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Disentangling Syntax and Intelligibility in Auditory Language Comprehension

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Abstract: Studies of the neural basis of spoken language comprehension typically focus on aspects of auditory processing by varying signal intelligibility, or on higher-level aspects of language processing such as syntax. Most studies in either of these threads of language research report brain activation including peaks in the superior temporal gyrus (STG) and/or the superior temporal sulcus (STS), but it is not clear why these areas are recruited in functionally different studies. The current fMRI study aims to disentangle the functional neuroanatomy of intelligibility and syntax in an orthogonal design. The data substantiate functional dissociations between STS and STG in the left and right hemispheres: first, manipulations of speech intelligibility yield bilateral mid-anterior STS peak activation, whereas syntactic phrase structure violations elicit strongly left-lateralized mid STG and posterior STS activation. Second, ROI analyses indicate all interactions of speech intelligibility and syntactic correctness to be located in the left frontal and temporal cortex, while the observed right-hemispheric activations reflect less specific responses to intelligibility and syntax. Our data demonstrate that the mid-to-anterior STS activation is associated with increasing speech intelligibility, while the mid-to-posterior STG/STS is more sensitive to syntactic information within the speech. *Hum Brain Mapp 31:448–457, 2010.* © **2009 Wiley-Liss, Inc.**

Key words: speech; fMRI; sentences; intelligibility; STS; STG

INTRODUCTION

The neural basis of the human ability to comprehend spoken language has been investigated in a number of studies either focusing on acoustic-phonetic aspects [Binder et al., 2000; Liebenthal et al., 2005; Obleser et al., 2007b; Scott et al., 2000], prosodic aspects [Friederici et al., 2007; Meyer et al., 2007], syntactic aspects [Friederici et al., 2000a], semantic aspects [Kotz et al., 2002; Wise et al., 1991] or both syntactic and semantic aspects of spoken language [Friederici et al., 2003; Humphries et al., 2006].

All these different aspects of language processing involve the temporal cortex to some degree. Semantic processes recruit the middle and superior temporal gyri bilaterally [Friederici et al., 2003; Kotz et al., 2002; Rossell et al., 2001], prosodic processes mainly rely on the right superior temporal gyrus (STG) [Gandour et al., 2004; Meyer et al., 2002; Zatorre et al., 1992], and syntactic processes involve different regions in the left temporal cortex. Within the domain of syntax increased activation of the left anterior superior temporal gyrus (aSTG) has been observed when comparing processing of simple spoken sentences to environmental sounds [Humphries et al., 2001], and bilaterally when comparing spoken sentences to word lists [Friederici et al., 2000b] or syntactically

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structured pseudo-word sentences to lists of pseudo-words [Friederici et al., 2000b]. The activation in the right hemisphere in addition to that in the left hemisphere was attributed to the fact that spoken sentences and word lists not only differ with respect to the presence of syntactic information but moreover with respect to prosodic parameters which are known to involve the right hemisphere. These studies led to the assumption that the left aSTG is involved in online processing of syntactically structured sequences [Friederici, 2002]. In line with this assumption the left aSTG in particular was found to show increased activation for sentences containing phrase structure errors, that is, errors which make it more difficult to build up a local phrase structure [Friederici and Kotz, 2003; Friederici et al., 2003]. The left posterior superior temporal cortex, i.e. the posterior STG (pSTG) and the posterior temporal sulcus (pSTS) seem to subserve a different aspect of syntax as it responds to correct, but syntactically complex, i.e. noncanonical sentences compared to correct canonical sentences in comprehension [Bornkessel et al., 2005; Friederici et al., 2009]. It has been proposed that this region in the left temporal cortex supports the assignment of thematic roles [Bornkessel et al., 2005] and more generally the integration of semantic and syntactic information during sentence comprehension [Friederici and Kotz, 2003]. Thus while the left anterior STG (aSTG) responds to local violation of phrase structure, the pSTG and pSTS respond to syntactic complexity in natural sentences which renders thematic role assignment difficult, and to syntactic as well as semantic violations.

Acoustic-phonetic aspects which are the primary basis for spoken language comprehension are subserved by the middle STG (mid STG) [e.g., Giraud and Price, 2001; Liebenthal et al., 2005] and STS [Scott et al., 2000]. In particular, speech intelligibility has been correlated with activation in the more anterior portion of the STS [Obleser et al., 2007a; Scott et al., 2000]. For the processing of speech a hierarchical organization along the entire STG and STS as a function of spectrotemporal complexity and intelligibility (i.e., increasing independence of acoustic form going from dorsal-posterior to ventral-anterior) has been proposed by Davis and Johnsrude [2003].

Thus the present overview of different syntactic studies and those investigating intelligibility of speech reveals a considerable overlap of the activation patterns found in syntactic analysis and intelligibility. If any systematic conclusion can be drawn from the existing literature, it appears that the most ventral anterior and most posterior temporal cortex is only recruited for syntactic analysis. The intelligibility-varying studies rather report the involvement of the entire STS/STG region. This, however, may not be surprising given that these latter studies not only vary acoustic parameters, but implicitly also vary the availability of syntactic and other linguistic information.

The goal of the present study was to systematically vary speech intelligibility and syntactic correctness in a 2 × 2 within-subjects design to determine whether subregions of the superior temporal cortex of both hemispheres can be functionally differentiated, along the posterior-to-anterior dimension or along the dorsal-to-ventral dimension with the STS supporting intelligibility of speech and the STG supporting syntax. Intelligibility of speech was varied by modifying acoustic parameters of speech signal (spectral rotation) whereas syntactic correctness was varied by introducing a phrase structure violation (insertion of a preposition before a verb). While spectral rotation makes syntactic (as well as phonological and semantic) information nonaccessible, a phrase structure violation taps the listeners' ability to make use of the syntactic information provided, and thus allows investigating syntax directly. The present factorial design, moreover, allows us to test whether the expected difference between syntactically incorrect and correct sentences is due to syntactic information provided in the intelligible speech version or due to any basic acoustic difference between the two conditions (e.g. an extra word in the incorrect condition and possible prosodic difference to the correct condition). Therefore, those brain areas that will reveal an interaction between the two factors with a major difference between syntactically incorrect and correct stimuli in the intelligible condition but not in the rotated condition can be considered as syntax-related. In terms of the hemispheric contributions to spoken language processing, the present study will allow us to evaluate whether intelligibility-driven brain activation is bilateral (irrespective of the syntactic correctness of an utterance) and whether activation driven by syntactic phrase-structure violations is exclusively localized in the left hemisphere.

METHODS

Participants

Seventeen participants (nine females; age range 20–30 years) took part in the fMRI experiment. All were native right-handed speakers of German and had normal hearing as well as no history of neurological or language-related problems. This information was assessed by self report. They also had had no previous experience with rotated speech. Participants received financial compensation (15 EUR). The present study was approved by the local ethics committee of the University of Leipzig.

Stimuli

We used a set of sentences that has been previously developed and thoroughly tested [Friederici et al., 2003]. The set consists of short German sentences containing transitive verbs in the imperfect passive form. Participial forms of 48 different transitive verbs, all of which started with the regular German participial morpheme "ge," were used to create the experimental sentences. For each participle, two different critical sentences were used; a correct

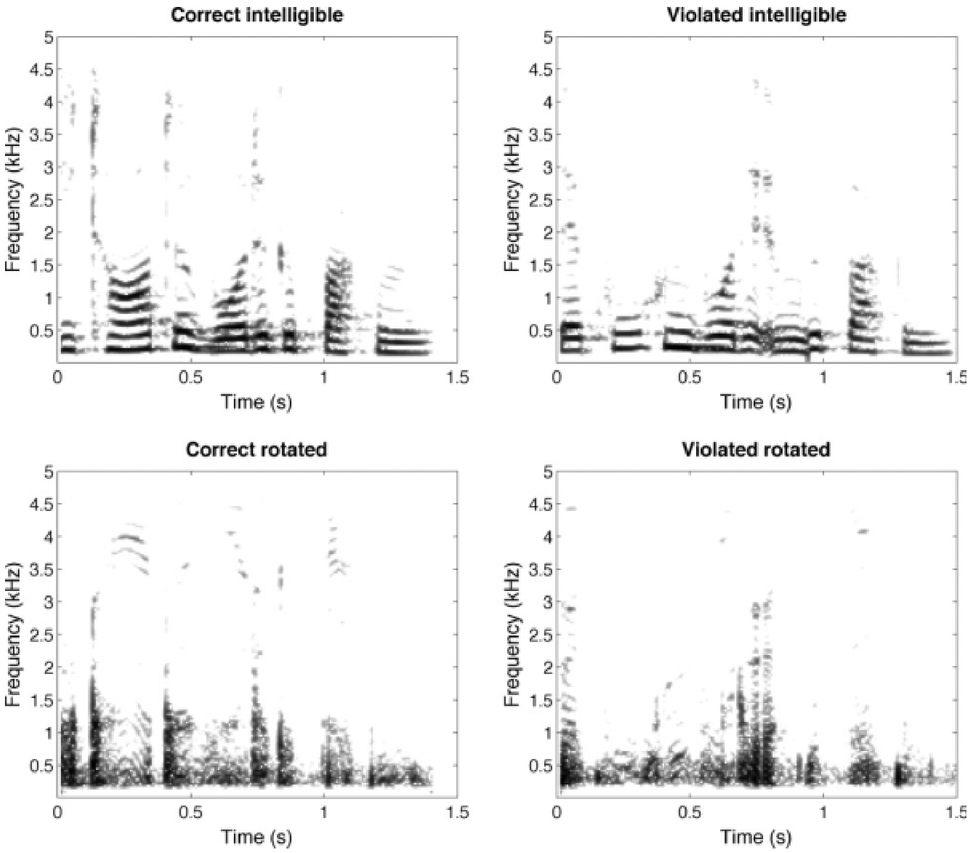

Figure 1.

Spectrograms for all four stimulus conditions. An example of a syntactically correct sentence (left panels) and its phrase-structure-violated complement (right panels) is shown in intelligible, unaltered (top panels) as well as unintelligible, spectrally rotated versions (bottom panels). Spectrally rotated analogues of the sentences (lower panels) preserve the spectrotemporal complexity, the envelope and some sense of intonation of the intelligible sentences.

sentence ("Die Pizza wurde gegessen" [The pizza was eaten]) and a syntactically incorrect sentence, where the participle immediately followed a preposition ("Die Pizza wurde *im* gegessen," [The pizza was *in the* eaten]), thus yielding a phrase structure violation. All sentences were spoken by a female native speaker of German. The sentences were recorded on digital-audio tape, and sampled at 20 kHz with a 16-bit resolution. Finally, pronouncing a syntactically malformed sentence may lead to acoustic or prosodic anomalies. To prevent such effects prior to the participle in the syntactically incorrect sentences, the speaker produced these sentences with a noun following the preposition. This noun always had the same onset-phoneme as the participle and ended in a phoneme which was identical to the last phoneme of the preposition occurring in that sentence. The sentences containing the syntactic violation were then created by eliminating the noun from the sentences produced as described above, thus avoiding an unnatural acoustic transition due to coarticulation differences [Hahne and Friederici, 1999]. The violated sentences turned out to be slightly longer in duration (1.69 ± 0.15 s) than the correct sentences (1.5 ± 0.13 s, M ± SD) because of the additional word, but the unintelligible control sets of stimuli described below retained (and thereby controlled for) this marginal difference.

The audio recordings of all sentences were then normalized for root mean square sound pressure, resampled to 22.05 kHz, and subjected to a Matlab(tm) script to create additional, unintelligible versions, using spectral rotation [Blesser, 1972]. Speech sounds were first low-passed filtered at 4 kHz and rotated around 2 kHz [cf. Scott et al., 2000]. Spectrally rotated speech has served as an unintelligible baseline condition in various neuroimaging experiments [Obleser et al., 2006, 2007a,b; Scott et al., 2000]. It allows the closest preservation of acoustic form while preventing analysis of phonology, syntax, or meaning. It retains aspects of some phonetic features (e.g. the frication in voiceless fricatives) and preserves the envelope shape and spectrotemporal complexity of the original speech. It also preserves a weak sense of the original pitch, and thus the original intonation, of speech. Figure 1 shows spectrograms for a set of examples of all four stimulus conditions.

Experimental Procedures

Scanning was performed using a Siemens 3-T scanner (Siemens, Erlangen) with a birdcage headcoil. Participants were comfortably positioned in the bore and wore air-conduction headphones (Resonance Technology, Los Angeles). After a brief (15-trial) familiarization period using sentences that were retained for demonstration purposes only, the actual experiment started.

Functional scans were acquired every 9 s, with a stimulus being presented 5.5 s before each scan [sparse temporal sampling; Edmister et al., 1999; Hall et al., 1999]. Participants were required to listen attentively to the stimuli, but no further task was employed [Obleser et al., 2007a,b; Scott et al., 2000].

Each trial's sentence was drawn pseudo-randomly from one of the five conditions (correct-intelligible, incorrect-intelligible, correct-rotated, incorrect-rotated, as well as no-stimulus baseline trials). About 48 trials (=48 volumes, in a sparse temporal sampling design) for each condition were acquired, amounting to a total of 240 acquired volumes/trials of interest.

Echo-planar imaging (EPI) scans were acquired in 26 axial slices covering the entire forebrain with an in-plane resolution of 3×3 mm^2 and a 3-mm slice thickness (repetition time TR = 9.0 s, acquisition time TA = 2.0 s, echo time TE = 30 ms, flip angle 90°, field of view 192 mm, matrix size 64×64, interleaved slice acquisition and no gap between slices). For each participant, the individual high-resolution 3D T1-weighted MR scan acquired in a previous session was available for normalization, coregistration, and data visualization.

Data Analysis

Functional data were analyzed using SPM5 (Wellcome Imaging Department, University College, London, UK). Functional MRI time series were resampled to a 2-mm^3 voxel size, realigned, and corrected for field inhomogeneities ("unwarped"), normalized (by segmenting each participant's T1-weighted image according to the SPM5 gray-matter template image and using the parameters gained for normalizing this participant' fMRI images), and smoothed using an isotropic 8-mm kernel.

In each participant, a general linear model using four regressors of interest (2 intelligibility levels $\times 2$ syntactic levels) was estimated with a finite impulse response basis function (order 1, window length 1). The no-stimulus (silent) trials in the time series formed an implicit baseline. Contrasts of all four conditions against the baseline from all 17 participants were submitted to the SPM5 module for second-level within-subject analysis of variance, from which main effects, interactions and specific contrasts could be assessed. Statistical parametric maps of the second-level analysis were thresholded at $q(\mathrm{FDR}) > 0.01$, $k > 30$ voxels [FDR, false discovery rate; Genovese et al., 2002].

TABLE I. List of brain structures activated in the two principal contrasts

Site	MNI peak coordinate	Z	Extent (in voxels)
Intelligible > rotated (in correct sentences only)			
Left anterior STS (BA 21/38)	−58, −4, 4	6.96	1,242
Right anterior STS (BA 21)	62, −4, −14	6.58	950
Incorrect > correct (in intelligible sentences only)			
Left middle STG (BA 22)	−54, −16, 4	5.44	763
Left posterior STS (BA 22)	−60, −42, 6	4.48	199
Left IFG (BA 44)	−62, 18, 16	4.08	55
Left Thalamus	−12, −28, 2	4.85	47
Right STG (BA 48)	44, −20, 6	5.06	255

SPMs were thresholded at a false-discovery rate (FDR) of $q > 0.01$ and a minimum cluster extent of $k > 30$ voxels. BA, Brodmann's area; IFG, Inferior frontal gyrus; STG, superior temporal gyrus; STS, superior temporal sulcus.

For further analyses of region of interest (ROI) data, the MaRsbar toolbox [Brett et al., 2002] was used to extract mean beta weights from peak-voxel-centered spheres of 4-mm radius (equalling ∼30 voxels or a volume of 268 μl; summed using the first Eigenvariate) as identified in the random-effects statistics (Table I). Seven regions of interest resulted directly from this. These regions have been found active in syntactic tasks in previous experiments conducted in the same laboratory [Bornkessel et al., 2004; Friederici et al., 2003, 2006, 2009]. All ROI-, condition- and participant-specific mean beta values were then transformed to percentage signal change (%SC) and assessed using Matlab(tm)-implemented repeated measures ANOVAs.

RESULTS

First, we tested two planned contrasts on the group fMRI data, to retest the main findings of Scott et al. [2000] on intelligibility and Friederici et al. [2000b, 2003] on syntactic violations, respectively: When comparing correct intelligible sentences to their unintelligible, rotated complements, activation was observed from mid-to-anterior STS bilaterally with significant peaks in the anterior STS (aSTS) (Fig. 2, Table I); conversely, intelligible sentences with violated syntax yielded a strongly left-lateralized peak in the mid STG when compared to intelligible correct sentences (Table I). Further peak activations in this comparison were observed in the left pSTS, left IFG (BA 44) the left thalamus, and also in the right mid STG.

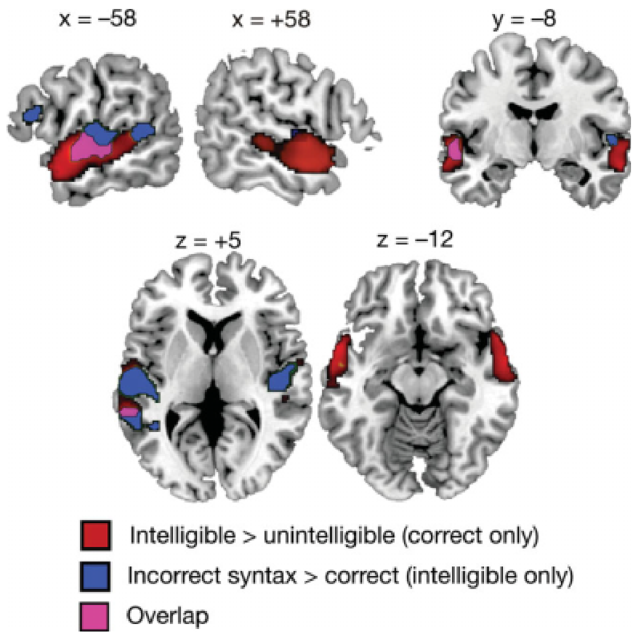

Figure 2.

Overlay of group activations in the two principal contrasts. *Intelligible > rotated (correct only)*, shown in red, *incorrect syntax > correct (intelligible only)* shown in blue (overlay in purple), thresholded at q(FDR) $>$ 0.01, cluster extent $k > 30$ voxels, in a left and right sagittal (top left panel), coronal (top right panel) and two axial slices (bottom panels); x, y, and z values indicate MNI coordinates of slices displayed.

Using the individual participants' percentage of signal change (%SC) data, the ANOVA for the temporal cortex with the factors: Syntax (correct/violated), Intelligibility (natural/spectrally rotated), Region (aSTS/mid STG), and Hemisphere (left/right) revealed a series of significant main effects and interactions.

There was a three-way interaction for the factors Syntax × Intelligibility × Hemisphere ($F(1,16) = 6.0$, $P < 0.03$) reflecting more activation of aSTS/mid STG in the left than in the right hemisphere for natural speech than for rotated speech. A main effect for the factor Intelligibility ($F(1,16) = 90.5$, $P < 0.001$) with higher activations for natural than for rotated speech extending to most anterior portions of the STS bilaterally is evident in Figure 2 (colored in red). The left localized main effect of Syntax ($F(1,16) = 73.5$, $P < 0.001$) extends not as far anterior but is present in the pSTS (Fig. 2, shown in blue; see also separate analysis below).

Figure 3 displays condition-specific activations in all seven ROIs. Those ROIs that show an interaction of Syntax and Intelligibility with more activation for the violated compared to correct sentences in the natural speech, but not in the rotated condition, are clearly those areas specifically reacting to syntactic information. They respond to information provided by the preposition and the resulting violation of an unfilled prepositional phrase and not simply to the fact that the violated stimuli contain one more syllable than the correct condition. This acoustic difference and any residual difference in prosody between correct and incorrect sentences is present in the natural as well as in the rotated versions, but only the natural versions reveal a significant difference. By this definition, all regions identified in the left hemisphere (left aSTS as well as pSTS, left mid-to-anterior STG, left thalamus and left IFG/BA 44) are sensitive to syntactic violation—unlike those in the right hemisphere (Table II).

The interaction pattern in the right STS does not attain significance. Likewise, the right-hemispheric mid STG peak (which does not show an interaction of Intelligibility and Syntax) only shows a strong main effect of Syntax. That is, this region appears to pick up on acoustic differences that may be elicited by the syntactic violation (prosody, number of syllables) and which are preserved in the rotated sentences.

Notably, when lowering the statistical threshold (FDR-corrected $q > 0.05$ and a cluster extent of 30), two additional bilateral peaks in more medial STG, i.e. in the transversal gyri housing primary auditory cortex, were observed in the contrast of incorrect rotated greater than correct rotated sentences (left MNI coordinate -50, -14, 4; right 48, -14, 6). This somewhat weaker effect amongst unintelligible sentences can be best attributed to the extra word and henceforth the extended length of the incorrect stimuli, eliciting more primary auditory activation.

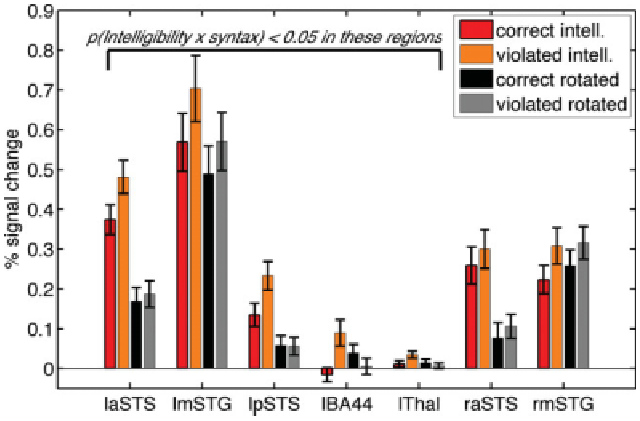

Figure 3.

Condition-specific activations in all regions of interest. The seven regions (groups of columns) refer directly to the seven clusters reported in Table I, and to the respective ROI statistics reported in Table II. laSTS, left anterior STS; lmSTG, left middle STG; lpSTS, left posterior STS; lBA44, left IFG/BA 44; lThal, left Thalamus; raSTS, right anterior STS; rmSTG, right middle STG.

TABLE II. Intelligibility and Syntax main effects and interaction in all regions of interest

Site	Main effect intelligibility	Main effect syntax	Intelligibility × syntax
Left anterior STS (BA 21/38)	****	****	*
Right anterior STS (BA 21)	****	****	—
Left middle STG (BA 22)	****	****	*
Right STG (BA 48)	—	****	—
Left thalamus	*	—	*
Left posterior STS (BA 22)	****	****	***
Left IFG (BA 44)	—	**	**

All effects reported are results of separate repeated-measures analyses of variance (ANOVA) with df = 1,16, where $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, and $^{****}P < 0.0001$.

DISCUSSION

The present study set out to investigate the contribution of the STS and the STG to syntactic processing and intelligibility of speech. Sentence material in the fMRI experiment varied with respect to its syntactic correctness and its acoustic parameters, namely intelligibility in a 2 × 2 design to functionally identify those brain regions that primarily support acoustic processes, and those that subserve syntactic processes during sentence comprehension.

Superior Temporal Gyrus and Sulcus

As Figure 2 shows, activation was observed in a number of different areas along the entire superior temporal cortex (in both STG and STS) for the two unrotated, intelligible sentence conditions carrying phonological, semantic, and syntactic information compared to their rotated baselines. These temporal areas are the aSTS bilaterally, the left mid STG, and the left pSTS. Only the right mid STG exhibits equally strong activation by intelligible and by rotated speech. All temporal areas in the left hemisphere also show a main effect of syntax (Fig. 2, Table II).

More importantly, however, the interaction of the two factors reveals a number of areas that showed more activation for syntactically incorrect than for correct sentences in the intelligible condition, but not for their rotated counterparts. These are the aSTG bilaterally, the left pSTS, in addition to left BA 44 and the left thalamus suggesting their specific involvement when syntactic processing demands increase (see Fig. 3).

Thus, although we observed a large overlap in activation (cf. purple areas in Fig. 2) both as a function of syntactic and acoustic features in the left superior temporal cortex, some areas increased their activation on top of a general enhancement for intelligible speech even more as a function of increased syntactic processing demands. Syntactic processes were more effective in driving the dorsal anterior and posterior parts of the STG/STS region in the left hemisphere in addition to the left BA 44.

Previous studies investigated acoustic parameters and syntactic parameters in spoken language only separately. Those focusing on acoustic parameters and intelligibility of speech reported that the STS responds to the presence of phonetic information [Liebenthal et al., 2005; Obleser et al., 2007b], and the aSTS to any intelligible speech compared to unintelligible speech [Scott et al., 2000]. A hierarchical organization from posterior to anterior regions has been proposed for the STG and STS with increasing sensitivity to spectrotemporal complexity and intelligibility of speech from posterior to anterior regions [Davis and Johnsrude, 2003; Scott et al., 2000; for an alternative view emphasizing a partly compatible dorsal-ventral gradient see Binder et al., 2000]. The present results are in general agreement with this view. Notably, the right-hemispheric activation in response to increasingly intelligible speech deviates from the original papers on intelligibility [Narain et al., 2003; Scott et al., 2000], but agrees with the case that several studies have reported bilateral suprathreshold activation [e.g., Binder et al., 2000; Davis and Johnsrude, 2003; Harris et al., 2009; Obleser et al., 2007a; Zekveld et al., 2006] for intelligible speech over adequate baseline conditions, although often skewed to the left. It is a matter of debate what the right-hemisphere is contributing to spoken language comprehension [e.g., Friederici and Alter, 2004; Hickok and Poeppel, 2007; Zatorre et al., 2002] and whether for example, speaker and intonation contour information can be more usefully extracted from clear than rotated speech. This only renders it more notable that all the interactions of syntax and intelligibility are observed in the left hemisphere.

In the syntactic domain, a comparable posterior to anterior gradient for complexity of the stimuli has not been reported. Rather, posterior STG/STS activations were found for the comprehension of syntactically complex sentence for which thematic role assignment requiring the integration of syntactic and semantic information is difficult [Bornkessel et al., 2002; Friederici et al., 2009; Roeder et al., 2002], and for both semantically and syntactically incorrect sentences [Friederici et al., 2003]. Anterior portions of the STG/STS (anterior to Heschl's gyrus), in contrast, have been observed specifically for sentences in which the local phrase structure is violated [Friederici et al., 2003; Rüschemeyer et al. 2005] or absent, i.e. word lists containing no syntactic structure compared to stimuli with syntactic structure thus rendering phrase structure building difficult [Friederici et al., 2000b; Humphries et al., 2005; Stowe et al., 1998]. The present data are compatible with previous studies on processing phrase structure violations in that we see a significant response of the aSTS as a function of the syntactic manipulation. To allow a direct comparison with a previous study using similar syntactic violations [Friederici et al., 2003], an additional ROI analysis with exactly those coordinates of the former study was calculated (Talairach coordinates $x = -53$, $y = -1$, $z = 0$; transformed to the MNI space of the current data using the Brett/mni2tal transformation). This analysis for the left aSTG ROI also revealed significantly more activation for violated compared to correct sentences (main effect of Syntax, $F(1,16) = 18.04$, $P < 0.001$; interaction n.s.). An involvement of the left posterior STG/STS was also observed in this previous study, but there it had not been specific to syntactic violations, but was observed in semantic violations as well. This area's sensitivity to syntactic and semantic violations is compatible with the present results revealing stronger activation for the left pSTS for intelligible speech carrying semantic and syntactic information compared to rotated speech in which this information is absent. Thus these results and others in the literature [Ben Shachar et al., 2003; Bornkessel et al., 2005] are in line with the previously formulated view that the posterior superior temporal cortex reacting to syntactic and semantic parameters should be seen as a region integrating different types of information subserving language comprehension [Grodzinsky and Friederici, 2006; see also below].

Of particular interest for the present work is a study by Giraud et al. [2004], which varied the complexity of speech-envelope noises during sentence comprehension. In this study the superior to middle STG and STS was found to respond to acoustic complexity and the ventral temporal regions to react to meaningfulness of the stimuli though modulated by their acoustic "quality." The left pSTG was reported sensitive both to auditory search and, similar to our study, to speech comprehensibility. In their study the additional activation observed in BA44 in the inferior frontal gyrus was interpreted to be associated with attentional effort of processing.

Frontal and Subcortical Structures

In our study we found BA44 to increase its activation with the processing of syntactically incorrect as compared to correct sentences. Earlier fMRI studies with adult listeners which had used similar stimulus material reported activation in the frontal operculum adjacent to the pars opercularis (BA44) rather than in BA 44 itself [Brauer and Friederici, 2007; Friederici et al., 2003]. Activation in BA44, however, was seen in children [Brauer and Friederici, 2007] and in adult second language learners [Rüschemeyer et al., 2005], that is, for groups for which the attentional processing effort is higher than in native adults. This later observation is compatible with the interpretation of BA44 involvement in attention related processing by Giraud et al. [2004]. The BA44 activation in the present study with native adults may result from increased attention-related processing demands. In contrast to the earlier fMRI studies, we used a sparse sampling approach with no specific task requirement other than attentive listening. Moreover, we presented naturally spoken sentences together with unintelligible sentences in a randomly mixed order [as in the study by Giraud et al., 2005]. This may have increased attentional demands while listening to, and extracting relevant information from speech.

Activation in the IFG has been observed not only with increased processing demands as a function of syntactic violations, but, moreover, as a function of syntactic complexity [Ben-Shachar et al., 2003; Fiebach et al., 2005; Friederici et al., 2006; Grodzinsky and Santi, 2008; Kuperberg et al., 2003; for reviews see Grodzinsky and Friederici, 2006; Vigneau et al., 2006]. Since activation of the IFG is also observed in processing hierarchically structured, complex sequences in semantic-free artificial grammars [Bahlmann et al., 2008; Friederici et al., 2006] we take this activity to reflect difficulty in structure building processes [for an overview see Grodzinsky and Friederici, 2006].

The left thalamus was also found to react systematically to syntactically violated sentences in the natural speech condition. This finding fits well with a recent study using the same material during intracranial recordings. It was found that the left thalamus more than the right thalamus was sensitive to syntactically (and semantically) violated sentences [Wahl et al., 2008]. Timing parameters of scalp and intracranial recordings suggested that the thalamus mediates between early syntactic processes in anterior fronto-temporal brain regions supporting phrase structure building [Friederici et al., 2000b] and late integration processes in more parieto-temporal brain regions.

Posterior Versus Anterior Superior Temporal Cortex

The present data are in line with the view that the left anterior and posterior STG/STS together with the ventral IFG and subcortical structures support syntactic processes [Friederici, 2002]. The mid STG bilaterally appears to react to more general aspects of acoustic processes such as stimulus length, as shown previously [e.g. Liebenthal et al., 2005; Obleser et al., 2007b; Scott et al., 2000].

In our study, those regions in the left temporal cortex which responded more strongly to the naturally spoken stimuli carrying phonological, semantic, and syntactic information than to rotated speech stimuli also reacted to the factor syntax in natural speech, however, specifically revealing additional reactiveness when syntactic processing demands increased due to syntactic violations. Effects of intelligibility were located more ventrally and more anteriorly, whereas syntax effects were located more dorsally extending to the posterior temporal region. General acoustic features such as stimulus length appear to be tracked by belt and parabelt areas [Rauschecker & Tian, 2000; Kaas & Hackett, 2000] in the mid STG bilaterally as evidenced by increased activation for the violation conditions independent of intelligibility. Acoustic-phonetic features as indicators of intelligible speech compared to unintelligible speech are of major interest for the mid-to-anterior superior temporal region, maximally though for aSTS in both hemispheres.

With respect to left pSTS, the activation patterns we report are consistent with this brain area's role of integrating various language and signal domains. Within the domain of sentence processing it seems to subserve the integration of semantic and syntactic information as necessary for thematic role assignment independent of the modality (auditory, visual) [e.g. Bornkessel et al., 2004; Keller et al., 2001; Friederici et al., 2009; Ni et al., 2000]. The left pSTS, extending into MTG has also been reported to show complex response patterns of integration within the auditory domain for lexical access [e.g., Kotz et al., 2002; Obleser & Kotz, 2009], semantic integration of ambiguous sentences [Rodd et al., 2005], as well as for multimodal language integration, such as gesture with speech [Holle et al., 2008]. Thus, the current evidence together with these results from the literature on language processing imply a functional distinction of pSTS from its more anterior parts, defining its functional role in terms of integration processes across different linguistic domains and levels.

The more general view on hierarchy of function promoted by our data is that basic acoustic aspects are processed in the auditory cortex, and regions located anterior and posterior to Heschl's gyrus are recruited for more complex yet distinguishable processes, i.e. acoustic-phonetic and syntactic processes. This view of a functional differentiation of the anterior and the posterior superior temporal cortex maps onto recent structural data that indicate two pathways from the primary auditory cortex, one to the posterior STG/STS and one to the anterior STG/STS [Upadhyay et al., 2008]. The present data shed some light on the suggestion that these two pathways within the superior temporal cortex may indeed be functionally distinct. In the left hemisphere the pathway to the anterior STG/STS appears to be involved in the online analysis of structured sequences, be they phonetic or syntactic, whereas the pathway to the posterior STG/STS (a region in which semantic and syntactic information are processed and possibly integrated) seems to be crucial for the comprehension of sentences.

CONCLUSION

In sum, this study distinguished how the mid-to-anterior STS activation is mainly driven by increasing intelligibility [Scott et al., 2000], while the mid-to-posterior STG is more sensitive to syntax [Friederici & Kotz, 2003]. The combination of syntactic and intelligibility manipulations within one experiment allowed us to discern meaningful differences in left and right STG/STS responses to these sentences: When carefully dissected, the left hemispheric predominance of the mid-to-posterior STG/STS in parsing sentences and a bilateral mid-to-anterior STS activation for acoustic-phonetic features, i.e. intelligibility of speech, can be unambiguously shown. It is, to our knowledge, the first study to experimentally disentangle brain activation patterns that accompany varying speech intelligibility from those additionally elicited by syntactic analysis.

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