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TASK-MODULATED ACTIVATION AND FUNCTIONAL CONNECTIVITY OF THE TEMPORAL AND FRONTAL AREAS DURING SPEECH COMPREHENSION

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Abstract—There is general consensus in the literature that a distributed network of temporal and frontal brain areas is involved in speech comprehension. However, how active versus passive tasks modulate the activation and the functional connectivity of the critical brain areas is not clearly understood. In this study, we used functional magnetic resonance imaging (fMRI) to identify intelligibility and task-related effects in speech comprehension. Participants performed a semantic judgment task on normal and time-reversed sentences, or passively listened to the sentences without making an overt response. The subtraction analysis demonstrated that passive sentence comprehension mainly engaged brain areas in the left anterior and posterior superior temporal sulcus and middle temporal gyrus (aSTS/MTG and pSTS/MTG), whereas active sentence comprehension recruited bilateral frontal regions in addition to the aSTS/MTG and pSTS/MTG regions. Functional connectivity analysis revealed that during passive sentence comprehension, the left aSTS/MTG was functionally connected with the left Heschl's gyrus (HG) and bilateral superior temporal gyrus (STG) but no area was functionally connected with the left pSTS/MTG; during active sentence comprehension, however, both the left aSTS/MTG and pSTS/MTG were functionally connected with bilateral superior temporal and inferior frontal areas. While these results are consistent with the view that the ventral stream of the temporo-frontal network subserves semantic processing, our findings further indicate that both the activation and the functional connectivity of the temporal and frontal areas are modulated by task demands.

Key words: task-modulated activation, functional connectivity, speech comprehension, inverse intelligibility effect, ventral stream, temporo-frontal brain network.

INTRODUCTION

Previous studies have shown that widely distributed brain areas in the left hemisphere including the superior and middle temporal, inferior parietal, and inferior frontal regions are involved in sentence-level speech comprehension (Tyler and Marslen-Wilson, 2008; Peelle et al., 2010; Price, 2010; Abrams et al., 2012). While the left mid-posterior inferior and middle temporal areas are considered to be critical for semantic store, the anterior temporal cortex is more involved in combinatorial operations that underlie sentence processing (Scott et al., 2000; Vandenberghe et al., 2002; Crinion et al., 2003; Spitsyna et al., 2006; Hickok and Poeppel, 2007; Abrams et al., 2012). Besides the temporal areas, the left inferior frontal gyrus (IFG), especially the anterior and ventrolateral regions have also been implicated in semantic processing (Davis and Johnsrude, 2003; Leff et al., 2008; Rogalsky and Hickok, 2011), perhaps more involved in semantic retrieval than semantic representation, compared with the temporal cortex. Specifically, activation in the left IFG subdivisions is thought to regulate the recovery of semantic information, presumably via top-down signals to temporal cortex (Wagner et al., 2001; Bookheimer, 2002; Badre et al., 2005; Whitney et al., 2011).

Although there is a broad consensus on the functional segregation of temporal and frontal brain areas in speech comprehension, how activation in these brain areas is modulated by passive versus active task demands is not completely understood. On the one hand, research using passive sentence comprehension has revealed either the exclusive involvement of the temporal cortex (Scott et al., 2000; Rogalsky and Hickok, 2009), or the involvement of additional frontal areas (Crinion et al., 2003; Whitney et al., 2011; Adank, 2012). For example, Scott et al. (2000) found that compared with unintelligible speech, passive listening to normal sentences only activated the left superior temporal sulcus (STS), while Crinion et al. (2003) found that the

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Abbreviations: aSTS/MTG, anterior superior temporal sulcus/middle temporal gyrus; fMRI, functional magnetic resonance imaging; FWHM, full-width half-maximum; GLM, general linear model; HG, Heschl's gyrus; IFG, inferior frontal gyrus; Porb, par orbitalis; pSTS/MTG, posterior superior temporal sulcus/middle temporal gyrus; PTr, par triangularis; ROI, region of interest; STG, superior temporal gyrus.

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left ventrolateral frontal regions were also engaged in automatic comprehension of simple narrative speech. On the other hand, most studies using active speech comprehension have adopted the strategy of comparing activation across different tasks but few studies have made direct comparison between passive and active sentence comprehension (Wagner et al., 2001; Badre et al., 2005; Nagel et al., 2008; Wright et al., 2011). Although these studies help to disentangle the patterns of activation associated with each active task, it is unclear how the activation in various brain areas is differentially affected by passive and active comprehension tasks. Such differences between studies clearly highlight the importance of task demands during language processing and the corresponding differences in patterns of brain responses. In this study, we attempt to examine further how passive versus active task-related effects contribute to patterns of activation in the temporal and frontal areas during speech comprehension.

In addition to the study of the functional segregation of brain regions, several studies have also examined the coordinated activities across the distributed areas and attempted to identify the temporo-frontal brain network underlying speech comprehension (Spitsyna et al., 2006; Obleser et al., 2007; Leff et al., 2008; Saur et al., 2010; Abrams et al., 2012). For example, Spitsyna et al. (2006) demonstrated the streams covering the left STS, temporal pole, fusiform gyrus and the junction of temporal, occipital, and parietal cortex for implicit language comprehension, while Saur et al. (2010) additionally argued for the fronto-temporal functional connections in the speech comprehension network, along with the inter-connections within the temporal lobe. These results are consistent with the prevailing dual-stream model of speech processing that assumes a ventral stream for sound-to-meaning processing. The ventral stream projects from the superior temporal gyrus (STG) anteriorly and ventrolaterally to the middle, inferior temporal and ventrolateral prefrontal cortices and maps sound-based representations of speech to widely distributed conceptual representations (Hickok and Poeppel, 2007; Saur et al., 2008; Friederici, 2012). Previous studies assigned a critical role to the functional connectivity between the temporal and prefrontal areas for selecting contextually appropriate word meanings (Rodd et al., 2005), processing semantic expectancy (Obleser and Kotz, 2010) and integrating linguistic meaning with world knowledge (Hagoort et al., 2004). As with the studies that examined the functional segregation of brain activation, the functional connectivity research in this domain also failed to look into how passive versus active tasks modulate the connections between critical brain regions during speech comprehension.

The existing gaps in the literature motivated our study to examine passive versus active listening tasks and investigate task-modulated activation and functional connectivity of the temporal and frontal brain areas during sentence comprehension. In the passive listening task, participants were told to listen to sentences carefully without overt responses, and in the active comprehension task, participants were instructed to comprehend the sentences attentively and to press a button whenever they heard of an anomalous sentence. We predicted that (1) the passive task would mainly activate the left temporal cortex with little involvement of the left IFG because of the nature of automatic comprehension of this task, and (2) the active task would recruit both the left temporal and the IFG areas reflecting controlled semantic processing. Furthermore, we predicted different functional connectivity patterns between the left temporal and frontal areas in the two tasks, although the specific patterns depend on the detailed analyses adopted.

EXPERIMENTAL PROCEDURES

Participants

Twenty Chinese native speakers participated in this study (11 females; mean age 20.8 years old, range 18–25). All the participants were right-handed according to a modified Chinese version of the Edinburgh Handedness Inventory (Oldfield, 1971), and none had 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 were paid for their participation. The study was approved by the research ethics committee at Beijing Normal University's Imaging Center for Brain Research.

Stimulus material

Two types of stimuli were used. (1) The first type comprised 48 spoken sentences in Mandarin Chinese, half of which was presented in the passive listening task and the other half in the active comprehension task. In each half of the sentences, six were semantically anomalous (e.g., 太阳每天从西边升起来, Every day the sun rises from the west) whereas the remaining were semantically normal. (2) The second type of stimuli was the time-reversed versions of the 48 normal sentences. The normal 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). The time-reversed stimuli were created by an established method of time-reversing the normal speech stimuli (Binder et al., 2000; Leff et al., 2008; Saur et al., 2010). The reversed sentence destroys the intelligibility of forward speech but preserves the overall acoustic complexity. The intelligible normal sentences and unintelligible time-reversed sentences were matched for amplitude of loudness to create a clean intelligibility variable of interest in our study.

Scanning procedure and functional magnetic resonance imaging (fMRI) protocol

Each participant went through two experimental sessions, one for the passive task run and the other for the active task run. The passive and active task runs were counterbalanced across subjects. Each run contained six 36-second sentence blocks, half of which were normal sentence blocks and half time-reversed sentence blocks. Seven 12-second silence resting blocks were interleaved with the sentence blocks. Each sentence block comprised eight stimuli and before each sentence, a 500-ms pure tone was presented as a cue. The normal sentence block and time-reversed sentence block were arranged in a random order within each run. Both the passive