Brain & Language 122 (2012) 135–141

Contents lists available at SciVerse ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Effective connectivity hierarchically links temporoparietal and frontal areas of the auditory dorsal stream with the motor cortex lip area during speech perception

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ARTICLE INFO

Article history:
Available online 24 October 2011

Keywords:
Sensorimotor integration of speech perception
Temporoparietal junction
Inferior frontal gyrus
Paired-coil transcranial magnetic stimulation
Effective connectivity

ABSTRACT

A left-hemispheric cortico-cortical network involving areas of the temporoparietal junction (Tpj) and the posterior inferior frontal gyrus (pIFG) is thought to support sensorimotor integration of speech perception into articulatory motor activation, but how this network links with the lip area of the primary motor cortex (M1) during speech perception is unclear. Using paired-coil focal transcranial magnetic stimulation (TMS) in healthy subjects, we demonstrate that Tpj → M1 and pIFG → M1 effective connectivity increased when listening to speech compared to white noise. A virtual lesion induced by continuous theta-burst TMS (cTBS) of the pIFG abolished the task-dependent increase in pIFG → M1 but not Tpj → M1 effective connectivity during speech perception, whereas cTBS of Tpj abolished the task-dependent increase of both effective connectivities. We conclude that speech perception enhances effective connectivity between areas of the auditory dorsal stream and M1. Tpj is situated at a hierarchically high level, integrating speech perception into motor activation through the pIFG.

1. Introduction

Language processing in humans occurs in an interconnected cortical network of distributed brain areas consisting of the bilateral temporal lobes (auditory and phonological processing), the left-hemispheric posterior inferior frontal gyrus (pIFG, overlapping with Broca's area) and the left-hemispheric dorsolateral premotor area. The left-hemispheric temporal and frontal areas are connected via the parietal–temporal junction (area Spt), forming an auditory dorsal stream sensorimotor integration pathway to map speech perception onto speech production processes (Buchsbaum et al., 2011; Hickok, Houde, & Rong, 2011; Hickok & Poeppel, 2007). Evidence for the existence of this auditory dorsal stream circuitry that maps acoustic speech signals to frontal lobe articulatory networks comes from functional magnetic resonance imaging (fMRI) studies (Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Watkins & Paus, 2004). Furthermore, lesions of the left-hemispheric temporoparietal junction (Tpj) areas around the posterior-most portion of the Sylvian fissure, including area Spt, the supramarginal gyrus and the posterior-most part of the superior temporal gyrus, are associated with conduction aphasia, a syndrome characterized by frequent phonemic paraphasias with often inefficient attempts of self-correction, and impaired verbatim repetition (Anderson et al., 1999; Buchsbaum et al., 2011; Hickok et al., 2000). These areas of the auditory dorsal stream are densely connected anatomically (Friederici, 2009) and functionally (Buchsbaum, Olsen, Koch, & Berman, 2005). However, although the components of this network are well established, virtually nothing is known on how their activity is linked together during speech perception to map speech signals onto articulatory motor activation.

Here, we used the novel technique of paired-coil conditioning-test focal transcranial magnetic stimulation (TMS) (Koch et al., 2008; Koch, Versace et al., 2010) to examine to what extent speech perception resulted in task-specific changes in effective connectivity between the left-hemispheric Tpj or pIFG with the primary motor cortex (M1) lip area.

Furthermore, we employed continuous theta-burst stimulation (cTBS) in the 'virtual lesion mode' (Ziemann, 2010) over the pIFG or Tpj to disrupt neuronal activity in the stimulated areas. This allowed testing of the critical dependence of pIFG → M1 and Tpj → M1 effective connectivity on the task-related neuronal activity in these areas.

We hypothesized that pIFG → M1 and Tpj → M1 effective connectivity would be enhanced during auditory speech perception. Furthermore, we hypothesized, in accord with previous connectivity models (Hickok et al., 2011; Hickok & Poeppel, 2007) that cortical areas of the Tpj would be placed hierarchically upstream of pIFG in sensorimotor integration of speech perception.

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doi:10.1016/j.bandl.2011.09.005

2. Materials and methods

2.1. Participants

Ten healthy volunteers (mean age ± SD, 28.3 ± 6.4 years, 6 female) participated in this study. The native language of all participants was German. Handedness was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), with a mean laterality score was 94.6 ± 7.7%, indicating right-handedness in all subjects. Written informed consent was obtained from all subjects prior to participation. None of the participants had a history of neuropsychiatric disease or was on CNS-active drugs at the time of the experiments. The study was approved by the ethics committee of the Medical Faculty of Goethe-University Frankfurt and conformed to the latest version of the Declaration of Helsinki.

2.2. Study design

This study consisted of two experiments. In Experiment 1, conditioning magnetic stimuli were applied to the Tpj or the pIFG of the left hemisphere and test stimuli were applied over the left M1 lip area while subjects listened to speech or white noise. Experiment 1 allowed examination of task-dependent modulation of Tpj → M1 and pIFG → M1 effective connectivity. In Experiment 2, a 'virtual lesion' was induced over the Tpj or the pIFG, and the consequences on task-dependent modulation of Tpj → M1 and pIFG → M1 effective connectivity were investigated. Eight subjects (mean age 28.6 ± 7.2 years, 4 female) were studied in Experiment 1 and eight subjects (mean age 28.3 ± 7.2 years, 4 female) in Experiment 2. Six subjects participated in both experiments.

2.3. Auditory tasks

Participants sat on a comfortable chair. TMS was performed while participants listened to auditory material: either short German speech sentences (80 dB sound pressure level) or auditory white noise (70 dB sound pressure level; Fig. 1A). The auditory material was presented through dual loudspeakers placed in front of the participants. To standardize visual input, visual noise was presented simultaneously in both conditions on a PC screen (Samsung SyncMaster 214T 21.3″LCD TFT monitor) at a distance of 1 m in front of the participant's head. The sentences were recorded from two female German native speakers by using a digital video camera. The auditory material was separated for presentation. In the speech condition, the participants were instructed to listen carefully and try to understand the meaning of the sentences. In the listening to speech condition, TMS was delivered always 1500 ms after presentation onset of a sentence, while during listening to continuous white noise TMS was applied every 4.5–5.5 s.

2.4. fMRI-guided TMS neuronavigation

High-resolution structural T1-weighted images and functional magnetic resonance imaging (fMRI) data were obtained from each subject prior to the TMS experiments. The fMRI data were obtained while subjects were engaged in the same audiovisual tasks as in Experiments 1 and 2. In addition, to identify the M1 lip area, fMRI data were obtained while the subjects performed repeated lip movements. 120 EPI volume images were obtained in a block design in each auditory task (listening to speech, listening to white noise), the repetitive lip movement task and a resting condition, respectively. The preprocessed images of each subject were analyzed using a standard general linear model approach. Simple *t*-contrast maps of the listening to speech vs. listening to white noise condition and lip movements vs. resting condition were calculated in each subject. Group data from the *t*-contrast images were analyzed using one-sample *t*-tests. Clusters were considered significant only if they consisted of at least 50 contiguous voxels, which passed the threshold of $P < 0.01$, family-wise error (FWE) corrected for the auditory task. The threshold for the lip movement task was set at cluster size >50 and at $P < 0.005$, FWE corrected.

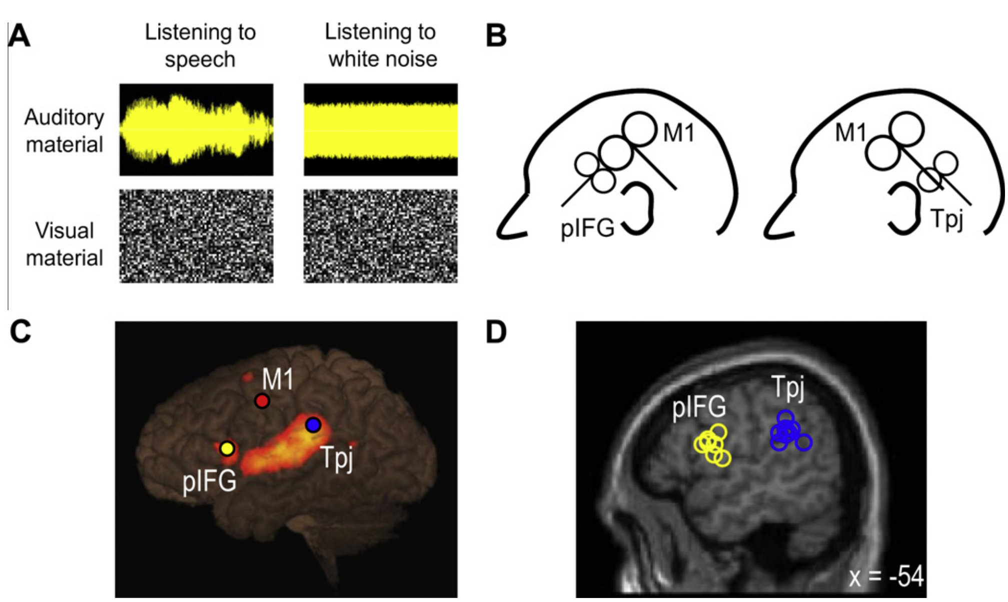

Fig. 1. (A) Schematic representation of experimental conditions in Experiments 1 and 2. (B) Focal conditioning TMS was applied to the Tpj or the pIFG of the left hemisphere. The TMS test pulse was delivered through another stimulating coil over the left-hemispheric M1 lip area. (C) Structural brain image and hemodynamic responses related to auditory speech perception in one representative subject. Red, yellow and blue dots show M1 lip area, pIFG and Tpj, respectively. (D) Sagittal view of the mean anatomical image ($x = -54$) indicating the individual coil locations (pooled data of Experiments 1 and 2, $n = 10$) over left-hemispheric Tpj (blue) and pIFG (yellow). These locations were defined by the maximum individual fMRI activations during auditory speech perception in close vicinity to the areas of activation in the group average, and targeted by using fMRI-guided TMS neuronavigation. Note, that the coil locations over Tpj were clustered around the posterior-most extent of the Sylvian fissure rostral to the superior temporal gyrus.