal gyrus elicits disorders of sub-lexical orthographic processing are supported by a massive literature involving both lesion-based and brain imaging studies (for a review Price, 2012). By contrast, the specific influence of stimulation of the posterior part of the left superior temporal cortex on the lexical procedure is by far less straightforward as this large region is a functional hub involved in many language functions primarily dominated by speech perception processes. Apart from the 4 dissociated cases we isolated in our patient sample, we also recorded a number of observations of phonemic paragraphias elicited by stimulation of this region, suggesting that diverse neural populations distributed over the superior temporal and inferior parietal areas participate in the sub-lexical orthographic procedure. Therefore, the 4 dissociated cases we observed with a clear-cut parietal versus temporal dichotomy for sub-lexical versus lexical orthographic procedure may represent extreme cases of anatomo-functional segregation while the majority of subjects would have more interspersed neural populations supporting the two orthographic procedures throughout the temporal parietal cortex. The variability in the degree of segregation of the two neural networks respectively in charge of the two orthographic procedures may also account for the rare and well-known observations of neuropsychological cases of "pure" phonological or surface dysgraphia, respectively reported by many authors (Baxter & Warrington, 1985, 1987; Bub & Kertesz, 1982; Roeltgen & Heilman, 1984; Shallice, 1981).

Thus, reading and writing processes could be similarly organized through a ventral, lexico-semantic and a dorsal, phonologic route. Short-range connection fibers could convey language information to areas responsible for semantic and phonological processing along the superior temporal and the supramarginal gyri (Friederici, 2012). More generally, the posterior part of the superior temporal gyrus (Démonet et al., 1992; Kim et al., 2002; Simos et al., 2002), supramarginal gyrus (Penniello et al., 1995; Roeltgen & Heilman, 1984) or both (Alexander, Friedman, Loverso, & Fischer, 1992) could sustain the "phonological route" for speech processing. Using fMRI and writing tasks in 20 volunteers, Sugihara et al. found that the anterior limb of the supramarginal gyrus was activated during phoneme to grapheme conversion (Sugihara et al., 2006). Perisylvian regions have been regularly described as being involved in phoneme to grapheme conversion as described in both lesion (Henry et al., 2007) and activation studies (Omura, Tsukamoto, Kotani, Ohgami, & Yoshigawa, 2004; Sakurai et al., 2008). Our results show that this phonological, dorsal comprehension stream, strongly left-hemisphere dominant (Hickok & Poeppel, 2007) and related to sensory-motor integration is involved in handwriting from dictation.

Finally, the current study did not focus on the angular gyrus, therefore less writing interferences in the angular gyrus were found than in one of our previous studies on this topic (Roux et al., 2003). The angular gyrus and left superior parietal gyrus have been shown to be involved in linguistic and high-level motor control aspects of writing respectively (Benson, 1979; Segal & Petrides, 2012). Previous studies have pointed to the involvement of the angular gyrus in reading and the spelling process used when writing (Benson, 1979; Deleon et al., 2007; Hillis & Rapp, 2004). The left superior parietal lobe could be involved in spatial and kinesthetic modulation of writing movements, its damage resulting in apractic agraphia (Auerbach & Alexander, 1981; Menon & Desmond, 2001). Functional MRI studies regularly demonstrate activation of this region during writing tasks contrasted with naming and finger tapping tasks (Katanoda et al., 2001; Segal & Petrides, 2012). Once decoded in the superior temporal gyrus and the inferior parietal lobe, the dictated message could then be transmitted, via long association fibers, such as the arcuate fasciculus and parts of the superior longitudinal fasciculus, to the upper parietal lobe and the premotor cortex (Friederici, 2011; Rauschecker, 2011). The planning of hand movements or the conversion of the dictated message from its graphemic form to its "allographic" form could involve other regions, such as left superior parietal (Segal & Petrides, 2012) or middle frontal gyrus (Roux et al., 2009). More work is needed to understand better the specific roles of the latter two functional entities in the latest stages of handwriting.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2013.09.012.

REFERENCES

Alexander, M. P., Friedman, R. B., Loverso, F., & Fischer, R. S. (1992). Lesion localization of phonological agraphia. *Brain and Language, 43*, 83–95.

Allen, E. A., Erhardt, E. B., Wei, Y., Eichele, T., & Calhoun, V. D. (2012). Capturing inter-subject variability with group independent component analysis of fMRI data: a simulation study. *NeuroImage, 59*, 4141–4159.

Auerbach, S. H., & Alexander, M. P. (1981). Pure agraphia and unilateral optic ataxia associated with a left superior parietal lobule lesion. *Journal of Neurology, Neurosurgery and Psychiatry, 44*, 430–432.

Baxter, D. M., & Warrington, E. K. (1985). Category specific phonological dysgraphia. *Neuropsychologia, 23*, 653–666.

Baxter, D. M., & Warrington, E. K. (1987). Transcoding sound to spelling: single or multiple sound unit correspondence? *Cortex, 23*, 11–28.

Beeson, P. M., Rapcsak, S. Z., Plante, E., Chargualaf, J., Chung, A., Johnson, S. C., et al. (2003). The neural substrate of writing: a functional magnetic resonance imaging study. *Aphasiology, 17*, 647–665.

Benson, D. F. (1979). *Aphasia, alexia and agraphia*. New York: Churchill Levingstone.

Binder, J. R., Liebenthal, E., Possing, E. T., Medler, D. A., & Ward, B. D. (2004). Neural correlates of sensory and decision processes in auditory object identification. *Nature Neuroscience, 7*, 295–301.

Binder, , Jr., Swanson, S. J., Hammeke, T. A., & Sabsevitz, D. S. (2008). A comparison of five protocols for mapping speech comprehension systems. *Epilepsia, 49*, 1980–1997.

Boatman, D. (2004). Cortical bases of speech perception: evidence from functional lesion studies. *Cognition, 92*, 47–65.

Boatman, D., Hart, J., Jr., Lesser, R. P., Honeycutt, N., Anderson, N. B., Miglioretti, D., et al. (1998). Right hemisphere speech perception revealed by amobarbital injection and electrical interference. *Neurology, 51*, 458–464.

Brett, M., Johnsrude, I., & Owen, A. (2002). The problem of functional localization in the human brain. *Nature Reviews Neuroscience, 3*, 243–249.

Bub, D., & Kertesz, A. (1982). Evidence for lexicographic processing in a patient with preserved written over oral single word naming. *Brain, 105*, 697–717.

Buchman, A. S., Garron, D. C., Trost-Cardamone, J. E., Wichter, M. D., & Schwartz, M. (1986). Word deafness: one hundred years later. *Journal of Neurology, Neurosurgery and Psychiatry, 49*, 489–499.

Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., & Zilles, K. (2006). The human inferior parietal cortex: cytoarchitectonic parcellation and interindividual variability. *NeuroImage, 33*, 430–448.

Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. D. R. C. (2001). A dual route cascaded model of visual word recognition and reading aloud. *Psychological Reviews, 108*, 204–256.

Creutzfeldt, O., Ojemann, G., & Lettich, E. (1989). Neuronal activity in the human lateral temporal lobe. I. Responses to speech. *Experimental Brain Research, 77*, 451–475.

Déjerine, J. (1891). Sur un cas de cécité verbale avec agraphie, suivi d'autopsie. *Compte Rendu de la Société de Biologie, 43*, 197–201.

Deleon, J., Gottesman, R. F., Kleinman, J. T., Newhart, M., Davis, C., Heidler-Gary, J., et al. (2007). Neural regions essential for distinct cognitive processes underlying picture naming. *Brain, 130*, 1408–1422.

Deloche, G. H., Metz-Lutz, M. N., & Kremin, H. (1997). *Test de dénomination orale de 80 images: DO 80*. Paris: ECPA.

Démonet, J. F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J. L., Wise, R., et al. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain, 115*, 1753–1768.

DeWitt, I., & Rauschecker, J. P. (2012). Phoneme and word recognition in the auditory ventral stream. *PNAS*, E505–E514.

Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Jr., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition, 92*, 145–177.

Fenoy, A. J., Severson, M. A., Volkov, I. O., Brugge, J. F., & Howard, M. A. (2006). Hearing suppression induced by electrical stimulation of human auditory cortex. *Brain Research, 1118*, 75–83.

Friederici, A. D. (2011). The brain basis of language processing: from structure to function. *Physiological Reviews, 91*, 1357–1392.

Friederici, A. D. (2012). The cortical language circuit: from auditory perception to sentence comprehension. *Trends in Cognitive Neurosciences, 16*, 262–268.

Griffiths, T. D., & Warren, J. D. (2002). The planum temporal as a computation hub. *Trends in Neurosciences, 25*, 348–353.

Henry, M. L., Beeson, P. M., Stark, A. J., & Rapcsak, S. Z. (2007). The role of left perisylvian cortical regions in spelling. *Brain and Language, 100*, 44–52.

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Neuroscience, 8*, 393–402.

Hillis, A. E., & Rapp, B. C. (2004). Cognitive and neural substrates of written language comprehension and production. In *The new cognitive neurosciences* (3rd ed..). (pp. 755–788) Cambridge MA: MIT press.

Just, M. A., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, K. R. (1996). Brain activation modulated by sentence comprehension. *Science, 274*, 114–116.

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

Kim, H. J., Chu, K., Lee, K. M., Kim, D. W., & Park, S. H. (2002). Phonological agraphia after superior temporal gyrus infarction. *Archives of Neurology, 59*, 1314–1316.

Kirshner, H. S., Webb, W. G., & Duncan, G. W. (1981). Word deafness in Wernicke's aphasia. *Journal of Neurology, Neurosurgery and Psychiatry, 44*, 197–201.

Lesser, R. P., Lueders, H., Dinner, D. S., Hahn, J., & Cohen, L. (1984). The location of speech and writing functions in the frontal language area. Results of extraoperative cortical stimulation. *Brain, 107*, 275–291.

Levy, J., Pernet, C., Treserras, S., Boulanouar, K., Aubry, F., Démonet, J. F., et al. (2009). Testing for the dual-route cascade reading model in the brain: an fMRI effective connectivity account of an efficient reading style. *PLoS One, 4*, e6675.

Lichtheim, L. (1885). On aphasia. *Brain, 7*, 433–484.

Lubrano, V., Draper, L., & Roux, F. E. (2010). What makes surgical tumor resection feasible in Broca's area? Insights into intraoperative brain mapping. *Neurosurgery, 66*, 868–875.

Lubrano, V., Roux, F. E., & Démonet, J. F. (2004). Writing-specific sites in frontal areas: a cortical stimulation study. *Journal of Neurosurgery, 101*, 787–798.

Lüders, H., Lesser, R. P., Hahn, J., Dinner, D. S., Morris, H. H., Wyllie, E., et al. (1991). Basal temporal language area. *Brain, 114*, 743–754.

Matsumoto, R., Imamura, H., Inouchi, M., Nakagawa, T., Yokoyama, Y., Matsuhashi, M., et al. (2011). Left Anterior temporal cortex actively engages in speech perception: a direct cortical stimulation study. *Neuropsychologia, 49*, 1350–1354.

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

Morosan, P., Rademacher, J., Schleicher, A., Amunts, K., Schormann, T., & Zilles, K. (2001). Human primary auditory cortex: cytoarchitectonic subdivisions and mapping into a spatial reference system. *NeuroImage, 13*, 684–701.

Nespoulous J. L., Joanette Y, Lecours A. R.. Ed. L'Ortho-Edition, Isbergues, France, 1992.

Ojemann, G., Ojemann, J., Lettich, E., & Berger, M. (1989). Cortical language localization in left, dominant hemisphere. *Journal of Neurosurgery, 71*, 316–326.

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

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

Penfield, W., & Robert, L. (1959). *Speech and brain mechanisms*. Princeton: Princeton University Press.

Penniello, M. J., Lambert, J., Eustache, F., Petit-Taboué, M. C., Barré, L., Viader, F., et al. (1995). A PET study of the functional neuroanatomy of writing impairment in Alzheimer's disease. *Brain, 118*, 697–706.

Poremba, A., Saunders, R. C., Crane, A. M., Cook, M., Sokoloff, L., & Mishkin, M. (2003). Functional mapping of the primate auditory system. *Science, 299*, 568–572.

Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage, 62*, 816–847.

Purcell, J. J., Napoliello, E. M., & Eden, G. F. (2011). A combined fMRI study of typed spelling and reading. *NeuroImage., 55*, 750–762.

Rapp, B., & Dufor, O. (2011). The neurotopography of written word production: an fMRI investigation of the distribution of sensitivity to length and frequency. *Journal of Cognitive Neuroscience, 23*, 4067–4081.

Rapp, B., & Lipka, K. (2011). The literate brain: the relationship between spelling and reading. *Journal of Cognitive Neuroscience, 23*, 1180–1197.

Rauschecker, J. P. (2011). An expanded role for the dorsal auditory pathway in sensorimotor control and integration. *Hearing Research, 271*, 16–25.

Roeltgen, D. P., & Heilman, K. M. (1984). Lexical agraphia. Further support for the two-system hypothesis of linguistic agraphia. *Brain, 107*, 811–827.

Rosati, G., & De Bastiani, P. (1979). Pure agraphia: a discrete form of aphasia. *Journal of Neurology, Neurosurgery and Psychiatry, 42*, 266–269.

Roux, F. E., Boetto, S., Sacko, O., Chollet, F., & Trémoulet, M. (2003). Writing, calculating, and finger recognition in the region of the angular gyrus: a cortical stimulation study of Gerstmann syndrome. *Journal of Neurosurgery, 99*, 716–727.

Roux, F. E., Dufor, O., Giussani, C., Wamain, Y., Draper, L., Longcamp, M., et al. (2009). The graphemic/motor frontal area Exner's area revisited. *Annals of Neurology, 66*, 537–545.

Roux, F. E., Durand, J. B., Jucla, M., Rehault, E., Reddy, M., & Demonet, J. F. (2012). Segregation of lexical and sub-lexical reading processes in the left perisylvian cortex. *PLoS One, 7*(11), e50665.

Roux, F. E., Lubrano, V., Lauwers-Cances, V., Giussani, C., & Demonet, J. F. (2008). Cortical areas involved in Arabic number reading. *Neurology, 70*, 210–217.

Sakurai, Y., Mimura, I., & Mannen, T. (2008). Agraphia for kanji resulting from a left posterior middle temporal gyrus lesion. *Behavioral Neurology, 19*, 93–106.

Schönwiesner, M., Novitski, N., Pakarinen, S., Carlson, S., Tervaniemi, M., & Näätänen, R. (2007). Heschl's gyrus, posterior superior temporal gyrus, and mid-ventrolateral prefrontal cortex have different roles in the detection of acoustic changes. *Journal of Neurophysiology, 97*, 2075–2082.

Scott, S. K., & Wise, R. J. S. (2004). The functional neuroanatomy of prelexical processing in speech perception. *Cognition, 92*, 13–45.

Segal, E., & Petrides, M. (2012). The anterior superior parietal lobule and its interactions with language and motor areas during writing. *European Journal of Neuroscience, 35*, 309–322.

Shallice, T. (1981). Phonological agraphia and the lexical route in writing. *Brain, 104*, 413–429.

Simos, P. G., Breier, J. I., Fletcher, J. M., Foorman, B. R., Castillo, E. M., & Papanicolaou, A. C. (2002). Brain mechanisms for reading words and pseudowords: an integrated approach. *Cerebral Cortex, 12*, 297–305.

Sugihara, G., Kaminaga, T., & Sugishita, M. (2006). Interindividual uniformity and variety of "writing center": a functional MRI study. *NeuroImage, 32*, 1837–1849.

Usui, K., Ikeda, A., Takayama, M., Matsuhashi, M., Yamamoto, J., Satoh, T., et al. (2003). Conversion of semantic information into phonological representation: a function in left posterior basal temporal area. *Brain, 126*, 632–641.

Uylings, H. B., Rajkowska, G., Sanz-Arigita, E., Amunts, K., & Zilles, K. (2005). Consequences of large interindividual variability for human brain atlases: converging macroscopical imaging and microscopical neuroanatomy. *Anatomy and Embryology (Berlin), 210*, 423–431.

Yokota, T., Ishiai, S., Furukawa, T., & Tsukagoshi, H. (1990). Pure agraphia of kanji due to thrombosis of the Labbé vein. *Journal of Neurology, Neurosurgery and Psychiatry, 53*, 335–338.