Available online at www.sciencedirect.com

ScienceDirect

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

Research report

Electrostimulation mapping of comprehension of auditory and visual words

Franck-Emmanuel Roux [a,b,c,*], *Krasimir Miskin* [d], *Jean-Baptiste Durand* [b], *Oumar Sacko* [a], *Emilie Réhault* [a], *Rositsa Tanova* [d] *and Jean-François Démonet* [e]

[a] *Pôle NeuroSciences (Neurochirurgie), Toulouse, France*
[b] *CNRS — centre de Recherche Cerveau et Cognition, Toulouse, France*
[c] *INSERM 825, Université de Toulouse UPS, Centres Hospitalo-Universitaires, Toulouse, France*
[d] *Department of Neurosurgery, University Hospital "St. Ivan Rilski", Sofia, Bulgaria*
[e] *Leenaards Memory Center, Department of Clinical Neurosciences CHUV & University of Lausanne, Switzerland*

ARTICLE INFO

Article history:
Received 9 December 2014
Reviewed 30 January 2015
Revised 19 March 2015
Accepted 2 July 2015
Action editor Rhonda Friedman
Published online 26 July 2015

Keywords:
Brain tumour
Cortical mapping
Speech comprehension
Auditory cortex

ABSTRACT

In order to spare functional areas during the removal of brain tumours, electrical stimulation mapping was used in 90 patients (77 in the left hemisphere and 13 in the right; 2754 cortical sites tested). Language functions were studied with a special focus on comprehension of auditory and visual words and the semantic system. In addition to naming, patients were asked to perform pointing tasks from auditory and visual stimuli (using sets of 4 different images controlled for familiarity), and also auditory object (sound recognition) and Token test tasks. Ninety-two auditory comprehension interference sites were observed. We found that the process of auditory comprehension involved a few, fine-grained, sub-centimetre cortical territories. Early stages of speech comprehension seem to relate to two posterior regions in the left superior temporal gyrus. Downstream lexical-semantic speech processing and sound analysis involved 2 pathways, along the anterior part of the left superior temporal gyrus, and posteriorly around the supramarginal and middle temporal gyri. Electrostimulation experimentally dissociated perceptual consciousness attached to speech comprehension. The initial word discrimination process can be considered as an "automatic" stage, the attention feedback not being impaired by stimulation as would be the case at the lexical-semantic stage. Multimodal organization of the superior temporal gyrus was also detected since some neurones could be involved in comprehension of visual material and naming. These findings demonstrate a fine graded, sub-centimetre, cortical representation of speech comprehension processing mainly in the left superior temporal gyrus and are in line with those described in dual stream models of language comprehension processing.

© 2015 Elsevier Ltd. All rights reserved.

* *Corresponding author*. 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.2015.07.001
0010-9452/© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

Both left and right superior temporal gyri are involved in early processes of speech perception (Binder, Swanson, Hammeke, & Sabsevitz, 2008; Buchman, Garron, Trost-Cardamone, Wichter, & Schwartz, 1986; Creutzfeldt, Ojemann, & Lettich, 1989; Dronkers, Wilkins, Van Valin Jr., Redfern, & Jaeger, 2004; Friederici, 2011; J.P. Rauschecker, 1998). However, the neural underpinnings of speech comprehension are thought to be hierarchically organized with increasing coding complexity along a caudal/rostral stream of neural activity in the left superior temporal gyrus (DeWitt & Rauschecker, 2012). This region has been described as supporting the functional gradient from phoneme to sentence comprehension (DeWitt & Rauschecker, 2012; Friederici, 2012). More specifically, decoding the speech message from initial prelexical processing (Scott & Wise, 2004) to the top-down semantic and syntactic processes (Hickok & Poeppel, 2007) is thought to involve a dedicated speech perception ventral pathway that spreads along the left superior temporal gyrus (DeWitt & Rauschecker, 2013). Accordingly, the processing of auditory word forms could be related to neural activities in the middle part of the left superior temporal gyrus (Binder, Liebenthal, Possing, Medler, & Ward, 2004; DeWitt & Rauschecker, 2012; Friederici, 2011, 2012). The dorsal comprehension pathway running from the left posterior temporal region to frontal premotor regions, through parts of the arcuate and superior longitudinal fasciculi, probably supports auditory motor integrations (Friederici, 2012; Hickok & Poeppel, 2007). In addition, the same territories in the superior temporal cortex would also be involved in other language functions such as naming (see C. Price, 2012 for review). One of the most intriguing issues in this field is whether the neural structures involved in the comprehension process (i.e., explored during a task involving semantic features of objects) are modality-specific (e.g., auditory input) or plurimodal (Hickok, 2012; Patterson, Nestor, & Rogers, 2007).

During the removal of brain tumours that lie close to brain regions related to language functions, it is standard clinical practice to wake the patient in order to precisely localize and spare functional areas (Boatman, 2004; Duffau, Gatignol, Moritz-Gasser, & Mandonnet, 2009; Lubrano, Draper, & Roux, 2010; Ojemann, Ojemann, Lettich, & Berger, 1989; Penfield & Robert, 1959; Roux et al., 2004; Roux et al., 2009; Schäffler, Lüders, Dinner, Lesser, & Chelune, 1993). This is achieved using electrostimulation of infra-centimetric portions of the brain while the patient is performing a task relating to the function being studied, e.g., picture naming, auditory and visual comprehension. Stimulation-induced impairment of the ability to perform the task (also named interference) indicates that the area beneath the electrode plays a role in processes involved in this task. Electrostimulation can evaluate inter-subject differences in cortical functional locations, frequent in some primary (Morosan et al., 2001; Uylings, Rajkowska, Sanz-Arigita, Amunts, & Zilles, 2005) or heteromodal areas of the human brain (Allen, Erhardt, Wei, Eichele, & Calhoun, 2012; Caspers et al., 2006; Penfield & Robert, 1959; Roux et al., 2009; Simos, Breier, Fletcher, Foorman, & Castillo, 2002; Uylings et al., 2005). Technical factors, such as the limitation of stimulation to gyral structures, the influence of epileptic activity, the level of stimulation (Lesser et al., 1986), and also the influence of some slow-growing tumours on the spatial reorganization of functional cortical representation, could account for cross-subject inconsistency (Lubrano et al., 2010). But the main advantages of this brain mapping technique are its high level of accuracy, its simplicity for trained teams and the absence of adverse affects for the patient (Lesser et al., 1986; Ojemann et al., 1989). Here, cortical electrostimulation was used to study the anatomical bases of the process of word comprehension in 90 patients who were operated on for various lesions in the left or the right cerebral hemisphere and to evaluate the existence of segregated speech comprehension pathways according to the above mentioned dorsal/ventral dichotomic organization in the superior temporal gyrus. In addition, we addressed the existence of common cortical territories for auditory and visual comprehension, as well as naming that would tend to confirm the hypothesis of a neural population supporting an amodal semantic system in this brain region.

2. Material and methods

2.1. Patients

The study involved 90 patients with the following inclusion criteria: 1) tumour resection with electrostimulation mapping, 2) no or minor language deficit pre-operatively. All patients underwent “awake surgery” (Roux et al., 2004) combining some comprehension tasks and naming, in order to directly map functional language areas. All patients and their families gave their informed consent to the study of their language areas by direct brain mapping. The consultative committee of INSERM (French national institute of health and medical research) gave its approval for the storage of patients' data and preservation of their anonymity. Data from successive brain mappings were prospectively collected throughout the 6 years of the study (January 2007–January 2013). When 90 patients had been included, the study was closed and the data analysed. All patients underwent an assessment of handedness (Oldfield, 1971) and completed the following standardized preoperative language tests: visual naming (Deloche & Hannequin, 1997), written, auditory and visual comprehension abilities, oral fluency, reading, dictation, repetition, written transcription, and object handling (Nespoulous, Joanette, & Lecours, 1992).

2.2. Tasks used

1) Auditory word–picture matching task

Items from a standardized test (Snodgrass & Vanderwart, 1980) were used for all patients. Stimuli consisted of sets of 4 line drawings of various objects with no direct relation between them; the French words corresponding to each object were clearly distinct from one another in phonological terms (Fig. 1a). Stimuli in each 4-image set were also selected so as to minimize familiarity differences among images according to the familiarity values provided by the Snodgrass and

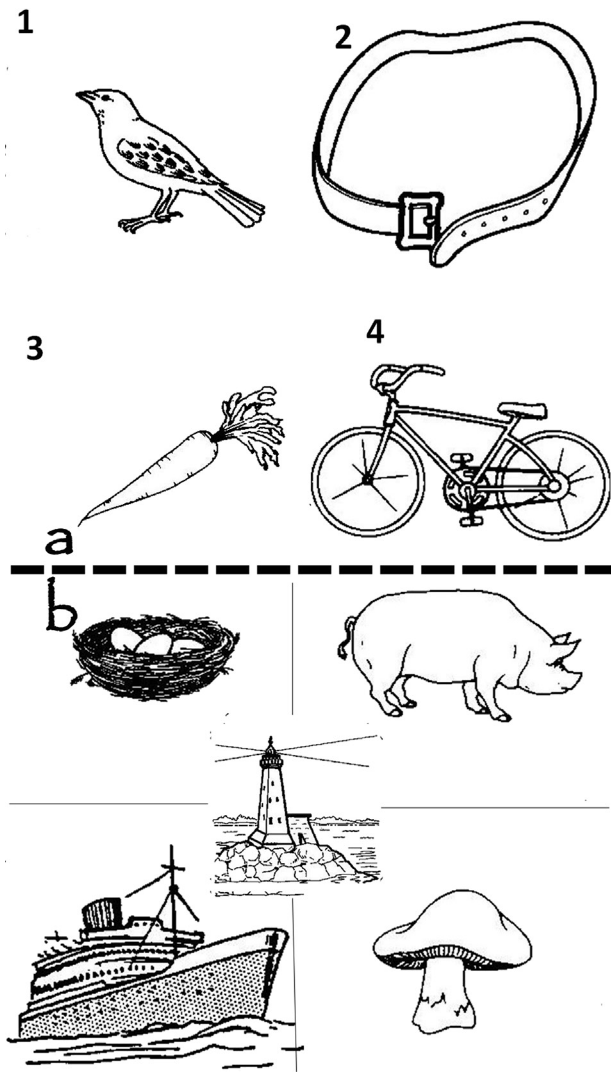

Fig. 1 – Examples of auditory (upper image) and visual (lower image) comprehension tasks used in this study. In the auditory comprehension task (1a), the patient had to match the auditorily perceived word with the correct visually presented picture among 4. Our auditory comprehension task focused on the word level of speech comprehension; the carrier sentence was always the same "where is the…?" For instance, in this figure, where is the belt? The patient had to answer "in 2". Stimulation was applied to the cortex 2 sec before the question. In the visual comprehension task (1b), stimulation was applied and, 2 sec later, a panel was shown to patients. No auditory instruction was given. They had to associate the central item with the directly related one among the other 4 by pointing to the two related items with one finger (here the lighthouse to the boat).

Vanderwart test. For instance, the mean familiarity of the 4 stimuli of the auditory comprehension set number 2 (*bed, bus, book, bread*) varied from 4.40 to 4.75 (standard deviation, .16). As shown in Appendix 1, the standard deviation of the familiarity of the 4 items of each set ranged from .09 to .42.

2) Visual naming task

During the naming procedure, a set of pictures from the Snodgrass test were randomly selected and the stimulation was applied just before the image was displayed. Stimuli were chosen for their high familiarity, with a mean familiarity above 2 according to the Snodgrass and Vanderwart test (Appendix 2). We refined this brain mapping set over more than 10 years, presenting only highly familiar stimuli to patients (Roux et al., 2004).

3) The visual two-picture matching task (Fig. 1b)

This visual comprehension task was derived from items of the Snodgrass test. It involved a centrally presented object picture that was to be matched by pointing to one of 4 peripherally depicted pictures in a given set of stimuli.

4) Abridged version of Token test

Ten patients took a more complex auditory comprehension task with two-step verbal directions from the "Token test" (identified by 3 parameters: colour, shape, size). This test contains drawings of squares and circles, large and small, of 5 different colours. For instance, for each stimulation patients were asked to choose the "small blue square" and the "large red round" (two-step verbal directions) and so on with different instructions. They had to point to the appropriate tokens with one finger.

5) Finally, in 5 patients, a *sound recognition* (or *auditory object naming*) *task* was also used. Patients had to listen to some selected sounds (for instance, horse whinnying, sheep grazing, doorbell ringing, or engine starting-up) from a sound library (Sound library, www.naïve.fr), recognize them and name them.

All patients were given auditory word–picture and visual naming tasks (see Table 1). Many of them also had a visual two-picture matching task. As the brain mapping procedure could be constrained by clinical requirements, the Token test and sound recognition tasks were used for some selected patients.

2.3. *Brain mapping procedure*

The level of electrostimulation was kept below that expected to cause electrical diffusion and afterdischarges to ensure that the stimulated area remained accurately localized in 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 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 in 1-mA steps. 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). The

Table 1 – Tasks administered in our group of 90 patients.

90 patients studied (87 right-handed) – 47 women, 43 men		
From 18 to 74 years old (mean: 48 years old – Standard Deviation: 10.4)		
77 left and 13 right hemispheres studied		
Auditory WORD–PICTURE MATCHING task AND NAMING in 90 patients		
In 75 patients (3 left-handed) – 62 left hemispheres, 13 right	In 10 right handed patients – 10 left hemispheres	In 5 right-handed patients – 5 left hemispheres
Visual comprehension task added	**Visual comprehension task, AND Token test added**	**Sound recognition task added**

intensity of stimulation varied from 4.0 to 12.0 mA in all patients (mean: 6.97 mA; standard deviation: 2.20).

All patients were tested at the same site for visual naming and other comprehension tasks. Before starting a direct cortical stimulation procedure, we chose a substantial number of sites on the brain surface. We kept the same areas and intensity of stimulation during the whole procedure of stimulation to test naming and comprehension. The number of stimulation sites varied from one patient to another depending on the size and location of the craniotomy.

When a functional site was found, it was marked by a sterile ticket of .25 cm^2, and then another area, 5 mm away, was tested. Direct brain mapping with the different tasks (naming and comprehension tasks) was usually completed in less than 25 min. Intra-operative photographs of the brain were taken, showing the sites validated according to this procedure. During the study, all data regarding brain mapping results were stored in an Excel database.

We classified the "visual naming interferences" found during the naming task as: 1) global behaviour arrest (patient stopped talking during stimulation); 2) anomia (patient said "yes, I know…yes…I know but I can't find the word…" and, as soon as stimulation was stopped, the target word was produced); 3) phonological interference (the target word seemed to be identified but was not correctly pronounced; for instance during stimulation one patient said "*c'est un arfitoqueur*" when the target was "*artichaut*" – artichoke); 4) semantic interference (the target word was not identified; patients showed verbal paraphasia suggesting semantic errors; for instance, one patient said "this is a banana" when a car was presented); 5) various other interferences were classified as "hesitation" (i.e., upon stimulation, patients did not produce the correct response at once, hesitated, and were not sure of their final response).

2.4. *Validation criteria of stimulation-interferences*

We included only reproducible and clear brain mapping data in the study. For the purpose of this study on speech comprehension function, only those sites provoking comprehension interferences (either isolated or associated with visual naming interferences) were considered. Our reproducibility criterion was 3/3. When a site had a reproducibility of 2/3 we stimulated it at least one more time: we validated reproducibility criteria of 3/4 (or 4/5) but *not* 2/4 or 3/5. For each task, at least 3 trials were performed on positive sites. When no interference was initially detected in a site, we only performed one other stimulation; if this stimulation was not positive, the site was considered as a null site for the task performed. Isolated visual naming interferences are not reported. No initial (i.e., pre-operative) instruction was given to the patients to report unintelligibility but the patients were systematically debriefed during the operation when they made comprehension errors.

During the electrostimulation process, items for which motor hand contractions or ocular movements could account for the observed comprehension disturbances were excluded from the results.

Strict criteria were applied to define language interference sites and are summarized in the following points:

1) To be accepted as a comprehension or naming interference, the interferences that we localized were tested at least three times. Non-reproducible interferences were not included in the study.
2) Because they can be considered as non-specific, the language interferences found in the pre- and postcentral gyrus (considered as language interferences due to blockade of articulatory mechanisms) were not included in the final analysis.
3) Finally, it must be emphasized that we qualified a site as specific to auditory comprehension when no interference in object naming or visual interference was found at that site. However we cannot completely exclude the possibility that other functions, not tested in this study, could be hampered by stimulation in our comprehension sites. Here specificity does not refer to the specificity of semantic processing but rather to the mere distinction between sites in which either auditory comprehension only or both auditory and visual modality of language input are affected by stimulation. The specificity does not address issues on "deep" semantic processing but only the effect of sensory-modality effect.

2.5. *Statistical analysis*

As the terms "Broca's" or "Wernicke's" regions were imprecise and not very informative, we decided to perform statistical analysis to define regions by using the gyral/sulcal anatomy. For instance, the supramarginal gyrus was considered as a region, as was the angular gyrus. Large gyri, such as the temporal gyri, for example, were arbitrarily divided into three segments by drawing an imaginary line extending the pre- and post-central sulci (see Appendix 3). Comparisons between regions were performed using this scheme. For each region, both the total number of stimulation sites and those leading to interferences in auditory and/or visual comprehension were counted, in order to compute the frequencies of auditory and visual interferences. For the statistical analysis, these regions were classified into four groups: two groups corresponding to the ventral (left superior temporal gyrus) and dorsal (left supramarginal and angular gyri) pathways, and two control groups in the frontal (left middle and superior frontal gyri) and temporal (left middle temporal gyrus) cortices. Pairwise comparisons of the auditory/visual interference frequencies across the four groups were achieved by using X^2 (chi-squared) statistics, with a threshold set at $p < .05$.

3. Results

Overall, 2754 cortical sites were stimulated in 90 patients (range, 10–68 sites per case; mean, 30.60 sites per mapping; SD: 12.18; see Fig. 2a). In a given cortical site, electrostimulation provoked either interferences affecting auditory comprehension only, or combined interferences with other tasks used (Appendix 4). We found 92 auditory comprehension interference areas in 49 patients (54%) – from 0 to 5 interferences – mean: 1.87 per patient- and no auditory comprehension interference in the other 41 patients. More specifically, electrostimulation included the left posterior temporal gyrus in a total 41 patients and at least one auditory comprehension interference was detected in 30 of them (73%).

In 32 of these cortical sites, stimulation impaired auditory and visual comprehension, and visual naming (global interference for the 3 tasks). Stimulation impaired only auditory comprehension and visual naming (no visual comprehension interference) at 48 other cortical sites. At 6 cortical sites (5 patients), auditory interferences were isolated, with neither visual comprehension nor visual naming interferences. Finally, in 6 other cortical sites, stimulation impaired auditory comprehension, and visual and auditory naming (sound recognition). All these comprehension interferences detected were located in discrete, sub-centimetre cortical sites. Each interference area was localized in an area 5 mm wide with distinct boundaries (See Fig. 2b and c for examples of brain mapping and the extremely localized pattern of these interferences).

Although 2 auditory interferences were detected in the right inferior frontal lobe in two left-handed patients, no auditory or visual comprehension interference was detected in the right hemispheres of any of our 10 right-handed patients. Overall, fewer auditory comprehension sites than visual naming interference sites were found (92 *vs* 203). Furthermore, most of the auditory comprehension sites (86 out of 92–93%) were also visual naming sites.

3.1. *The two types of interference affecting auditory comprehension*

Two different types of verbal auditory comprehension disorders were detected during electrostimulation depending on whether patients were aware of their comprehension deficit or not (detailed in Fig. 3a):

- In the *first type* of interference, patients were aware that they failed to understand the auditorily presented question (e.g., the patient said: "I don't understand your question?!" or "please repeat the sentence"). Patients perceived that someone was speaking (they did not complain of sudden hearing loss) but they complained about the intelligibility of the sentence or the instruction they were to follow. Once stimulation was stopped and the question was repeated, patients addressed the task correctly after a few seconds. These interferences mimicking "word deafness" were called "speech discrimination" interference. We noticed visually that some points were gathered or occurred closely together (each point separated from the following one by a distance of less than 3 mm on the Y axis). Such interferences found at 23 cortical sites formed two clusters (two regions where these points were gathered, with a gap of 8 mm between the two regions with no positive point), located rostrally and caudally along the superior temporal gyrus. The centre of mass or barycentric coordinates [$X = -61.4$; $Y = -23.9$; $Z = 6.7$] of the anterior cluster (16 areas) was located in the superior temporal gyrus (BA42), rostrally and laterally to Heschl's gyrus. The centre of mass or barycentric coordinates [$X = -60.0$; $Y = -42.2$; $Z = 10.2$] of the posterior cluster (7 areas) was located in the superior temporal gyrus (BA22), slightly ventrally and laterally to the planum temporale.
- *In the second type* of interference, patients were *not* aware of their mistakes (i.e., repeated errors on identifying the image corresponding to the auditorily presented word). This type of interference was observed at 53 cortical sites and was clearly related to disorders of lexical-semantic processes involved in matching a picture to the auditory word form. The patient was able to speak and understood that (s)he was asked to point to an object that would match a heard stimulus; the patient did not complain of difficulties in perceiving the auditory instruction. However, he/she did not perform the task accurately. As before, when stimulation was removed and the question was repeated, patients performed correctly after a few seconds. These lexical semantic interferences were mostly localized in territories farther away from Heschl's gyrus than the locations observed in the first type of interference, either rostrally in the superior temporal gyrus or caudally in the supramarginal or posterior middle temporal gyri.

Yet another, more massive, type of disorder, which we termed global behaviour arrest, was observed. In this case, although awake, the patient neither performed the comprehension task nor reacted by any means, either verbally or with a motor response. In these cases, observed at 16 additional sites (localized in the same regions), patients were apparently not aware of their global behaviour arrest, although positive evidence is lacking. As mentioned above, once stimulation was removed, the patients performed correctly after a few seconds.

Interferences observed during the "Token test" verbal comprehension task (Appendix 5) and the sound recognition test (Appendix 6) were similar to those observed in the standard auditory comprehension task: in some areas, patients acknowledged they were unable to understand the auditorily presented question or sound; in other stimulated areas, the patient did not complain of difficulties in perceiving the auditory instruction but did not perform the task accurately (see Fig. 3b and c for details).

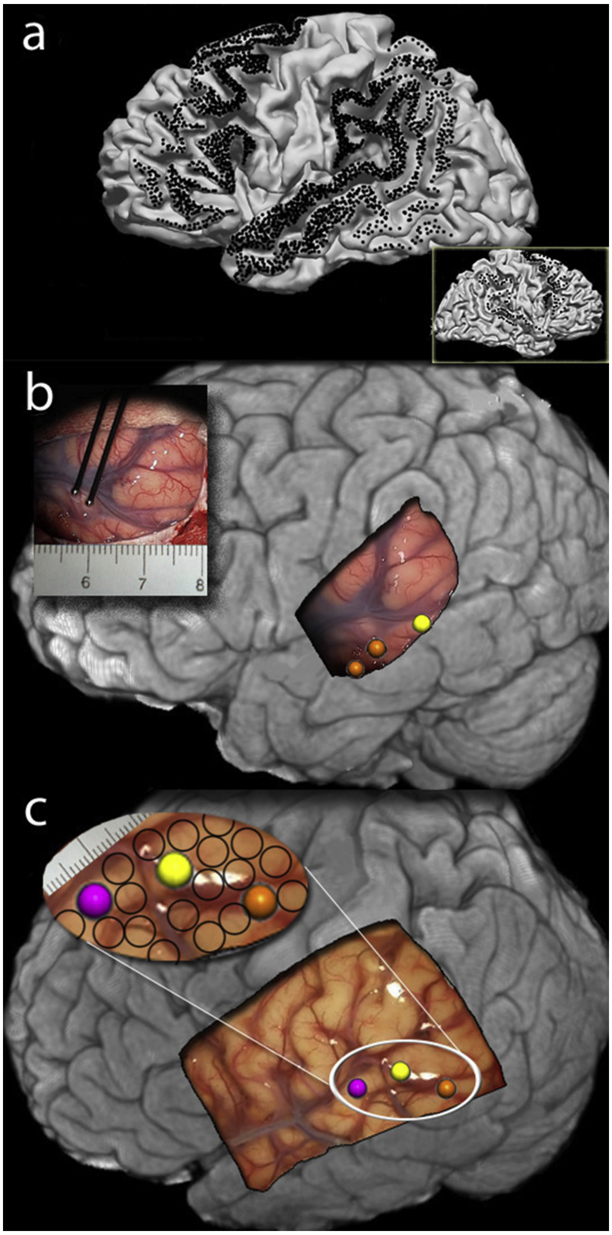

Fig. 2 – Regions of the brain stimulated and examples of auditory comprehension interferences from two direct brain mapping procedures in 2 patients: 2a Scheme of the regions of the left hemisphere stimulated and localized using the system described in Appendix 3 with stimulation points overlaid on a standard brain 3D. All frontal and temporo-parietal left hemispheric regions of the convexity were studied (contrary to inferior temporal, interhemispheric cortical regions that are not easily accessible by direct electrostimulation). In right hemispheres (small box), brain mapping focused on inferior frontal, superior temporal and supramarginal gyri. Pre- and postcentral gyri were not tested with speech comprehension tasks. 2b operative pictures superimposed onto 3D reconstructions of the patients' brains. The picture shows the level of accuracy that can be obtained with electrostimulation (5 mm distance between the 2 stimulating probes). The interference sites were discretely located in small sites of the cortex and had distinct boundaries, so a small displacement of the electrode into an adjacent cortical area located 5 mm away in the same gyrus made the interference disappear. This patient had 3 auditory comprehension interferences in the superior temporal gyrus, one leading to an impossibility to understand the question (yellow dot) and two where the patient made errors in pointing to the required item (lexical-semantic error – orange dots). 2c picture showing the number of stimulations (black circles: no comprehension interference detected) performed in one region. In this case, the patient had 3 comprehension interferences: a discrimination (yellow dot), a complete behaviour arrest (purple dot), and a lexical-semantic (orange dot) interference.

3.2. *Visual comprehension type of interference*

Visual comprehension interference areas were detected in 21 patients, and less frequently than auditory interferences, i.e., 32 times (from 0 to 3 interferences – mean: 1.5 interference per patient). They were all combined with auditory comprehension and visual naming interferences (see localization in Fig. 3d). Overall, either patients were unable to perform the visual matching task correctly (8 interferences), or they had global behaviour arrests with no specific performance during the task (24 interferences).

3.3. *Visual naming with auditory comprehension interferences*

Overall, 203 visual naming interferences were found in 71 patients. They included 52 areas of global behaviour arrest, 56 areas of anomia, 30 semantic errors, 24 phonological errors, and 41 hesitation interferences. Although it was not always clear-cut in all interferences, in most cases of global behaviour arrest, or semantic and phonological errors, patients were not conscious of their errors and, when stimulation was stopped, they resumed the task without notifying that they had made errors during it. In cases of anomia, patients were mostly aware of their difficulties in finding the target word.

Over these 56 anomia and 30 semantic sites detected during visual naming tasks, 21 were associated with lexical semantic auditory comprehension interferences (patient made errors pointing to the designated item) during speech comprehension tasks. These joint interferences, probably affecting lexical semantic processes in both speech production and comprehension, classified as *central lexical* semantic, were mainly located in the anterior part of the superior temporal gyrus (see Fig. 4 and Appendix 7). Other anomia or semantic interferences during visual naming tasks (65 areas) were isolated in sites that elicited either no comprehension interferences at all, or gave rise to various non-semantic comprehension interferences.

Overall, 24 cortical sites eliciting phonological naming were detected. Among these 24 sites, 6 were associated with lexical semantic auditory comprehension interferences (errors when designating the required item – for instance mistaking the “belt” for the “carrot”); all these areas were

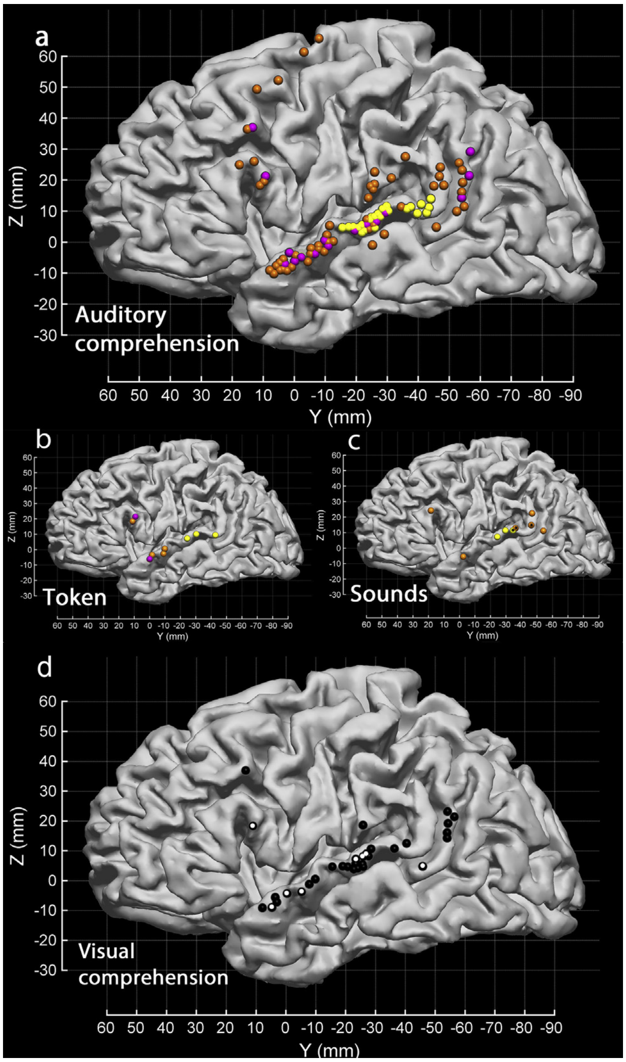

Fig. 3 – Localization of the types of verbal auditory comprehension, Token test, auditory object (sound recognition) naming, and visual comprehension interferences. Each patient had her/his 3D brain volume normalized in the Talairach space and parameters were used to obtain normalized coordinates from stimulation site locations which were per-operatively visualized and positioned on 3D original images provided by neuronavigation software (Medtronic®). The structural scans of all the patients were normalized into MNI space by using SPM8 and its standard T1 template (ICBM152). MNI coordinates were converted to Talairach coordinates by using a non-linear transform implemented in the mni2tal.m function by Mathew Brett (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach). In 3a, yellow dots represent sites where patients did not understand the question (verbal auditory discrimination impaired). They are divided into two clusters in the posterior part of the left superior temporal gyrus. At this stage, patients were conscious of their errors. Further, in orange dots (lexical-semantic interference areas: for example, when asked to show a belt the patient verbally designated the bicycle) or in purple dots (complete speech comprehension arrest: once stimulation was applied, the patient did nothing) patients were not conscious of their comprehension difficulties. Two left-handed patients who had their right hemispheres studied were found to have auditory comprehension interferences shown in this figure on the left hemisphere. Compared to the left middle and superior frontal gyri, the left superior temporal ($X^2 = 31.9$, $p < 10^5$), and the left supramarginal and angular gyri ($X^2 = 7.2$, $p < 10^{-2}$) were significantly involved in auditory comprehension tasks. Similar significant results were also obtained when comparing these two regions to the left middle temporal gyrus. In 3b, Token test interference areas were found 9 times in 7 patients of the 10 tested (the same colour scheme was used). No specific area was detected for the Token task. In 3c, nine auditory object recognition interferences were found in the 5 patients tested. Patients were not able to discriminate any sound at the yellow dots (Patients said: "I really don't know; I hear something but I can't say what it is"). Stimulation at this stage did not impair consciousness; patients knew they were unable to identify the sound. Patients also made lexical-semantic errors (orange dots) outside the posterior superior temporal region (hearing a sheep grazing the patient said "it is a door bell"). These mistakes were not conscious. Three dissociated sound/verbal recognition interferences were found (marked with "*") in 3 different patients: stimulation of these areas induced errors only in sound recognition and not in verbal recognition. Lesion studies also suggest that neural substrates for environmental sound and spoken language could be partially separable at some level (Saygin, Dick, Wilson, Dronkers, & Bates, 2003; Vignolo, 2003), though closely linked to one another (Cummings et al., 2006; Lewis et al., 2004; Saygin et al., 2003). In 3d, localization of the visual comprehension interferences detected (black dots: global behavioural arrest; white and black dots: incorrect visual matching); all 32 areas were combined with naming and auditory comprehension interferences and mainly located in the superior temporal gyrus. Compared to the left middle and superior frontal gyri, the left superior temporal ($X^2 = 78.4$, $p < 10^{-5}$), and supramarginal and angular gyri ($X^2 = 18.1$, $p < 10^{-4}$) were significantly involved in visual comprehension tasks. Similar significant results were also obtained when comparing these two regions to the left middle temporal gyri.

located in the inferior part of the supramarginal gyrus. The other 18 sites were isolated, without comprehension interference, and were located in the upper part of the supramarginal gyrus or in the middle part of the superior temporal gyrus.

3.4. *Clinical viewpoint*

The possibility of exploring speech comprehension interference might seem appealing, especially for surgery focused in posterior temporal areas. However, adding an auditory comprehension task to a standard visual naming task was not decisive; only 6 specific auditory comprehension areas were isolated. In 93% of cases (86 areas out of 92), a visual naming

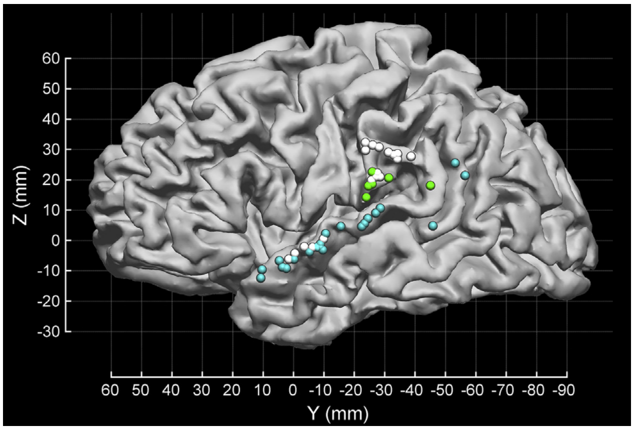

Fig. 4 – Dissociation of the naming process regarding the response to the auditory comprehension tasks. Positioned on a 3D brain volume normalized in the Talairach space, 1) blue dots represent cortical areas associating semantic naming or typical anomia interferences with lexical-semantic interferences during auditory comprehension tasks, 2) green dots represent phonological interferences during naming tasks associated with lexical-semantic auditory comprehension interference, and 3) white dots represent the areas of phonological interference during naming tasks without any impairment of the auditory comprehension tasks (see coordinates of all these points in Appendix 7). Anatomical segregation of naming process was detected between the superior temporal gyrus (mainly involved in the lexical semantic naming process) and the supramarginal gyrus (involved in the phonological part of the naming process).

task would have been sufficient to detect language areas. The vertical projection of the sylvian ramus segregating the pars opercularis and the pars triangularis on the superior temporal gyrus corresponded to the most rostral area ($y = +10$) involved in comprehension of auditory and visual words in this study. This would represent the anterior limit of the territory of the superior temporal gyrus that needs to be spared during surgery so as to avoid speech comprehension deficits.

4. Discussion

We found that the process of auditory comprehension involved a few, fine-grained, sub-centimetre cortical territories mainly centred along the left superior temporal gyrus with some individual variability. Areas involved in auditory comprehension were organized hierarchically, from areas related to mere auditory discrimination to regions supporting higher level processes. The latter involved two discrete regions: one located along the anterior part of the left superior temporal gyrus and the other in the left supramarginal gyrus. These anatomical findings are in line with those described in dual stream models of language comprehension processing (DeWitt & Rauschecker, 2013; Friederici, 2011; Hickok & Poeppel, 2007; Rauschecker, 2011) and those demonstrating an extremely localized cortical representation of speech comprehension processing in the superior temporal gyrus (Chang et al., 2010). We found that, while generally involved in auditory comprehension, some territories in the superior temporal cortex harboured neural populations supporting a heteromodal, possibly amodal, semantic system as stimulation of the same territory could result in comprehension errors relating to either auditory or visual stimuli. This multimodal comprehension organization has also been detected in the fusiform gyrus in other studies, where stimulation of the “basal temporal language area” resulted in global language dysfunction in the visual and auditory realms (Mani et al., 2008; Trébuchon-Da Fonseca et al., 2009). In addition, cortical stimulation could induce 2 distinct speech comprehension disturbances. In some cases, patients complained of word deafness and this functional deficit most likely corresponded to the activity of the attention-based feedback system that monitors lower levels of speech representation (Hickok, 2012). These results may also be interpreted as disruption of the hierarchical feed-forward processing network postulated to subserve auditory word-form recognition (DeWitt & Rauschecker, 2012). In other cases, electrical stimulation of either the anterior part of the left superior temporal gyrus or more posterior temporal territories resulted in lexical semantic errors that participants were not aware of. By combining visual naming and comprehension tasks, we showed that naming-related territories could be anatomically separated into two different types, a superior, temporal territory and an inferior, parietal territory, respectively affecting lexical-semantic and phonological processes.

4.1. *Speech discrimination level*

As shown in many studies (Johnsrude, Giraud, & Frackowiak, 2002; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Price, 2012), Heschl's gyrus is activated indifferently by all types of sound i.e. the earliest, pre-phonological, steps of speech signal processing (Scott & Wise, 2004). As the present study did not assess discrimination ability for simple acoustic features, our first type of interferences, mimicking “word deafness”, which we called “speech discrimination” interferences, may have arisen from disruption of object recognition processing at any stage between acoustic-phonetic feature recognition and word-form recognition. It is worth noting that no speech discrimination deficit (at least for the tasks we used) was detected in our patients during stimulation of right temporal cortex, implying a further leftward lateralization of speech analysis. After activation of the Heschl's gyri, the following processing of auditory phonological structures could be performed in two adjacent left regions, i.e., the antero-lateral Heschl's gyrus in the planum polare (Ahveninen et al., 2006; Obleser, Zimmermann, Van Meter, & Rauschecker, 2007) or the planum temporale and posterior superior temporal gyrus (Dehaene-Lambertz et al., 2005). Short range fibres would connect the primary auditory cortex in Heschl's gyrus to these areas specialized for speech discrimination, and located laterally slightly anterior or posterior to it (Upadhyay et al., 2008). The region anterior and lateral to Heschl's gyrus corresponds to the phoneme decoding step of auditory comprehension (Démonet et al., 1992) and has been considered as the "word form" phonological decoding region (Cohen, Jobert, Le Bihan, & Dehaene, 2004; DeWitt & Rauschecker, 2012).

The two discrete regions involved in auditory word discrimination that we found in the left posterior temporal gyrus matched the data of these studies. Rather constant in localization, they are similar to the two-syllable discrimination areas located in the left posterior superior temporal gyrus described by Miglioretti and Boatman using electrostimulation in 13 patients (Miglioretti & Boatman, 2003). Convergent results have been reported by other electrostimulation, electrocorticographic, and functional imaging studies (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Boatman, 2004; Just et al., 1996; Matsumoto et al., 2011; Rapp & Dufor, 2011). Electrocorticographic recordings showed that the left posterior superior temporal gyrus was a site in which speech sound encoding involved integration from the acoustic signal to a higher order phonetic level (Chang et al., 2010; Edwards et al., 2009). The two regions we detected could correspond to the pathway stem from which the two above-mentioned auditory comprehension pathways diverge (Ahveninen, 2006).

4.2. Word auditory lexical-semantic comprehension level

Anatomically, neural territories associated with this lexical-semantic processing stage were not sharply localized in precise cortical zones. They were distributed mainly along the middle part of the left superior temporal gyrus, or more scattered around the supramarginal gyrus and posterior part of the middle temporal gyrus, and were assumed to involve short range fibres to transfer neural impulses between them (Brugge, Volkov, Garell, Reale, & Howard 3rd, 2003). As in 2 other neurosurgical mapping studies, other temporal gyri were very rarely or never involved in speech comprehension (Boatman, 2004; Creuztfeldt et al., 1989). Although classical studies localized this lexical-semantic process in the posterior temporo-parietal region (Geschwind, 1970), some recent studies have pointed out the role of the anterior superior temporal gyrus in the comprehension process. In primates, electrophysiological studies have shown that the supratemporal plane could contain a hierarchically organized auditory processing stream (Bornkessel-Schlesewsky, Schlesewsky, Small, & Rauschecker, 2015; Kaas, Hackett, & Tramo, 1999; Rauschecker & Scott, 2009; Rauschecker, Tian, & Hauser, 1995) with gradually increasing stimulus selectivity (Kikuchi, Horwitz, & Mishkin, 2010). In humans, the anterior superior temporal gyrus is involved in word and sentence-level semantic domains (Rogalsky & Hickok, 2009; Vandenberghe, Nobre, & Price, 2002) with a hierarchical anteriorly-directed decoding gradient (DeWitt & Rauschecker, 2012) from phonemes to words to sentences. In an electrophysiological study, single units were found to respond to word and sentence decoding in the middle to anterior part of the superior temporal gyrus (Creutzfeldt et al., 1989). Brain activation studies reported similar auditory word form decoding in this region (Dehaene-Lambertz et al., 2006). Our findings suggest that stimulation in the anterior superior temporal, supramarginal, and posterior middle temporal gyri impaired the core semantic system associated with words rather than impairing access from auditory pathways.

4.3. Speech feedback control

Within this speech comprehension pathway, electrostimulation experimentally identified the neural system of speech feedback control depending on the presence or absence of involvement of on-line conscious attentional control of the phonological representation of perceived words. The stimulation of the 2 posterior temporal regions involved in the processing of the auditory word form provoked an immediate report from the patient that (s)he did not perceive the stimulus correctly and could not reproduce it orally. Long described in neuro-functional models of speech, this feedback control of speech (Chang, Niziolek, Knight, Nagarajan, & Houde, 2013) has been demonstrated at the phonological level but seems absent at the lexical conceptual level (Hickok, 2012). Along the anterior superior temporal and supramarginal gyri, stimulation resulted in comprehension errors but not in any complaint from the patient about misperception of the auditory stimuli. During electrostimulation of the lexical conceptual system (located downstream in the speech analysis process), the forms of the words were perceived as correct (due to the previous phonological feedback control) but, when participants pointed to wrong items during stimulation, they failed to report an erroneous association between correctly perceived word forms and unrelated concepts. In other words, electrostimulation of these regions may not distort the acoustic/phonological representations of words heard whereas the lexical semantic processing of these phonologically correct traces is deeply affected. This led to erroneous responses that proved to be beyond the participant's conscious speech control. These symptoms, which we have already described in a previous work on the neural processes of word writing under dictation (Roux et al., 2014), mimic word deafness or auditory verbal agnosia symptoms (Buchman et al., 1986; Kirshner, Webb, & Duncan, 1981; Slevc, Martin, Hamilton, & Joanisse, 2011). Word deafness symptoms could thus be related to a lesion critically located in these "auditory speech discrimination" areas of the left superior temporal gyrus. In patients with bilateral damage, this region could be the zone of convergence of the commissural projections of the left and right auditory cortex (Lee, 2013).

4.4. Visual word naming and comprehension

Errors in speech comprehension tasks were observed in an auditory word – picture matching task. In addition, these interference sites were also eloquent for picture naming tasks. Many studies have shown that the naming process is deeply linked to the comprehension process (Hillis & Caramazza, 1991). Combining visual naming and auditory comprehension interferences, we hypothesized that naming troubles observed in patients with brain lesions could be due to: 1) a difficulty in accessing the central semantic representation (Hillis, Rapp, Romani, & Caramazza, 1990) of the presented item (common anomia and lexical-semantic comprehension interferences) along the anterior part of the superior temporal gyrus (amodal semantic neurons); 2) a perturbation of the phonological output lexicon (phonological anomia and auditory comprehension interferences) along the supramarginal gyrus. Electrostimulation of some areas in this gyrus showed that phonological lexical representations could also be affected in isolation, without semantic interferences, as already suggested in previous studies focusing not on auditory tasks but on word reading (Roux et al., 2012; Simos et al., 2002). In the naming process, this region would harbour the neural populations that support the phonological output component of naming, just upstream of the involvement of the articulatory functional areas in the Rolandic region needed to pronounce the target word.

In conclusion, these findings are in line with the current conceptualizations of the neural correlates of speech comprehension. However, the direct cortical stimulation method also demonstrates a large amount of variability among participants, possibly linked to the underlying effects of brain pathology, which may distort cortical representations of language processes, but possibly also related to individual variations, especially for the higher level representations such as territories supporting lexical semantic processes.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2015.07.001.

REFERENCES

Ahveninen, J., Jääskeläinen, I. P., Raij, T., Bonmassar, G., Devore, S., Hämäläinen, M., et al. (2006 Sep 26). Task-modulated "what" and "where" pathways in human auditory cortex. *Proceedings of the National Academy of Sciences of the United States of America, 103*(39), 14608–14613.

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.

Belin, P., Zatorre, R. J., Lafaille, P., Ahad, P., & Pike, B. (2000). Voice-selective areas in human auditory cortex. *Nature, 403*, 309–312.

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, J. R., 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.

Bornkessel-Schlesewsky, I., Schlesewsky, M., Small, S. L., & Rauschecker, J. P. (2015). Neurobiological roots of language in primate audition: common computational properties. *Trends in Cognitive Sciences, 19*(3), 142–150.

Brugge, J. F., Volkov, I. O., Garell, P. C., Reale, R. A., & Howard, M. A., 3rd (2003). Functional connections between auditory cortex on Heschl's gyrus and on the lateral superior temporal gyrus in humans. *Journal of Neurophysiology, 90*, 3750–3763.

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.

Chang, E. F., Niziolek, C. A., Knight, R. T., Nagarajan, S. S., & Houde, J. F. (2013). Human cortical sensorimotor network underlying feedback control of vocal pitch. *Proceedings of the National Academy of Sciences of the United States of America, 110*, 2653–2658.

Chang, E. F., Rieger, J. W., Johnson, K., Berger, M. S., Barbaro, N. M., & Knight, R. T. (2010). Categorical speech representation in human superior temporal gyrus. *Nature Neuroscience, 13*, 1428–1432.

Cohen, L., Jobert, A., Le Bihan, D., & Dehaene, S. (2004). Distinct unimodal and multimodal regions for word processing in the left temporal cortex. *NeuroImage, 23*, 1256–1270.

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.

Cummings, A., Ceponiene, R., Koyama, A., Saygin, A. P., Townsend, J., & Dick, F. (2006). Auditory semantic networks for words and natural sounds. *Brain Research, 1115*, 92–107.

Dehaene-Lambertz, G., Dehaene, S., Anton, J. L., Campagne, A., Ciuciu, P., Dehaene, G. P., et al. (2006). Functional segregation of cortical language areas by sentence repetition. *Human Brain Mapping, 27*, 360–371.

Dehaene-Lambertz, G., Pallier, C., Serniclaes, W., Sprenger-Charolles, L., Jobert, A., & Dehaene, S. (2005). Neural correlates of switching from auditory to speech perception. *NeuroImage, 24*, 21–33.

Deloche, G. H., & Hannequin, D. (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. *Proceedings of the National Academy of Sciences of the United States of America*, E505–E514.

DeWitt, I., & Rauschecker, J. P. (2013 Nov). Wernicke's area revisited: parallel streams and word processing. *Brain and Language, 127*(2), 181–191.

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.

Duffau, H., Gatignol, P., Moritz-Gasser, S., & Mandonnet, E. (2009). Is the left uncinate fasciculus essential for language? A cerebral stimulation study. *Journal of Neurology, 256*, 382–389.

Edwards, E., Soltani, M., Kim, W., Dalal, S. S., Nagarajan, S. S., Berger, M. S., et al. (2009). Comparison of time-frequency responses and the event-related potential to auditory speech stimuli in human cortex. *Journal of Neurophysiology, 102*, 377–386.

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.

Geschwind, N. (1970). The organization of language and the brain. *Science, 170*, 940–944.

Hickok, G. (2012). Computational neuroanatomy of speech production. *Nature Reviews Neuroscience, 13*, 135–145.

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

Hillis, A. E., & Caramazza, A. (1991). Category-specific naming and comprehension impairment: a double dissociation. *Brain, 114*, 2081–2094.

Hillis, A. E., Rapp, B., Romani, C., & Caramazza, A. (1990). Selective impairment of semantics in lexical processing. *Cognitive Neuropsychology, 7*, 191–243.

Johnsrude, I. S., Giraud, A. L., & Frackowiak, R. S. (2002). Functional imaging of the auditory system: the use of positron emission tomography. *Audiology and Neuro-otology, 7*, 251–276.
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.
Kaas, J. H., Hackett, T. A., & Tramo, M. J. (1999). Auditory processing in primate cerebral cortex. *Current Opinion in Neurobiology, 9*, 164–170.
Kikuchi, Y., Horwitz, B., & Mishkin, M. (2010). Hierarchical auditory processing directed rostrally along the monkey's supratemporal plane. *Journal of Neuroscience, 30*, 13021–13030.
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.
Lee, C. (2013). Thalamic and cortical pathways supporting auditory processing. *Brain and Language, 126*, 22–28.
Lesser, R. P., Lüders, H., Morris, H. H., Dinner, D. S., Klem, G., Hahn, J., et al. (1986). Electrical stimulation of Wernicke's area interferes with comprehension. *Neurology, 36*, 658–663.
Lewis, J. W., Wightman, F. L., Brefczynski, J. A., Phinney, R. E., Binder, J. R., & DeYoe, E. A. (2004). Human brain regions involved in recognizing environmental sounds. *Cerebral Cortex, 14*, 1008–1021.
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.
Mani, J., Diehl, B., Piao, Z., Schuele, S. S., Lapresto, E., Liu, P., et al. (2008). Evidence for a basal temporal visual language center: cortical stimulation producing pure alexia. *Neurology, 71*, 1621–1627.
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.
Miglioretti, D. L., & Boatman, D. (2003). Modelling variability in cortical representations of human complex sound perception. *Experimental Brain Research, 153*, 382–387.
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. (Eds.). (1992). *L'Ortho-Edition*. Isbergues, France.
Obleser, J., Zimmermann, J., Van Meter, J., & Rauschecker, J. P. (2007). Multiple stages of auditory speech perception reflected in event-related FMRI. *Cerebral Cortex, 17*, 2251–2257.
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.
Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? the representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience, 8*, 976–987.
Penfield, W., & Robert, L. (1959). *Speech and brain mechanisms*. Princeton: Princeton University Press.
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.
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.
Rauschecker, J. P. (1998). Cortical processing of complex sounds. *Current Opinion in Neurobiology, 8*, 516–521.
Rauschecker, J. P. (2011). An expanded role for the dorsal auditory pathway in sensorimotor control and integration. *Hearing Research, 271*, 16–25.
Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: non-human primates illuminate human speech processing. *Nature Neuroscience, 12*, 718–724.
Rauschecker, J. P., Tian, B., & Hauser, M. (1995). Processing of complex sounds in the macaque nonprimary auditory cortex. *Science, 268*, 111–114.
Rogalsky, C., & Hickok, G. (2009). Selective attention to semantic and syntactic features modulates sentence processing networks in anterior temporal cortex. *Cerebral Cortex, 19*, 786–796.
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*, e50665.
Roux, F. E., Durand, J. B., Rehault, E., Planton, S., Draper, L., & Démonet, J. F. (2014). The neural basis for writing from dictation in the temporoparietal cortex. *Cortex, 50*, 64–75.
Roux, F. E., Lubrano, V., Lauwers-Cances, V., Trémoulet, M., Mascott, C. R., & Démonet, J. F. (2004). Intra-operative mapping of cortical areas involved in reading in mono- and bilingual patients. *Brain, 127*, 1796–1810.
Saygin, A. P., Dick, F., Wilson, S. M., Dronkers, N. F., & Bates, E. (2003). Neural resources for processing language and environmental sounds: evidence from aphasia. *Brain, 126*, 928–945. Erratum in: *Brain*, 2003, 126, 1507.
Schäffler, L., Lüders, H. O., Dinner, D. S., Lesser, R. P., & Chelune, G. J. (1993). Comprehension deficits elicited by electrical stimulation of Broca's area. *Brain, 116*, 695–715.
Scott, S. K., & Wise, R. J. S. (2004). The functional neuroanatomy of prelexical processing in speech perception. *Cognition, 92*, 13–45.
Simos, P. G., Breier, J. I., Fletcher, J. M., Foorman, B. R., & Castillo, E. M. (2002). Brain mechanisms for reading words and pseudowords: an integrated approach. *Cerebral Cortex, 12*, 297–305.
Slevc, L. R., Martin, R. C., Hamilton, A. C., & Joanisse, M. F. (2011). Speech perception, rapid temporal processing, and the left hemisphere: a case study of unilateral pure word deafness. *Neuropsychologia, 2011*(49), 216–230.
Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Perception and Performance, 6*, 174–215.
Trébuchon-Da Fonseca, A., Bénar, C. G., Bartoloméi, F., Régis, J., Démonet, J. F., Chauvel, P., et al. (2009). Electrophysiological study of the basal temporal language area: a convergence zone between language perception and production networks. *Clinical Neurophysiology, 120*, 539–550.
Upadhyay, J., Silver, A., Knaus, T. A., Lindgren, K. A., Ducros, M., Kim, D. S., et al. (2008). Effective and structural connectivity in the human auditory cortex. *Journal of Neuroscience, 28*, 3341–3349.
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 (Berl), 210*, 423–431.
Vandenberghe, R., Nobre, A. C., & Price, C. J. (2002). The response of left temporal cortex to sentences. *Journal of Cognitive Neuroscience, 14*, 550–560.
Vignolo, L. A. (2003). Music agnosia and auditory agnosia. Dissociations in stroke patients. *Annals of the New York Academy of Sciences, 999*, 50–57.