Sensory-Motor Brain Network Connectivity for Speech Comprehension

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Abstract: The act of listening to speech activates a large network of brain areas. In the present work, a novel data-driven technique (the combination of independent component analysis and Granger causality) was used to extract brain network dynamics from an fMRI study of passive listening to Words, Pseudo-Words, and Reverse-played words. Using this method we show the functional connectivity modulations among classical language regions (Broca's and Wernicke's areas) and inferior parietal, somatosensory, and motor areas and right cerebellum. Word listening elicited a compact pattern of connectivity within a parieto-somato-motor network and between the superior temporal and inferior frontal gyri. Pseudo-Word stimuli induced activities similar to the Word condition, which were characterized by a highly recurrent connectivity pattern, mostly driven by the temporal lobe activity. Also the Reversed-Word condition revealed an important influence of temporal cortices, but no integrated activity of the parieto-somato-motor network. In parallel, the right cerebellum lost its functional connection with motor areas, present in both Word and Pseudo-Word listening. The inability of the participant to produce the Reversed-Word stimuli also evidenced two separate networks: the first was driven by frontal areas and the right cerebellum toward somatosensory cortices; the second was triggered by temporal and parietal sites towards motor areas. Summing up, our results suggest that semantic content modulates the general compactness of network dynamics as well as the balance between frontal and temporal language areas in driving those dynamics. The degree of reproducibility of auditory speech material modulates the connectivity pattern within and toward somatosensory and motor areas. *Hum Brain Mapp* 31:567–580, 2010. © 2009 Wiley-Liss, Inc.

Key words: speech perception; language network; motor theory of speech perception; granger causality; independent component analysis; fMRI; brain functional connectivity
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INTRODUCTION

Classic aphasiology research has shown an anterior-posterior distinction in characterizing speech-related brain areas. Anterior sites (Broca's area) have been associated with motor production, while posterior areas (Wernicke's area) with receptive functions [Lichtheim, 1885; Wernicke, 1874]. This basic model has been challenged since the early stages of neuropsychological research by other less modular and more integrated views [Berker et al., 1986]. More recently, neuroimaging and neurophysiological works showed that areas classically thought to be involved in motor production might be recruited also in speech perception and language comprehension [D'Ausilio et al., 2009; Fadiga et al., 2002; Meister et al., 2007; Pulvermüller et al., 2006; Sato et al., in press; Watkins et al., 2003; Wilson and Iacoboni, 2006]. These findings might not be surprising if one considers the brain from a network perspective. Neuropsychological [Basso et al., 1977; Moineau et al., 2005], modeling data [Guenther et al., 2006], anatomical pathways [Catani et al., 2005], and cortico-cortical functional connectivity studies [Matsumoto et al., 2004] have suggested, from very different perspectives, that the connection among posterior and anterior language sites as well as inferior parietal, somatosensory, and motor-premotor areas and the cerebellum could be critical in allowing speech comprehension and production.

The involvement of brain areas, other than sensory cortices, in speech comprehension led to a resurgence of interest for a network-oriented view of speech-related brain processing [Hickok and Poeppel, 2007]. Current models agree on the idea that perception and production of speech sounds rely on complex interactions among sensory and motor cortices. Skipper et al. [2006] suggests that anterior and posterior brain areas balance their relative importance according to environmental and contextual constraints. Similarly, Watkins et al. [2003] proposed that the speech system may perform two computations involving both anterior and posterior areas: (1) motor-to-sensory flow: motor efference copies, necessary to update the sensory systems and aid in vocal learning and control processes (see also Guenther's model on this issues [Guenther et al., 2006]); and (2) sensory-to-motor flow: sensory inputs, translated into motor coordinates to aid in speech perception. In this latter computation, the motor system might be particularly important offering at least four different contributions: (i) disambiguating degraded or noisy speech signals [D'Ausilio et al., 2009]; (ii) segmenting incoming speech units [Sato et al., in press]; (iii) enabling predictive coding of incoming information [Pickering and Garrod, 2007]; (iv) facilitating turn-taking behaviors during conversation [Scott et al., 2009].

As these hypotheses are necessarily specified in terms of the network relationship amongst areas, more typical univariate approaches to analysis are not feasible. In fact, the critical side is the lack of a satisfactory description of the relationships among the functional units belonging to the

speech perception-production network. Several possible methods have been proposed [Friston, 2002; Lee et al., 2003] to extract brain functional connectivity from fMRI data, starting from some pioneering studies in the mid-90s [Friston et al., 1993; McIntosh et al., 1994]. Most of them, however, require a large amount of a-priori knowledge during analysis [Friston et al., 2003]. This a priori knowledge consists of both the use of statistical models imposed on the data and the definition of which areas form the network to test.

Our approach instead enables the study of brain functional connectivity severely limiting the amount of a priori constraints. The spatial independent component analysis (sICA) is first used to extract the activities that are statistically independent from each other. Then, the Granger causality (GC) algorithm is applied to the associated temporal evolutions (ATEs) of each independent component (IC) to map relations among the many ICs. ICA is a statistical method used to extract spatially independent sources of information from a data-set [Hyvärinen, 1999] that has been extensively used in neuroimaging literature [Beckmann and Smith, 2004; Calhoun et al., 2005; Esposito et al., 2002; McKeown, 2000; McKeown and Sejnowski, 1998; McKeown et al., 1998a, 1998b]. Granger's method estimates the causality between time series by evaluating how much the past of a signal can predict another signal [Geweke, 1982; Granger, 1969]. This method has been successfully applied in recent fMRI studies [Abler et al., 2006; Goebel et al., 2003; Roebroeck et al., 2005; Sridharan et al., 2007]. Compared to other methods implemented to detect connectivity patterns based on correlations among ATEs [i.e., Jafri et al., 2008], the joint use of ICA and GC allows the study of the relationships among ICs. The ICA and GC technique has been successfully tested on a simulated dataset [Londei et al., 2006] and then refined for single-subject fMRI data [Londei et al., 2007]. The present study is a significant advancement with respect to the previous works, especially in terms of generalization power of neuropsychological findings, and in verifying the feasibility of the ICA-GC method to group data.

Therefore, the aim of this study is to disclose the functional brain circuits responsible for speech perception, by means of a predominantly data-driven methodology. We hypothesize that speech comprehension may be a continuous process of motor and sensory hypothesis generation [Callan et al., 2004]. The modulation of sensory-motor areas connectivity should reflect the ability to transform auditory speech into appropriate sensory and motor representations. This mechanism might be driven by a balanced causal influence of both anterior and posterior language areas [Skipper et al., 2006]. These two poles of the language network should endorse top-down and bottom-up processing, whose net ratio is modulated by the semantic content. Specifically, we seek to verify this model by using a passive word listening task with three sets of stimuli: Words, Pseudo-Words, and Reversed-Words. Previous neuroimaging studies showed, for all three conditions, the

major involvement of the superior temporal gyrus, with little agreement on the activation of Broca's area or motor and premotor regions [Price, 2000; Gernsbacher and Kaschak, 2003; Benson et al., 2001]. Our prediction is that the connectivity pattern among motor, somatosensory, and parietal areas, as well as the right cerebellum, will be substantially modulated by the degree of stimuli reproducibility. More specifically, listening to reproducible speech (as is the case for Words and Pseudo-Words) should elicit the activation of the classical language network together with inferior parietal areas and the motor system (for sake of simplicity we will refer to a parieto-somato-motor network) as well as the cerebellar-motor connection. On the other hand, we predict that the lack of reproducibility (as in Reversed-Words) should induce an altered connectivity among areas performing the sensory-motor coordinate transformation. Finally, word meaning (as in Words) should not change the global pattern of sensory-motor connectivity but rather affect the balance between anterior and posterior language brain areas. We predict a greater activity, in network dynamics, for anterior frontal areas (top-down processes) and a reduced driving role for temporal regions (bottom-up processes) when Words are presented.

METHODS

Subjects

Eight right-handed [Oldfield, 1971] males volunteered to participate in the study. All of them were native Italian speakers, with normal audition. Only male subject were selected to have a more homogeneous sample. Female usually show larger variability in language lateralization [Mc Glone, 1977]. Participants (mean age: 29.75, SD: 3.1) were screened to exclude any form of cerebral trauma, dementia, or language deficit. A written informed consent was obtained before beginning the study, in conformity to the principles of the Declaration of Helsinki (1964) and the ethical guidelines approved by the "G. D'Annunzio" University of Chieti.

Stimuli and Procedures

Stimuli were 90 audio files, 30 for each of the three categories: (i) Words—trisyllabic high frequency concrete words according to the Italian norms [De Mauro et al., 1993]; (ii) Pseudo-Words—trisyllabic meaningless but phonologically and phonotactically legal words, created by mixing the syllables forming the Words; (iii) Reversed-Words—same words of the first two categories (randomly chosen among Words and Pseudo-Words, 15 in each), but reversely played by using an audio-editing software. Action-verbs were excluded to avoid motor activities often observed during listening to them and eventually associated to action simulation strategies [Pulvermüller, 2005].

Word and Pseudo-Word stimuli were digitally recorded by a professional male actor. The design consisted in 12 stimulation blocks (30 s duration each) interleaved with a rest reference (30 s duration), and starting with rest. Thus, the whole experiment lasted 12 min and 30 s. Each stimulation block (four each condition) consisted of 15 stimuli taken from Words, Pseudo-Words, or Reversed-Words groups. Blocks contained only one kind of stimuli at a time. Stimuli were presented at a constant rate (0.5 Hz, onset of stimuli set every 2 s). Each block of 15 was repeated two times during the experiment, and the order of presentation was randomized across subjects to avoid any order or sequence effects. Stimuli were administered via MRI-compatible headphones connected to a personal computer. Subjects were only asked to passively listen while paying attention to the stimuli. Subjects had no overt or covert task to perform on the stimuli and each block contained the same category of stimuli and expectation was never violated. Therefore, no processing strategy was suggested and each condition could be considered as a separate task-set, inducing dissociable activations.

Data Acquisition

BOLD contrast functional images were acquired with a SIEMENS MAGNETOM VISION scanner at 1.5 T by means of T2*-weighted echo planar imaging free induction decay sequences with the following parameters: TR, 2,095 ms; TE, 60 ms; matrix size, 64 × 64; FOV, 256 mm; in-plane voxel size, 4 mm × 4 mm; flip angle, 90°; slice thickness, 6 mm; and no gap; 365 functional volumes consisting of 16 transaxial slices were acquired. High-resolution structural volume was acquired at the end of the session via a 3D MPRAGE sequence with the following features: sagittal, matrix 256 × 256, FOV 256 mm, slice thickness 1 mm, no gap, in-plane voxel size 1 mm × 1 mm, flip angle 12°, TR = 9.7 ms, TE = 4 ms. Data were preprocessed using SPM2 (Wellcome Department of Cognitive Neurology, London, UK) for realignment, slice timing, coregistration, and normalization. To avoid T1 effects, the first five scans were discarded, thus obtaining 360 volumes each subject.

ICA-GC Combination

The data was submitted to a noise and dimensionality reduction by using a principal component analysis (PCA). The group-ICA and GC was then applied in succession [Londei et al., 2006, 2007]. The ICA is a data-driven multivariate statistical technique that uses higher-order statistics to perform the decomposition of linearly combined statistically independent sources [Hyvärinen, 1999]. Every IC (spatial ICA) is spatially independent on any other IC and represents a specific map of activity whose time evolution is denoted by its ATE. The contribution of a spatial IC to each voxel is given by the IC magnitude at that point

modulated in time by the ATE. We selected the IC with an ATE that was most strongly correlated with the external stimulus evolution (named IC1). The reference stimulus was built by convolving the boxcar describing the on/off stimulations with an artificial model of hemodynamic response function (two gamma function HRF). This procedure was used to detect the first activity triggered by the experimental stimuli in the group data. We postulate that the first cortical activity locked to stimuli processing is strongly correlated to the HRF convoluted experimental boxcar. It is possible that other task-irrelevant activities were present before and after stimulus presentation. However, we were not interested in those processes. Subsequently, GC was applied between the IC1 and the other ICs, showing a reduced set of secondary areas causally related to IC1 (first-order connectivity). The ICs found in this first GC analysis were afterwards introduced in a further GC computation to evaluate the interaction among them (second-order connectivity) (see “Granger’s Causality and Bootstrap Analysis” section for details).

Group ICA

The spatial IC group analysis performed in the present experiment is similar to the method of Calhoun et al. [2001]. This approach is based on the assumption that the data collected from individual subjects are statistically independent observations. Therefore, each subject is treated as an observation of the statistics of the population. After a dimensional reduction step operated on each subject, the full data set is given by the temporal concatenation of the reduced data (30 components for each subject for a total number of 240). Dimensional reduction is performed by applying the PCA on the covariance matrix of the single subject data and by selecting the first greatest L eigenvalues. If Y_i is the K -by- V raw data from the i th subject and F_i^{-1} is the associated L -by- K reduction matrix, where K is the amount of temporal samples (volumes), V is the number of voxels, L is the size of time dimension following reduction, and M is the amount of subjects, the ICA is performed on the concatenated LM -by- V $\mathbf{X}$ matrix given by

$$\mathbf{X} = \mathbf{G}^{-1} \begin{bmatrix} \mathbf{F}_1^{-1} \mathbf{Y}_1 \\ \vdots \\ \mathbf{F}_M^{-1} \mathbf{Y}_M \end{bmatrix} \quad (1)$$

where $\mathbf{G}^1$ is a further N -by- LM dimension reduction matrix. After the ICA estimation, the data matrix $\mathbf{X}$ can be written as

$$\mathbf{X} = \mathbf{A} \cdot \mathbf{S} \quad (2)$$

where $\mathbf{A}$ is the N -by- N mixing matrix and $\mathbf{S}$ is the N -by- V IC matrix.

In this study, to perform a group analysis on ICs, a different approach with respect to Calhoun’s method has been used [Calhoun et al., 2001]. Actually, Calhoun’s approach allows recovering the original subject brain activation related to the independent source detected by the group ICA. In the present work, the aim is to detect the causal relationships between the spatial sources of the group analysis to extract the common temporal features of the components. Hence, the same result shown in (2) would have been obtained if the concatenated $\mathbf{X}$ matrix had been built as

$$\mathbf{X} = \mathbf{G}^{-1} \begin{bmatrix} \mathbf{F}_1^{-1} \\ \vdots \\ \mathbf{F}_M^{-1} \end{bmatrix} \tilde{\mathbf{Y}} = \mathbf{G}^{-1} \mathbf{F}^{-1} \tilde{\mathbf{Y}} \quad (3)$$

where $\tilde{\mathbf{Y}}$ may be considered as a virtual raw data matrix (K -by- V) containing the common spatiotemporal features of all subjects taken as a whole. The mathematical description of $\tilde{\mathbf{Y}}$ is $\tilde{\mathbf{Y}} = \mathbf{F} \begin{bmatrix} \mathbf{F}_1^{-1} \mathbf{Y}_1 \\ \vdots \\ \mathbf{F}_M^{-1} \mathbf{Y}_M \end{bmatrix}$. By substituting (3) in (2), the final ICA is given by

$$\mathbf{X} = \mathbf{G}^{-1} \mathbf{F}^{-1} \tilde{\mathbf{Y}} = \mathbf{A} \mathbf{S} \quad (4)$$

Therefore, the evaluation of causal relationships between the group activations is performed by analyzing the ATEs extracted by the modified $\tilde{\mathbf{A}}$ matrix is given by

$$\begin{aligned} \tilde{\mathbf{A}} &= \mathbf{F} \mathbf{G} \mathbf{A} \\ \tilde{\mathbf{Y}} &= \tilde{\mathbf{A}} \mathbf{S} \end{aligned} \quad (5)$$

This approach allows extracting the group temporal features associated with the spatial ICs by the virtual raw data matrix $\tilde{\mathbf{Y}}$. Note that $\tilde{\mathbf{A}}$ is a K -by- N matrix, where N is the number of extracted spatial ICs and K is the original temporal length (volumes), and $\mathbf{S} = \mathbf{A}^{-1} \mathbf{X} = \tilde{\mathbf{A}}^{-1} \tilde{\mathbf{Y}}$. All the inverse matrices involved in the present description have been calculated by Penrose’s pseudo-inverse approach.

Granger’s Causality and Bootstrap Analysis

The GC [Granger, 1969] is a regressive technique for the evaluation of the relationships between temporal series. This method is based on the assumption that the variances of the residuals after a regressive analysis decrease when the specific time-course A can be explained by the past values of a second causal time series. Geweke [1982] introduced a further elaboration of GC by describing three specific parameters: $F_{A \rightarrow B}$, $F_{B \rightarrow A}$, $F_{A \cdot B}$. Each parameter is given by the logarithm of a particular variance ratio between residuals of the regressive

model of A added to the past description of B, and the residuals variance of B alone. $F_{A \rightarrow B}$ (or $F_{B \rightarrow A}$) represents the amount of causality given by A (or B), when applied to the prediction of B (or A). $F_{A \cdot B}$ describes the total linear dependence between A and B in terms of undirected instantaneous influence.

Although some problems and limitation in the interpretation of GC as applied to fMRI data have to be considered such as hemodynamic delays, the method has been successfully applied to fMRI analysis with the purpose of highlighting functional connections between brain areas [for an extensive discussion, refer Abler et al., 2006; Goebel et al., 2003; Roebroeck et al., 2005]. However, the intervening hemodynamic delays, peculiar to different brain regions, have to be acknowledged as a possible source of confound. Granger parameters might in fact suffer from these delays and generate spurious causalities. Different insightful interpretations have emerged for the use of GC on the BOLD signal [for more details, Abler et al., 2006; Goebel et al., 2003; Roebroeck et al., 2005], and beside those we will offer a post-hoc verification by showing a pattern of connections highly consistent with previous reports. The extraction of these relations allows a rough determination of time delay between the ICs, which may be smaller than a sampling time TR. However, it has been shown that sub-TR-delayed influences can be captured in TR level vector autoregressive models and directed GC [Goebel, 2003; Roebroeck et al., 2005]. To reduce the bidirectional interaction due to bias effect of hemodynamics, the subtraction between $F_{A \rightarrow B}$ and $F_{B \rightarrow A}$ has been considered according to Roebroeck et al. [2005]. Therefore, only the time series whose parameter $F_d = F_{A \rightarrow B} - F_{B \rightarrow A}$ is greater than a given significant statistical threshold are considered. Actually, sub-TR-delayed influences can be captured in TR level-directed GC [Goebel et al., 2003; Roebroeck et al., 2005] and can be described by the specific values of F_d and $F_{A \cdot B}$.

Therefore, our GC algorithm implementation extracts two parameters with different functional meaning. $F_{A \cdot B}$ represents a simultaneous bidirectional influence between two ICs, whereas F_d is to be considered as a time-delayed (1 TR) directed causal link. The conjunction of the previous two parameters instead represents the strongest connection possible, involving a notion of directed causality as well as a simultaneous and bidirectional link. Granger tests, applied on different conditions, were performed by selecting and concatenating the correct fragments of ATEs related to the conditions Words, Pseudo-Words, and Reversed-Words. Each temporal fragment starts with a stimulation block (on) followed by rest (off), repeated until the end of the specific condition. The time-series extraction was performed by the application of an operator H (specific for each condition) on the matrix $\mathbf{A}$. H was built taking into account the stimuli position in time and the temporal extension, by opportunely combining identity submatrices.

TABLE I. Primary and secondary activities: Extension, peak location in MNI coordinates, P-value, and Z-score levels

IC no.	MNI coordinates			Z-score	Area (mm ³)	BA
	X	Y	Z			
IC1	-65	-13	12	26.3	18,816	42
	-45	-7	58	8.73	2,688	6
	57	13	-6	16.54	18,432	22
IC2	-60	-51	40	5.84	2,784	40
	-60	10	8	27.23	7,872	44
	62	9	7	12.65	2,946	44
	59	-37	49	7	1,056	40
IC3	-57	-19	45	18.3	10,848	4
	48	-39	45	17.33	7,680	40
IC4	-57	-23	49	14.61	9,600	2
	45	-48	50	29.26	10,080	40
IC5	-48	-35	56	30.36	14,208	40
	28	-40	57	23.49	8,640	40
IC6	-55	-34	44	5.75	768	40
	52	-37	59	7.69	1,440	40
IC7	-49	-65	42	6.76	2,208	39
IC8	-53	-21	5	10.68	3,648	41
	41	-76	-23	22.32	5,184	Post. cerebellum

The statistical threshold for selecting significant Granger's f -values can be evaluated by means of bootstraps. The bootstrap technique is mainly applied for estimating unknown quantities associated with statistical models. In particular, the bootstrap may either be used to estimate the intervals of confidence for a specific parameter or to find P -values for statistical tests under a null hypothesis [Boos, 2003]. In our case, we tested the Granger's f -values against the null hypothesis of no causal relation between couples of ICs time series. Specifically, we evaluated parameters F_d and $F_{A \cdot B}$ on several time courses built by combining the first-order autoregressive model and the randomly sampled versions of the residuals. Mathematical details can be found in Londei et al. [2007]. The parameters F_d and $F_{A \cdot B}$ are therefore validated if their values do not fulfill the bootstrap null hypothesis, i.e., $F_d(\text{measured}) > F_{th}$ ($P = 0.05$). Statistical threshold have been set by applying 5,000 cycles of the bootstrap procedure. In addition to that, we also double-checked the significance of Granger's parameters across conditions. Specifically, we tested whether any presence/absence of effect between conditions was confirmed by a further bootstrap analysis. The nominal differences, between F_d and $F_{A \cdot B}$ values fulfilled the inferences found by means of this additional bootstrap analysis. Finally, the validity of the uncorrected statistical threshold is further motivated by the evaluation of the Cramer's ϕ as an objective and standardized measure of the magnitude of observed effect, also known as effect size [Rosenthal and Di Matteo, 2001].

Figure 1.

Primary activity. Among all independent component's temporal evolutions one showed the greatest correlation with the experimental boxcar (lower panel). The signal associated with this primary IC (whole group) was located in the bilateral superior temporal gyrus and in the premotor cortex with a larger distribution on the left hemisphere (upper panel).

The evaluation of ϕ is given by

$$\phi = \sqrt{\frac{\chi_k^2}{N}} \quad (6)$$

where χ_k^2 is the chi-squared variable associated with any Granger's causality parameter, as described in Geweke [1982]. χ_k^2 has than been estimated by the inverse chi-squared cumulative distribution applied to the probability level given by the bootstrap. We computed the ϕ values of each GC relationship, and according to previous reports we set the threshold of 0.20 as the value to consider each effect large enough to be reliable [Rosenthal and Di Matteo, 2001].

RESULTS

Primary Activity

The primary activity was defined as the IC with the highest correlation with stimulus temporal evolution. This

IC was located in the bilateral superior temporal gyrus and the left premotor cortex (STG/PM) (IC1; correlation coefficient with the convoluted boxcar: Pearson's $r = 0.663$, $P < 0.00001$; Fig. 1). Extension, peak location in MNI coordinates, P -value, and Z -score levels are given in Table I.

Secondary Activities

Secondary activities are those ICs whose ATEs were not significantly correlated with the convoluted experimental boxcar. However, they had significant GC relationship with the primary IC as defined by the GC tests. The GC algorithm was run separately for each condition to search for interactions between IC1 and all other ICs. A total number of seven ICs were significantly associated with the three conditions taken together. These seven components were then used for further analysis: IC2 in the posterior inferior frontal gyrus and bilaterally in the inferior parietal lobule (IFG/IPL; Fig. 2a); IC3 was located in the left pre-central gyrus (Fig. 2b); both IC4 and IC5 in the left post-central gyrus (Fig. 2c,d); IC6 in the bilateral anterior inferior parietal lobule (Fig. 2e); IC7 in the left posterior inferior parietal lobule (Fig. 2f); IC8 in the right cerebellum and the left Heschl's gyrus (Fig. 2g). Extension, peak location in MNI coordinates, P -value, and Z -score levels are given in Table I.

Connectivity Analysis

GC analysis described the interactions between the primary IC and all other ICs and the modulation according to experimental condition. Figure 3a presents the connectivity that the primary IC holds with all other ICs. Furthermore, we run a second session of GC tests between all eight ICs obtained in the previous step. Figure 3b shows a graphical representation of all GC relations in the three experimental conditions, obtained with the second run of GC tests. Table II contains the GC values (F_d and F_{A-B}) and related probability levels among all eight ICs. Cramer's ϕ values of each significant causal relationship was also greater than 0.23. Overall, the connectivity pattern was strongly modulated according to the kind of stimuli presented, as shown in Figure 3. The critical modulation was at the connection between motor (IC3) and somatosensory activities (IC4). Word (directed connection: $P = 0.0005$, $\phi = 0.37$) and Pseudo-Word (directed connection: $P = 0.0214$, $\phi = 0.26$) presentations maintained such a connection that was instead missing in Reversed-Word listening (directed connection: $P = \text{n.s.}$). This connectivity pattern was also confirmed by the further bootstrap analysis between conditions [IC3-IC4: Fd(Word vs. Reversed-Word) = 0.1306, Pd(Word vs. Reversed-Word) = 0.0006; Fd(Pseudo-Word vs. Reversed-Word) = 0.0695, Pd(Pseudo-Word vs. Reversed-Word) = 0.0118].

Moreover, the connection between inferior frontal gyrus/inferior parietal lobule (IC2) and the somatosensory

Figure 2.

cortex (IC4) was similarly modulated by condition (Words-directed connection: $P = 0.0102$, $\phi = 0.28$; simultaneous connection: $P = 0.0358$, $\phi = 0.24$. Pseudo-Words-directed connection: $P = 0.007$, $\phi = 0.30$; simultaneous connection: $P = 0.0053$, $\phi = 0.30$. Reversed-Words-directed connection: $P = \text{n.s.}$; simultaneous connection: $P = \text{n.s.}$). The subsequent bootstrap analysis between conditions yielded the same results [IC2–IC4: $F_d(\text{Word vs. Reversed-Word}) = 0.0709$, $P_d(\text{Word vs. Reversed-Word}) = 0.0108$; $F_d(\text{Pseudo-Word vs. Reversed-Word}) = 0.0848$, $P_d(\text{Pseudo-Word vs. Reversed-Word}) = 0.0070$; $F_{A,B}(\text{Word vs. Reversed-Word}) = 0.0370$, $P_{A,B}(\text{Word vs. Reversed-Word}) = 0.0266$, $F_{A,B}(\text{Pseudo-Word vs. Reversed-Word}) = 0.0670$, $P_{A,B}(\text{Pseudo-Word vs. Reversed-Word}) = 0.0052$].

Finally, the connectivity modulations originating from the right cerebellum and Heschl gyrus (IC8) toward frontal activities (motor cortex: IC3; inferior frontal gyrus and inferior parietal lobule: IC2) are also critically important. A significant connection was present only for Words and Pseudo-Words between IC8 and IC3 (Words-directed connection: $P = 0.014$, $\phi = 0.27$. Pseudo-Words-directed connection: $P = 0.0157$, $\phi = 0.27$. Reversed-Words-directed connection: $P = \text{n.s.}$). Bootstrap analysis between conditions yielded the same results [IC8–IC3: $F_d(\text{Word vs. Reversed-Word}) = 0.0508$, $P_d(\text{Word vs. Reversed-Word}) = 0.0336$; $F_d(\text{Pseudo-Word vs. Reversed-Word}) = 0.0468$, $P_d(\text{Pseudo-Word vs. Reversed-Word}) = 0.0468$]. Similarly, IC8 and IC2 (Words simultaneous connection: $P < 0.0001$, $\phi = 0.39$. Pseudo-Words simultaneous connection: $P = 0.0005$, $\phi = 0.37$. Reversed-Words simultaneous connection: $P = \text{n.s.}$) showed the same pattern further confirmed by the bootstrap between conditions [IC8–IC2: $F_{A,B}(\text{Word vs. Reversed-Word}) = 0.1084$, $P_{A,B}(\text{Word vs. Reversed-Word}) = 0.0006$; $F_{A,B}(\text{Pseudo-Word vs. Reversed-Word}) = 0.0844$, $P_{A,B}(\text{Pseudo-Word vs. Reversed-Word}) = 0.0020$].

DISCUSSION

The brain speech network relies on the integrated processing of several functional units to fulfill a critical and complex task that is particularly relevant for human behavior. Indeed, the successful transformation of a sound stream into a set of discrete meaningful motor-based units

Secondary activities. Here we show the activities whose connectivity is significant and modulated by the experimental manipulations. Each panel includes the 3D rendering of the left hemisphere activations (except for IC8) and the associated temporal evolution of each independent component. (a) IC2 in the posterior inferior frontal gyrus and inferior parietal lobule; (b) IC3 in the precentral gyrus; (c) IC4 in the somatosensory area; (d) IC5 in the postcentral gyrus; (e) IC6 in the anterior inferior parietal lobule; (f) IC7 in the posterior inferior parietal lobule; (g) IC8 in the Heschl's gyrus; (h) right cerebellum.

Figure 3.

Connectivity schematics. (a) Graphical representation of the first-order connectivity pattern between the primary activity (IC1) located in the bilateral superior temporal gyrus and the other seven ICs. (b) Graphical representation of the second-order connectivity pattern between all 8 ICs found in the previous step of analysis. W, P, and R labels represents Word, Pseudo-Word, and Reversed-Word conditions, respectively.

might be an important aspect of speech processing and requires the concerted activity of sensory and motor brain areas [Callan et al., 2004; D'Ausilio et al., 2009; Fadiga et al., 2002; Meister et al., 2007; Pickering and Garrod, 2007; Pulvermüller et al., 2006; Scott et al., 2009; Skipper et al., 2006; Watkins et al., 2003; Wilson and Iacoboni, 2004]. Our study supports this view by describing the network dynamics among several sensory-motor brain areas implicated in a speech perception task. The primary focus of activity was located in the superior temporal gyrus, predominantly on the left side, probably including Wernicke's territory. Additionally, IC1 also included an activity in the left precentral gyrus. The premotor cortex has been recently associated to both listening and producing speech sounds [Wilson et al., 2004].

First-Order Connectivity

Listening to all three kinds of stimuli elicited an instantaneous connection between the primary IC and the right posterior cerebellum and Heschl's gyrus. The right cerebellum is a predominantly motor structure that recently has been shown to be involved in a variety of language tasks [Jansen

et al., 2005; Marien et al., 2001]. Mathiak et al. [2002] further demonstrated its role in evaluating the duration of speech segments in accordance with its canonical role in time perception [Ivry et al., 2002]. In addition to that, listening to Words produced an instantaneous signal toward the IFG/IPL network (IC2) and a directed influence toward somatosensory cortices (IC5). The posterior inferior frontal gyrus, also known as Broca's area, is a region classically associated with speech output functions and implicated in language understanding as well [Schäffler et al., 1993]. Catani et al. [2005] considered the inferior parietal lobule, renamed Geschwind's territory, as the third language area anatomically connected to both Wernicke's and Broca's territories by separate segments of the arcuate fasciculus. The pattern of connectivity originating from IC1 when listening to Pseudo-Word stimuli was partly different. A directed influence toward the IFG/IPL network (IC2), motor (IC3), and somatosensory cortices (IC4) as well as an instantaneous connection with a postcentral activity (IC5) and the anterior inferior parietal lobule (IC6) were present. The connections stemming from the STG/PM network were similar to the those found in the Word condition, with the addition of inferior parietal, motor, and somatosensory cortices. Pseudo-Words could be assimilated to real words with a very low

TABLE II. Granger connectivity among all relevant ICs: Pattern of F_d , F_{dA-B} GC values, and relative P -levels found with the bootstrap method between all eight ICs. Significant P -values are in bold

Words															
F_d								P -values							
IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8	IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8
IC1	–	0.0000	–0.0014	0.0286	0.0353	0.0138	0.0087	–	0.4913	0.5848	0.0580	0.0354	0.2102	0.1612	0.2372
IC2	0.0000	–	0.0648	0.0563	0.0041	0.0117	–0.0214	0.5087	–	0.0064	0.0102	0.3180	0.8193	0.1823	0.8947
IC3	0.0014	–0.0648	–	–0.1041	0.0861	0.0039	–0.0529	0.4152	0.9936	–	0.9995	0.0020	0.9228	0.3187	0.9860
IC4	–0.0286	–0.0563	0.1041	–	0.0295	–0.0944	–0.1675	0.9420	0.9898	0.0005	–	0.0484	0.9984	0.4654	1.0000
IC5	–0.0353	–0.0041	–0.0861	–0.0295	–	–0.0424	0.0017	0.9646	0.6820	0.9980	0.9516	–	0.9770	0.3925	0.9997
IC6	–0.0108	0.0126	0.0241	0.0944	0.0424	–	–0.0002	0.7898	0.1807	0.0772	0.0016	0.0230	–	0.5270	0.9566
IC7	–0.0138	–0.0117	–0.0039	–0.0003	–0.0017	0.0002	–	0.8388	0.8177	0.6813	0.5346	0.6075	0.4730	–	0.1198
IC8	–0.0087	0.0214	0.0529	0.1675	0.1267	0.0397	–0.0181	0.7628	0.1053	0.0140	0.0000	0.0003	0.0434	0.8802	–
F_{A-B}								P -values							
IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8	IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8
IC1	–	0.1233	0.0176	0.0130	0.0014	0.0158	0.2009	–	0.0002	0.1683	0.2330	0.6906	0.1936	0.6606	0.0000
IC2	0.1233	–	0.0135	0.0408	0.0105	0.0347	0.0019	0.0002	–	0.2336	0.0358	0.2860	0.0523	0.6498	0.0002
IC3	0.0176	0.0135	–	0.0009	0.0001	0.0243	0.1615	0.1683	0.2336	–	0.7569	0.9125	0.1012	0.0000	0.2705
IC4	0.0130	0.0408	0.0009	–	0.0006	0.0207	0.0012	0.2330	0.0358	0.7569	–	0.7921	0.1407	0.7207	0.0160
IC5	0.0014	0.0105	0.0001	0.0006	–	0.0512	0.0041	0.6906	0.2860	0.9125	0.7921	–	0.0170	0.5054	0.9339
IC6	0.0158	0.0347	0.0243	0.0207	0.0512	–	0.0133	0.1936	0.0523	0.1012	0.1407	0.0170	–	0.2281	0.0010
IC7	0.0017	0.0019	0.1615	0.0012	0.0041	0.0133	–	0.6606	0.6498	0.0000	0.7207	0.5054	0.2281	–	0.2819
IC8	0.2009	0.1337	0.0115	0.0542	0.0001	0.0962	0.0108	0.0000	0.0002	0.2705	0.0160	0.9339	0.0010	0.2819	–
Pseudo-Words															
F_d								P -values							
IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8	IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8
IC1	–	0.0447	0.0990	0.1181	0.1206	0.0371	–0.0015	–	0.0275	0.0014	0.0002	0.0001	0.0382	0.5919	0.5673
IC2	–0.0447	–	–0.0177	0.0702	0.0698	–0.0144	0.0179	0.9725	–	0.8914	0.0070	0.0053	0.8524	0.1188	0.7605
IC3	–0.0990	0.0177	–	–0.0430	0.0358	–0.0011	–0.0030	0.9986	0.1086	–	0.9786	0.0343	0.5741	0.6460	0.9843
IC4	–0.1181	–0.0702	0.0430	–	0.0130	0.0510	0.0077	0.9998	0.9930	0.0214	–	0.1560	0.0147	0.2468	0.9998
IC5	–0.1206	–0.0698	–0.0358	–0.0130	–	0.0013	0.0335	0.9999	0.9947	0.9657	0.8440	–	0.4195	0.0407	0.9986
IC6	–0.0371	0.0144	0.0011	–0.0510	–0.0013	–	–0.0085	0.9618	0.1476	0.4259	0.9853	0.5805	–	0.7843	0.9900
IC7	0.0015	–0.0179	0.0030	–0.0077	–0.0335	0.0085	–	0.4081	0.8812	0.3540	0.7532	0.9593	0.2157	–	0.9783
IC8	0.0012	0.0087	0.0489	0.1194	0.0866	0.0634	0.0453	0.4327	0.2395	0.0157	0.0002	0.0014	0.0100	0.0217	–

TABLE II. (Continued)

F_{AB}									P -values								
IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8		IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8	
IC1	–	0.1030	0.0053	0.0111	0.0276	0.0724	0.0020	0.1412	–	0.0010	0.4621	0.2683	0.0843	0.0054	0.6419	0.0000	
IC2	0.1030	–	0.0121	0.0708	0.0812	0.0021	0.0008	0.1098	0.0010	–	0.2529	0.0053	0.0039	0.6297	0.7694	0.0005	
IC3	0.0053	0.0121	–	0.0045	0.1036	0.0087	0.1942	0.0076	0.4621	0.2529	–	0.4861	0.0007	0.3381	0.0000	0.3737	
IC4	0.0111	0.0708	0.0045	–	0.0069	0.0159	0.0142	0.0075	0.2683	0.0053	0.4861	–	0.3834	0.1881	0.2149	0.3654	
IC5	0.0276	0.0812	0.1036	0.0069	–	0.0029	0.0294	0.0530	0.0843	0.0039	0.0007	0.3834	–	0.5816	0.0714	0.0159	
IC6	0.0724	0.0021	0.0087	0.0159	0.0029	–	0.0284	0.0841	0.0054	0.6297	0.3381	0.1881	0.5816	–	0.0775	0.0018	
IC7	0.0020	0.0008	0.1942	0.0142	0.0294	0.0284	–	0.0783	0.6419	0.7694	0.0000	0.2149	0.0714	0.0775	–	0.0036	
IC8	0.1412	0.1098	0.0076	0.0075	0.0530	0.0841	0.0783	–	0.0000	0.0005	0.3737	0.3654	0.0159	0.0018	0.0036	–	
F_d									Reversed Words								
IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8		IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8	
IC1	–	0.0346	–0.0616	0.0645	0.0205	0.0066	–0.0165	–0.0165	–	0.0465	0.9938	0.0061	0.0908	0.2682	0.8670	0.8537	
IC2	–0.0346	–	–0.0102	–0.0147	0.0350	0.0048	–0.0233	–0.0276	0.9535	–	0.8075	0.8620	0.0397	0.3102	0.9227	0.9365	
IC3	0.0616	0.0102	–	0.0265	–0.0248	–0.0135	0.0008	–0.0021	0.0062	0.1925	–	0.0616	0.9332	0.8516	0.4290	0.6080	
IC4	–0.0645	0.0147	–0.0265	–	–0.0646	0.0081	0.0291	–0.1027	0.9939	0.1380	0.9384	–	0.9943	0.2192	0.0511	0.9992	
IC5	–0.0205	–0.0350	0.0248	0.0646	–	–0.0190	–0.0247	–0.0632	0.9092	0.9603	0.0668	0.0057	–	0.8971	0.9333	0.9930	
IC6	–0.0066	–0.0048	0.0135	–0.0081	0.0190	–	–0.0317	–0.1460	0.7318	0.6898	0.1484	0.7808	0.1029	–	0.9503	0.9998	
IC7	0.0165	0.0233	–0.0008	–0.0291	0.0247	0.0317	–	–0.0417	0.1330	0.0773	0.5710	0.9489	0.0667	0.0497	–	0.9710	
IC8	0.0165	0.0276	0.0021	0.1027	0.0632	0.1460	0.0417	–	0.1463	0.0635	0.3920	0.0008	0.0070	0.0002	0.0290	–	
F_{AB}									P -values								
IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8		IC1	IC2	IC3	IC4	IC5	IC6	IC7	IC8	
IC1	–	0.0744	0.0014	0.0022	0.0119	0.1068	0.1234	0.2042	–	0.0049	0.6969	0.6210	0.2616	0.0007	0.0004	0.0000	
IC2	0.0744	–	0.0026	0.0038	0.0000	0.0002	0.0066	0.0253	0.0049	–	0.5879	0.5106	0.9747	0.8747	0.3996	0.0990	
IC3	0.0014	0.0026	–	0.0000	0.0030	0.0027	0.1871	0.0304	0.6969	0.5879	–	0.9536	0.5599	0.5841	0.0000	0.0685	
IC4	0.0022	0.0038	0.0000	–	0.0217	0.0088	0.0037	0.0089	0.6210	0.5106	0.9536	–	0.1295	0.3274	0.5241	0.3259	
IC5	0.0119	0.0000	0.0030	0.0217	–	0.0091	0.0082	0.0033	0.2616	0.9747	0.5599	0.1295	–	0.3230	0.3459	0.5524	
IC6	0.1068	0.0002	0.0027	0.0088	0.0091	–	0.0088	0.1305	0.0007	0.8747	0.5841	0.3274	0.3230	–	0.3357	0.0000	
IC7	0.1234	0.0066	0.1871	0.0037	0.0082	0.0088	–	0.0009	0.0004	0.3996	0.0000	0.5241	0.3459	0.3357	–	0.7493	
IC8	0.2042	0.0253	0.0304	0.0089	0.0033	0.1305	0.0009	–	0.0000	0.0990	0.0685	0.3259	0.5524	0.0000	0.7493	–	

frequency of use [Roy et al., 2008]; our results are consistent with the finding that lower frequency words elicit larger parietal activities [Zhang et al., 2005]. Finally, Reversed-Words are stimuli that cannot be easily reproduced by any speaker. Nevertheless, they still maintain the necessary information to recognize different human speakers, estimate the length of the stimuli, and perform some rudimentary phonological analysis. Phoneme recognition, in fact, is strongly impaired but not completely suppressed [Binder et al., 2000]. We found that IC1 had an instantaneous connection with the IFG/IPL network (IC2), as for the Word and Pseudo-Word conditions. Additionally, a directed connection toward the left somatosensory activity (IC4) was found as in Pseudo-Words. Finally IC1 was connected with the anterior inferior parietal lobule (IC6) as in the Pseudo-Words condition, whereas the connection with a more posterior site (IC7) was unique to Reversed-Word listening.

In summary, the STG/PM (IC1) was constantly connected to the IFG/IPL network (IC2) and the right cerebellum/Heschl gyrus activity (IC8), as expected when listening to language material [Gernsbacher and Kaschak, 2003; Price, 2000]. On the other hand, the number of independent cortical activities causally associated with the primary input cortices was highly varied. Word listening evidenced a basic network of areas comprising an inferior parietal region. Pseudo-Words showed a much wider pattern including parietal, early somatosensory, and motor connections. This observation is in line with other studies reporting increased activities when listening to less frequent words [Chee et al., 2002; Nakic et al., 2006; Zhang et al., 2005]. Reversed-Words, instead, maintained parietal and somatosensory connections while lacking motor components.

We hypothesize that the presence of meaning, in the Words condition, helps the comprehension process via top-down influences [Chee et al., 2002]. These influences reduce the need for a sensory-motor translation, and in fact only one parietal activity was found. Pseudo-Words encoding, instead, might only rely on low-level analyses [Zhang et al., 2005]. Therefore, we interpret in this light the activation of the motor and somatosensory nodes and the more widespread computation. The lack of meaning together with the poor reproducibility of Reversed-Word stimuli induces, instead, the system to attempt a sensory-motor translation. As a matter of facts, no motor components were found and two inferior parietal components were activated.

Second-Order Connectivity

Word listening showed a compact network of areas revolving around the parieto-somato-motor network (IC3-4-5-6) and the linkage between the somatosensory component (IC4) and the motor activity (IC3). The parieto-somato-motor network was mainly driven by the IFG/IPL network (IC2). Indeed, the IFG/IPL activated both the primary motor (IC3) and somatosensory components (IC4). Interestingly, the IFG/IPL played a more important role than STG/PM in causing the parieto-somato-motor net-

work activation. This finding is in line with previous reports showing the involvement of inferior frontal areas in lexical decision tasks [Nakic et al., 2006]. Word meaning might reduce the need for phonological analysis and take advantage from top-down hypothesis-dependent processing [Chee et al., 2002]. Finally, the right cerebellum (IC8) maintained connectivity relationships with the primary activity (IC1), the parieto-somato-motor (IC3-4-5-6) as well as the IFG/IPL network (IC2).

Instead, Pseudo-Word stimuli still evoked the parieto-somato-motor network, but using a larger network of connections. The IFG/IPL was less implicated in triggering the parieto-somato-motor network, whereas the STG/PM increased its driving force. This is testified by the connection that all components of the parieto-somato-motor network receive from the primary IC and is further corroborated by previous studies [Newman and Twieg, 2001; Rauschecker et al., 2008]. The processing of meaningless stimuli can only rely on bottom-up, sound-based analysis, sustained for longer times [Roy et al., 2008]. These stimuli are nevertheless phonologically and phonotactically legal in Italian, and as a consequence were able to evidence, as in the Words condition, the linkage between somatosensory and motor areas. Also in this condition, the right cerebellum (IC8) showed a pattern of connectivity with the primary component (IC1), the parieto-somato-motor (IC3-4-5-6-7) as well as the IFG/IPL network (IC2).

Reversed-Words are peculiar stimuli lacking both meaning and, more interestingly, motor reproducibility. In this case, the main source of causal drive was derived from the STG/PM, supporting the impossibility of making use of any top-down strategies [Chee et al., 2002]. Moreover, in accordance with previous reports, this condition induced more activation of parietal areas [Zhang et al., 2005]. Remarkably, these stimuli induced a rather different pattern of connectivity within the parieto-somato-motor network. First, the direct connection between somatosensory and motor components was completely lacking (IC3 and IC4). More specifically, two independent circuits emerged, one including parieto-motor areas (IC1-6-7-3) and the other parieto-somatosensory cortices (IC1-2-4-5), with almost no cross talk between the two. Moreover, the right cerebellum/Heschl gyrus (IC8) showed an altered pattern of connectivity when compared to the Words and Pseudo-Words conditions. Indeed, apart from the instantaneous connection with the STG/PM network (IC1), we could measure only a directed influence toward somatosensory (IC4) and parietal components (IC5-6). Thus, its connectivity with motor components (IC3) and the IFG/IPL network (IC2) was completely missing. We propose that while listening to irreproducible speech the system still tries to assign labels to what is heard. The bottom-up analysis tries to fit the input with both its own motor repertoire and known somatosensory categories [Ito et al., 2009; Pulvermüller et al., 2006; Skipper et al., 2005]. However, sensory and motor components are not connected as if the two sources of hypothesis never agree on what is being heard.

Our hypothesis is that comprehension is a continuous process of hypothesis generation in both motor and sensory codes [Callan et al., 2004]. This mechanism is driven by a balanced influence of both IFG/IPL and STG/PM networks, whose ratio is modulated by the semantic content. On one hand, there are high frequency meaningful words, where past knowledge might guide comprehension. Listening to these stimuli should induce the parieto-somato-motor network to act efficiently; the IFG/IPL–STG/PM balance is shifted toward the first. On the other hand, Pseudo-Words (or very low frequency and unknown words) allow only a bottom-up analysis driven by the STG/PM network, whose result is a less compact parieto-somato-motor connectivity. Finally, irreproducible speech sounds cannot permit a real motor comprehension as in Words and Pseudo-Words conditions. This translates into a split of the parieto-somato-motor network into separate somatosensory and motor sub-networks, as well as into the abolition of the functional connections between the right cerebellum and motor cortices. In our view, the activation of the parieto-somato-motor network and cerebellar-motor connection during speech perception describes the successful mapping of heard sounds onto motor and somatosensory representations (see Fig. 4 for a schematic representation).

General Discussion

The reproducibility of an incoming speech stimulus has proven to be a critical feature in modulating the speech perception network. For instance, Wilson and Iacoboni [2006] showed that listening to phonemes of other languages—which were hard to reproduce for the experimental subjects—elicited weaker motor connections with the STG. The properties of these circuits support the idea of a re-enactment of the sensori-motor plans to execute articulatory gestures [Callan et al., 2004]. Such a re-enactment might share strong similarities with the plan to actually control the vocal tract and articulators and associated somatosensory feedback [D'Ausilio et al., 2009; Ito et al., 2009; Pulvermüller et al., 2006].

From a functional point of view, the activation of sensory-motor and cerebellar-motor circuits when listening to speech could serve in principle as an inverse model predictor. Learning and development of speech production might shape the mapping between sensory and motor maps [Guenther et al., 2006] that later might become useful in predicting and generating hypotheses on the incoming information. These mechanisms might be critical in adults to (i) disambiguate noisy speech signals [D'Ausilio et al., 2009]; (ii) segment incoming speech units [Sato et al., in press]; (iii) enable top-down predictive coding [Pickering and Garrod, 2007]; (iv) facilitate turn-taking in conversation [Scott et al., 2009]. In line with such hypotheses, we found a disconnection between motor and somatosensory areas, as well as of the motor-cerebellar connections, when listening to irreproducible speech (Reversed-Words) if compared to reproducible sounds

Figure 4.

Model of the speech perception network separated for condition. Each box represents a different area or network (PSM, parieto-somato-motor network; M, motor component; S, somatosensory component; aIPL, anterior inferior parietal lobule component; pIPL, posterior inferior parietal lobule component; IFG/IPL, inferior frontal gyrus and inferior parietal lobule component; STG/PM, superior temporal gyrus and pre-motor component; R Cerebellum, right cerebellum). Links represent a simplified and schematic depiction of a functional connection between two components. Thick lines represent connections originating from the cerebellum as opposes to cortico-cortical connections. Word meaning induce a stronger causal drive originating from anterior language areas. Meaningless stimuli prompt a more evident role played by the STG/PM in shaping networks dynamics. Reproducibility evoked a tight connection among parietal, somatosensory, and motor areas (here named parieto-somato-motor network) together with the involvement of the right cerebellum. Unpronounceable speech stimuli instead caused a split in this parieto-somato-motor network, and in addition to that, the motor-cerebellar functional connection was cancelled.

(Words, Pseudo-Words). Moreover, we found that speech sounds belonging to the subjects' motor repertoire elicited interesting differences depending on the presence of meaning. Meaningless (Pseudo-Words) stimuli unbalanced the overall causal drive toward language input areas and induced the system in a more complex pattern of connections when compared to meaningful stimuli (Words).

However, in neuroimaging research, the risk of erroneously associating a given brain activity to a particular cognitive function is extremely high [Poldrack, 2006]. In fact, each area is by no means an isolated module, and its function needs to be considered in a network-oriented view. Therefore, typical neuroimaging research must be complemented by data gathered with other complementary methodologies (such as transcranial magnetic stimulation, electroencephalography, etc.), by studies on different populations (neurological, psychiatric, or brain-lesioned patients) or by disclosing the structural connectivity pattern of the area of interest [Ffytche and Catani, 2005]. In this vein, we are indeed exploring how functional connectivity might define the function of a given area, using fMRI data and a novel data analysis approach. To our knowledge, this is among the first studies (as well as van de Ven et al. [in press]) showing connectivity modulations between and within sensory-motor cortices while listening to speech sounds with varying degree of reproducibility and semantic content.

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