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The causal role of right posterior superior temporal sulcus in prosody perception: a combined TMS-fMRI study

Carried out in Otto Hahn Group, Neural Bases of Intonation in Speech and Music
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The causal role of right pSTS in the prosody-associated network

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Abstract

Prosody is a language feature that enables us to express meaningful intentions or emotions by means of vocal tone and rhythm variations. Recent neural models of prosody comprehension proposed that a right hemispheric network is specialized for the processing of linguistic prosody, and that it is divided into two pathways with a common core area: posterior superior temporal sulcus (pSTS). The present study investigated whether right pSTS provides a crucial brain basis for prosody perception, in a paradigm combining fMRI with disruptive inhibitory transcranial magnetic stimulation. 29 participants executed prosody and phoneme categorization tasks in the MRI scanner, after application of TMS to one of three different stimulation sites: right pSTS, left pSTS or vertex. The stimulus material consisted in recordings of single words, morphed along phoneme (between "Bear" and Pear") and prosody (between question/statement) continua. Stimuli were identical for both tasks, individually selected according to each participant's perception and were matched for difficulty. The data show that behavioural performance was not affected by TMS, and that according to the imaging data, no decrease of activation was found in the targeted areas after TMS application. No brain area, except for supplementary motor area, was more strongly activated during prosody than phoneme task execution. However, phoneme task induced stronger activation in frontal areas -superior frontal gyrus and middle frontal gyrus- after left pSTS and vertex stimulation, as well as in right angular gyrus after left pSTS stimulation. While the data do not exclude a role of right pSTS in perception of prosodic stimulus features, that may have cancelled out in the present contrasts, the results call for further pitch-wise analyses in order to distinguish between clear and ambiguous prosody perception. Moreover, the results invite the reflection on improving powerful and reliable TMS protocols to study higher-order cognitive processes.

Abbreviations

RpSTS	Right superior temporal sulcus
LpSTS	Left superior temporal sulcus
V	Vertex site in stimulation condition
R	RpSTS site in stimulation condition
L	LpSTS site in stimulation condition
AG	Angular gyrus
SFG	Superior frontal gyrus
MFG	Medial frontal gyrus
SMA	Supplementary motor area
TMS	Transcranial magnetic stimulation
cTBS	continuous theta burst stimulation
R, L as prefix	right and left hemisphere

Contents

Chapter 1

Introduction

Language is an essential human faculty that enables us to communicate with each other, to exchange information and ideas by way of constructed sentences. Language relies not only on features such as semantics, phonology and syntax in order to convey the meaning of an utterance, but also on the rhythmic and melodic variations of language, called prosody (Frazier, Carlson, & Clifton Jr, 2006). Prosody can carry prominent and subtle information about the speaker's emotional state, through slow modulations of loudness, pitch and duration (Pichon & Kell, 2013; Ethofer, Van De Ville, Scherer, & Vuilleumier, 2009) and is, hence, essential for smooth social interactions. With the same feature variations, prosody can also have linguistic function, e.g. to convey sentence mode (question/statement) through distinct prosodic contours, or to mark word stress. The present study asked how pitch variation - also known as intonation- can affect the perceived meaning of an utterance. The focus of the present study was put on two basic categories of linguistic prosody, which enable speakers to achieve different communicative goals, e.g. naming/declaring (statement) or asking/requesting (question). For the sake of simplicity, intonation and prosody will be use synonymously in the present report.

At the brain level, language processing in terms of perception and production relies on different brain areas interacting with one another in the form of networks (Friederici & Gierhan, 2013; Ross & Monnot, 2008). Core linguistic aptitude is associated with left-hemispheric networks, which have been well studied and characterized (Rauschecker, 2012; Hickok & Poeppel, 2004, 2007). They are composed of both ventral and dorsal white matter pathways, connecting prefrontal regions with temporal language-relevant areas (Friederici & Gierhan, 2013). While the ventral tracts support semantics and basic syntactic processes, the dorsal tracts enable complex syntactic structure building as well as the sensory-motor coupling for speech repetition (Saur et al., 2008; Friederici, 2011). Recently, a network with similar architecture has been identified for the perception of linguistic prosody, but with rightward asymmetry (Sammler, Grosbras, Anwander, Bestelmeyer, & Belin, 2015). This right hemispheric lateralization of prosody processing is also supported by studies which investigated emotional prosody perception (Frühholz, Ceravolo, & Grandjean, 2011). *Sammler et al. (2015)* designed a study where participants had to execute a two-alternative forced-choiced prosody task compared to a similar phoneme recognition task. The authors used an audio morphing paradigm, in which the stimulus material was composed of single-word utterances varying from question to statement (prosody task), or from "Bear" to "Pear" (phoneme task). They found that linguistic prosody recognition involved different brains areas that were connected with each other through two pathways in the right hemisphere. Particularly, dual routes along dorsal and ventral pathways seem to be implicated in prosody perception and suggest a division of labor to process this language feature. The dorsal pathway connects posterior superior temporal sulcus (pSTS) to premotor cortex (PMC) and inferior frontal gyrus (IFG) via arcuate/superior longitudinal fascicle (AF/SLF). As PMC has been linked to pitch control in vocalizations, it has been proposed that pSTS projects sound perception to PMC in order to trigger a motor representation of the articulation process needed to produce this sound. Audio and motor patterns of prosody could in a second phase be evaluated and integrated by IFG, located at the end of the stream (Sammler et al., 2015; Glasser & Rilling, 2008). The ventral pathway, on the other side, which connects pSTS to anterior STS (aSTS) via middle longitudinal fascicle (MdLF) has been suggested to play a role in the categorization of prosody percepts. Additionally to those pathways, left intra parietal sulcus (IPS) and supplementary motor area (SMA) were also identified as prosody-related regions. Notably, pSTS has a core position in this network, as it is part of ventral and dorsal pathways at the same time. Moreover, right pSTS has previously been associated with the integration of complex acoustic percepts and may be especially sensitive to human voices (Ethofer et al., 2011). Yet, right pSTS's role has only been shown in studies correlating its activation with prosody tasks, while its *causal* role in prosody perception remains to be investigated.

A good way to address this question is the use of transcranial magnetic stimulation (TMS). TMS consists in non-invasive magnetic field stimulation inducing electric current flow in targeted brain regions, leading to temporary reduced or enhanced activity in this area.

Continuous theta burst stimulation (cTBS) is a specific TMS protocol that can be adapted to provoke partial disruption of a specific cortex area during or after short stimulation. Hence, cTBS is a powerful tool to investigate the *causal* relationship between the activation of specific brain regions and behaviour. First applied to motor areas, disruptive TMS is nowadays also used to stimulate language areas in order to observe the involvement of various language-network nodes in speech production or speech perception (Hartwigsen et al., 2013, 2010; Devlin & Watkins, 2006).

TMS effects result from network activation disturbance and can consequently influence behavioural performances. Usually, studies apply TMS over a region of interest, and register the behavioural variations while participants perform a task related to the stimulated areas' function. Nonetheless, only a coupling with imaging technique such as functional magnetic resonance imaging (fMRI) can prove its effect at the brain network level and allow to deduce links between specific cortical activation and behaviour. Hence, novel paradigms combining those two techniques are emerging, and seem to be an optimal way to conduct neurocognitive research.

Here, we present an experiment with a combined TMS-fMRI design which aimed to transiently inhibit right pSTS and register the effect on behaviour and brain activation while subjects performed a prosody task. The goal was to highlight the central role of right pSTS in prosody processing. Given its language-related function (Willems, Özyürek, & Hagoort, 2009) and its contralateral position, left pSTS was stimulated as a control for site specificity of TMS effect and right hemispheric lateralization of pSTS activation during prosody perception. Furthermore, vertex was stimulated as non-active control site. A modified version of *Sammler et al. (2015)* paradigm comparing phoneme and prosody recognition in the same simulus material was employed. In order to avoid any discrepancy due to differences in task difficulty, the stimuli were individually adapted for each participant. Participants came for four sessions, including one preparation session and three TMS-fMRI sessions. During these scanning sessions, participants categorized stimuli in terms of prosody and phoneme in the MR bore, after TMS stimulation of: right pSTS, left pSTS or Vertex. We expected a decrease of activity in pSTS after TMS, that would cause a decrease in prosody perception in the right but not the left pSTS stimulation condition, and possibly provoke compensatory effect in other language-related areas. Furthermore, we aimed to replicate the prosody network in the vertex stimulation condition.

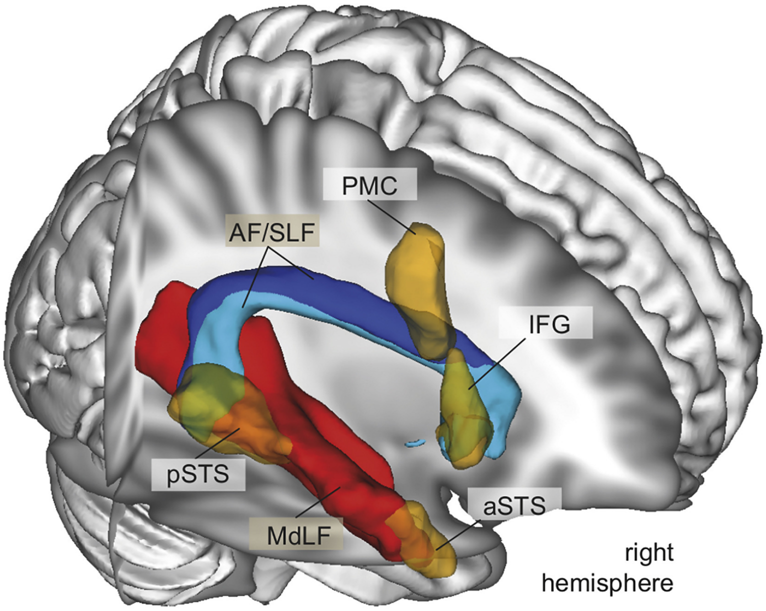

Figure 1.1: Dorsal and ventral pathways for prosody in the right hemisphere, taken from *Sammler et al. (2015)*. Right pSTS is a key node in both pathways. PMC: premotor cortex, IFG: inferior frontal gyrus, a/p STS: anterior/posterior superior temporal sulcus, AF/SLF: arcuate/superior longitudinal fascicle, MdLF: middle longitudinal fascicle. Color code indicates: orange for areas showing stronger activity in prosody than phoneme categorization; blue for dorsal pathway; red for ventral pathway.

Chapter 2

Methods

This study used a set of raw imaging and behavioural data acquired for the PRONET project at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig between September 2017 and January 2018. Approval from the local ethics committee at the University of Leipzig was granted before the beginning of the study. The following sections describe the experimental steps for the data acquisition performed beforehand as well as the analysis procedure, which was applied in this Master thesis. Abbreviations L, R and V refer respectively to L-pSTS, RpSTS and Vertex as stimulation condition in the following sections.

2.1 Participants

Twenty-nine healthy participants (age range: 21-36 years, mean age: 27.6, SD: 4.0) were recruited from the Max Planck Institute data base. They provided written informed consent prior to inclusion in the study and received a financial compensation for their participation. Each participant fulfilled the following conditions : German native speaker, right handed, normal hearing, no TMS or MRI contraindications. All of them had a structural T1-weighted scan which was available in the data base allowing to orientate the TMS coil to the desired brain areas.

2.2 Structure of the study

The study included four sessions. The first session was a preparation session during which participants received instructions about the experimental procedure, and different calibration parameters were determined: individual active motor threshold (AMT) for TMS and individualized stimulus selection. A so-called -staircase procedure- was carried out to choose stimuli from a pool of morphed single-word stimuli (along phoneme and prosody continua), that were fully-matched in difficulty (see below for details). In the remaining three sessions, one of three areas was stimulated with TMS: left pSTS, right pSTS or Vertex (see below for TMS parameters). The order of stimulation site was balanced across participants. Each experimental session started with 40 seconds of TMS stimulation before participants were rapidly (within 5 minutes) moved to the MRI scanner where they performed a phoneme and prosody categorization task on the preselected stimuli. They pressed one of two different buttons with their right hand to judge whether the word was "Bar" or "Paar" for the phoneme task or, spoken as question/statement for the prosody task. Finally, after the fMRI-experiment, participants filled in a questionnaire on their strategies during the tasks.

2.3 Stimuli and experimental procedure

2.3.1 Stimuli

Similarly to *Sammler et al. (2015)*, stimuli of the present study consisted of single words in order to prevent an interaction between prosody perception and left-hemispheric sentence-level language processing. The two German words “Bar” and “Paar” (meaning “pub” and “pair”, respectively), were recorded (16 kHz, 16 bit, mono) from two native German speakers (one male and one female), with either falling (statement) or rising (question) pitch contour. The audio-morphing toolbox STRAIGHT was used in MatlabR2009 (The MathWorks, Inc., Natick, MA, USA) to create continua between the 4 recorded utterances (i.e. “Bar.”, “Bar?”, “Paar.”, “Paar?”). The audio morphing enabled to produce continua of prosody stimuli (from statement to question, for any phoneme level) and continua of phoneme stimuli (from “Bar” to “Paar”, for any level of prosody), with 61 steps between the recorded originals. While phoneme continua were produced by gradually varying the voice onset time (e.g., when ‘the voice comes in’ after the plosive), prosody continua were produced by progressively increasing the pitch contour (from a falling (statement) to a rising contour (question)). **Figure 2.1** displays the original recordings in the centre and examples of continua used in the experiment in the outer rows and columns

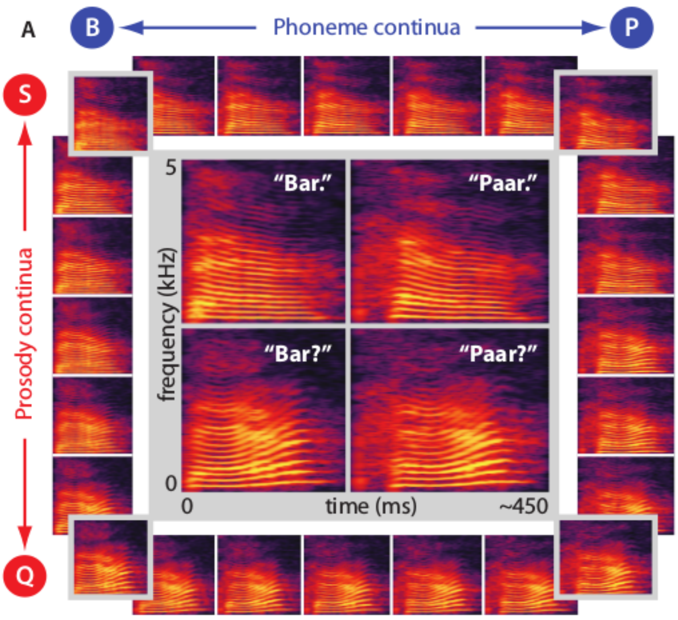

Figure 2.1: Examples of stimuli used in the present study. The words "Bar" (B) and "Paar" (P) spoken as statement (S) or question (Q) depicted in the central panel were used to construct continua along prosody (vertical), and word-initial phoneme (horizontal) dimensions.

2.3.2 Individual difficulty adjustment

The set of stimuli obtained with the audio morphing underwent an individual selection for each participant using a staircase procedure, in order to fairly tune the difficulty between the two tasks and across participants. In fact, prosody and phoneme perception are subjective capabilities and can vary from one person to another. The goal of the procedure was to select 5 morph steps along each continuum (prosody and phoneme), spaced to match the two tasks in difficulty. First, participants were presented with stimuli along each continuum at a time, in a staircase order, until reaching the point of subjective equality (PSE). The PSE represents the morph value at which the stimulus is perceived as 50% "Bar" and 50% "Paar" for the phoneme task (as 50% question and 50% statement for the prosody task). Responses during the staircase procedure were used to fit a psychophysical functions, centered on the PSE, using a function of the following form:

$$y = a + \frac{b}{1 + exp(\frac{c-x}{s})} \tag{2.3.1}$$

with a and b representing the lower and upper asymptotes, c the center of symmetry of the curve (PSE), and s the slope of the curve at c. The slope of the curve was defined to reflect categorization difficulty (with shallower slopes reflecting higher task difficulty). In the end, from each psychophysical function, the PSE value was selected, as well as two morph-values on each side whose spread along each continua was determined based on the corresponding curve's slope, in order to select identical difficulty values for both prosody and phoneme stimuli.

2.3.3 Experimental procedure

Stimuli were presented via headphones (MR-compatible) using Presentation® software (version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA). Phoneme and prosody morph values selected during the staircase procedure were assembled following a type-1 index-1 sequence to produce stimuli blocks (Nonyane & Theobald, 2007). Identical blocks were presented during prosody and phoneme tasks. The experiment consisted of 24 blocks, each split into 2 mini-blocks of 39 seconds, interspersed by resting periods of 15 seconds (**Figure 2.2**). A full block consisted in 2 × 13 stimuli that were presented with a jittered stimulus onset asynchrony of 2.5-3.5 seconds. Each trial block started with a fixation cross followed by an instruction-page ("intonation" or "phoneme") to inform the participant whether they should evaluate the stimuli in terms of one or the other. In total, the experiment lasted two hours including preparation, cTBS application and 44 minutes for the task in the scanner.

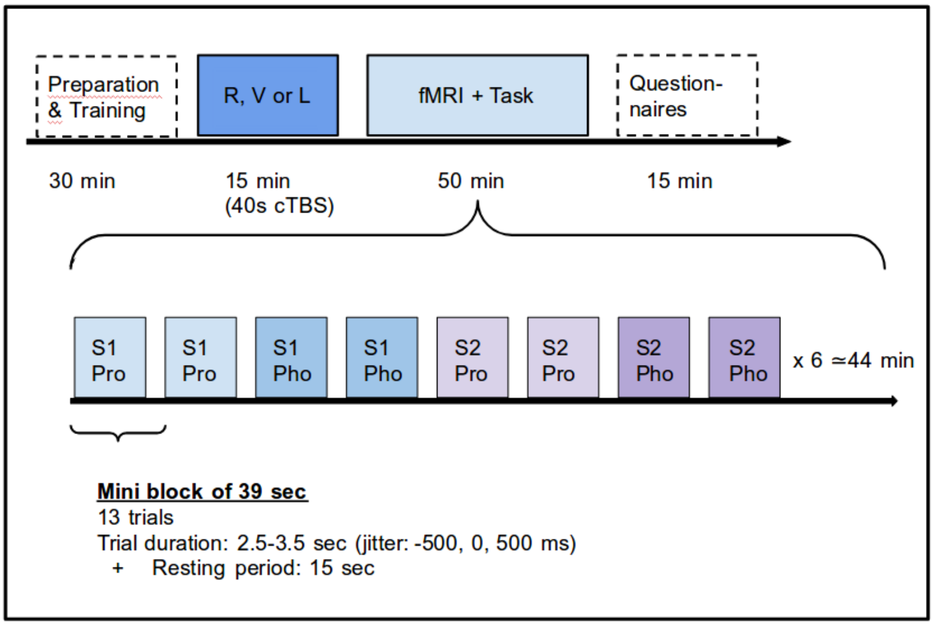

Figure 2.2: TMS-fMRI session timeline and task organisation. S1 and S2 represent two different stimuli blocks, "Pro" stands for prosody (intonation) task, and "Pho" for phoneme task. R, L and V correspond to the stimulation condition for cTBS application.

2.4 TMS parameters

Inhibitory transcranial magnetic stimulation was applied offline prior to the fMRI experiment with a figure-of-eight coil (double 75mm; coil type CB-60) connected to a MagPro X100 stimulator (MagVenture 4.3.20, Medtronic, Fridley, MN). Neuronavigation (TMS Navigator; Localite) and individual T1-weighted MRI images were used to navigate the TMS coil to the desired area and maintain its exact location and orientation throughout stimulation. Left and right pSTS location were targeted using the Montreal Neurological Institute (MNI) coordinates reported by *Sammler et al. (2015)*: left pSTS (x, y, z =-48, -40, 10), right pSTS (x, y, z= 45, -37, 1). They were converted to native space of each participant by applying the inverse of the normalization transformation to the MNI coordinates with SPM software. Vertex was defined as the center of the upper surface of the head, and was also targeted with the neuro-navigation system. The coil was placed tangentially with the handle pointing at 45° to the sagittal plane (315° for the R stimulation session). A continuous theta burst stimulation (cTBS) protocol was used (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). Stimulation protocol was set to 600 pulses at 50Hz in trains of 3 stimuli at an interburst-interval of 200 ms for 40s at 80-90% of the individual AMT, following the experimental setup of *Hartwigsen et al. (2013)* . AMT was individually determined during the preparation session. It was defined as the lowest intensity targeted towards left M1 (x, y, z= -37, -21, 58, (Mayka, Corcos, Leurgans, & Vaillancourt, 2006)) to elicit a motor evocked potential (MEP) $\geq 150\ \mu$V in right FDI (first dorsal interosseous) -in 5 out of 10 consecutive trials- during an isometric contraction.

2.5 MRI parameters

A high-resolution T1-weighted dataset ($1 \times 1 \times 1$ mm^3 voxel size) of each participant was taken from the data base for co-registration of fMRI scans and neuronavigation during TMS. The acquisition was done with the standard institute setup in a 3T scanner (*Siemens*), using a magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence (TR = 2300 ms, TE = 2.98 ms, 176 axial slices, FOV =240×256mm^2, matrix size = 256×256 pixels,flip angle = 9°). Functional MRI was performed at the MPI in a 3T Siemens Skyra scanner. A series of 1385 T2*-weighted functional images were acquired with a simultaneous multi-slices echo-planar gradient (EPI) pulse sequence (TR = 1900 ms, TE = 23.2 ms). Sixty slices ($2 \times 2 \times 2.5$ mm^3 voxel size, flip angle 80°) were collected with a 32-channel head coil.

2.6 Questionnaires

After each session, participants filled out a questionnaire on their strategies in the prosody task, the phoneme task and with general questions about the experiment.

2.7 Data analysis

2.7.1 Behavioural analysis

Task performance

A psychometric function was fit to the data obtained during the fMRI sessions with Palamedes toolbox in Matlab. PSE and slope values were retrieved from this function and analysed with repeated measures ANOVAs with a 3×2 design, to compare between tasks (prosody/phoneme), and across TMS sessions (L, R and V).

Questionnaire analysis

Subjective task difficulty (reported in ratings from ”1” -very easy- to ”9” -very difficult-) were compared by means of 3 × 2 repeated-measures ANOVA with factors stimulation condition (L, R and V) and task (prosody and phoneme), computed with SPSS Software.

2.7.2 fMRI data analysis

fMRI data analysis was performed using Statistical Parametric Mapping software SPM 12 (Wellcome Trust Centre for Neuroimaging; www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB 12 (The Mathworks, Inc., Natick, MA).

Preprocessing

The imaging data were first converted from DICOM to 4D nifti format to make them SPM-readable. The data underwent the classical preprocessing protocol for multiband sequence fMRI data through a matlab metabatch adapted to the experiment (Hartwigsen et al., 2017). Functional images of each scanning session were realigned to the first acquired image in order to correct for participants' head movements in the scanner. As a sanity check, preprocessing SPM report of each subject were controlled for the range of movement in the scanner (which should not exceed one voxel size), and no participant had to be excluded for head movement. Jointly with realignment, the unwarping function reduced the susceptibility-by-movement variance (movement-caused image deformations) due to magnetic field inhomogeneities in the scanner bore. Given that no field map was acquired during the scanning sessions, no further magnetic field inhomogeneities due to different tissue-susceptibilities were corrected. Afterwards, the MR images were segmented into different tissue classes (white matter, grey matter and cerebro-spinal fluid). Resulting images were used for co-registration of functional and anatomical data, and normalization (which allow, respectively, to align functional and anatomical images of each subject and to map them into the standard stereotaxic anatomical MNI space). During this step, functional images were resampled to 2 × 2 × 2 mm voxel size. This step allowed to overcome the brain shape variability between participants and to make it possible to compare and analyse images from different participants and TMS sessions. Finally, the normalized images were spatially smoothed with an 8 mm FWHM isotropic Gaussian kernel to further accommodate intersubject variation in brain anatomy.

First level Analysis

The individual first level analysis was implemented with a General Linear Model ('GLM'), by including the scans of the three sessions in the same design, each of them represented by a different block in the design matrix (see **Figure 2.4**). In each session block, three regressors of interest were convolved with a canonical hemodynamic response function, representing the two task phases (phoneme and intonation task). One additional regressor of interest coding for the begining of each block, and six nuisance regressors with the realignment parameters (3 rotations and 3 translations along the axis x, y and z) were added in order to reduce noise caused by movements. A high-pass filter with a cutoff frequency of 1/128 Hz was used to correct for low frequency components. The model was estimated with the SPM 'Classical method', which calculates the model parameters using Restricted Maximum Likelihood (ReML). Finally, different contrasts were computed at the subject level. Six t-contrasts were set to highlight the specific task-related activations against baseline: prosody and phoneme tasks vs. baseline, in each of the three fMRI sessions. As a sanity check, a t-contrast 'all tasks vs baseline' was calculated in order to check for auditory cortex and left motor cortex activations (due to right-handed button press) for each subject. The 'Slicer' tool of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/FSL) was used to verify correct estimation in every subject (see example in supplementary material).

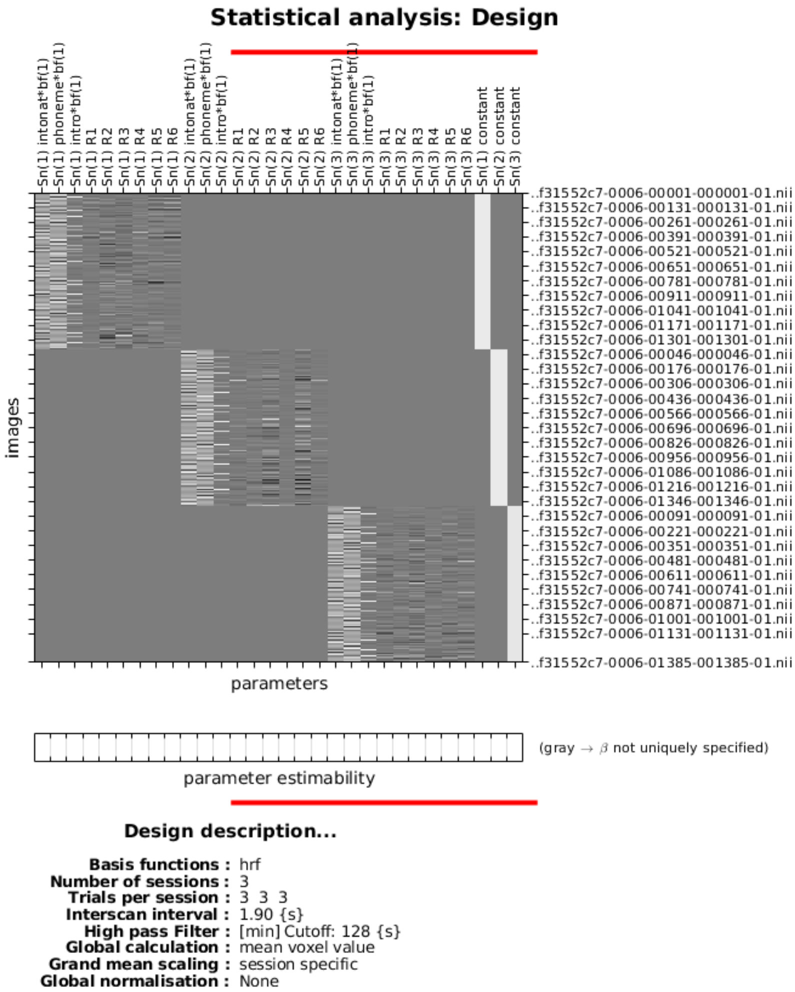

Figure 2.3: Example of first level design matrix containing one regressor for each task and session, as well as 6 nuisance regressors with motion parameters.

An analogous analysis was carried out after splitting the experiment into 2 parts to estimate TMS inhibition in the targeted areas more closely to the stimulation procedure, and the potential decay of its effects. Therefore, new sets of onset regressors were computed in order to divide the experiment in time by two **(Figure 2.5)**. Like this, new regressors comprised subsets of consecutive onsets which were individually used to compute the related t-contrasts, comparing tasks against baseline.

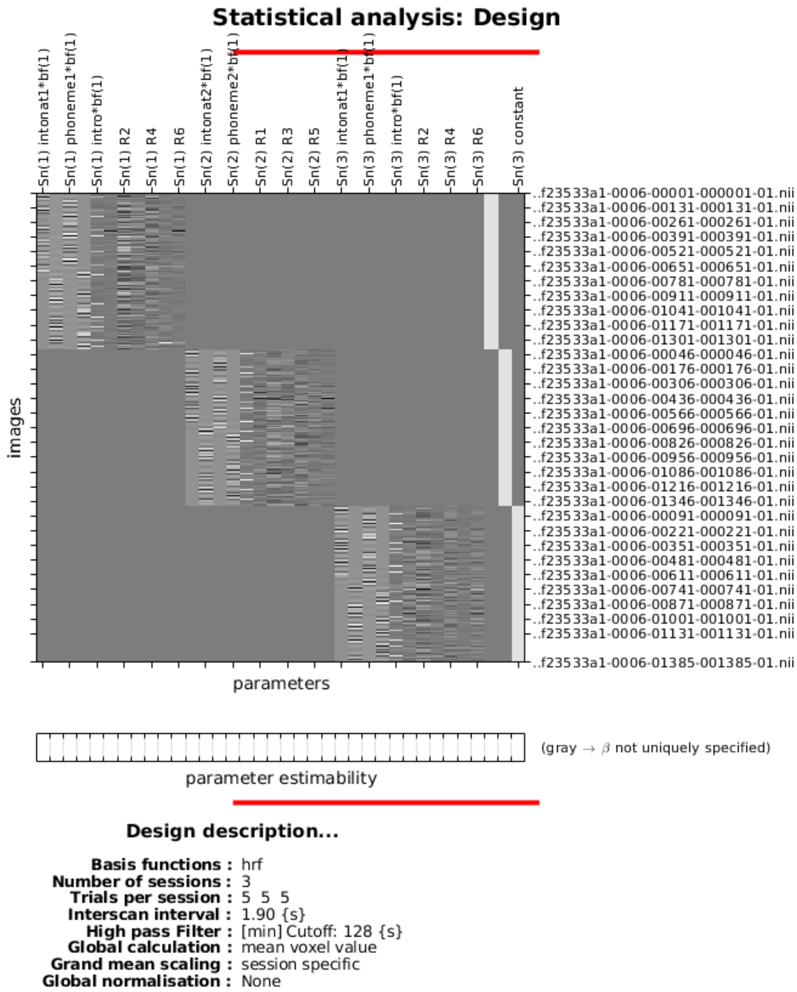

Figure 2.4: Example of first level design matrix containing two regressors for each task, dividing the experiment into two parts

Second level analysis

Here, several steps and strategies have been successively applied in order to refine the analysis and to try to correct for different kinds of disruptive elements (participant performance, TMS effect decrease etc.).

Whole experiment, whole brain

In a first phase, contrast images of all participants from the first level were gathered in a second level analysis using paired t-test. Every task and stimulation condition (R, L and V) was compared against baseline. Then, phoneme and prosody tasks were compared against each other, separately for each stimulation condition. Finally, the same task (prosody or phoneme) was compared across stimulation conditions (R was compared with V, L with R and L with V, for prosody and phoneme independently).

Region of interest (ROI) analyses

To perform ROI analyses, effect sizes of first-level regressors of interest were extracted from a set of areas by means of the SPM8 toolbox RFX-plot (J. Glascher Visualization of group inference data in functional neuroimaging 2009). Effect sizes were extracted from 8 mm spheres centered around each analysed-area coordinates. Aiming to check for TMS effects on targeted areas, we first focused the ROI analysis on the stimulated coordinates: left pSTS (x, y, z =-48, -40, 10) and right pSTS (x, y, z= 45, -37, 1). T-tests were calculated with effect sizes of each area to compare the tasks against each other within each session and to compare each, R and L condition, with V condition. Afterwards, seven ROIs in prosody-related areas were defined based on peak coordinates in baseline contrast: left and right auditory cortex, left and right insula, left and right inferior frontal gyrus, and supplementary motor area (SMA) (coordinates available in supplementary material) . Two-way repeated measures ANOVAs were calculated with SPSS software (IBM Corp. Released 2017. IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY: IBM Corp.) for each ROI, using within-subject factors task (prosody vs.phoneme) and TMS stimulation condition (V, R and L).

Splitting the experiment in 2

The experiment was split into 2 parts according to the 2-parts first level design described above. ROI analyses and whole brain analyses were applied as described above for each of the two parts.

Chapter 3

Results

3.1 Behavioural data

Repeated measures ANOVA with factors task and stimulation condition reported no effect of task nor of stimulation on the slope of the curve (all $p > .229$)(**Figure 3.1**). The fact that no task effect was discovered indicates that phoneme and intonation stimuli were well-matched for difficulty, as intended by the staircase procedure. The fact that no stimulation effect was discovered indicates that TMS did not interfere with task performance.

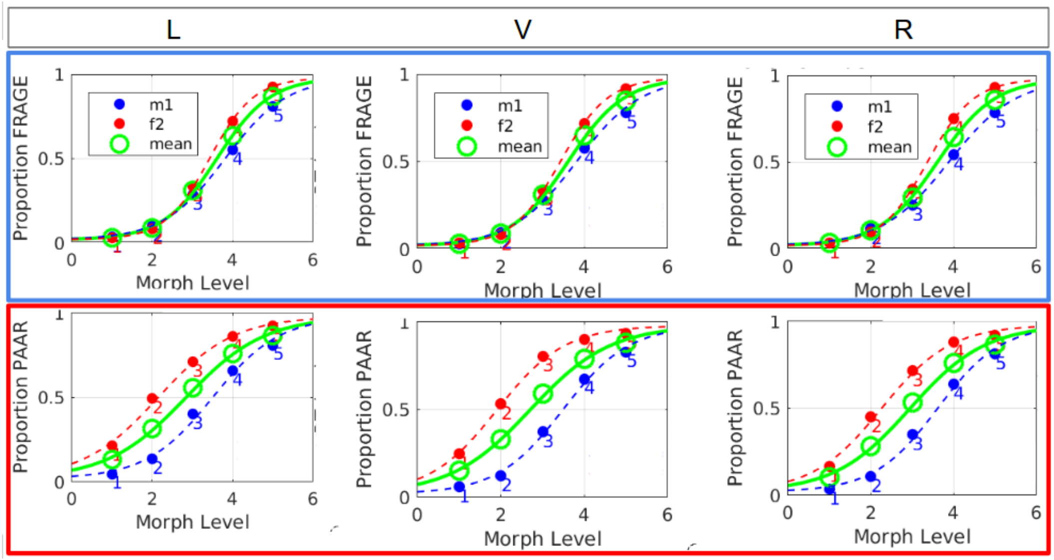

Figure 3.1: Response functions averaged across participants for each task (prosody displayed in the blue box, phoneme in the red box), and each condition (L, V and R). m1 and f1 stand for male and female speakers respectively, response to both are averaged in the mean response function.

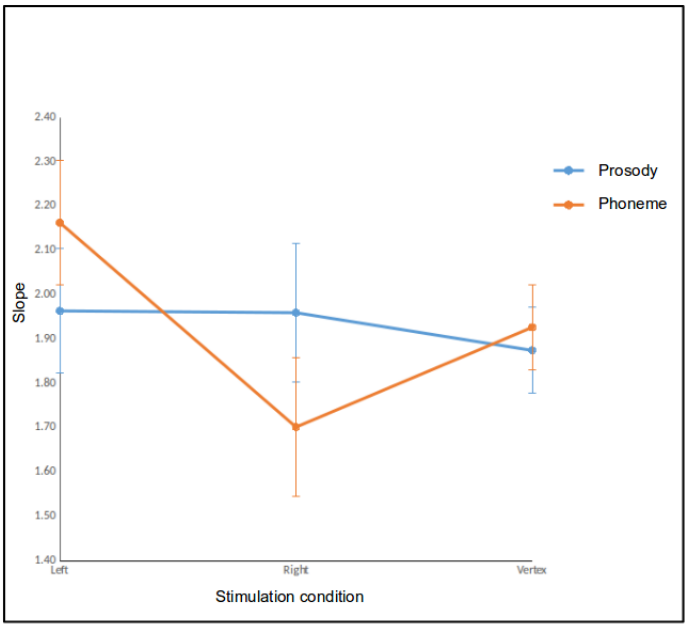

Figure 3.2: Mean slope for each stimulation condition and task. Error bars indicate ±1 SEM.

However, participants reported in the post-experimental questionnaire that they found the phoneme task more difficult than the intonation task. Repeated measures 3×2 ANOVA with factors task and stimulation condition reported a main effect of task (F(1,28)= 16.256, p<.001, η_{p2}= 0.367).

3.2 Sanity check of the images, co-registration and general activity

In the following results, brain regions showing activity were labeled using Neuromorphometrics tool implemented in SPM (Neuromorphometrics, Inc. Somerville, MA). Using baseline contrasts we checked whether the co-registration was done correctly and general activity was in the right place. Baseline contrasts were calculated for each task and each stimulation condition separately. Contrast threshold was set to p<.05 at the voxel level (FWE corrected).**Figure 3.2** and **Figure 3.3** display the results for intonation and phoneme respectively. Global activations looked similar between the two tasks, as well as between the three stimulation conditions. They all showed activation in bilateral auditory cortex, left motor cortex, thalamus and cerebellum.

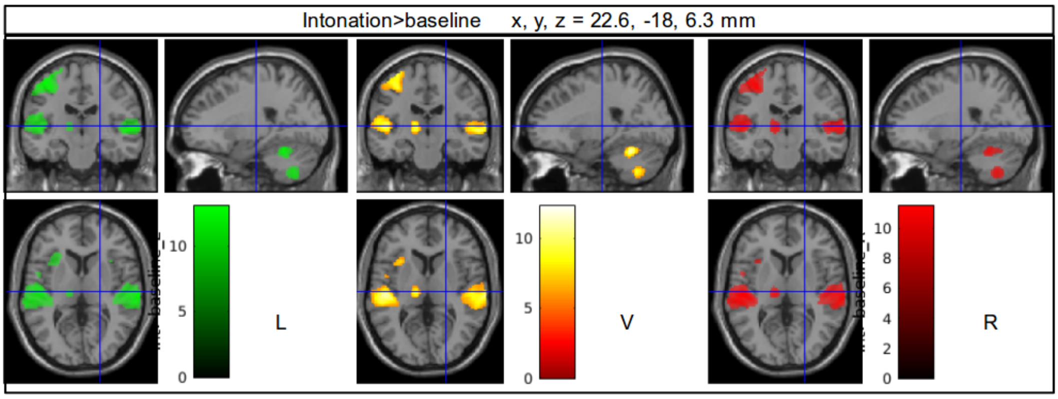

Figure 3.3: Baseline contrasts for prosody task, after L, V and R cTBS stimulation across all subjects and the full experimental session. (Result tables available in supplementary material)

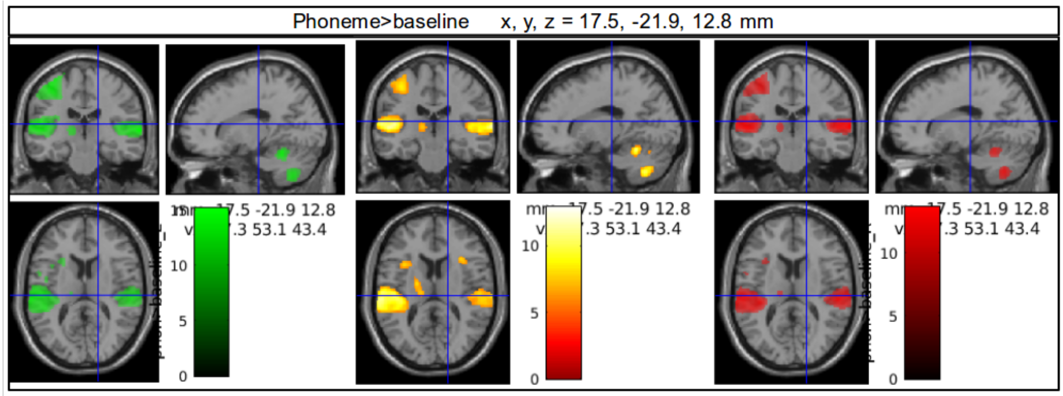

Figure 3.4: Baseline contrasts for phoneme task, after L, V and R cTBS stimulation across all subjects and the full experimental session. (Result tables available in supplementary material)

3.3 Inhibitory effect of TMS on targeted areas and effects on other network-related areas

In order to verify whether TMS had an effect on the stimulated area activation, ROI analyses were done for right and left pSTS. With the results in R-pSTS, a 2×2 repeated-measures ANOVA with factors TMS conditions (V and R) and tasks (prosody and phoneme) was done. Similar repeated-measures ANOVA was calculated for the results in L-pSTS, but with factors TMS condition (V and L) and tasks. The analysis comprising the whole experiment in one block did not reveal any stimulation condition or task effect in both

ANOVAs (all p>.05). Yet a task effect was not found, it is interesting to mention that it was approaching significance in R-pSTS (p=.07), with a tendency for higher activation during prosody than phoneme task.

When looking at the same analysis but with the experiment split into 2 parts, (see **Figure 3.5**), activity had a tendency to decrease with time in both regions, but did not differ between stimulation conditions nor between the tasks. Repeated measures ANOVAs with a $3 \times 2 \times 2$ factors design (TMS/task/time) reported a main effect of time for both regions (LpSTS: $F(1,28)= 17.525$, $p<.001$, $\eta_{p2}= 0.385$; RpSTS: $F(1,28)= 35.350$, $p<.001$, $\eta_{p2}= 0.558$).

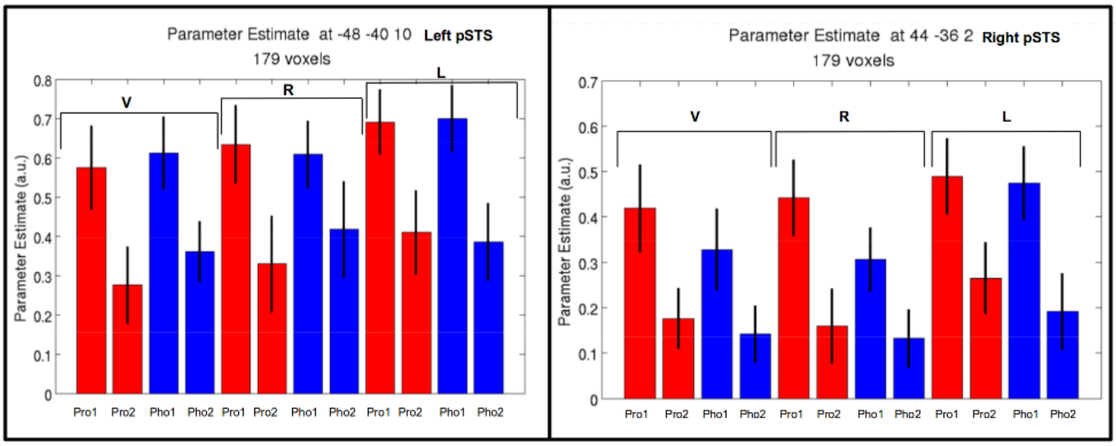

Figure 3.5: Bar graphs of the ROIs analyses in right and left pSTS (stimulated coordinates), for the experiment divided in two. Red bars indicate the prosody task, blue bars indicate the phoneme task. 1 and 2 refer to first and second part of the experiment, respectively. Error bars indicate ±1 SEM.

3.4 Comparison of tasks in the three stimulation conditions

In a third analysis, contrasts comparing the two tasks in each stimulation condition, and each task across different stimulation conditions were computed. Voxel threshold was set to p<.05 (without correction), and cluster level threshold to p<.05 (FWE corrected).

Task-comparing contrasts (phoneme>prosody & prosody>phoneme) in each stimulation condition revealed regions significantly more activated in phoneme than prosody task in both L and V stimulation conditions. Phoneme>prosody highlighted: right superior frontal gyrus (SFG) in both L and V; in L additionally, right middle frontal gyrus (MFG) and right angular gyrus (AG); in R nothing was revealed at this threshold (see **Figure**

3.5). The contrast prosody>phoneme in V did not reveal any significant area and thus did not replicate the prosody network found by *Sammler et al. (2015)*.

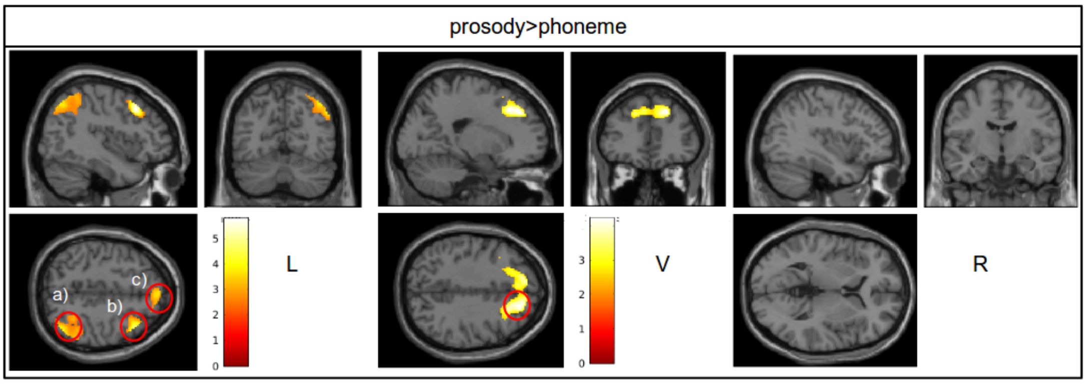

Figure 3.6: Significant phoneme (*vs.* intonation) task-related activation peaks in each stimulation condition. For results in L, a), b) and c) show R-AG, R-MFG and R-SFG respectively; in V, the only circled area is R-SFG. (Results table available in supplementary material.)

The ROI analysis was done in order to focus the analysis on peak activation coordinates coming out of the baseline contrasts and to compare the sessions and tasks at a smaller scale. Globally, bar graphs that were plotted for each region of interest, with parameter estimates of each condition and task, showed a high similarity across the different conditions, for same task. However, the analysis revealed significant differences between parameter estimates when the area of interest was the left supplementary motor area (x, y, z = -6,6,51) (see **Figure 3.7**). Especially, the conducted ANOVA reported a main effect of task (p = 0.015) , indicating an increased left SMA activation for intonation relative to phoneme task independent of the TMS stimulation condition. However, this result this not survive multiple comparison correction (Bonferroni adjusted p-value=0.007).

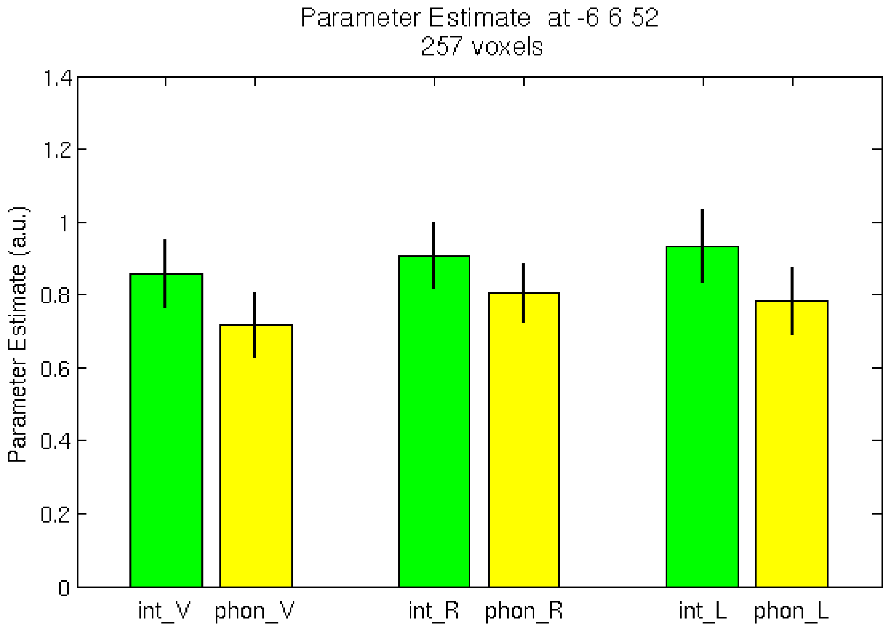

Figure 3.7: Bar graph of the ROI analysis results for supplementary motor area (SMA, x, y, z = -6, 6, 51). Intonation task is represented in green bars whereas phoneme task is shown in yellow bars. Error bars indicate ±1 SEM.

Chapter 4

Discussion

The goal of this study was to investigate the causal role of right pSTS in prosody perception. Therefore, a combined TMS-fMRI experiment was conducted, where participants had to perform a prosody and a phoneme task (as control) in the scanner, after TMS one of three different sites: right pSTS, left pSTS, and Vertex (the last two being control areas for right pSTS). Tasks were successfully matched for difficulty. Results show: (i) prosody and phoneme perception were not disrupted by TMS, (iii) TMS did not decrease pSTS activity, (iv) comparison between activation related to prosody and phoneme task did not reveal the right hemispheric prosody network, independently of the stimulation condition, except for SMA which was shown in the ROI analysis, (iv) frontal and temporal brain regions were more strongly involved in phoneme than prosody processing during V and L sessions. The findings will be discussed in turn.

TMS effect

Surprisingly, ROI analyses at the stimulated coordinates reported no activation decrease in these areas after they were stimulated with cTBS, whereas a decrease was expected in L-pSTS and R-pSTS when comparing L&V and R&V respectively. Therefore, we did not go into network analysis. Nonetheless the absence of activation decrease fits to the behavioural results, as stimulation conditions did not affect the behavioural performance. Various reasons can be suggested to explain the lack of TMS effect, starting with the fact that left and right pSTS coordinates used as target regions in the present study lie rather deep in the sulcus, which makes them more difficult areas to reach with TMS. Indeed, the protocol used here (Huang et al., 2005) has been more often tested in surface regions of the cortex. Moreover, regarding the activation threshold, previous studies which succeeded to disrupt pSTS with the same type of coil used stimulation intensities which ranged from 40% (van Kemenade, Muggleton, Walsh, & Saygin, 2012) to 60% of the maximal stimulator output (Grossman, Battelli, & Pascual-Leone, 2005). Here, we set the stimulation intensity to 80% of individual AMT. This resulted in slightly lower intensities, ranging from 27 to 50% of the maximal stimulator output, which might have been too low to reach the desired perturbing effect in all participants. Finally, it is important to mention that even though the theory about TMS functioning is accepted, the underlying physiological mechanisms of this technique are not fully described yet and their understanding remains a critical step in order to develop powerful and reliable protocols (Chervyakov, Chernyavsky, Sinitsyn, & Piradov, 2015). Thus far, we can notice variable inter and intra-subject responses to TMS in the literature (Martin-Trias et al., 2018; Maeda, Keenan, Tormos, Topka, & Pascual-Leone, 2000). For example, reproducibility of TMS effects over time within the same subjects can be unsuccessful, as reported by *Martin-Trias et al. (2018)* (Martin-Trias et al., 2018). Here, the authors selected subjects who responded positively to a first TMS-session, but failed to reproduce the previous results when they invited them for a second identical session. Regarding inter-subject variability, differences in cortical neurons network and recruitment between subjects has been linked to highly variable response after cTBS (Hamada, Murase, Hasan, Balaratnam, & Rothwell, 2012). Altogether, those facts raise concerns about the reliability of TMS, and illustrate the difficulty to adjust the right protocol to each experimental aim as well as the necessity to verify the induced effect in each subject. We can then wonder whether the overall trend of scientific literature to only report successful studies whose paradigm worked but not those which failed to do so despite careful methods execution, limit the critical mind of the scientific community on this technique. Thus, it could make researchers overestimate the current mastery of TMS and the present results might not be an isolated case but could show a common unreported-tendency of TMS experiments. Pre-registration of studies could work against that, and represent high hopes for fruitful research in the future.

Prosody network and differences to the results of *Sammler et al. (2015)*

Replication of the prosody network found by *Sammler et al. (2015)* was one of the first objectives of the second level analysis given that this finding was the grounding material for the present experimental paradigm. Nonetheless, the reported results failed to bring the network out after comparing prosody with phoneme blood oxygenation level response in the V session. Only SMA, which was also part of the reported prosody network (Sammler et al., 2015), showed a trend towards significance in the ROI analysis. Reasons for this can be numerous, starting with the stimulus material differences between the two experiments, suggesting that the present study might have too carefully matched the tasks. Stimulus material used by *Sammler et al. (2015)*, was also individually shaped with the staircase procedure in order to match the difficulty between phoneme and prosody task. However, task blocks were composed of stimuli varying only along one dimension (e.g. prosody), keeping the respective other feature constant (e.g. phoneme). In other words, blocks did not only differ in task but also in stimuli, whereas here, they were composed of stimuli varying along both continua dimensions and the exact same stimuli were used for both tasks. That way, we can not exclude that the prosody network, and especially right pSTS, -highlighted by contrasting prosody *vs.* phoneme task- was driven by stimulus properties in *Sammler et al. (2015).* Stimulus blocks varying only along one continua at a time may have induced repetition suppression effects on the steady factor (Grill-Spector, Henson, & Martin, 2006; Breiter et al., 1996), while the varying-factor processing was additionally task-relevant. Using the same stimulus material for both tasks in the present study, may have reduce differences between task activations.

The fact that right pSTS was not significantly more active in prosody than phoneme task during the V session does not necessarily question the central role of this area in prosody perception. *Sammler et al. (2015)* suggested that pSTS was the initial network-receiver of basic sound features related to prosody, and which further transmitted this primary information to the two processing streams. On one hand, right pSTS may be sensitive to stimulus feature (i.e, pitch variation) that were kept constant between both tasks here, and cancelled out in the contrast. On the other hand, right pSTS could specifically be sensitive to relatively sharp variations in prosody contour, but less to subtle differences as the ones used in the present stimulus material. An interesting investigation could be to compare the average pitch contours used by *Sammler et al. (2015)* with the one used in this study. As the two paradigms were not exactly the same, and also that the stimulus material selection depended on the recruited-participants performance, the variance of the pitch contours used in the present study may have been smaller and could then be a relevant reason for reduced effect. Following this logic which leads to a low pSTS activation during the prosody task, it would then explain why TMS could not downregulate it further.

ROI analysis, on the other hand, revealed that SMA was more activated during the prosody task than during the phoneme task, for all three sessions. This is something we expected to find, as SMA is part of the prosody network (Sammler et al., 2015). SMA is also part of the multi-demand system (Duncan, 2010), which is described as a pattern of frontal and parietal activity associated with different types of cognitive demands. This could suggest that prosody recognition of mono-syllabic stimuli is cognitively more demanding compared to mono-syllabic phoneme recognition. Another explanation for stronger SMA activation in prosody than phoneme may be that, together with pre-SMA, they have been proposed to play a role in facilitating spontaneous motor responses to sound and to support sensorimotor processes to guide auditory perception (Lima, Krishnan, & Scott, 2016). Thus, prosody perception could drive an imagery representation of the sound in order to be successfully integrated, which is in line with the suggested role of the dorsal pathways in *Sammler et al. (2015)*.

Phoneme perception

Even if not in prosody, we found activity for the phoneme task. Right SFG was more activated during the phoneme than during the prosody task in V and L sessions. Phoneme also induced a higher activation of right MFG and AG compared to prosody task in the L session. Although intonation and phoneme tasks were matched in difficulty and the behavioural results are in agreement with that, participants' subjective estimation revealed that they actually found the phoneme task more difficult. Phoneme categorization relied on voice onset during the first few milliseconds of the stimulus whereas intonation discrimination relied on the sound contour of the entire stimulus. Hence, it is reasonable to think that the phoneme task may require more focused attention (at the very beginning of the stimuli) from the participant than the prosody task. The lateral prefrontal cortex has been associated with control of attention and awareness, related to both stimulus-driven and goal-directed attention (Asplund, Todd, Snyder, & Marois, 2010). SFG activation has been reported to correlate with attention shift between different visual recognition tasks (Nagahama et al., 1999). MFG lesions have been identified as predictor for attention neglect (Ptak, 2012), and more particularly, right MFG activation has been associated with attention reorientation (Japee, Holiday, Satyshur, Mukai, & Ungerleider, 2015). Concerning right AG, several studies reported a role of this region in spatial attention (Chambers, Payne, Stokes, & Mattingley, 2004; Cattaneo, Silvanto, Pascual-Leone, & Battelli, 2009), but no literature was found regarding its implication in auditory attention or phoneme

processing tasks.
However, right AG was only involved after stimulation of left pSTS, a crucial area for phoneme decoding (Chang et al., 2010), and also left AG is also known as a language-related area (Seghier, 2013). That way, one could argue that the stronger activity of right AG during phoneme than prosody task after left pSTS disruption might reflect a compensatory process in the contra-lateral hemisphere to sustain phoneme processing (Hartwigsen et al., 2017).
Overall, the fact that right MFG and right AG are activated in the L session may represent a potential compensatory mechanism to offset the temporary loss of function on left pSTS, which is involved in phonological processing (Vaden Jr, Muftuler, & Hickok, 2010). As right pSTS is not involved in phoneme perception, it would then explain why similar activation was not highlighted in R-pSTS stimulation condition.

Conclusion

Finally, the results reported here underline the difficulty of designing an experiment to draw an undeniable conclusion from the output, as well as the necessity of combining brain stimulation paradigms with imaging techniques in order to verify the effects at the activation level. Furthermore, very few studies aiming to explain the brain mechanisms associated with prosody perception have been using the same stimulus material for both prosody and control task, and matched them in difficulty as well. Thus, it seems essential to carefully discuss prosody-related studies in term of the stimuli employed, as it may highly influence the outcome (Frühholz, Jellinghaus, & Herrmann, 2011).
The collected data require further analysis in order to be accurately interpreted. In fact, the complexity of the stimulus material and general paradigm may produce different results according to the strategy adopted in the data analysis. Given the individual adjustment, it would be interesting to describe the overall stimulus material in term of acoustic properties. Recently published results from a study investigating the neural underpinning of prosody integration (Hellbernd & Sammler, 2018) suggest that morph-wise analysis of the imaging and behavioural data could be profitable. In other words, by grouping and separately analyzing the results related to similar morph values in terms of difficulty (ambiguous vs typical stimuli), we could expect to see variable activation in pitch and phoneme related areas.

I declare that, except where explicit reference is made to the contribution of others, that this dissertation is the result of my own work and has not been submitted for any other degree at the Ecole Polytechnique Federale de Lausanne or any other institution.

Eléa Dheilly

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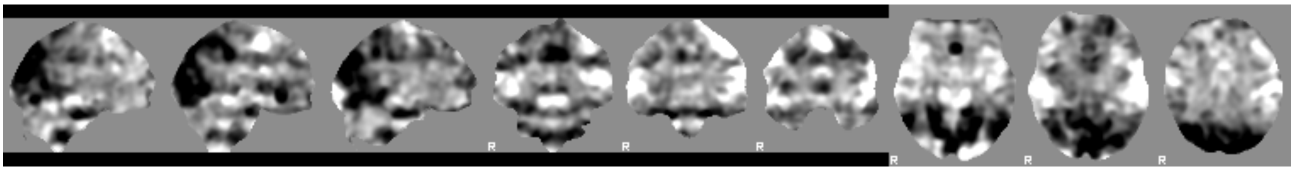
Chapter 5

Supplementary Material

Figure S1. Results of Slice tool in FSL with the contrast phoneme>baseline in the first level analysis.



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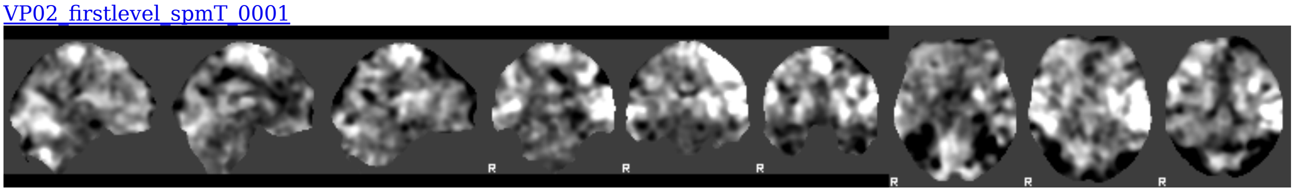

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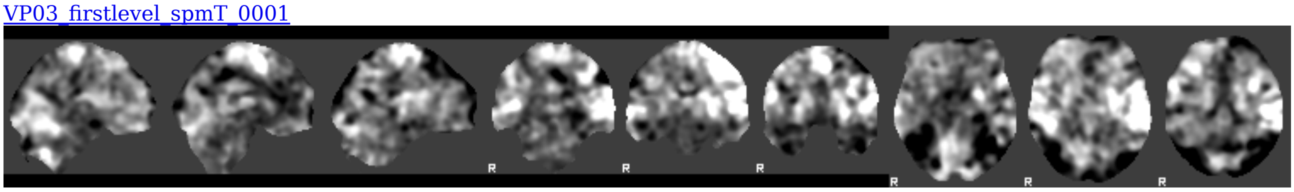

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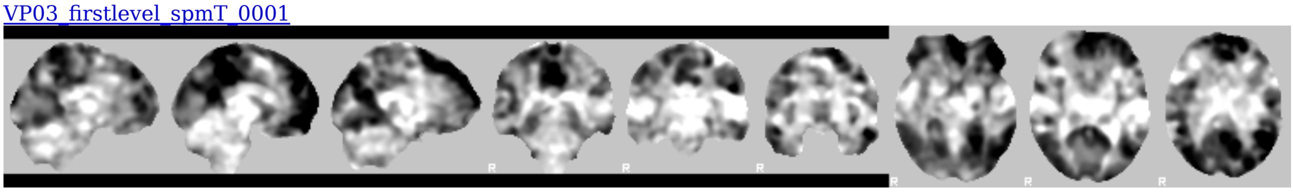

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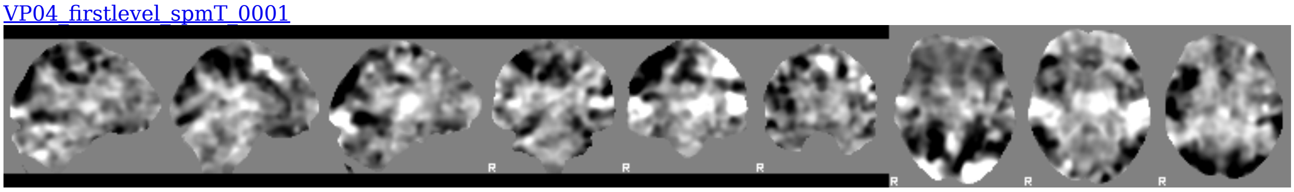

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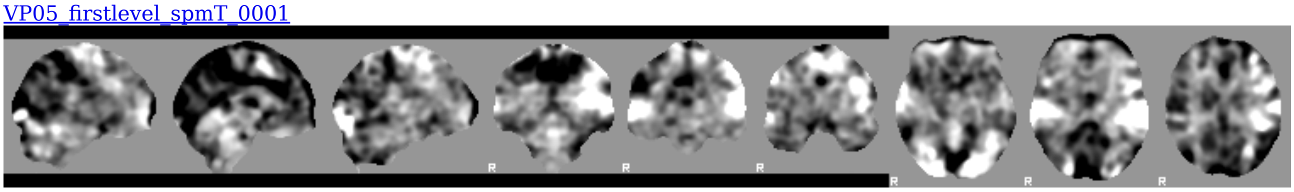

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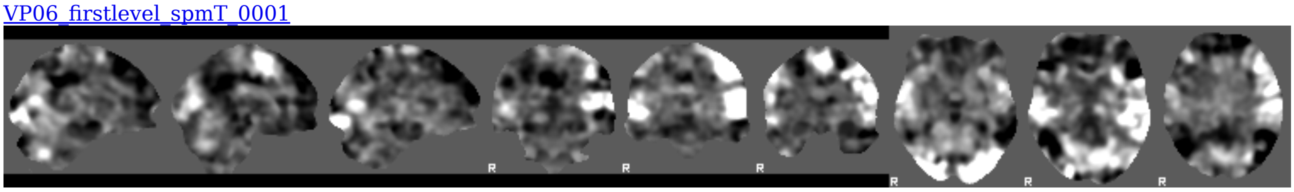

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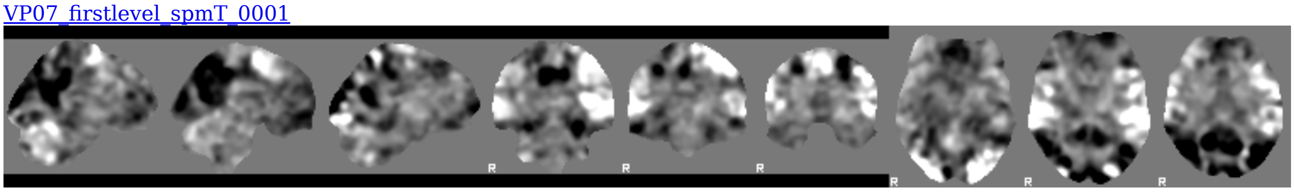

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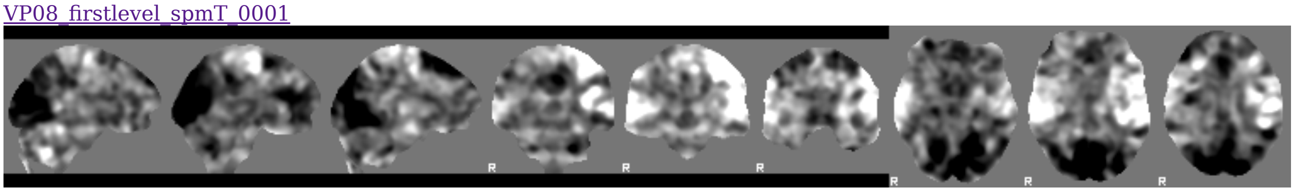

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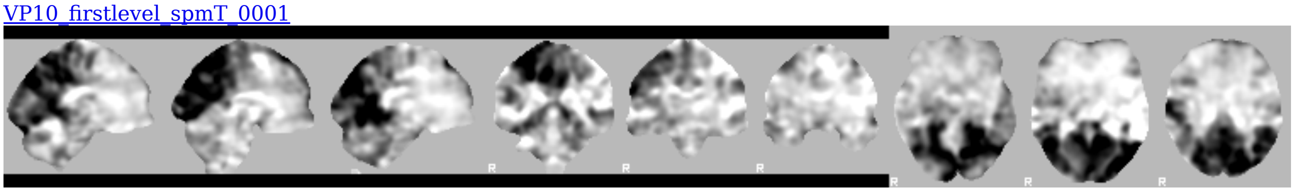

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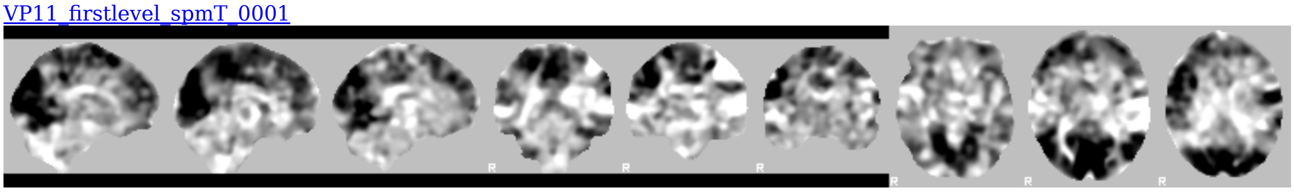

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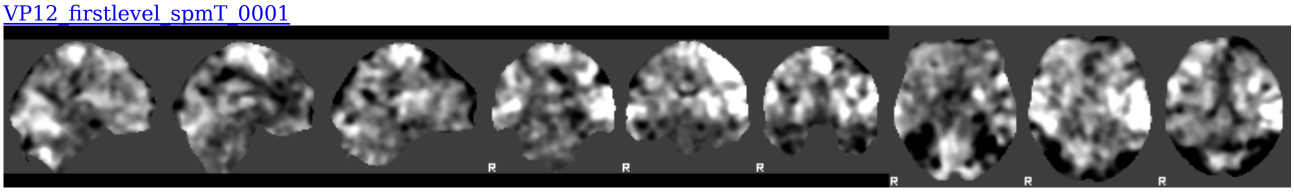

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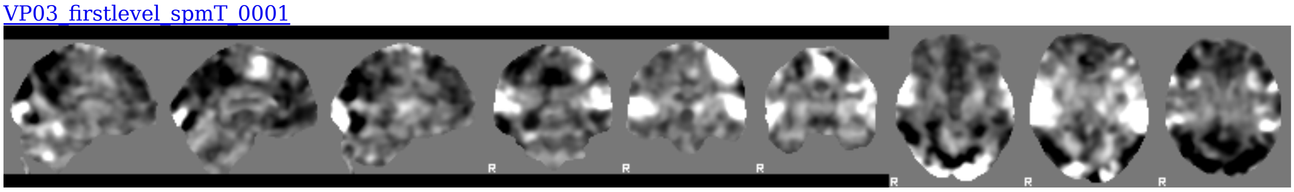

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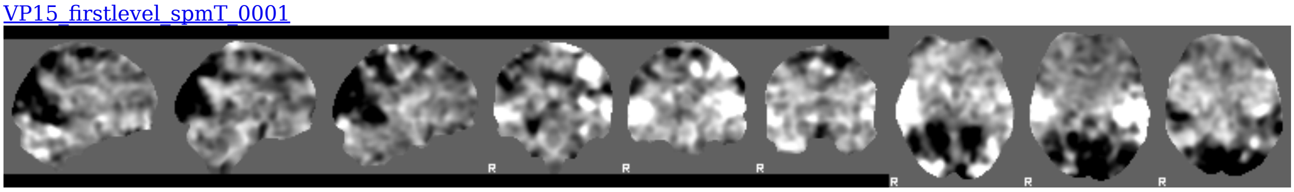

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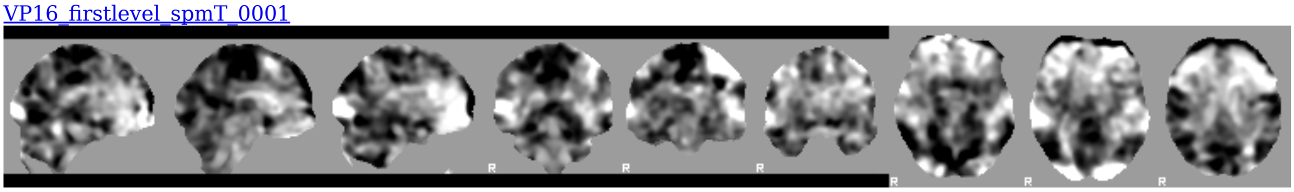
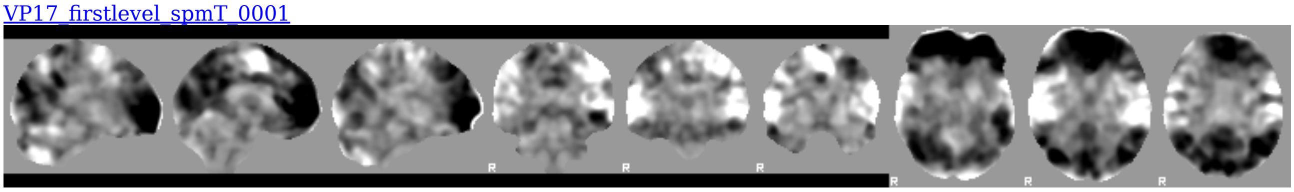
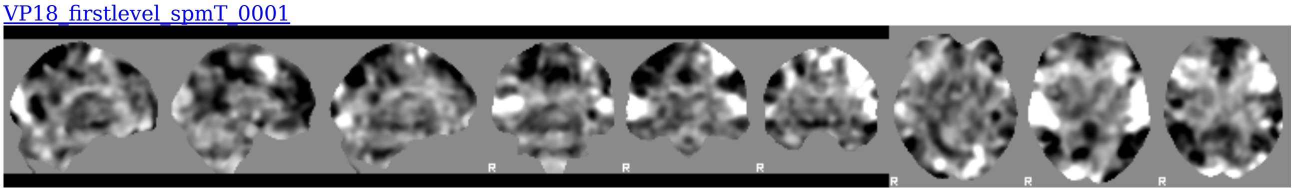


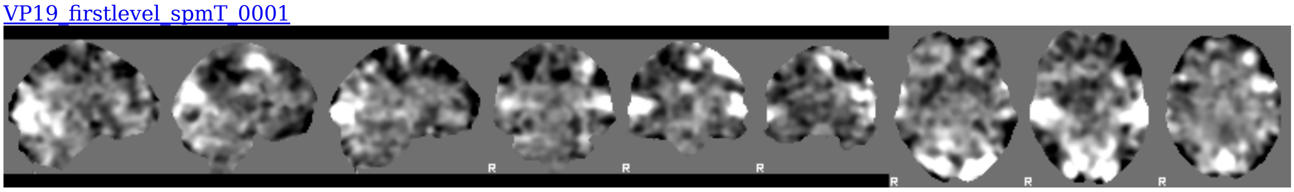
VP17_firstlevel_spmT_0001



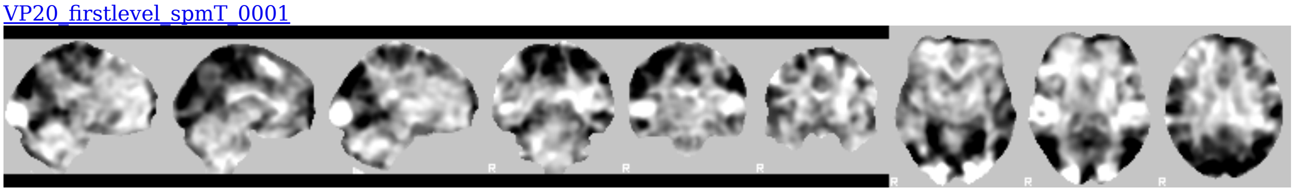
VP18_firstlevel_spmT_0001



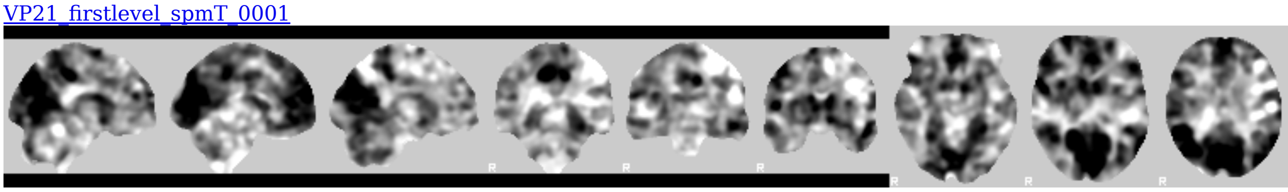
VP19_firstlevel_spmT_0001



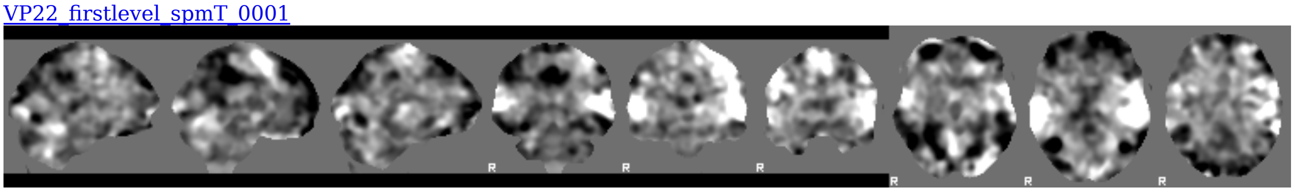
VP20_firstlevel_spmT_0001



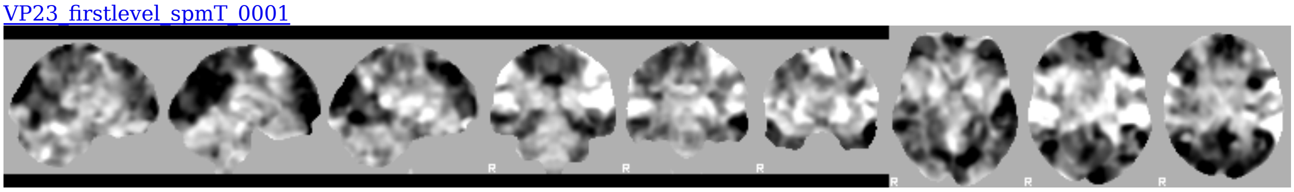
VP21_firstlevel_spmT_0001



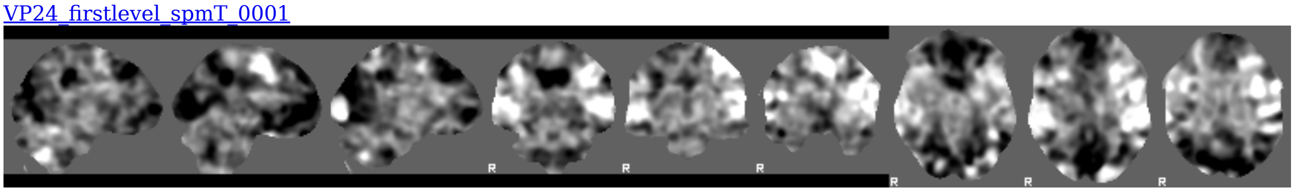
VP22_firstlevel_spmT_0001



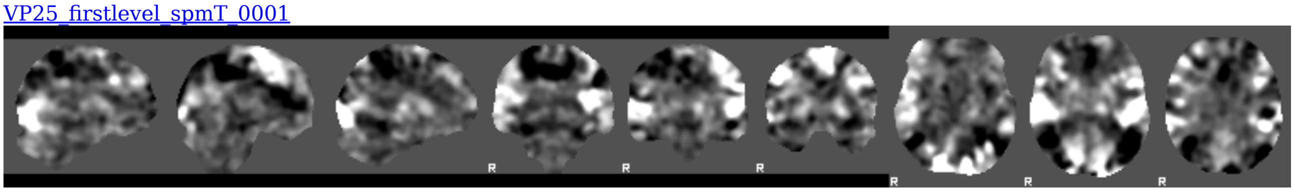
VP23_firstlevel_spmT_0001



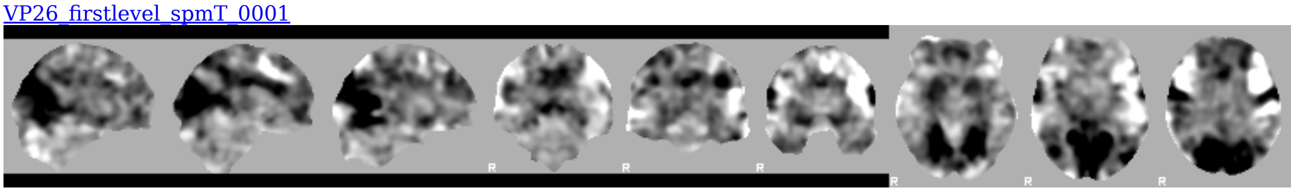
VP24_firstlevel_spmT_0001



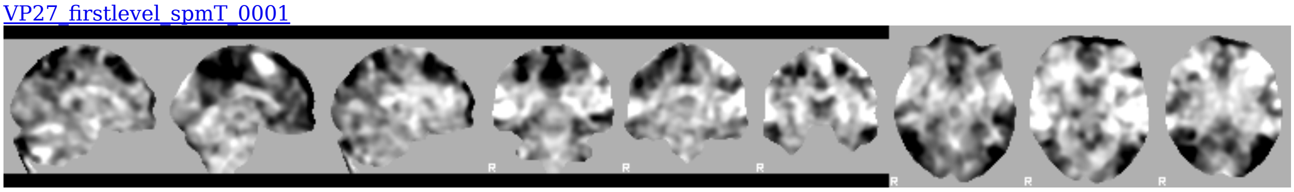
VP25_firstlevel_spmT_0001



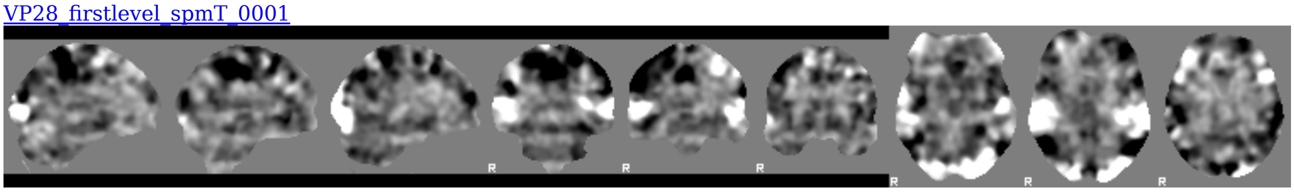
VP26_firstlevel_spmT_0001



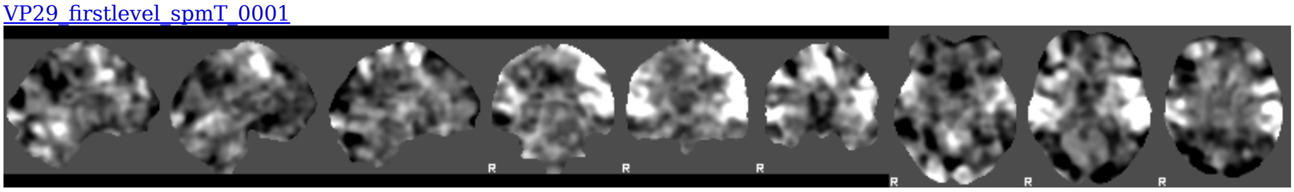
VP27_firstlevel_spmT_0001



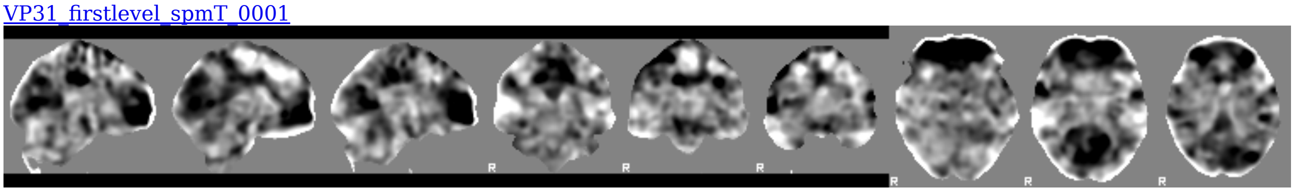
VP28_firstlevel_spmT_0001



VP29_firstlevel_spmT_0001

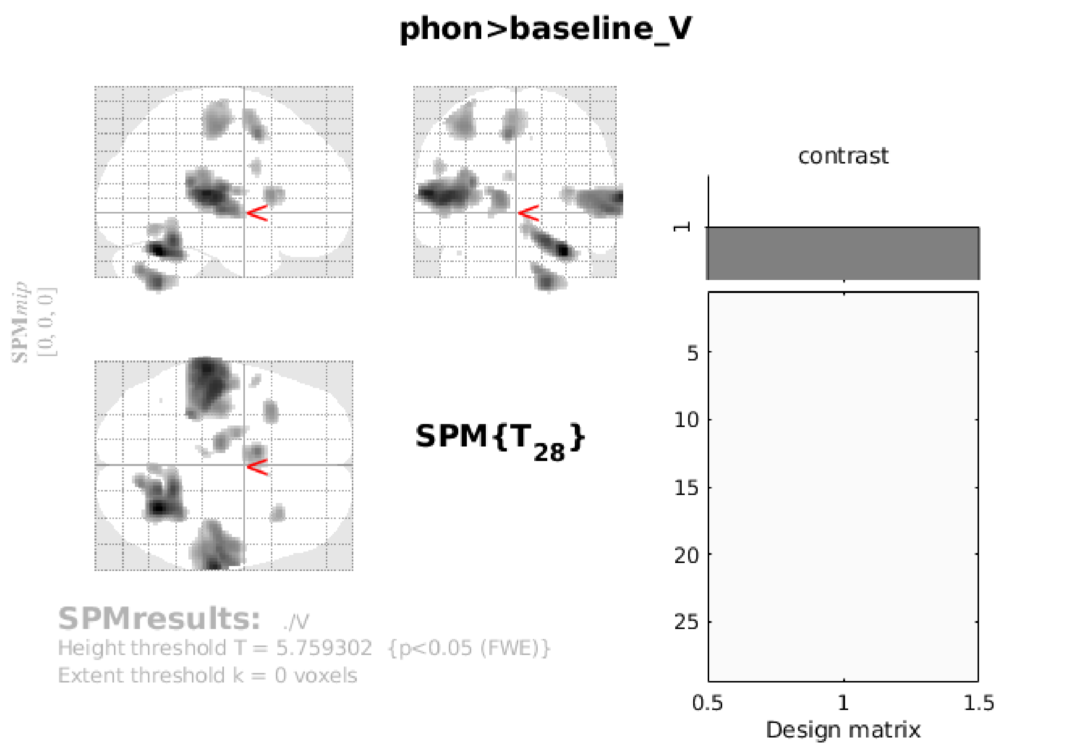


VP31_firstlevel_spmT_0001



VP32_firstlevel_spmT_0001

Figure S2. Results table of the contrast phoneme>baseline in the vertex stimulation condition.



Statistics: ***p-values adjusted for search volume***

set-level		cluster-level				peak-level							
p	c	$p_{FWE\text{-}corr}$	$q_{FDR\text{-}corr}$	k_E	p_{uncorr}	$p_{FWE\text{-}corr}$	$q_{FDR\text{-}corr}$	T	$(Z_{\equiv})$	p_{uncorr}	mm	mm	mm
0.000	13	0.000	0.000	714	0.000	0.000	0.000	12.93	7.32	0.000	30	-60	-26
						0.000	0.000	10.46	6.62	0.000	18	-50	-20
						0.001	0.035	7.43	5.48	0.000	4	-62	-12
		0.000	0.000	1886	0.000	0.000	0.000	11.80	7.02	0.000	-60	-28	10
						0.000	0.000	11.23	6.86	0.000	-50	-22	6
						0.000	0.000	10.17	6.53	0.000	-58	-18	12
		0.000	0.000	1262	0.000	0.000	0.000	11.45	6.92	0.000	68	-22	8
						0.000	0.001	9.83	6.41	0.000	62	-16	0
						0.000	0.003	8.99	6.12	0.000	50	-20	8
		0.000	0.000	396	0.000	0.000	0.000	10.12	6.51	0.000	18	-60	-46
						0.000	0.005	8.57	5.96	0.000	14	-72	-40
		0.000	0.000	276	0.000	0.000	0.003	8.99	6.12	0.000	-6	6	50
						0.001	0.022	7.69	5.59	0.000	-4	2	58
		0.000	0.000	258	0.000	0.000	0.004	8.66	5.99	0.000	-12	-18	6
						0.001	0.020	7.76	5.62	0.000	-18	-8	12
		0.000	0.000	535	0.000	0.000	0.006	8.45	5.91	0.000	-38	-22	54
						0.002	0.047	7.26	5.40	0.000	-34	-18	68
		0.000	0.000	144	0.000	0.000	0.008	8.23	5.82	0.000	-34	16	10
		0.000	0.004	73	0.003	0.001	0.024	7.62	5.56	0.000	34	20	12
		0.002	0.047	31	0.036	0.004	0.086	6.96	5.26	0.000	-54	6	28
		0.006	0.128	17	0.109	0.004	0.090	6.92	5.24	0.000	-6	-28	22
		0.036	0.715	1	0.715	0.047	0.971	5.79	4.66	0.000	-40	-58	-28

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 5.76, p = 0.000 (0.050)
Extent threshold: k = 0 voxels
Expected voxels per cluster, <k> = 6.831
Expected number of clusters, <c> = 0.05
FWEp: 5.759, FDRp: 7.258, FWEc: 1, FDRc: 31

Degrees of freedom = [1.0, 28.0]
FWHM = 14.9 14.4 13.8 mm mm mm; 7.5 7.2 6.9 {voxels}
Volume: 1487984 = 185998 voxels = 465.6 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 370.23 voxels)
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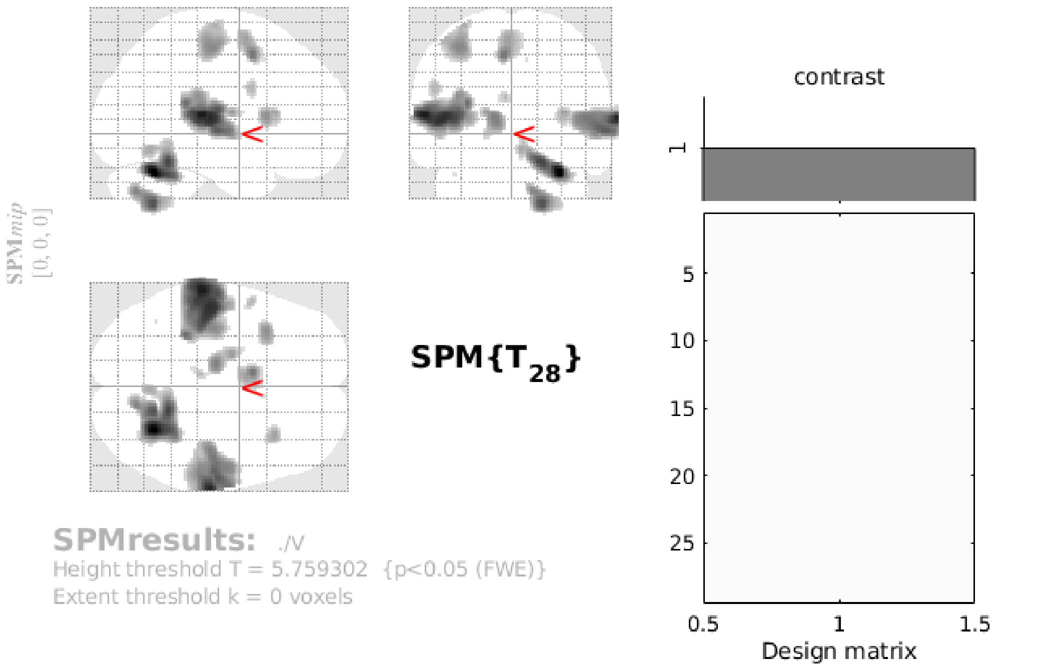
phon>baseline_V



Statistics: ***p-values adjusted for search volume***

set-level		cluster-level				peak-level					mm mm mm
p	c	$p_{FWE-corr}$	$q_{FDR-corr}$	k_E	p_{uncorr}	$p_{FWE-corr}$	$q_{FDR-corr}$	T	$(Z_{\equiv})$	p_{uncorr}	
		0.036	0.715	1	0.715	0.050	1.000	5.76	4.64	0.000	8 14 46

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 5.76, p = 0.000 (0.050)
Extent threshold: k = 0 voxels
Expected voxels per cluster, <k> = 6.831
Expected number of clusters, <c> = 0.05
FWEp: 5.759, FDRp: 7.258, FWEc: 1, FDRc: 31

Degrees of freedom = [1.0, 28.0]
FWHM = 14.9 14.4 13.8 mm mm mm; 7.5 7.2 6.9 {voxels}
Volume: 1487984 = 185998 voxels = 465.6 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 370.23 voxels)
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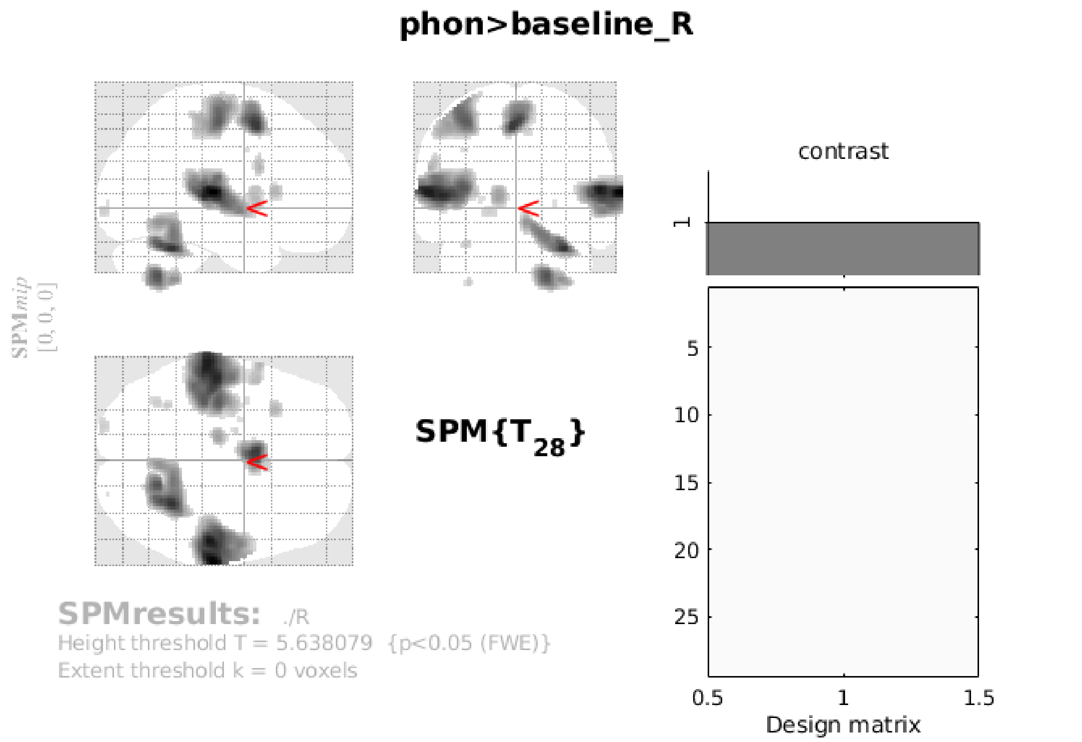
Figure S3. Results table of the contrast phoneme>baseline in the right pSTS stimulation condition.



Statistics: ***p-values adjusted for search volume***

set-level		cluster-level				peak-level							
p	c	$p_{FWE-corr}$	$q_{FDR-corr}$	k_E	p_{uncorr}	$p_{FWE-corr}$	$q_{FDR-corr}$	T	$(Z_{\equiv})$	p_{uncorr}	mm	mm	mm
0.000	16	0.000	0.000	1572	0.000	0.000	0.000	13.66	7.49	0.000	68	-22	8
						0.000	0.000	12.58	7.23	0.000	54	-26	10
						0.000	0.002	8.89	6.08	0.000	56	-6	-4
		0.000	0.000	2230	0.000	0.000	0.000	12.49	7.21	0.000	-62	-26	8
						0.000	0.000	12.03	7.08	0.000	-52	-22	6
						0.000	0.000	10.40	6.60	0.000	-38	-30	12
		0.000	0.000	801	0.000	0.000	0.000	11.62	6.97	0.000	30	-50	-28
						0.000	0.000	10.59	6.66	0.000	28	-58	-26
						0.000	0.001	9.28	6.22	0.000	16	-50	-20
		0.000	0.000	617	0.000	0.000	0.000	11.33	6.89	0.000	-4	6	52
		0.000	0.000	464	0.000	0.000	0.000	10.46	6.62	0.000	18	-60	-46
						0.000	0.006	8.30	5.85	0.000	28	-50	-48
		0.000	0.000	1049	0.000	0.000	0.000	10.23	6.55	0.000	-36	-20	54
						0.000	0.013	7.88	5.68	0.000	-48	-26	52
		0.000	0.004	116	0.002	0.000	0.013	7.85	5.66	0.000	-14	-20	6
		0.002	0.064	44	0.036	0.002	0.043	7.23	5.39	0.000	-60	8	24
		0.000	0.015	78	0.008	0.002	0.053	7.11	5.33	0.000	-32	18	8
		0.015	0.387	10	0.290	0.009	0.228	6.41	4.99	0.000	-34	-54	-50
		0.011	0.309	14	0.213	0.012	0.288	6.28	4.92	0.000	-36	-60	-26
		0.005	0.145	27	0.091	0.013	0.288	6.26	4.91	0.000	-20	-98	-4
		0.026	0.584	4	0.511	0.023	0.511	5.99	4.77	0.000	-16	-8	-4
		0.033	0.655	2	0.655	0.039	0.831	5.75	4.64	0.000	24	-94	0

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 5.64, p = 0.000 (0.050)
Extent threshold: k = 0 voxels
Expected voxels per cluster, <k> = 9.657
Expected number of clusters, <c> = 0.05
FWEp: 5.638, FDRp: 7.234, FWEc: 2, FDRc: 78

Degrees of freedom = [1.0, 28.0]
FWHM = 16.2 16.0 15.1 mm mm mm; 8.1 8.0 7.6 {voxels}
Volume: 1487984 = 185998 voxels = 351.2 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 490.85 voxels)
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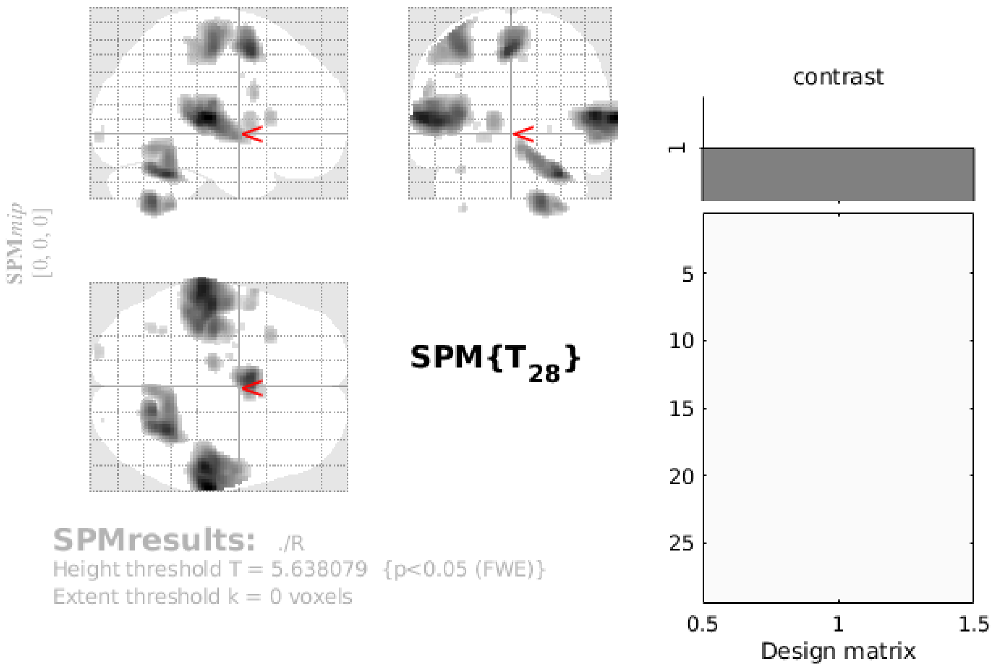
phon>baseline_R



Statistics: ***p-values adjusted for search volume***

set-level		cluster-level				peak-level							
p	c	$p_{FWE-corr}$	$q_{FDR-corr}$	k_E	p_{uncorr}	$p_{FWE-corr}$	$q_{FDR-corr}$	T	$(Z_{\equiv})$	p_{uncorr}	mm	mm	mm
		0.026	0.584	4	0.511	0.041	0.846	5.73	4.62	0.000	-26	-6	4
		0.033	0.655	2	0.655	0.043	0.862	5.71	4.61	0.000	-36	0	36

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 5.64, p = 0.000 (0.050)
Extent threshold: k = 0 voxels
Expected voxels per cluster, <k> = 9.657
Expected number of clusters, <c> = 0.05
FWEp: 5.638, FDRp: 7.234, FWEc: 2, FDRc: 78

Degrees of freedom = [1.0, 28.0]
FWHM = 16.2 16.0 15.1 mm mm mm; 8.1 8.0 7.6 {voxels}
Volume: 1487984 = 185998 voxels = 351.2 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 490.85 voxels)
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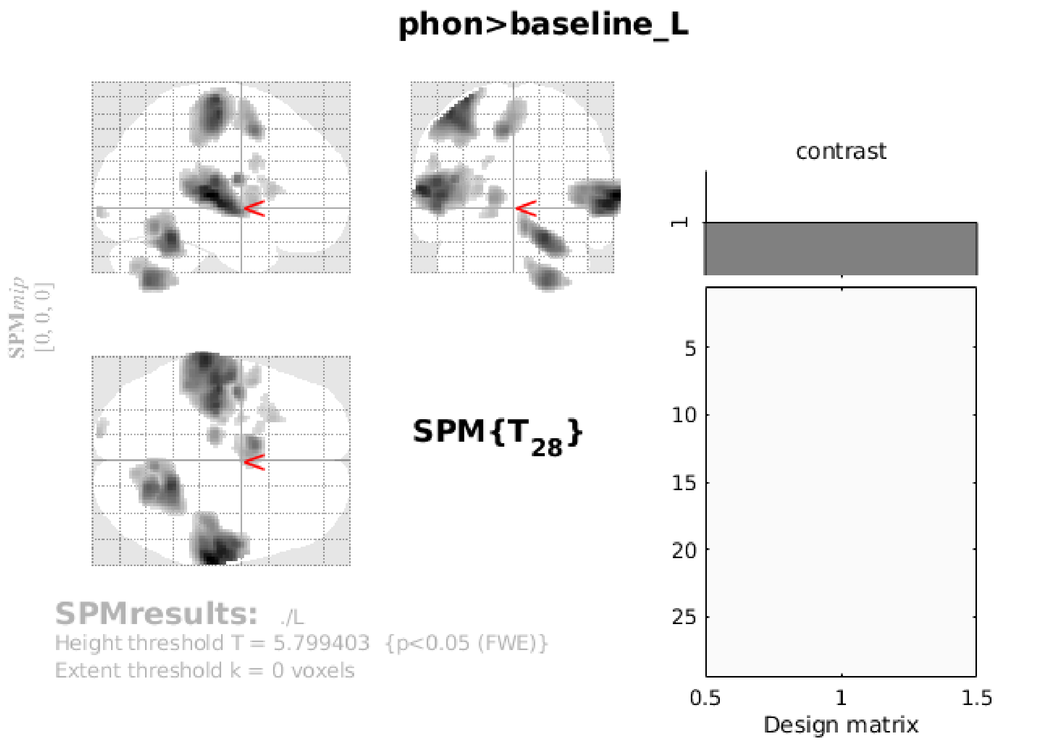
Figure S4. Results table of the contrast phoneme>baseline in the left pSTS stimulation condition.



Statistics: ***p-values adjusted for search volume***

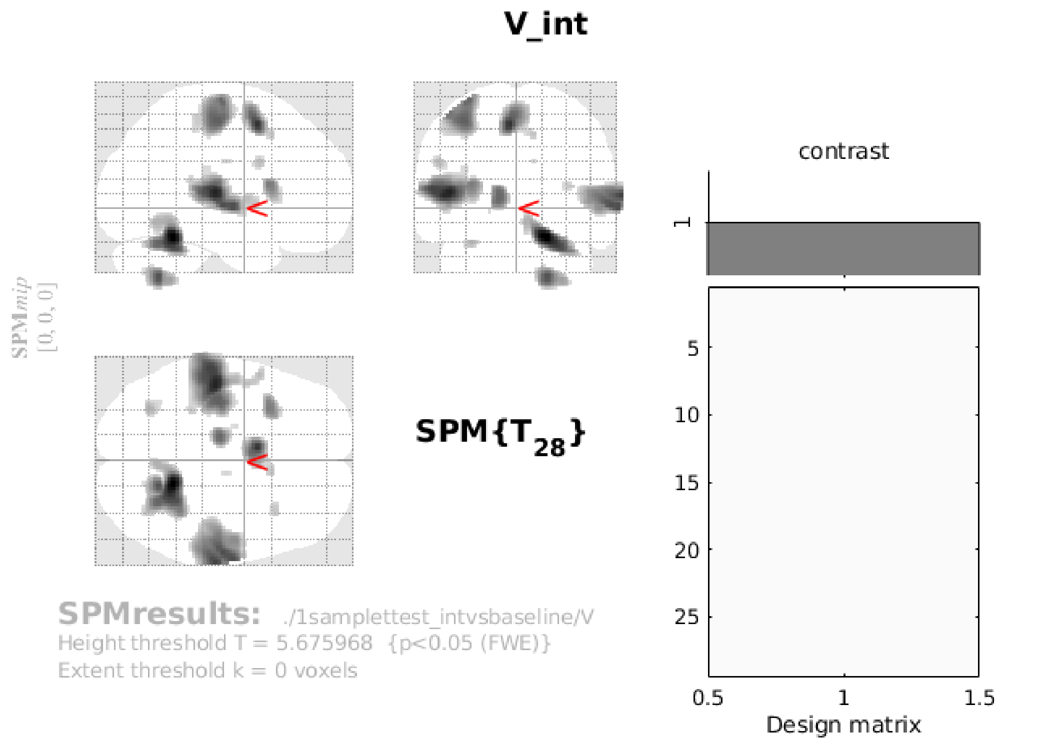
set-level		cluster-level				peak-level					mm	mm	mm
p	c	$p_{FWE-corr}$	$q_{FDR-corr}$	k_E	p_{uncorr}	$p_{FWE-corr}$	$q_{FDR-corr}$	T	$(Z_\equiv)$	p_{uncorr}			
0.000	12	0.000	0.000	1697	0.000	0.000	0.000	15.17	7.82	0.000	68	-22	6
						0.000	0.000	13.76	7.52	0.000	62	-16	2
						0.000	0.000	11.64	6.98	0.000	56	-8	-4
		0.000	0.000	2574	0.000	0.000	0.000	13.30	7.41	0.000	-64	-26	10
						0.000	0.000	12.32	7.16	0.000	-52	-20	6
						0.000	0.000	11.90	7.05	0.000	-52	-20	16
		0.000	0.000	1444	0.000	0.000	0.000	12.70	7.26	0.000	-44	-18	60
						0.000	0.000	12.32	7.16	0.000	-34	-20	68
						0.001	0.017	7.86	5.67	0.000	-38	-32	42
		0.000	0.000	776	0.000	0.000	0.000	12.43	7.19	0.000	18	-50	-22
						0.000	0.001	9.34	6.24	0.000	6	-60	-14
		0.000	0.000	712	0.000	0.000	0.000	11.11	6.82	0.000	20	-64	-50
						0.001	0.026	7.66	5.58	0.000	10	-72	-40
						0.002	0.043	7.37	5.45	0.000	34	-48	-50
		0.000	0.000	472	0.000	0.000	0.000	10.25	6.56	0.000	-8	6	48
		0.000	0.000	129	0.000	0.000	0.003	8.69	6.00	0.000	-14	-20	4
		0.000	0.000	112	0.000	0.002	0.055	7.23	5.39	0.000	-26	20	10
						0.013	0.269	6.42	4.99	0.000	-32	12	16
		0.001	0.017	42	0.013	0.002	0.058	7.18	5.36	0.000	-16	-98	-6
		0.001	0.023	36	0.019	0.004	0.087	6.98	5.27	0.000	-56	8	28
		0.003	0.069	21	0.063	0.006	0.129	6.77	5.17	0.000	-26	-2	18
		0.004	0.069	20	0.069	0.015	0.303	6.35	4.96	0.000	-18	10	30

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 5.80, p = 0.000 (0.050)
Extent threshold: k = 0 voxels
Expected voxels per cluster, <k> = 6.096
Expected number of clusters, <c> = 0.05
FWEp: 5.799, FDRp: 7.342, FWEc: 20, FDRc: 36

Degrees of freedom = [1.0, 28.0]
FWHM = 14.4 14.0 13.3 mm mm mm; 7.2 7.0 6.7 {voxels}
Volume: 1487984 = 185998 voxels = 510.9 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 337.35 voxels)

Figure S5. Results table of the contrast prosody>baseline in the vertex stimulation condition.



Statistics: ***p-values adjusted for search volume***

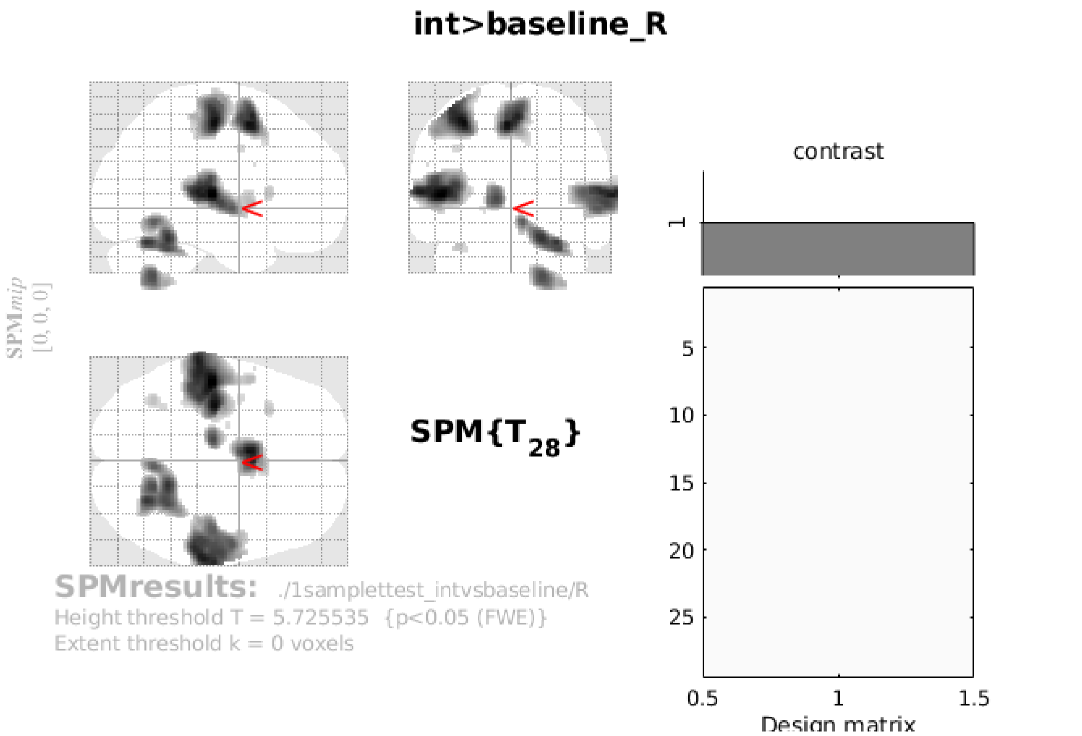
set-level p	set-level c	cluster-level $p_{FWE-corr}$	cluster-level $q_{FDR-corr}$	cluster-level k_E	cluster-level p_{uncorr}	peak-level $p_{FWE-corr}$	peak-level $q_{FDR-corr}$	peak-level T	peak-level $(Z_{\equiv})$	peak-level p_{uncorr}	mm	mm	mm
0.000	13	0.000	0.000	681	0.000	0.000	0.000	12.28	7.15	0.000	16	-50	-20
						0.003	0.082	6.99	5.27	0.000	4	-60	-12
		0.000	0.000	1357	0.000	0.000	0.000	11.09	6.82	0.000	-46	-22	8
						0.000	0.000	10.15	6.52	0.000	-58	-24	10
						0.006	0.168	6.61	5.09	0.000	-48	0	4
		0.000	0.000	411	0.000	0.000	0.000	10.61	6.67	0.000	-6	6	52
						0.010	0.243	6.40	4.98	0.000	8	16	46
		0.000	0.000	1104	0.000	0.000	0.000	10.12	6.51	0.000	68	-22	6
						0.000	0.001	9.83	6.42	0.000	66	-10	-2
						0.000	0.001	9.52	6.31	0.000	58	-20	2
		0.000	0.000	303	0.000	0.000	0.001	9.61	6.34	0.000	18	-60	-46
						0.001	0.031	7.48	5.50	0.000	28	-54	-48
		0.000	0.000	840	0.000	0.000	0.001	9.36	6.25	0.000	-38	-22	54
						0.000	0.002	9.07	6.15	0.000	-34	-18	68
						0.000	0.003	8.70	6.00	0.000	-46	-22	60
		0.000	0.000	185	0.000	0.000	0.002	9.08	6.15	0.000	-14	-18	4
		0.000	0.000	181	0.000	0.000	0.004	8.50	5.93	0.000	-32	14	14
		0.002	0.063	36	0.044	0.002	0.075	7.05	5.30	0.000	-32	-66	-24
		0.003	0.087	29	0.067	0.004	0.114	6.81	5.19	0.000	-54	8	28
		0.005	0.125	22	0.105	0.009	0.227	6.46	5.01	0.000	34	18	12
		0.028	0.597	3	0.551	0.026	0.557	5.97	4.76	0.000	10	-14	28
		0.032	0.634	2	0.634	0.032	0.655	5.88	4.71	0.000	-20	-8	-4

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 5.68, p = 0.000 (0.050)
Extent threshold: k = 0 voxels
Expected voxels per cluster, <k> = 8.664
Expected number of clusters, <c> = 0.05
FWEp: 5.676, FDRp: 7.481, FWEc: 2, FDRc: 181

Degrees of freedom = [1.0, 28.0]
FWHM = 15.9 15.5 14.7 mm mm mm; 7.9 7.7 7.3 {voxels}
Volume: 1487984 = 185998 voxels = 383.6 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 449.37 voxels)

Figure S6. Results table of the contrast prosody>baseline in the right pSTS stimulation condition.



Statistics: ***p-values adjusted for search volume***

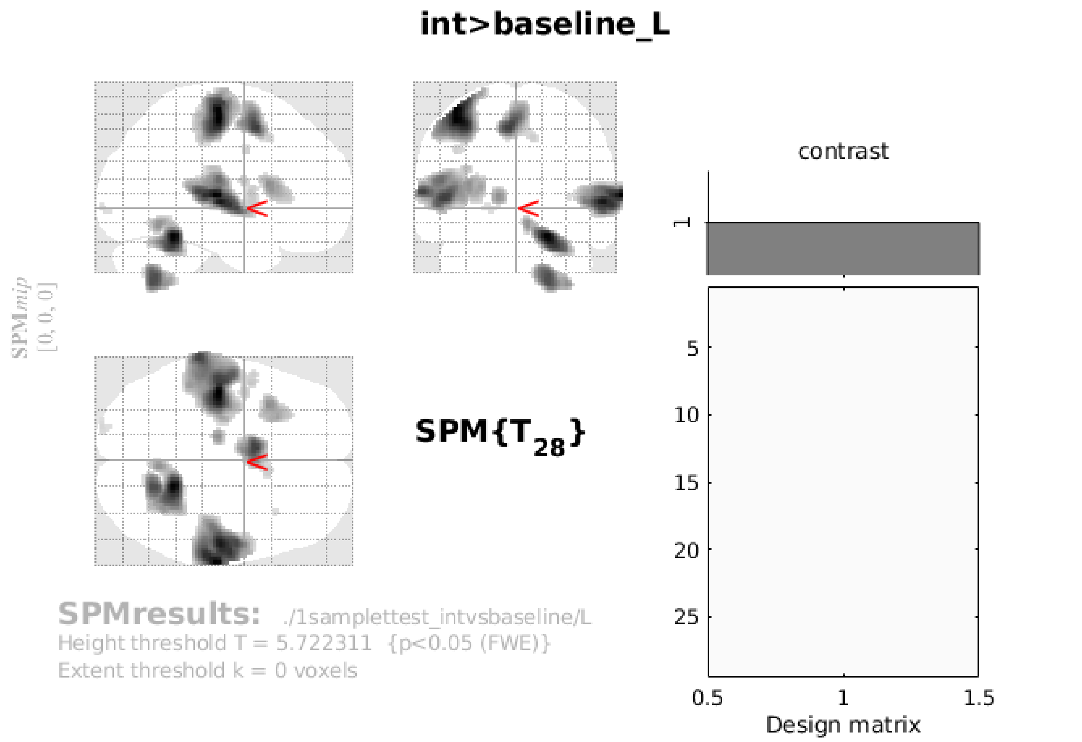
set-level		cluster-level				peak-level					mm mm mm		
p	c	$p_{FWE-corr}$	$q_{FDR-corr}$	k_E	p_{uncorr}	$p_{FWE-corr}$	$q_{FDR-corr}$	T	$(Z_{\equiv})$	p_{uncorr}			
0.000	12	0.000	0.000	1718	0.000	0.000	0.000	11.47	6.93	0.000	-50	-20	6
						0.000	0.000	10.64	6.68	0.000	-62	-30	8
						0.000	0.000	9.82	6.41	0.000	-40	-28	12
		0.000	0.000	1087	0.000	0.000	0.000	11.01	6.79	0.000	-34	-18	54
						0.001	0.021	7.66	5.58	0.000	-52	-22	48
						0.004	0.113	6.83	5.20	0.000	-48	-34	58
		0.000	0.000	751	0.000	0.000	0.000	10.93	6.77	0.000	-4	4	52
						0.000	0.000	10.42	6.61	0.000	2	6	58
		0.000	0.000	1336	0.000	0.000	0.000	10.59	6.66	0.000	66	-26	6
						0.000	0.000	10.25	6.56	0.000	58	-32	8
						0.000	0.001	9.61	6.34	0.000	62	-16	2
		0.000	0.000	680	0.000	0.000	0.000	9.97	6.46	0.000	18	-50	-22
						0.000	0.000	9.94	6.45	0.000	28	-64	-24
						0.000	0.001	9.39	6.26	0.000	30	-50	-28
		0.000	0.000	216	0.000	0.000	0.001	9.36	6.25	0.000	-12	-20	4
		0.000	0.000	399	0.000	0.000	0.001	9.31	6.23	0.000	18	-60	-46
						0.003	0.074	7.05	5.30	0.000	32	-52	-52
		0.003	0.068	29	0.051	0.010	0.231	6.47	5.02	0.000	-38	-60	-26
						0.028	0.620	5.99	4.77	0.000	-32	-54	-28
		0.002	0.055	34	0.037	0.011	0.253	6.41	4.99	0.000	-32	18	8
		0.014	0.340	8	0.284	0.030	0.630	5.97	4.75	0.000	-38	0	36
		0.026	0.567	3	0.519	0.034	0.707	5.90	4.72	0.000	-20	-10	-2
		0.037	0.730	1	0.730	0.039	0.769	5.84	4.69	0.000	-58	8	26

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 5.73, p = 0.000 (0.050)
Extent threshold: k = 0 voxels
Expected voxels per cluster, <k> = 7.520
Expected number of clusters, <c> = 0.05
FWEp: 5.726, FDRp: 7.656, FWEc: 1, FDRc: 216

Degrees of freedom = [1.0, 28.0]
FWHM = 15.1 15.0 14.2 mm mm mm; 7.5 7.5 7.1 {voxels}
Volume: 1487984 = 185998 voxels = 430.5 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 400.40 voxels)

Figure S7. Results table of the contrast prosody>baseline in the left pSTS stimulation condition.



Statistics: ***p-values adjusted for search volume***

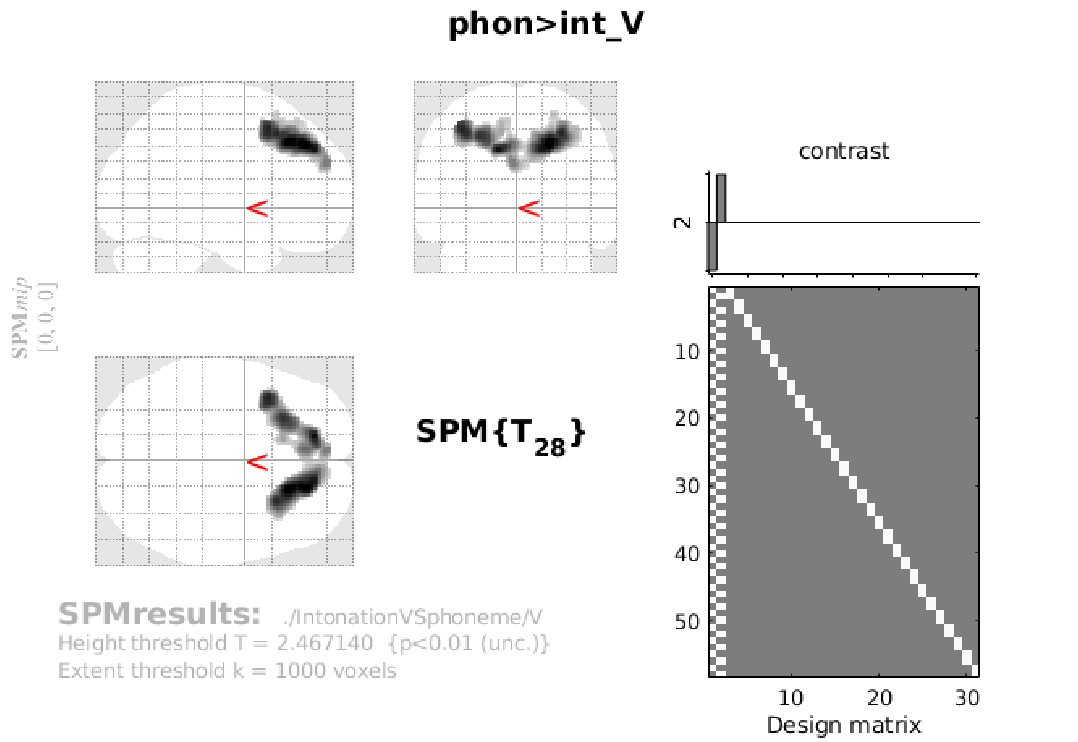
set-level p	set-level c	cluster-level $p_{FWE-corr}$	cluster-level $q_{FDR-corr}$	cluster-level k_E	cluster-level p_{uncorr}	peak-level $p_{FWE-corr}$	peak-level $q_{FDR-corr}$	peak-level T	peak-level $(Z_{\equiv})$	peak-level p_{uncorr}	mm	mm	mm
0.000	12	0.000	0.000	1306	0.000	0.000	0.000	13.03	7.34	0.000	-42	-20	56
						0.001	0.019	7.74	5.61	0.000	-26	-18	72
		0.000	0.000	1375	0.000	0.000	0.000	12.77	7.28	0.000	68	-22	6
						0.000	0.000	12.03	7.08	0.000	56	-18	2
						0.000	0.000	11.23	6.86	0.000	62	-12	0
		0.000	0.000	638	0.000	0.000	0.000	12.71	7.26	0.000	18	-50	-20
						0.000	0.009	8.12	5.77	0.000	6	-60	-14
		0.000	0.000	1854	0.000	0.000	0.000	10.77	6.72	0.000	-50	-20	4
						0.000	0.000	10.60	6.67	0.000	-64	-32	8
						0.000	0.001	9.34	6.25	0.000	-52	-20	16
		0.000	0.000	569	0.000	0.000	0.000	10.76	6.72	0.000	-6	6	50
						0.016	0.372	6.25	4.90	0.000	8	14	44
		0.000	0.000	474	0.000	0.000	0.000	10.29	6.57	0.000	20	-62	-48
						0.000	0.009	8.18	5.80	0.000	32	-56	-52
		0.000	0.000	344	0.000	0.000	0.009	8.18	5.80	0.000	-34	14	14
						0.001	0.022	7.65	5.57	0.000	-26	20	12
		0.000	0.007	72	0.004	0.000	0.009	8.17	5.79	0.000	-14	-20	6
		0.004	0.092	25	0.069	0.006	0.162	6.68	5.12	0.000	-42	-2	16
		0.012	0.255	10	0.234	0.019	0.410	6.17	4.86	0.000	-42	0	36
		0.008	0.179	15	0.149	0.028	0.597	5.99	4.76	0.000	-20	-98	-2
		0.023	0.454	4	0.454	0.041	0.840	5.82	4.67	0.000	34	18	6

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 5.72, p = 0.000 (0.050)
Extent threshold: k = 0 voxels
Expected voxels per cluster, <k> = 7.590
Expected number of clusters, <c> = 0.05
FWEp: 5.722, FDRp: 7.646, FWEc: 4, FDRc: 72

Degrees of freedom = [1.0, 28.0]
FWHM = 15.4 14.7 14.2 mm mm mm; 7.7 7.4 7.1 {voxels}
Volume: 1487984 = 185998 voxels = 427.2 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 403.45 voxels)

Figure S8. Results table of the contrast phoneme>prosody in the vertex stimulation condition.



Statistics: ***p-values adjusted for search volume***

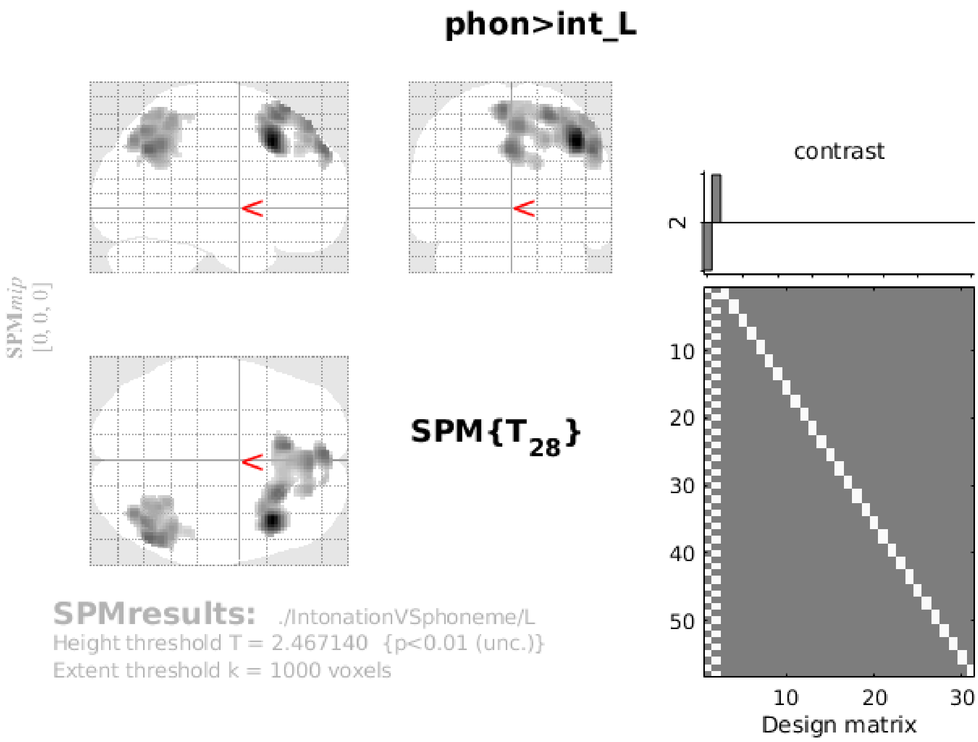
cluster-level				peak-level					mm mm mm
$p_{FWE-corr}$	$q_{FDR-corr}$	k_E	p_{uncorr}	$p_{FWE-corr}$	$q_{FDR-corr}$	T	$(Z_{\equiv})$	p_{uncorr}	
0.003	0.005	2374	0.000	0.673	0.565	4.22	3.68	0.000	20 28 42
				0.677	0.565	4.22	3.68	0.000	20 40 38
				0.799	0.565	4.04	3.56	0.000	-14 44 36

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 2.47, p = 0.010 (1.000)
Extent threshold: k = 1000 voxels, p = 0.007 (0.134)
Expected voxels per cluster, <k> = 117.861
Expected number of clusters, <c> = 0.14
FWEp: 5.655, FDRp: Inf, FWEc: 2374, FDRc: 2374

Degrees of freedom = [1.0, 28.0]
FWHM = 16.3 15.9 14.6 mm mm mm; 8.1 7.9 7.3 {voxels}
Volume: 1487984 = 185998 voxels = 365.5 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 471.56 voxels)

Figure S9. Results table of the contrast phoneme>prosody in the left pSTS stimulation condition.



Statistics: ***p-values adjusted for search volume***

set-level		cluster-level				peak-level					mm mm mm		
p	c	$p_{FWE-corr}$	$q_{FDR-corr}$	k_E	p_{uncorr}	$p_{FWE-corr}$	$q_{FDR-corr}$	T	$(Z_\equiv)$	p_{uncorr}			
0.013	2	0.016	0.037	1825	0.001	0.037	0.197	5.77	4.64	0.000	42	20	42
						0.709	0.674	4.14	3.63	0.000	22	24	58
						0.736	0.674	4.10	3.60	0.000	-2	54	36
		0.032	0.038	1556	0.002	0.629	0.674	4.25	3.70	0.000	52	-62	36
						0.836	0.674	3.95	3.49	0.000	54	-54	40
						0.908	0.674	3.81	3.39	0.000	42	-66	48

table shows 3 local maxima more than 8.0mm apart

Height threshold: T = 2.47, p = 0.010 (1.000)
Extent threshold: k = 1000 voxels, p = 0.008 (0.157)
Expected voxels per cluster, <k> = 126.667
Expected number of clusters, <c> = 0.17
FWEp: 5.624, FDRp: Inf, FWEc: 1556, FDRc: 1556

Degrees of freedom = [1.0, 28.0]
FWHM = 16.7 16.1 15.0 mm mm mm; 8.4 8.1 7.5 {voxels}
Volume: 1487984 = 185998 voxels = 340.1 resels
Voxel size: 2.0 2.0 2.0 mm mm mm; (resel = 506.79 voxels)

Figure S10. Averaged coordinates of the peak activation in the six baseline contrasts.

Area	x (mm)	y (mm)	z (mm)
Right cerebellum exterior	17.33	-50	-20.67
Right cerebellum exterior (ventral)	18.67	-61	-47
Right AC lateral	67.67	-22.66	6.67
Right AC medial	52.67	-19	4.33
Right insula	29.2	21.6	12
Right IFG	50	14	7
Left AC lateral	-61.67	-27.67	8.8
Left AC medial	-50	-21	6
Left thalamus proper	-13.33	-19.33	5
Left insula	-32.5	17.2	10
Left IFG	-55.33	7.33	27.33
Left SMA (ventral)	-5.67	5.67	50.67
Left MC, (medial)	-37.67	-22.33	52.33
Left MC (lateral)	-42	-20.5	60.5
Left cerebellum exterior	-37.2	-61.6	-26
Left cerebellum exterior	-35.2	-54.4	-28.4
Left pallidum	-18.67	-8.67	-3.33
Left V1	-18	-98	-4