



## Syntactic and auditory spatial processing in the human temporal cortex: An MEG study

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### ABSTRACT

Processing syntax is believed to be a higher cognitive function involving cortical regions outside sensory cortices. In particular, previous studies revealed that early syntactic processes at around 100–200 ms affect brain activations in anterior regions of the superior temporal gyrus (STG), while independent studies showed that pure auditory perceptual processing is related to sensory cortex activations. However, syntax-related modulations of sensory cortices were reported recently, thereby adding diverging findings to the previous studies. The goal of the present magnetoencephalography study was to localize the cortical regions underlying early syntactic processes and those underlying perceptual processes using a within-subject design. Sentences varying the factors syntax (correct vs. incorrect) and auditory space (standard vs. change of interaural time difference (ITD)) were auditorily presented. Both syntactic and auditory spatial anomalies led to very early activations (40–90 ms) in the STG. Around 135 ms after violation onset, differential effects were observed for syntax and auditory space, with syntactically incorrect sentences leading to activations in the anterior STG, whereas ITD changes elicited activations more posterior in the STG. Furthermore, our observations strongly indicate that the anterior and the posterior STG are activated simultaneously when a double violation is encountered. Thus, the present findings provide evidence of a dissociation of speech-related processes in the anterior STG and the processing of auditory spatial information in the posterior STG, compatible with the view of different processing streams in the temporal cortex.

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### Introduction

Previous studies investigating early syntactic processes in auditory sentence comprehension reported an enhanced negativity around 100–200 ms, labeled early left anterior negativity (ELAN), that was elicited by sentences containing a syntactic word category violation (Friederici et al., 1993; Hahne and Friederici, 1999, 2002). It has been a point of discussion whether prosodic effects contribute to such early syntax-related responses. However, a recent finding provides contradicting evidence by showing that a change in the prosodic contour cannot account for the ELAN effect, thereby highlighting the interpretation of the ELAN as a marker for initial syntactic processes (B. Herrmann et al., 2011).

Another question that has been raised in the context of the interpretation of the ELAN is whether this component belongs to the family of the mismatch negativity (MMN), an early negativity associated with rule violations in auditory perception (Näätänen et al., 1978). The MMN is elicited by an infrequently presented auditory event among a series of frequently repeated auditory events reflecting a memory

comparison process (Schröger, 2005). The MMN has its maximum at around 100–200 ms following the onset of the infrequent event and has been reported for frequency (Näätänen et al., 1978; Shalgi and Deouell, 2007), duration (Jemel et al., 2002) or spatial deviations (Schröger, 1996; Nager et al., 2003), for example.

The relation between processing syntactic and auditory perceptual information was first investigated by Hahne et al. (2002) who studied early syntactic and auditory spatial processing in combination using electroencephalography (EEG). In this study, infrequent spatial deviations within a spoken sentence elicited a MMN, whereas sentences containing a syntactic word category violation elicited an ELAN. Sentences including an infrequent spatial deviation as well as a syntactic violation led to a larger negativity around 125–175 ms than the single violations, although the amplitude was less than a complete addition of the two single violations. The results were taken as an indicator that early syntactic and physical acoustic information can be processed in parallel within the first 200 ms (Hahne et al., 2002).

However, it remains an open question what parallel processing in this context means as only slight differences in the EEG scalp distribution of the syntactic and auditory spatial violation effects were reported in the study of Hahne et al. (2002). The present magnetoencephalography (MEG) study aims to shed more light on this issue. It might be the case that both types of single deviations

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recruit the same brain regions and that the double deviation thus leads to stronger activation in these very same regions. On the other hand, different brain regions might be involved in processing syntactic versus spatial deviations and that these regions are activated simultaneously when a combined violation is encountered. According to dual stream auditory processing models (Rauschecker and Scott, 2009) spatial information is processed in the dorsal stream involving the posterior portion of the superior temporal cortex, while speech (intelligibility of speech) processes recruit regions anterior to Heschl's gyrus in the ventral stream. It could, therefore, be hypothesized that partly different regions are activated when speech-related and auditory spatial features are processed in parallel.

Previous studies on the localizations of the neural mechanisms that underlie early syntactic processes, have localized the sources of the magnetic ELAN (ELANm) to the superior temporal cortex (Groß et al., 1998; Knösche et al., 1999), and more specifically to the anterior parts of the superior temporal gyrus (aSTG) and the inferior frontal cortex (IFC; Friederici et al., 2000). More recently, a so called “sensory hypothesis” for early syntactic effects has been introduced in the visual domain (Dikker et al., 2009). This hypothesis is based on the observation that early sensory cortex activations were affected at around 100–200 ms when participants encountered a syntactic word category violation (Dikker et al., 2009, 2010; B. Herrmann et al., 2009). It has been suggested that these early sensory effects rely on form properties associated with the syntactic category, e.g. overt category marking by an affix (Dikker et al., 2010). For the processing of syntactic violations in an auditory oddball paradigm, B. Herrmann et al. (2009) observed modulations of the primary auditory cortex (AC) and the superior temporal sulcus, thus, suggesting activations in regions different from previous localizations showing aSTG and IFC activations in processing word category violations (Friederici et al., 2000). One explanation for these diverging findings that has been proposed relates to the methodological approaches applied (Dikker et al., 2009). In the study conducted by Friederici et al. (2000), for instance, dipole modeling was constrained by functional magnetic resonance imaging (fMRI) results from a previous sentence processing study (Meyer et al., 2000). Dikker et al. (2009) argued that this constraint might not be valid, as fMRI lacks the temporal resolution to derive solid assumptions about an early stage in sentence processing. In the study by B. Herrmann et al. (2009), on the other hand, two-word utterances were presented in an auditory oddball paradigm in which syntactic processing is accompanied by an acoustic change (Shtyrov and Pulvermüller, 2007), thus, possibly biasing the source localization towards primary regions.

The underlying neural sources of the MMN have mainly been localized to auditory sensory cortex regions (Giard et al., 1990; Alho et al., 1998; Maess et al., 2007). Particularly relevant for the current study, the MMN and its magnetic counterpart (MMF, mismatch field) has been found sensitive to infrequent changes of interaural time and interaural level differences (ITD, ILD; Schröger, 1996; Schröger and Wolff, 1996; Kaiser et al., 2000; Nager et al., 2003). The ITD and ILD are two important auditory cues which allow spatial sound localization (Middlebrooks and Green, 1991). The MMN to changes in ITD/ILD has been shown to modulate brain activations in the posterior STG/AC (Kaiser et al., 2000; Tata and Ward, 2005; Sonnada et al., 2006; Deouell et al., 2006). Sometimes, an additional neural generator localized to the right IFC has been reported to underlie the MMN mechanism (Giard et al., 1990; Jemel et al., 2002; Shalgi and Deouell, 2007).

In addition to the ELAN effect in the 100–200 ms time window, previous studies were able to disentangle the “early syntax effect” into different sub-stages, observing an additional very early syntax-related effect that modulated the M50 component (C. S. Herrmann et al., 2000; B. Herrmann et al., 2009, 2011). Furthermore, the detection of simple rule violations in an auditory oddball paradigm has not only been shown to elicit the MMN, but also to modulate the brain's

activity very early, starting at around 30 ms (Boutros and Belger, 1999; Ermutlu et al., 2005; Slabu et al., 2010; Grimm et al., 2011).

In the present study, anatomically constrained magnetoencephalography (MEG) was used to further investigate the early syntactic and auditory perceptual parallel processing effect in the brain. On this account, auditory sentence materials were presented that varied in syntax (syntactically correct vs. syntactically incorrect) and auditory space (standard vs. infrequent ITD change). For the source analysis, a distributed source model was used without any priors regarding the location of the underlying cortical regions modulated by syntax and auditory space. Our main goals were to examine the neural mechanisms that underlie the processing of (1) syntactic violations, (2) auditory spatial violations (ITD change), and (3) double violations, i.e. in syntax and auditory space.

- (1) The localization of the neural responses elicited by syntactic violations allowed us to test previous localizations of the ELANm (Friederici et al., 2000), and to examine whether auditory sensory cortices are sensitive to syntactic manipulations (Dikker et al., 2009). The former study predicts activations in the anterior STG with additional weaker frontal activations, whereas the latter view predicts the ELANm to be localized in auditory sensory cortices.
- (2) We sought to localize the neural sources of the MMF elicited by infrequent ITD changes within naturally spoken sentences in order to have a condition which reflects auditory perceptual rule processing (Schröger, 1996, 2005). We expected the posterior STG/AC to be sensitive to auditory spatial deviations (Kaiser et al., 2000; Deouell et al., 2006). Based on the dual pathways in the auditory system (Rauschecker and Scott, 2009), the neural sources of the ELANm and MMF were expected to differ in location.
- (3) By localizing the neural responses to sentences including a double violation, we aimed to investigate how processing a syntactic violation and an auditory spatial violation in parallel is accomplished by different regions in the temporal cortex (Rauschecker and Scott, 2009). We expected the brain regions involved in processing the single syntactic and those involved in processing the auditory spatial violations to be activated simultaneously for sentences containing both violations.

Apart from the effects in the 100–200 ms time window (i.e., the ELANm and MMF), we intended to further elucidate on the very early syntax and simple rule violation effects that precede the ELANm and MMF, and ask whether parallel processing can be observed already at this processing stage.

## Methods and materials

### Participants

Twenty-four healthy, native German-speaking adults (11 female, mean age = 25.3 years, standard error of the mean (SEM) = 1) participated in the MEG study. They were all right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). The 20th percentile of the laterality quotient was 100 (range: 83–100). All participants gave written consent prior to testing and were paid seven Euros per hour. They had no known hearing deficit or neurological diseases in their history.

### Stimulus material

The material comprised 192 syntactically correct sentences and 192 sentences which included a syntactic word category violation. Stimuli were taken from a previous EEG experiment (Hahne et al., 2002). They were spoken by a trained female native speaker of German and digitized at 44.1 kHz (16 bit, stereo). The factor syntax

was tested by introducing syntactically correct sentences consisting either of a “determiner–noun–auxiliary–past participle” sequence (e.g., “Das Obst wurde geerntet.”, Engl. “The fruit was harvested.”) or of a “determiner–noun–auxiliary–preposition–noun–past participle” sequence (e.g., “Das Gemüse wurde im Herbst geerntet.”, Engl. “The vegetable was in-the autumn harvested.”). Syntactically incorrect sentences consisted of a “determiner–noun–auxiliary–preposition–past participle” sequence (e.g., “Die Gerste wurde im geerntet.”, Engl. “The barley was in-the harvested.”). In these sentences, the preposition was directly followed by the past participle, causing a word category violation. The participle of each sentence was overtly marked by closed class morphology (i.e., by the prefix “ge-” and a suffix, e.g., “-t”). Incorrect sentences were created following the procedure described by Hahne and Friederici (1999), and have been evaluated to avoid unwanted acoustic and/or prosodic effects (Hahne and Friederici, 1999; B. Herrmann et al., 2011).

In order to test for the factor auditory space, a standard and a deviant condition were created for each of the 384 sentences. The deviant condition included an infrequent ITD change of 0.2 ms (the left channel was delayed) starting at the onset of the participle, thus giving a right-lateralized impression. No such ITD change was included in the standard condition. Based on the number of words, an ITD change occurred in only 10% of the words, while 90% of the words did not include a lateralization effect. Correct sentences without an ITD change are henceforth called “correct standard condition”, syntactically incorrect sentences without an ITD change “incorrect standard condition”, correct sentences including an ITD change “correct deviant condition” and syntactically incorrect sentences containing an ITD change “incorrect deviant condition” (see Table 1).

#### Design and procedure

The present experiment used a within-subject design. All 384 sentences were presented via in-ear headphones at an intensity of 55 dB above a participant's individual hearing threshold. One half of the sentences was randomly selected as standards, while the other half was selected as deviants. Sentences were randomly distributed over four blocks with equal probability for each condition. Sentences within each block were randomized with the constraint that no more than three stimuli of the same type were presented in a row. During auditory stimulation, participants looked at a small fixation square in the middle of a screen to reduce eye movements. In order to avoid motor preparation, a variable response key assignment was used. One thousand five hundred milliseconds after the sentence ended, a picture was presented showing a happy and sad smiley next to each other. Participants were instructed to press the button for the happy smiley whenever the sentence was syntactically correct and to press the button for the sad smiley whenever the sentence was syntactically

incorrect. The positions (left vs. right) of the happy and sad smiley were randomized uniformly within each block and across conditions. Participants were instructed to ignore lateralization effects in the auditory stimulation. All steps of randomization were conducted individually.

#### MEG data recording and processing

Participants sat in an electromagnetically shielded room (Vacuumschmelze, Hanau, Germany). MEG signals were recorded with a 306-channel MEG device (Vectorview, Elekta-Neuromag, Helsinki, Finland) at 500 Hz and online filtered with a band-pass of 0.1–160 Hz. Two pairs of electrodes recorded a bipolar electrooculogram (EOG). Triggers marked the onset of the sentences as well as the onset of the participle within all sentences. During blocks, the position of the participant's head was quasi-continuously measured by five HPI (head position indicator) coils to correct the magnetic fields for head movements. Head movement correction, bad channel interpolation and external interference suppression were obtained by applying the Signal Space Separation Method (Taulu et al., 2004). The MEG recordings were filtered with a high-pass of 2 Hz to avoid baseline correction and a low-pass of 10 Hz to maximize the signal-to-noise-ratio. By leaving the broad deflections untouched, this procedure has proven to be useful when investigating language- or memory-related processes (Tervaniemi et al., 1999; Friederici et al., 2000; C. S. Herrmann et al., 2000; Maess et al., 2006). The data was divided into epochs of 700 ms (–200 ms to 500 ms) that were time-locked to the onset of the participle and to the sentence onset. Epochs were screened for blinks and other artifacts and excluded from averaging if they contained a signal change of more than 200 pT/m (gradiometer), 4 pT (magnetometer) or 100  $\mu$ V (EOG).

#### Source reconstruction

Individual T1-weighted MRI images were obtained with a 3 T MRI scanner (Magnetom Trio, Siemens AG, Germany). The software Freesurfer (<http://surfer.nmr.mgh.harvard.edu/>) was applied to construct individual topological representations of the cortical surface for each hemisphere using the individual MRI images.

The MNE package provided by M. Hämäläinen, MGH, Boston, MA, USA (<http://www.nmr.mgh.harvard.edu/martinos/userInfo/data/>) was used to compute forward and inverse solutions. On this basis, inner skull surfaces were extracted using the above-mentioned T1-weighted MRI images in order to construct individual boundary element models (BEM) for the volume conductor. Such a single compartment volume conductor has been shown to be sufficient for solving the MEG forward problem (Hämäläinen and Sarvas, 1989). The MRI coordinate system was transformed into the MEG coordinate system using the HPI coils and about 50 additional points on the head surface estimated by a Polhemus FASTRAK 3D digitizer. As source space, the individual white matter surface was adopted.

For the inverse solution, the approximately 130,000 vertices needed to describe single hemispheres were reduced to approximately 5000 dipoles, resulting in approximately one dipole in 10 mm<sup>2</sup>. The standardized low resolution brain electromagnetic tomography (sLORETA) method was used to compute individual brain activations (Pascual-Marqui, 2002). In order to average solutions across participants, the individual cortical representations were transformed to a sphere representation, providing a unique coordinate system for all participants (Fischl et al., 1999a). For visualization purposes, this representation was morphed to the inflated cortical surface of one participant (Fischl et al., 1999b).

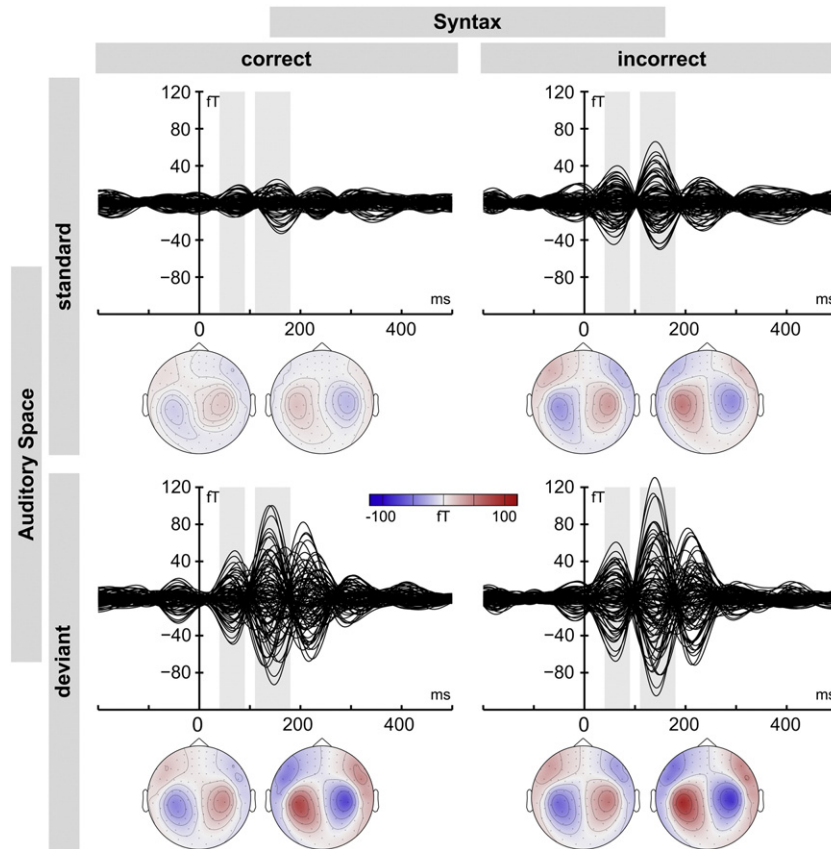
#### Statistical analysis

Based on the visual inspection of the grand average data displayed in Figs. 1 and 3, two time windows were selected for the statistical analyses. The first time window (40–90 ms) was centered at the peak

**Table 1**

Examples of the sentence materials. The asterisk marks syntactically incorrect sentences and the underlined participle highlights the interaural time difference change of 0.2 ms within the sentence. The number of sentences presented to the participants is provided in parentheses.

Sentence, e.g.:	Syntax	Auditory space
Das Obst wurde geerntet. (48) + <i>The fruit was harvested. +</i>	Correct	0.0 ms/standard
Die Gerste wurde im Herbst geerntet. (48) <i>The barley was in-the autumn harvested.</i>		
*Die Gerste wurde im geerntet. (96) <i>*The barley was in-the harvested.</i>	Incorrect	0.0 ms/standard
Das Obst wurde <u>geerntet</u> . (48) + <i>The fruit was harvested. +</i>	Correct	0.2 ms/deviant
Die Gerste wurde im Herbst <u>geerntet</u> . (48) <i>The barley was in-the autumn harvested.</i>		
*Die Gerste wurde im <u>geerntet</u> . (96) <i>*The barley was in-the harvested.</i>	Incorrect	0.2 ms/deviant



**Fig. 1.** Grand average ERFs time-locked to the onset of the particle are depicted for each condition. The gray bars highlight the time windows (40–90 ms, 110–180 ms) used for the statistical analyses and corresponding topographical distributions are provided below. Only magnetometer channels were used in this figure.

of the very early deflection. The second time window (110–180 ms) included the peak of the ELANm/MMF at around 135 ms. These time windows are in perfect agreement with previous studies (Schröger, 1996; Friederici et al., 2000; B. Herrmann et al., 2009, 2011). Additionally, a third component, peaking at around 220 ms, is visible in Figs. 1 and 3. This possibly reflects the MEG correlate of the P2 response (for a review see Crowley and Colrain, 2004) and appears to be sensitive to both auditory spatial and syntactic manipulations. Here, however, we focus on the ELANm/MMF time window and the preceding M50 time window.<sup>1</sup>

#### Statistical analysis of activation strength

Mean individual time courses for each condition were extracted from a region of interest (ROI) in the left and right hemisphere, covering the STG from the planum polare to the planum temporale by including the lower wall of the Sylvian fissure and the upper wall of the superior temporal sulcus (see Fig. 3). These cortical regions have also been shown previously to be involved in early syntactic and auditory spatial processing (Friederici et al., 2000; Deouell et al., 2006). Here, only one ROI was applied per hemisphere because grand average activations of the conditions overlapped in the STG (see Fig. 2). Inferior frontal regions did not display independent local maxima and were therefore not included in the analysis.

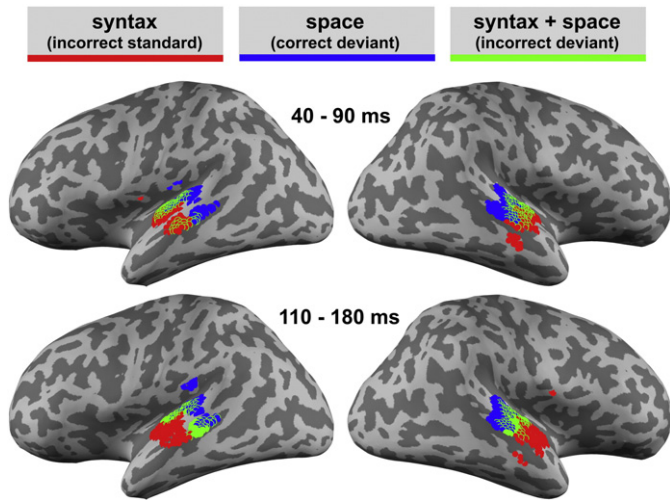
To test for STG activity differences between conditions, a three-way repeated measures analysis of variance (rmANOVA) including

the factors Syntax (correct; incorrect), Auditory space (standard; deviant) and Hemisphere (left; right) was conducted for all time windows separately. Effect Sizes are provided as generalized eta-squared ( $\eta^2_G$ ; Bakeman, 2005). Post-hoc tests were conducted whenever significant effects occurred. False discovery rate (FDR) was applied in order to prevent false positives among significant post-hoc comparisons (Benjamini and Hochberg, 1995; Genovese et al., 2002).

#### Statistical analysis of local maxima

Previous studies investigating early syntactic (e.g., Friederici et al., 2000) or auditory spatial processing (e.g., Deouell et al., 2006) as well as the present grand average data show activations along the anterior–posterior gradient of the STG (see Fig. 2). In order to evaluate the condition-specific differences of the local activation maxima in the temporal cortex, the following procedure was applied. First, a region covering most of the temporal cortex was selected for each hemisphere. Second, for each time window (40–90 ms; 110–180 ms) individual local maxima were extracted from the temporal cortex regions for the incorrect standard condition, the correct deviant condition and the incorrect deviant condition. Third, individual local maxima extracted from the temporal cortex regions for the time window of 20–50 ms following the onset of the sentence were used as an auditory cortex reference for the violation conditions in the other two time windows (see Fig. S1 in the supplemental materials; for a similar approach see e.g. Huotilainen et al., 1998). Acoustic stimulation after a period of silence is known to elicit the M50 component, which has been repeatedly localized to the auditory cortex (e.g., Mäkelä et al., 1994; Huotilainen et al., 1998; Thoma et al.,

<sup>1</sup> It is noteworthy, nevertheless, that visual inspection of the amplitudes in the P2 time window (see Fig. 3) suggests the effects of the auditory manipulation to be unaffected by the syntax manipulation, i.e. that there are only effects of syntax in cases of no additional auditory manipulation.



**Fig. 2.** Display of the location of the 100 vertices in each hemisphere that show the strongest grand average activations (syntax violation: incorrect standard condition, red; auditory space violation: correct deviant condition, blue; syntax + auditory space violation: incorrect deviant condition, green). Brain activity is displayed on the inflated surface, with dark gray representing sulci and light gray representing gyri.

2003, 2008). As brain activations were distributed parallel to the Sylvian fissure and not along one of the Cartesian axes of the source space, the final step consisted of feeding these extracted individual coordinates into a principal component analysis (PCA). A PCA identifies a coordinate system whose axes follow the most prominent spreadings of the data distribution. This allowed us to replace the 3D statistical analysis of the locations by a 1D analysis of the axis which corresponded to the anterior–posterior gradient of the temporal cortex. The correct standard condition was not included in this analysis as only weak activations were observed (see Fig. 3).

Location differences were tested using a two-way rmANOVA that included the factors Condition (incorrect standard; correct deviant; incorrect deviant; sentence onset) and Hemisphere (left; right). The

rmANOVA used the coordinates of the axis corresponding to the anterior–posterior gradient of the temporal cortex as a dependent measure and was conducted for each time window separately. The Greenhouse–Geisser correction was applied when the assumption of sphericity was violated (Greenhouse and Geisser, 1959). The original degrees of freedom are reported along with the Epsilon correction coefficient and the corrected probability. Effect Sizes are provided as  $\eta^2_G$  (Bakeman, 2005). In the case of significant effects, post-hoc tests using FDR were conducted.

## Results

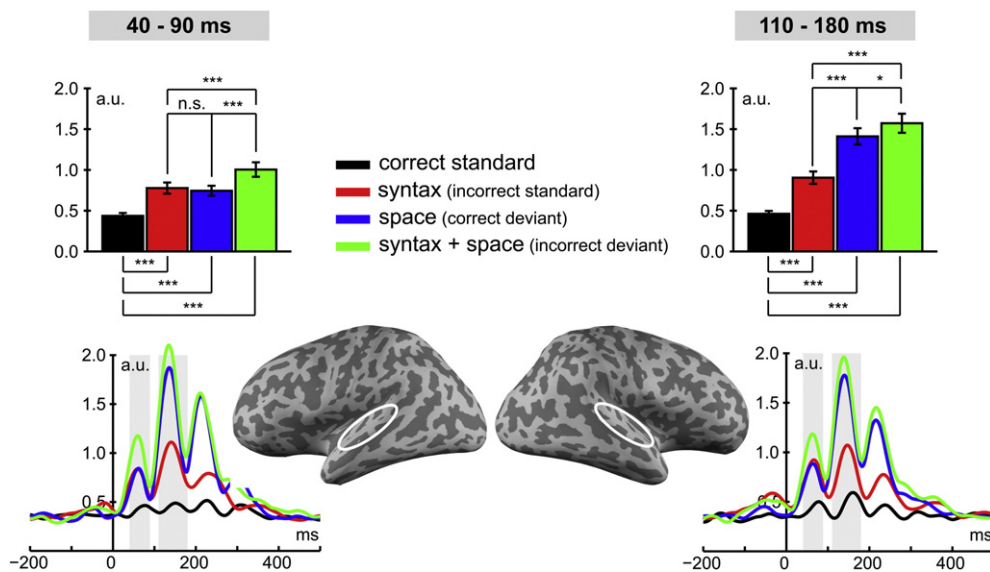
### Behavioral task

The overall mean error rate was 2.9% (SEM=0.5). Statistical comparisons did not reveal any differences between conditions.

### Source localization—activation strength

For each time window, the grand average activations of the violation conditions are depicted in Fig. 2. The corresponding STG activation time courses as well as a summary of the statistical comparisons for the two time windows are displayed in Fig. 3.

In the very early time window from 40 to 90 ms, the rmANOVA revealed a main effect of Syntax ( $F(1,23) = 33.82$ ,  $P < 0.001$ ,  $\eta^2_G = 0.150$ ) and a main effect of Auditory space ( $F(1,23) = 48.83$ ,  $P < 0.001$ ,  $\eta^2_G = 0.123$ ). Additionally, the Syntax  $\times$  Auditory space interaction was significant ( $F(1,23) = 4.67$ ,  $P = 0.041$ ,  $\eta^2_G = 0.005$ ). Post-hoc tests showed stronger activation for each of the violation conditions when compared to the correct standard condition (incorrect standard:  $F(1,23) = 50.71$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.298$ ; correct deviant:  $F(1,23) = 46.01$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.292$ ; incorrect deviant:  $F(1,23) = 64.44$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.433$ ). Furthermore, the incorrect deviant condition elicited stronger activation compared to the incorrect standard and the correct deviant condition ( $F(1,23) = 32.90$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.082$ ;  $F(1,23) = 18.04$ ,  $P_{FDR} = 0.001$ ,  $\eta^2_G = 0.111$ ; respectively). No difference was found between the incorrect standard and the correct deviant condition ( $F(1,23) = 0.32$ ,  $P_{FDR} > 0.05$ ). In other words, effects to the violation conditions were



**Fig. 3.** Time course of STG grand average brain activity (in a.u.—arbitrary units) for each condition (correct standard condition, black; syntax violation: incorrect standard condition, red; auditory space violation: correct deviant condition, blue; syntax + auditory space violation: incorrect deviant condition, green). Bar graphs depict the statistical comparisons between conditions for each time window ( $*P_{FDR} \leq 0.05$ ,  $***P_{FDR} \leq 0.001$ , n.s.—not significant).

highly significant, but the effect to the double violation was smaller than the sum of the effects to the single violations, thereby causing the interaction. There was no main effect of Hemisphere ( $F(1,23) = 0.92$ ,  $P = 0.35$ ). None of the other interactions was significant (for all,  $P > 0.15$ ).

In the time window of the ELANm/MMF (110–180 ms), the rmANOVA revealed a main effect of Syntax ( $F(1,23) = 32.53$ ,  $P < 0.001$ ,  $\eta^2_G = 0.088$ ) as well as a main effect of Auditory space ( $F(1,23) = 99.59$ ,  $P < 0.001$ ,  $\eta^2_G = 0.409$ ). These main effects were specified by a significant Syntax  $\times$  Auditory space interaction ( $F(1,23) = 27.19$ ,  $P < 0.001$ ,  $\eta^2_G = 0.021$ ). Post-hoc tests revealed that the correct standard condition elicited significantly weaker activation compared to each of the three violation conditions (incorrect standard:  $F(1,23) = 58.30$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.378$ ; correct deviant:  $F(1,23) = 118.92$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.637$ ; incorrect deviant:  $F(1,23) = 108.36$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.642$ ). Thus, the effects to the violation conditions were highly significant. Moreover, the correct deviant condition and the incorrect deviant condition elicited significantly stronger activation than the incorrect standard condition ( $F(1,23) = 34.84$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.262$ ;  $F(1,23) = 63.50$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.332$ ; respectively). In addition, the incorrect deviant condition led to greater activation than the correct deviant condition ( $F(1,23) = 6.98$ ,  $P_{FDR} = 0.05$ ,  $\eta^2_G = 0.023$ ), although this difference was much smaller than for the other comparisons, causing the significant interaction. There was no main effect of Hemisphere ( $F(1,23) = 0.14$ ,  $P = 0.71$ ). None of the other interactions was significant (for all,  $P > 0.15$ ).

**Source localization—local maxima**

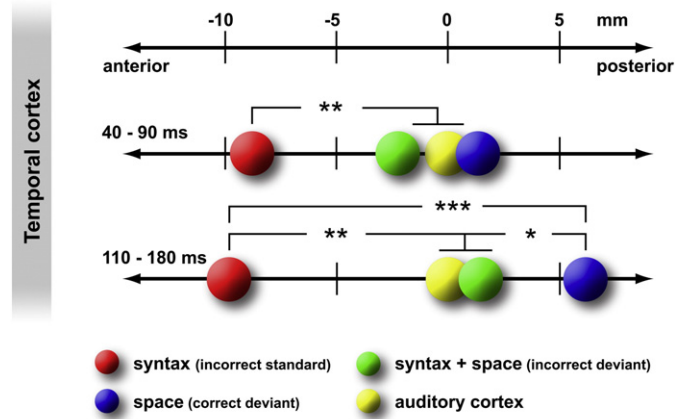
Talairach coordinates for the mean of the 100 most activated vertices of the grand average activations of the three violation conditions and the sentence onset M50 component are provided in Table 2 (Talairach and Tournoux, 1988). These were obtained using the icbm2tal transformation (Lancaster et al., 2007). An approximation to the corresponding Brodmann areas was acquired using the Talairach Client (Lancaster et al., 2000). Fig. 4 depicts the results of the statistical analysis of the local maxima along the anterior–posterior gradient of the temporal cortex for each time window.

The rmANOVA conducted for the 40–90 ms time window showed a significant main effect of Condition ( $F(3,69) = 8.72$ ,  $P < 0.001$ ,  $\epsilon = 0.760$ ,  $\eta^2_G = 0.078$ ). Post-hoc tests revealed that the incorrect standard condition was significantly more anterior compared to the correct deviant condition, the incorrect deviant condition and the sentence onset ( $F(1,23) = 18.11$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.198$ , 10 mm;  $F(1,23) = 26.62$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.147$ , 7 mm;  $F(1,23) = 12.39$ ,  $P_{FDR} = 0.01$ ,  $\eta^2_G = 0.187$ , 9 mm; respectively). No significant differences were found between the correct deviant condition, the incorrect deviant condition and the sentence onset (for all,  $P_{FDR} > 0.05$ ). There

**Table 2**

Talairach coordinates and corresponding Brodmann areas for the incorrect standard condition, the correct deviant condition, the incorrect deviant condition and the sentence-onset M50 component. The coordinates reflect the mean of the 100 most activated vertices of the grand average source localizations (BA—Brodmann area; STG—superior temporal gyrus).

Time window	Condition	Left hemisphere				Right hemisphere			
		x	y	z	Region	x	y	z	Region
40–90 ms	Incorrect standard	-49	-18	2	STG	52	-12	3	BA22
	Correct deviant	-47	-28	8	BA41	51	-23	7	BA41
	Incorrect deviant	-45	-22	4	BA22	52	-16	7	BA22
110–180 ms	Incorrect standard	-52	-16	2	BA22	52	-6	2	BA22
	Correct deviant	-49	-32	10	BA41	53	-24	9	BA41
	Incorrect deviant	-46	-28	7	BA41	53	-19	8	BA41
20–50 ms	Sentence onset	-54	-30	8	BA41	55	-24	8	BA41



**Fig. 4.** Results of the local maxima analysis in the temporal cortex for the two time windows defined (syntax violation: incorrect standard condition, red; auditory space violation: correct deviant condition, blue; syntax + auditory space violation: incorrect deviant condition, green; auditory cortex: sentence onset M50 as reference to the auditory cortex, yellow; \* $P_{FDR} \leq 0.05$ ; \*\* $P_{FDR} \leq 0.01$ ; \*\*\* $P_{FDR} \leq 0.001$ ).

was no main effect of Hemisphere and no Condition  $\times$  Hemisphere interaction ( $F(1,23) < 0.01$ ,  $P = 0.94$ ;  $F(3,69) = 0.23$ ,  $P = 0.87$ ; respectively).

In the ELANm/MMF time window (110–180 ms), a main effect of Condition was found ( $F(3,69) = 15.04$ ,  $P < 0.001$ ,  $\eta^2_G = 0.167$ ). Post-hoc tests showed that the incorrect standard condition was significantly more anterior compared to the correct deviant condition, the incorrect deviant condition as well as the sentence onset ( $F(1,23) = 41.01$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.448$ , 16 mm;  $F(1,23) = 20.65$ ,  $P_{FDR} < 0.001$ ,  $\eta^2_G = 0.205$ , 11 mm;  $F(1,23) = 13.91$ ,  $P_{FDR} < 0.01$ ,  $\eta^2_G = 0.235$ , 10 mm; respectively). In addition, the correct deviant condition was significantly more posterior compared to the incorrect deviant condition and the sentence onset ( $F(1,23) = 8.34$ ,  $P_{FDR} < 0.05$ ,  $\eta^2_G = 0.064$ , 5 mm;  $F(1,23) = 7.45$ ,  $P_{FDR} < 0.05$ ,  $\eta^2_G = 0.107$ , 6 mm; respectively), whereas no difference was found between the incorrect deviant condition and the sentence onset ( $F(1,23) = 0.06$ ,  $P_{FDR} > 0.05$ ). There was no main effect of Hemisphere and no Condition  $\times$  Hemisphere interaction ( $F(1,23) = 0.02$ ,  $P = 0.90$ ;  $F(3,69) = 1.22$ ,  $P = 0.31$ ; respectively).

**Discussion**

The goal of the present MEG study was to investigate the underlying neural mechanisms of the parallel processing effect observed for early syntax-related and auditory perceptual-related responses, and to test previous localizations of early responses to syntactically incorrect sentences. The present data replicate earlier findings (Friederici et al., 1993, 2000; Schröger, 1996; Hahne and Friederici, 1999, 2002; Hahne et al., 2002; Nager et al., 2003), by showing stronger activation in the STG for sentences including a syntactic or an auditory spatial violation than correct standard sentences (reflecting the ELANm and MMF). Going beyond these earlier findings, the present study found differences between the temporal cortex activation maxima of the violation effects reflecting syntax and auditory space. Syntactically incorrect sentences elicited activations anterior to the auditory cortex, whereas infrequent ITD changes led to activations more posterior in the STG. Sentences containing both violations led to even stronger activations in the STG with its activation maximum between the activation maxima of the single violations. Moreover, we observed very early modulations of STG activations at around 60 ms which preceded the ELANm and MMF. These results are discussed in detail below.

### *Very early effects (40–90 ms)*

After approximately 60 ms, syntactically incorrect sentences and sentences including an ITD change led to stronger neural activations in the STG compared to correct standard sentences. Moreover, STG activations were even further increased for sentences containing both a syntactic violation and an ITD change. These findings suggest parallel processing of syntactic and auditory spatial information already within the first 100 ms after violation onset.

In previous studies, very early syntax-related effects (C. S. Herrmann et al., 2000; B. Herrmann et al., 2009, 2011) and effects to deviances of auditory stimulus regularities (Boutros and Belger, 1999; Ermutlu et al., 2005) have been reported on the P50/M50 components. More recently, auditory deviancy detection effects have been observed already around 30–40 ms. Based on these findings and observed MMN effects, auditory violation detection mechanisms were suggested to expand along multiple stages that are organized hierarchically (Slabu et al., 2010; Grimm et al., 2011).

Furthermore, it has been proposed that early syntactic processing draws on syntactic templates, where local syntactic dependencies are preprocessed and stored in memory in the form of templates (Bornkessel and Schlesewsky, 2006; Kaan, 2009). Thus, the fastness of early syntax-related responses might be due to this precompilation of phrase structure representations. If predictions during sentence comprehension were the basis of the early syntax effects (Dikker et al., 2009), then such predictions could be driven by the head of the phrase, which would then activate the respective templates, thereby allowing for fast neural responses.

Crucially, there are some differences regarding the source locations of our M50-related effects and previous findings. Here, we observed the responses to syntactic violations more anterior in the temporal cortex compared to the other violations and the AC reference. Previously, the neural sources of the P50/M50 have been localized to the auditory cortex (Mäkelä et al., 1994; Huotilainen et al., 1998; Thoma et al., 2003, 2008). While this also holds true for sentences including an ITD change in the current study and for the very early syntax effect found by B. Herrmann et al. (2009), the current very early syntax-related effect was localized more anterior. However, in the localization study of B. Herrmann et al. (2009), two-word utterances were presented in an oddball paradigm, in which syntactic processing is accompanied by an acoustic change (see Shtyrov and Pulvermüller, 2007). This might bias the source analysis towards (primary) auditory cortices, and does not allow for direct comparisons with the current results.

### *Auditory space processing: MMF—infrequent ITD change (110–180 ms)*

In the present study, naturally spoken sentences that included an infrequent ITD change allowing to test for processing of auditory space elicited a magnetic mismatch response at around 110–180 ms. This is compatible with previous studies investigating the MMN/MMF to infrequent ITD changes using simpler stimuli (Schröger, 1996; Schröger and Wolff, 1996; Kaiser et al., 2000; Nager et al., 2003).

Regarding our aim to localize the cortical regions affected by auditory spatial processing, the local activation maximum in the temporal cortex elicited by the ITD change was found about 6 mm more posterior to the local activation maximum of the sentence onset M50 component serving as reference to the auditory cortex. In line with our observation, activations in posterior parts of the STG have been reported in EEG/MEG studies localizing the MMN/MMF to infrequent auditory location changes (Kaiser et al., 2000; Tata and Ward, 2005; Sonnadara et al., 2006; Deouell et al., 2006) as well as in fMRI studies varying the stimulus's ITD (Warren and Griffiths, 2003; Krumbholz et al., 2005; Altmann et al., 2008).

Importantly, the estimated local maxima in the temporal cortex for auditory space processing, i.e. the MMF to infrequent ITD changes,

was significantly different from that found for the ELANm elicited by the syntactic violation. Sentences containing an ITD change elicited a local maximum in the temporal cortex about 16 mm more posterior than syntactically incorrect sentences. This difference of processing spatial vs. non-spatial sounds along the superior temporal cortex has been found in fMRI studies as well (Warren and Griffiths, 2003; Altmann et al., 2008) and can be related to the dual processing pathways proposed in the auditory domain (for a recent review see Rauschecker and Scott, 2009).

Regarding hemispheric differences, no difference between hemispheres was found in the present study for processing auditory spatial information. In previous research, two opposing views have been proposed, one suggesting a right-hemispheric predominance for processing auditory spatial cues (e.g., Kaiser et al., 2000; Krumbholz et al., 2005), while the other argues for strongest activations elicited in areas contralateral to the stimulation (e.g., Nager et al., 2003; Richter et al., 2009). If the latter were the case, we would have expected left-lateralized activations because the ITD of 0.2 ms we used resulted in a right-lateralized perception. Nevertheless, the present findings do not allow a direct comparison with these previous studies as much simpler stimuli such as noise bursts or syllables have been presented (Kaiser et al., 2000; Nager et al., 2003; Richter et al., 2009). The current sentence processing paradigm, on the other hand, might have influenced the MMF to ITD changes regarding the hemispheric lateralization.

Previous EEG studies investigating the MMN to duration and frequency deviations reported activations in right-hemispheric frontal areas as an additional source to the STG (Giard et al., 1990; Jemel et al., 2002; Shalgi and Deouell, 2007). Similarly, using dynamic causal modeling (DCM) in an EEG study, it has been shown that the best model to explain MMN data also includes a right frontal source (Garrido et al., 2008). However, in the present MEG study, no local inferior frontal activation maximum was observed. This difference might be due to different sensitivities of EEG vs. MEG regarding the dipole orientations. Activations from radial sources are mostly invisible in MEG, whereas EEG shows strong sensitivity to radial generators (Ahlfors et al., 2010). Consistent with this interpretation, in an MEG experiment using DCM, it was recently shown that models excluding the right inferior frontal source led to better explanation of the MMF data than models which included an inferior frontal generator (Schofield et al., 2009).

### *Syntactic processing: ELANm (110–180 ms)*

Regarding the ELANm component, our results replicate previous EEG and MEG findings in which syntactically incorrect sentences led to larger brain activation compared to syntactically correct ones (Friederici et al., 1993, 2000; Knösche et al., 1999; Hahne and Friederici, 1999, 2002; C. S. Herrmann et al., 2000; Kubota et al., 2003).

In terms of our goal to localize the neural mechanisms underlying early syntactic processing, the present STG activations elicited by auditorily presented syntactically incorrect sentences were localized anterior to the M50 auditory cortex reference. This is consistent with previous reports on the ELANm showing strongest activation in the anterior STG (Friederici et al., 2000) and the superior temporal cortex (Groß et al., 1998; Knösche et al., 1999). Recently, sentence processing experiments in the visual domain have led to a “sensory hypothesis” for early syntactic effects (Dikker et al., 2009) by showing early modulations of visual sensory cortex activations caused by syntactic anomalies (Dikker et al., 2009, 2010). However, Dikker et al.'s localization approach did not allow them to further elaborate on the exact location of their visual sensory effect, i.e. whether activation was modulated in primary visual areas or outside of those (Dikker et al., 2009, 2010). Here we show for the auditory domain that it is not the auditory core regions which are modulated by syntactic violations, but rather cortical regions anterior to it. This in line with recent findings

using fMRI, showing regions outside sensory cortices to be involved in early syntactic processing (B. Herrmann et al., *in press*). The present observations are also in general agreement with the view that more complex auditory stimulus processing is accomplished in belt and parabelt regions of the auditory system rather than in its core areas (Kaas and Hackett, 2000; Rauschecker and Tian, 2004).

By introducing the “sensory hypothesis” in the visual domain, Dikker et al. (2009, 2010) not only reported visual sensory cortex activations in response to syntactic word category violations, but moreover suggested that syntactic predictions provide the basis for a top-down selection of syntactically relevant information at the phonological level. In particular, the authors showed that the early syntax-related effects rely on phonological form properties associated with the syntactic category, e.g. an affix marking the syntactic category (Dikker et al., 2009, 2010). In the auditory sentence materials used in the present study, the word category was indeed overtly marked by the prefix “ge-” and a suffix (e.g., “-t”). Thus, overt phonological marking of the word category may cause the detection of word category violations leading to early syntax effects. The present results could, therefore, be seen in relation to a study of Ahveninen et al. (2006) showing that anterior parts of the STG are tuned to phonetic/phonological information, whereas posterior parts are tuned to spatial information, and that this difference is already present at around 70–150 ms, partly overlapping with the current time window of the syntax effect (110–180 ms). Thus, in the auditory domain it appears that both the phonological effect observed by Ahveninen et al. (2006) and the present syntax effect are not localized in the auditory cortex, but rather more anteriorly to it.

In the present study, no difference in activation strength was found between the left and right STG. While some previous studies reported stronger activation in left- than right-hemispheric areas when syntactic violations were encountered (Friederici et al., 2000; Shtyrov et al., 2003; B. Herrmann et al., 2009, 2011), other studies suggest a bihemispheric involvement in early syntactic processing (Knösche et al., 1999; C. S. Herrmann et al., 2000; Kubota et al., 2003). Recent findings in fMRI that were explicitly attributed to early syntactic processes showed left and right superior temporal cortices activated in a conventional analysis, while a multivariate pattern classification approach on the same data revealed left-hemispheric regions carrying the syntax-relevant information (B. Herrmann et al., *in press*). Taking these previous findings into account it seems that there is a tendency towards left-hemispheric regions being most important for syntactic processing. This preference has also been shown in an EEG study reporting a bilateral ELAN distribution in healthy adults and a left-lateralized one in patients with right anterior temporal lesions, whereas no ELAN was observed in patients with lesions in the left anterior temporal cortex (Kotz et al., 2003).

In contrast to some of the earlier studies (Groß et al., 1998; Knösche et al., 1999; Friederici et al., 2000), no frontal activation maximum was found in the present study for sentences including a syntactic violation. However, different source reconstruction models were applied in the prior studies and the present one. Some of the studies reporting statistical differences in frontal areas for syntactically incorrect sentences when compared to syntactically correct ones had used current source density analysis (Groß et al., 1998; Knösche et al., 1999). In the present study, a distributed source model was used, which accounts for activations over the whole cortical surface. No prior assumptions about source locations were made. In contrast, in the study by Friederici et al. (2000), two dipoles were explicitly seeded in each hemisphere (one in the IFC and one in the anterior STG) using the results of an fMRI study as prior (Meyer et al., 2000). The finding that dipole strength was significantly weaker in the IFC than in the anterior STG (Friederici et al., 2000) can be related to the present results, suggesting that MEG responds strongly to the temporal source of the ELANm component, but not as much to a frontal source. EEG studies, on the

other hand, suggest strong involvement of frontal areas in the detection of syntactic violations (Pulvermüller and Shtyrov, 2003), as the distribution of the ELAN was not only found very focal in frontal electrodes (Friederici et al., 1996; Hahne and Friederici, 2002), but was moreover absent in patients with selective lesions in the left IFC (for a review see Friederici and Kotz, 2003). In addition to these findings, fMRI activations in the IFC have been recently related to early syntactic processes as well (B. Herrmann et al., *in press*). From this point of view, EEG and MEG may measure different parts of the same phenomenon, due to the orientation of the dipoles (see also the discussion above). Explicitly fitting a dipole into the frontal cortex could account for the explanation of additional variance (Friederici et al., 2000) which might be concealed when using distributed source models without such a prior. Therefore, with MEG alone, the question about a frontal source of the ELAN/ELANm component is not conclusive.

#### *Processing syntax and auditory space in parallel (110–180 ms)*

With respect to the third research question outlined in the Introduction, we aimed to further investigate parallel processing of syntactic and auditory perceptual information in the 110–180 ms time window. Such an effect has already been observed in a previous EEG study (Hahne et al., 2002). In their study, however, the analysis was conducted for the EEG electrodes placed on the scalp. Here, we used MEG which allows for a much more fine-grained topographic analysis to investigate this parallel processing effect in the brain. Local neural activations in the temporal cortex elicited by sentences including the combination of a syntactic violation and an ITD change were found significantly more anterior compared to the MMF maximum and significantly more posterior to the ELANm maximum. No difference was found to the M50 reference to the auditory cortex. In order to interpret this finding, there are three different alternatives that need to be considered.

First, the current finding that the double violation was localized in an intermediate location between the activation maxima of the single violations could in principle be due to averaging across participants, in which a few participants were processing only the syntactic part of these double violation sentences (i.e., more anterior), and the remaining participants only the ITD change (i.e., more posterior). However, if that were the case, one would have expected reduced activation strength for the double violation compared to the correct deviant condition. Since the opposite was found, the present observations cannot be explained by this argument.

A second explanation might be that a completely independent mechanism underlies the processing of such a double violation compared to the single violations. According to such an explanation, activations in cortical regions different from the regions activated by single violations must be assumed. However, the current analysis did not reveal a difference between the location of the M50 auditory cortex reference and the local maximum elicited by the double violation, whereas single violations recruited cortical regions more anterior and posterior in the STG. Consequently, processing the double violation should lead to activations in distinct areas as well, because the AC was found to respond strongly to simple, but less strongly to more complex stimuli (Kaas and Hackett, 2000; Rauschecker and Tian, 2004). Hence, this explanation very unlikely accounts for the present results.

A third alternative, however, might be that the double violation simultaneously elicited activations in those temporal cortex regions that were independently activated by the single violations. Within one condition, it is fairly difficult to separate two very close sources activated at the same time using distributed source models. As a result, source reconstruction would reveal one source for the corresponding condition somewhere between the true activations. On this account, the current data can be taken as indirect evidence



that the auditory system is able to process these syntactic and auditory spatial violations in parallel by activating different brain regions simultaneously.

While the latter is the most likely explanation of the intermediate temporal cortex maximum to the double violations, such an activation shift due to two (or more) truly activated regions in close proximity could in principle also account for the present syntactic and auditory spatial localizations. However, this is very unlikely because previous fMRI studies also showed anterior STG activations for syntactic processing (Friederici et al., 2003; B. Herrmann et al., in press) and posterior STG activations for auditory spatial processing (Warren and Griffiths, 2003; Krumbholz et al., 2005; Altmann et al., 2008).

Taken together, the present findings strongly indicate that processing the combination of a syntactic violation and an auditory spatial violation simultaneously recruits brain regions in the anterior STG as well as in the posterior STG.

## Conclusions

The present MEG study revealed a number of similarities and differences in processing syntactic and auditory spatial information. Approximately 60 ms after stimulus onset, processing of syntactic and auditory spatial deviations led to modulations in the STG, showing that both deviations are processed in parallel when encountered in combination. Following these very early effects, clear evidence of a dissociation of speech-related processes and auditory spatial processes was observed in the superior temporal cortex. Syntactically incorrect sentences elicited activations in the anterior STG at around 110–180 ms, while auditory spatial deviations elicited activations in the posterior STG. The current observations, moreover, suggest that brain regions independently activated by single violations are activated simultaneously in case of a combined violation. These findings are compatible with the view of different processing streams in the temporal cortex involved in syntactic and auditory spatial processing.

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