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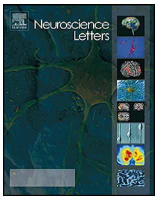

Short communication

# Task-dependent modulation of regions in the left temporal cortex during auditory sentence comprehension

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## HIGHLIGHTS

- The left lateral temporal cortex is sensitive to sentence intelligibility.
- The anterior and posterior STS/MTG regions are involved in both passive and active sentence comprehension.
- The middle STS/MTG regions respond to sentence intelligibility only during the active task.

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## ABSTRACT

Numerous studies have revealed the essential role of the left lateral temporal cortex in auditory sentence comprehension along with evidence of the functional specialization of the anterior and posterior temporal sub-areas. However, it is unclear whether task demands (*e.g.*, active *vs.* passive listening) modulate the functional specificity of these sub-areas. In the present functional magnetic resonance imaging (fMRI) study, we addressed this issue by applying both independent component analysis (ICA) and general linear model (GLM) methods. Consistent with previous studies, intelligible sentences elicited greater activity in the left lateral temporal cortex relative to unintelligible sentences. Moreover, responses to intelligibility in the sub-regions were differentially modulated by task demands. While the overall activation patterns of the anterior and posterior superior temporal sulcus and middle temporal gyrus (STS/MTG) were equivalent during both passive and active tasks, a middle portion of the STS/MTG was found to be selectively activated only during the active task under a refined analysis of sub-regional contributions. Our results not only confirm the critical role of the left lateral temporal cortex in auditory sentence comprehension but further demonstrate that task demands modulate functional specialization of the anterior–middle–posterior temporal sub-areas.

## 1. Introduction

Recent neurolinguistic work has highlighted the critical role of the left lateral temporal cortex in auditory sentence comprehension [1,13,14,23,30]. Neural models for speech comprehension hold that the left lateral temporal cortex together with the left frontal areas such as par triangularis and par orbitalis forms the ventral pathway responsible for auditory-to-meaning processing [12,26]. However, there is evidence that sub-regions of the left lateral temporal cortex are functionally specialized, although the specific functions of the different areas in auditory sentence comprehension are still being debated. For example, the posterior areas are considered to be critical for semantic store at the lexical level, whereas the anterior regions are more involved in combinatorial semantic processes [3,16,23]. There may even exist subtle separation of functions within the left anterior temporal region, with the most anterior portion of the superior temporal sulcus and middle temporal gyrus (STS/MTG) primarily responding to syntactic

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*Abbreviations:* fMRI, functional magnetic resonance imaging; GLM, general linear model; ICA, independent component analysis; ROI, region of interest; STS/MTG, superior temporal sulcus and middle temporal gyrus.

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structure and a region directly posterior to it reflecting the interaction of syntactic and semantic information [13].

The existing studies on functional heterogeneity of the left lateral temporal cortex have used stimulus manipulations in either a passive listening condition [1,25,30] or active anomaly detection/selective attention conditions [10,20,23]. These studies adopted the strategy of comparing activation across different types of stimuli or across active tasks to isolate semantic and syntactic processing in either passive or active listening conditions. While the results helped to disentangle functional divisions of the sub-regions in the left lateral temporal cortex and how they were associated with syntactic and sentence-level semantic processing, the previous studies have not successfully addressed how task demands may differentially affect the functional specificity of the sub-regions in this important brain area. To our knowledge, only one study has made direct comparison between passive and active sentence comprehension [11]. By use of sentence repetition paradigm, this study reported null findings on this issue as similar activation reductions were found in the lateral aspects of STS/MTG for the different tasks.

In the current study, we attempted to further address whether and how passive *vs.* active task-related effects contribute to different activation patterns in various sub-regions of the left temporal cortex during auditory sentence comprehension. Of these sub-regions, the middle area is of special interest because functions of this area in auditory sentence comprehension have not been clearly specified, although it is implicated as an important part of the ventral pathway subserving semantic processing [8]. We asked participants to listen to normal and time-reversed sentences in both passive and active task conditions. In the passive listening task, participants were told to listen to sentences carefully without overt responses, and in the active comprehension task, they were instructed to comprehend the sentences attentively and to press a button whenever they detected an anomalous sentence. We first adopted probabilistic independent component analysis (ICA) [2] to identify the functional regions of interest (ROIs) in order to avoid the issues of circularity that may characterize the traditional two-step model-driven identifications of ROIs [15,29]. And then anatomical parcellation masks from Freesurfer [7] were used to create sub-ROIs in order to examine the possible functional heterogeneity of the left lateral temporal cortex that is modulated by passive and active task demands.

## 2. Materials and methods

### 2.1. Participants

Twenty undergraduate and postgraduate students (11 females) with a mean age of 20.8 years (range 18–25) participated in this study. They were all native Chinese speakers, and were right-handed according to a modified Chinese version of the Edinburgh Handedness Inventory [21]. No participant reported a history of a hearing, neurological or psychiatric disorder. Written informed consent was obtained from all participants after they were given a complete description of the study and all received monetary compensation for their participation. The study was approved by the research ethics committee at Beijing Normal University's Imaging Center for Brain Research.

### 2.2. Stimulus material

Two types of stimuli were used: (1) 48 spoken sentences in Mandarin Chinese, half of which were presented in the passive listening task and the other half in the active comprehension task, and (2) time-reversed versions of the 48 sentences. For the first type, six sentences were semantically anomalous (*e.g.*, 太阳每天从西边升起来, "The sun rises from the west everyday") for both the passive and the active tasks, intermixed with the remaining normal sentences presented to participants. The sentences were produced by a female Chinese native speaker and recorded in an anechoic chamber at a sampling rate of 44.1 kHz. Each sentence consisted of 10 ± 1 Chinese syllables with an average duration of 2289 ms (SD = 115 ms). For the second type, the intelligibility of the speech was destroyed but the overall acoustic complexity was preserved, following an established method previously used by other researchers [17,24]. All stimuli were normalized for average root mean square intensity amplitude.

### 2.3. Functional magnetic resonance imaging (fMRI) procedure and data acquisition

Two runs of scanning were collected from each participant, one for the passive task and the other for the active task. The passive and active task runs were counterbalanced across participants. Each run consisted of six 36-s sentence blocks, half of which were normal sentence blocks and half time-reversed sentence blocks, interleaved with seven 12-s silent resting blocks. Each sentence block comprised eight sentences and before each sentence, a 500-ms pure tone was presented as a cue. The normal sentence blocks and time-reversed sentence blocks were arranged in random order within each run. The passive and active task runs each lasted 302 s.

During the passive task run, participants were required to listen to the stimuli carefully without any explicit response. During the active task run, they were instructed to comprehend the stimuli and make a judgment by pressing a button when they heard any semantically anomalous sentence. This anomaly detection paradigm was used to ensure that participants did comprehend each stimulus carefully. Semantically anomalous sentences occurred in 25% of the total trials and were not used in the analysis to avoid measuring activations associated with error detection [23].

Magnetic resonance images were obtained on a Siemens Magnetom Trio Tim 3-T scanner at the Beijing normal university's imaging center for brain research. Foam pads were used to keep participant's head still as far as possible within the head coil. We collected two sessions of fast echo planar imaging sequence with the following parameters: TR = 2 s, TE = 30 ms, FA = 90°, matrix size = 64 × 64, voxel size = 3.125 × 3.125 × 4 $\text{mm}^3$. Each session had 151 volumes and each volume had 33 slices to cover the whole brain. After two EPI scans, a high-resolution 3-dimension anatomical image was acquired using MPRAGE sequence in axial plane with the following parameters: TR = 2.53 s, TE = 3.45 ms, FA = 7°, matrix size = 256 × 256, voxel size = 1 × 1 × 1 $\text{mm}^3$. During the scanning, the auditory stimuli were presented binaurally *via* MRI-compatible headphone SereneSound (Resonance Technology Inc., Northridge, CA, USA), which reduced the background scanner noise to about 70 dB. A short pre-test scanning was administered to ensure that participants could hear the sentences clearly and the sound volume was adjusted to a comfortable level for each participant.

### 2.4. Data analysis

#### 2.4.1. Preprocessing and independent component analysis

Functional image preprocessing was conducted using the AFNI software package [4], including the correction for slice timing and head motion, alignment between functional images and structural images, normalization, spatial smoothing and scaling. In order to increase the signal to noise ratio, the passive task run and active task run were concatenated together for each participant, and an average concatenated time series was calculated across all participants as the input data for the following ICA analysis.

A participant-average cortical surface model was created by using Freesurfer for display and reference [5,6].

Probabilistic independent component analysis was carried out using MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components) Version 3.10, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) [2]. The ICA procedure resulted in 28 independent components across the whole brain gray matter regions, each containing a temporal mode representing its temporally dynamic changes (time series) and a spatial mode which consisted of voxels having the representative time courses in its temporal mode. In order to identify the independent component activities related to the stimuli, simple correlation analyses were conducted between every temporal mode of all the 28 ICs and every ideal time series of all types of stimuli was convolved with a hypothetical hemodynamic response function. Only independent components significantly correlated ($p < 10^{-5}$) with any type of stimuli were considered as the stimuli-related components. Meanwhile, the spatially discrete cortical regions were identified in the spatial map of each significantly temporally-correlated component by thresholding the amplitude of spatial map Z-score (the probability of representing its temporal mode in that spatial map) at a voxel-wise threshold ($Z > 3.72$, $p < 10^{-4}$), corrected at cluster-wise extent (voxel size > 20, $2 \times 2 \times 2$ mm, $p < 0.005$ corrected) [19,31]. These spatially discrete regions were then used as masks to extract regression coefficient for each stimulus condition from traditional individual GLM analysis.

### 2.4.2. *Effects of stimulus and task analysis*

In order to analyze the effects of stimulus and task within the ROIs identified by the ICA method, repeated-measure ANOVAs were conducted on the regression coefficients with stimulus and task as fixed factors and participant as a random factor. Regression coefficients were estimated using standard GLM in AFNI. Two regressors of interest for each sentence condition (normal sentence and time-reversed sentence), as well as six regressors from head motion parameters and one regressor from responses in the active task run, were modeled in GLM. The regression coefficients (beta values) of each sentence condition for every task were obtained from individual GLM analysis. A strict significance threshold ($p < 0.01$) for any main effect or interaction was used to control for Type I error due to the multiple tests. In order to examine whether functional specialization of the sub-areas in the left lateral temporal cortex is modulated by tasks, the anatomical parcellation masks from Freesurfer [7] were applied in creating the sub-ROIs. Then the differences in intelligibility contrast coefficients were calculated for each sub-ROI between the passive and active tasks.

## 3. Results

### 3.1. *Behavioral data*

For the active task runs, behavioral responses of all the participants approached ceiling-level performance (mean accuracy = 99%), indicating that the participants maintained vigilance during the task and that the anomaly detection paradigm successfully directed participants' attention to semantic integration of the sentences.

### 3.2. *Intelligibility and task effects*

Of the twenty-eight independent components decomposed by ICA analysis, five components were identified as stimulus-related (significantly correlated with any type of sentences), which was confirmed by *t*-tests on simple correlations between time modes of components and hemodynamic response function for

**Table 1**
Independent components correlated with stimuli ($p < 10^{-5}$).

| IC# | Regions | EV (%) | *t*-value | | |
|---|---|---|---|---|---|
| | | | All stimuli | Sentence | Reversed |
| 3 | HG (*b*), STG (*b*), STS (*b*), precentral (*r*) | 5.09 | 28.75 | 6.61 | 8.00 |
| 6 | ATL (*b*), ITG (*b*) | 3.92 | 34.65 | 8.40 | 6.97 |
| 9 | MTG (*b*), STS (*b*), precentral (*b*), SMA (*b*), MCC (*b*) IFG p.tri (*l*), IFG p.orb (*l*), MFG (*l*), Insula lobe (*l*), | 3.39 | 9.52 | 13.45 | – |
| 27 | SFG (*b*), calcarine (*b*), MCC (*r*), thalamus (*l*), SPL (*l*), MFG (*l*), MOG (*l*) | 1.56 | – | 10.02 | – |
| 28 | ACC (*b*), insular lobe (*b*), MFG (*b*), orbital (*r*) | 1.45 | – | 4.71 | – |

IC#: independent component number; EV:explained variance; HG:Heschl's gyrus; STG:superior temporal gyrus; STS:superior temporal sulcus; ATL:anterior temopral lobe; ITG:inferior temoral gyrus; MTG:middle temporal gyrus; SMA:supplementary motor area; MCC:middle cingulate cortex; IFG p.tri:inferior frontal gyrus par triangularis; IFG p.orb:par orbitalaris; MFG:middle frontal gyrus; SFG:superior frontal gyrus; SPL: superior parietal lobule; MOG:middle occipital gyrus; ACC:anterior cingulate cortex; (*l*):left hemisphere; (*r*): right hemisphere; (*b*):both hemispheres; -:no significant correlation.

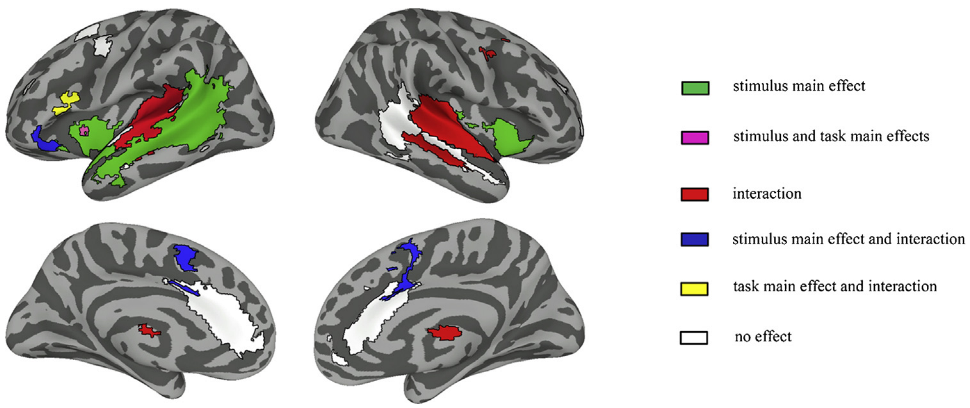

**Fig. 1.** Stimuli by task ANOVA analyses within all stimuli-related clusters.

different stimulus models (see Table 1). The five components explained 15.41% of the variance in the data.

The five components contained in total 31 discrete clusters distributing over the bilateral temporal and frontal regions. These clusters were used as ROIs to further examine response patterns in different regions with regard to intelligibility and task demands. As shown in Fig. 1, a large cluster in the left lateral temporal cortex and two clusters in the bilateral insular lobe showed a significant main effect of stimulus, indicating their sensitivities to sentence intelligibility (normal sentences > time-reversed sentences) in both passive and active tasks. In the bilateral superior temporal gyri including Heschl's gyri, there was only a significant stimulus by task interaction effect with time-reversed sentences eliciting stronger activation than normal sentences in the passive task and an opposite pattern of activation in the active task. A cluster in the dorsal part of the left inferior frontal cortex showed a significant main effect of task (active > passive) and stimulus by task interaction with normal sentences eliciting stronger activation than time-reversed sentences only in the active task. Unlike the dorsal activation pattern, a cluster in the ventral part of the left inferior frontal cortex and two clusters near the medial superior frontal region had a significant main effect of stimulus (normal sentences > time-reversed sentences) and stimulus by task interaction with active task only increasing activation of the normal sentences but not the time-reversed sentences. In a tiny cluster of the left insular cortex, there were only significant stimulus (normal sentences > time-reversed sentences) and task (active > passive) main effects, but no stimulus by task interaction.

### 3.3. *Functional heterogeneity of the left lateral temporal cortex*

The cluster in the left lateral temporal cortex was very large covering a wide range of anterior, middle, and posterior temporal regions. In order to find out whether activation patterns of various sub-regions was modulated by task demands during auditory sentence comprehension, we created sub-ROIs by using the left STS mask from Freesurfer anatomical parcellation and anterior-posterior gradient mask along $y$-axis direction (Talairach standard space) [28], and then tested task by sub-ROIs interaction. The results showed that the sub-ROIs by task interaction was significant ($F(7,133) = 5.38$, $p < 0.001$), indicating that responses to sentence intelligibility in these sub-regions were differentially modulated by passive/active task demands although all the sub-areas in the large cluster discriminate between intelligible and unintelligible sentences. Paired sample $t$-test further revealed that task-modulated intelligibility effect was only observed in the middle parts ($y$ coordinates of the sub-ROIs: $-0.5 \leq y \leq -40.5$; $t(19) \geq 2.564$, $p < 0.05$), but not in either the anterior or posterior parts of the left lateral temporal cortex (anterior part, $y = 9.5$; $t(19) = 1.598$, $p > 0.1$; posterior parts, $y = -50.5$, $-60.5$; $t(19) = 1.054$, $0.947$, $p > 0.3$) Fig. 2.

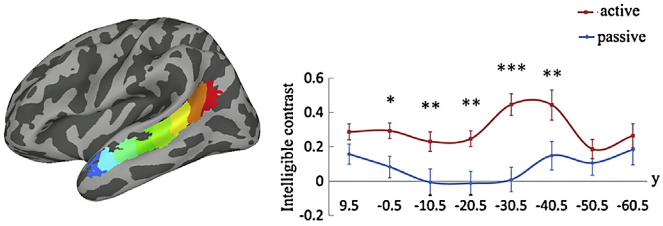

**Fig. 2.** Task effects on the processing of intelligible sentences along the left superior temporal sulcus. Left: sub-ROIs with each marked in a different color; right: intelligibility effect with the y scale representing beta values.

## 4. Discussion

Although multiple methodological approaches have identified the left lateral temporal cortex as one of the most important areas responsible for sentence-level speech comprehension, there remain substantial disagreements in the literature with respect to the precise functions of its sub-regions [1,12,13,23,25,30]. Specifically, it is unclear whether and how functions of the various sub-regions are modulated by passive/active task demands during auditory sentence comprehension. To address this issue, we combined ICA and GLM analyses of fMRI data to elucidate the subareas of the left lateral temporal cortex respectively involved in the passive and active processing of sentence intelligibility. Consistent with previous research, a large cluster of the left lateral temporal cortex but not the primary auditory cortex showed greater activity for intelligible relative to unintelligible sentences, reflecting its critical role in sentence comprehension. Further analyses revealed that the anterior and posterior sub-regions of the left lateral temporal cortex were equally activated during both passive and active comprehension, whereas the middle sub-regions were only activated during the active task. These findings indicate that the anterior-middle-posterior sub-areas of the left lateral temporal cortex are differentially affected by passive and active task demands during sentence comprehension.

Previous studies have provided evidence implicating functional separation between the anterior and posterior sub-regions of the left lateral temporal cortex in speech intelligibility. Evidence from semantic dementia has led some researchers to emphasize the role of the anterior regions in word-level semantic processes [25,27], while other researchers have highlighted the role of posterior regions for storage of lexical representations based on functional imaging data [12,22]. Moreover, the anterior regions have been found to contribute to combinatorial semantic and syntactic computations because the anterior but not the posterior areas are more active when listening to sentences than to word lists and pseudoword sentences [9,14]. While many studies have examined the anterior and posterior sub-regions, few have investigated the functional role(s) of the middle regions in sentence comprehension. The mid-STS/MTG regions, especially in the left hemisphere, have been suggested to be involved in phoneme recognition processes and represent an intermediate processing stage in which combinations of phonemes activate semantic representations of single words [13,18].

In contrast to studies that have focused on the functional differentiation of the sub-regions of the left lateral temporal cortex in semantic, syntactic and phonological processes *per se*, our study was designed to provide new insights into the functional similarity or specialization of the anterior–middle–posterior sub-areas. We demonstrated their different activation patterns in passive and active sentence comprehension tasks. On the one hand, a small anterior region and large posterior regions were sensitive to sentence intelligibility irrespective of task demands, which implicates the essential role of the anterior and posterior regions in sentence comprehension. On the other hand, a large portion of the middle regions occupying the majority of the STS/MTG cluster showed intelligibility effect only in the active but not the passive task, which reflects its role in controlled semantic processing of sentences. It is clear from these results that functional similarity and specialization of these sub-regions is task-dependent during sentence comprehension. Our results suggest when investigating the neural substrates for sentence comprehension and integrating the data with the literature, researchers need to take into account task-dependent functional modulation of individual brain regions and possible discrepancies due to differences in the tasks of interest. Given the mounting evidence pointing to different roles of the sub-regions of the left lateral temporal cortex in phonemic, semantic and syntactic processing, future studies can be designed to investigate how phonemic/semantic/syntactic processes are differentially susceptible to attentional processing demands and how the interactions between task demands and linguistic processing modulate functional similarity and specialization of these sub-regions in order to elucidate brain systems underlying the processing of intelligible speech.

## 5. Conclusion

In sum, our fMRI data indicate the existence of two classes of sub-regions in the left lateral temporal cortex that are differentially sensitive to sentence intelligibility depending on the demands of the listening task. First, the anterior and posterior sub-regions respond similarly to intelligibility of spoken sentences regardless of task demands. Second, the middle sub-regions selectively respond to controlled processing of intelligibility that requires overt behavioral response. Thus, functional heterogeneity of the left lateral temporal cortex and specialization of the anterior–middle–posterior sub-areas are modulated by task demands during auditory sentence comprehension.

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