NeuroImage 86 (2014) 525–535

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

A bilateral cortical network responds to pitch perturbations in speech feedback

Naomi S. Kort [a,b,*], Srikantan S. Nagarajan [a,1], John F. Houde [c,1]

[a] Department of Radiology, University of California, San Francisco, and University of California, Berkeley USA
[b] Joint Graduate Group in Bioengineering, University of California, San Francisco, USA
[c] Department of Otolaryngology—Head and Neck Surgery, University of California, San Francisco, USA

ARTICLE INFO

Article history:
Accepted 15 September 2013
Available online 25 September 2013

Keywords:
Speech motor control
Sensorimotor
Auditory feedback
Magnetoencephalography

ABSTRACT

Auditory feedback is used to monitor and correct for errors in speech production, and one of the clearest demonstrations of this is the pitch perturbation reflex. During ongoing phonation, speakers respond rapidly to shifts of the pitch of their auditory feedback, altering their pitch production to oppose the direction of the applied pitch shift. In this study, we examine the timing of activity within a network of brain regions thought to be involved in mediating this behavior. To isolate auditory feedback processing relevant for motor control of speech, we used magnetoencephalography (MEG) to compare neural responses to speech onset and to transient (400 ms) pitch feedback perturbations during speaking with responses to identical acoustic stimuli during passive listening. We found overlapping, but distinct bilateral cortical networks involved in monitoring speech onset and feedback alterations in ongoing speech. Responses to speech onset during speaking were suppressed in bilateral auditory and left ventral supramarginal gyrus/posterior superior temporal sulcus (vSMG/pSTS). In contrast, during pitch perturbations, activity was enhanced in bilateral vSMG/pSTS, bilateral premotor cortex, right primary auditory cortex, and left higher order auditory cortex. We also found speaking-induced delays in responses to both unaltered and altered speech in bilateral primary and secondary auditory regions, left vSMG/pSTS and right premotor cortex. The network dynamics reveal the cortical processing involved in both detecting the speech error and updating the motor plan to create the new pitch output. These results implicate vSMG/pSTS as critical in both monitoring auditory feedback and initiating rapid compensation to feedback errors.

© 2013 Published by Elsevier Inc.

Introduction

Speaking is a complex motor process where the goal is to produce sounds that convey an intended message; if the right sounds are produced, the listener will correctly comprehend the speaker's message. It is not surprising, therefore, that speakers monitor their sound output, and that this auditory feedback exerts a powerful influence on their speech. Indeed, the motor skill of speaking is very difficult to acquire without auditory feedback, and, once acquired, the skill is gradually lost in the absence of auditory feedback (Cowie et al., 1982). The control of the fundamental frequency of speech (F0), perceived as pitch, is rapidly lost in the absence of auditory feedback (Lane and Webster, 1991), demonstrating that pitch, along with other suprasegmental features, requires aural monitoring. However, the control of pitch during speech, given that the auditory feedback is both noisy and delayed, is still poorly understood. Precise control of pitch is essential for the prosodic content of speech — providing the speaker with information on emphasis, emotional content, and form of the utterance (e.g. question or statement). The failure to properly modulate pitch is an impediment in communication, and the result of several neurological and psychiatric disorders, including schizophrenia and Parkinson's disease.

When auditory feedback is present, its alteration can have immediate effects on ongoing production. It has long been known, for example, that delaying auditory feedback can immediately render a speaker disfluent (Lee, 1950; Yates, 1963). More recently, experiments have altered specific features of auditory feedback, and the responses of speakers have been particularly revealing. In response to brief perturbations of the pitch, loudness, and formant frequencies of their auditory feedback, speakers will make quick adjustments to their speech that reduce the perceived effect of the perturbations on their auditory feedback (Chang-Yit et al., 1975; Houde and Jordan, 1998, 2002; Lane and Tranel, 1971; Lombard, 1911). These experiments, in which a feedback perturbation elicits a quick compensatory response, demonstrate the existence of speech sensorimotor pathways in the CNS that convey corrective information from auditory areas to speech motor areas during ongoing speaking. Behavioral experiments have further shown that

* Corresponding author at: Department of Radiology and Biomedical Imaging, University of California, San Francisco, 513 Parnassus Avenue, S362, San Francisco, CA 94143, USA.
E-mail addresses: naomi.kort@ucsf.edu (N.S. Kort), Srikantan.Nagarajan@ucsf.edu (S.S. Nagarajan), houde@phy.ucsf.edu (J.F. Houde).
[1] Department of Radiology and Biomedical Imaging, University of California, San Francisco, 513 Parnassus Avenue, S362, San Francisco, CA 94143, USA.

1053-8119/$ – see front matter © 2013 Published by Elsevier Inc.
http://dx.doi.org/10.1016/j.neuroimage.2013.09.042

auditory feedback is important for online control of pitch both in words and sentences. Altered pitch feedback on the first syllable of a nonsense word impacts the pitch of the second syllable, even when the first syllable is short and unstressed (Donath et al., 2002; Natke and Kalveram, 2001). Compensation to pitch-altered feedback influencing either the stress in a sentence (Patel et al., 2011) or the form of the sentence (Chen et al., 2007) has been observed. These studies have shown the importance of auditory feedback in controlling pitch both within a syllable, and on a suprasegmental level. This behavior may be used to compensate for disturbances in output pitch known to arise from a number of natural sources, including an error in the complex coordination of vocal fold tension (Lane and Webster, 1991), aerodynamic instability, and even heartbeat (Orlikoff and Baken, 1989). The rapid compensation to altered pitch feedback occurs both in continuous speech (sentence production) and during single vowel phonation. This is not surprising given that phonation is an important part of speech. While the pitch perturbation response has been well-characterized in behavioral studies, very little is known about the neural substrate of these sensorimotor pathways.

Until recently, the study of the neural circuitry monitoring self-produced speech has primarily focused on auditory cortex during correct (unaltered) vocalization. Work in non-human primates found that the majority of call-responsive neurons was inhibited during phonation (Eliades and Wang, 2002, 2005, 2008; Muller-Preuss and Ploog, 1981). Extensive work has been done to study this suppression effect in humans (Chang et al., 2013; Curio et al., 2000; Greenlee et al., 2011; Houde et al., 2002; Ventura et al., 2009). Studies using magnetoencephalography (MEG) in humans similarly found suppressed neural activity in auditory areas during self-produced speech compared to the neural activity while listening to the playback of recorded speech (Curio et al., 2000; Houde et al., 2002). This effect has been termed speaking-induced suppression (SIS). SIS is a specific example of the broader phenomenon of motor-induced suppression (MIS) (Aliu et al., 2009), where sensory responses to stimuli triggered by self-initiated motor act are suppressed. However, in these studies, it was difficult to localize the SIS effect to specific areas of auditory cortex. Better localization of SIS has been seen in studies based on intracranial recording (ECoG) in neurosurgery patients. One study found that the SIS response only occurred in circumscribed areas of auditory cortical areas, and in fact some areas show an anti-SIS effect (Greenlee et al., 2011). Another ECoG study focusing on responses in the left hemisphere found SIS primarily in electrodes clustered in posterior superior temporal cortex (Chang et al., 2013). However, the spatial coverage of ECoG is limited, and, as yet, no studies to date have examined more completely the spatial distribution of SIS along the speech sensorimotor pathways.

Monitoring feedback to confirm that speech motor acts give rise to the expected auditory outputs (resulting in SIS) is only one important role of the speech sensorimotor pathways. When feedback is altered and mismatches expectations, these pathways take on the additional role of conveying the mismatch to motor areas and generating a compensatory production change. What are the neural correlates of this process? Several SIS studies have showed that altering feedback at speech onset reduces SIS (Heinks-Maldonado et al., 2006; Houde et al., 2002). A few recent studies have looked at responses to feedback alterations during ongoing speech to pitch perturbations of auditory feedback using EEG (Behroozmand and Larson, 2011; Behroozmand et al., 2009, 2011). These studies found that perturbations of ongoing vocal feedback evoked larger responses than did perturbations passively heard during the subsequent playback of feedback. We term this effect speech perturbation response enhancement (SPRE). Although EEG studies to date have not been able to localize SPRE to particular brain areas, in two recent ECoG studies the spatial distribution of SPRE was mapped (Chang et al., 2013; Greenlee et al., 2013). One study from our group looked at high gamma responses to pitch-altered feedback in the left hemisphere, finding SPRE responses clustered in ventral premotor cortex and posterior superior temporal cortex including the parietal–temporal junction (Chang et al., 2013). A second study, using ECoG, found enhanced evoked and high gamma responses in both left and right mid-to-anterior superior temporal gyri (Greenlee et al., 2013). Coverage limitations of ECoG restrict the analysis to the individual subject's placement of the grid electrodes. Furthermore, since each patient's grid is uniquely placed ECoG studies cannot easily compare results across subjects, or across hemispheres within a subject.

The relationship between SIS and SPRE is largely unexplored. A recent study in marmosets found auditory neurons that show suppression at the onset of vocalization are more likely to have an enhanced response to a perturbation, suggesting a direct link between the mechanisms suppressing self-produced speech to those recognizing errors in self-produced speech (Eliades and Wang, 2008). In contradiction with these findings, an ECoG study of SPRE found only a small number of electrodes displaying both SIS and SPRE, in contrast to a larger number of electrodes which preferentially display one or the other (Chang et al., 2013).

To more completely define the speech sensorimotor network, other studies have used whole-head functional imaging to look at how the speech motor system responds to feedback alterations. The spatial resolution of fMRI has allowed several studies to identify specific areas in the auditory and motor cortices that respond when auditory feedback is altered during speaking (Parkinson et al., 2012; Tourville et al., 2008; Toyomura et al., 2007). When the results from the altered auditory feedback fMRI studies are combined with other pertinent speech studies, several cortical regions emerge as likely computational nodes in processing and responding to an error in auditory feedback (Andersen et al., 1997; Buchsbaum et al., 2011; Fu et al., 2006; Gelfand and Bookheimer, 2003; Grefkes and Fink, 2005; Hickok and Poeppel, 2007; Hickok et al., 2009, 2011; Rauschecker and Scott, 2009; Shadmehr and Krakauer, 2008; Tourville et al., 2008; Toyomura et al., 2007): primary auditory cortex, the superior temporal gyrus/middle temporal gyrus (STG/MTG), ventral supramarginal gyrus/posterior superior temporal sulcus (vSMG/pSTS) and premotor cortex, summarized in Table 1.

Unfortunately, the lack of temporal resolution in the fMRI studies and the limitations of ERP studies leave many questions unanswered. fMRI studies have helped to define the speech sensorimotor pathways, but due to the lack of temporal resolution, these studies have not revealed the dynamics of the network's behavior. In particular, do the areas identified in the fMRI studies also exhibit SPRE, and, if so, what is the time course of SPRE over these areas? Do the areas that exhibit SPRE also exhibit SIS? Do the areas that exhibit SPRE show correlations across subjects with behavior? The advent of new source localization algorithms for magnetoencephalography (MEG) gives us a unique, unexploited opportunity to answer these questions using the millisecond time resolution of MEG.

The present study used MEG to investigate the cortical neural responses at speech onset (to examine SIS) and during brief, unexpected shifts in the pitch of subjects' audio feedback (to examine SPRE) during the phonation of a single vowel. By using a single vowel utterance we were able to isolate phonation from additional (linguistic) aspects of speech to specifically study pitch production. In this study, we tested several hypotheses. First, given that SIS has been shown to be involved in auditory self-monitoring, we hypothesized that there would be spatial overlap between the monitoring role of SIS and the error recognition part of the SPRE network. Second, we hypothesized that SPRE would be seen to propagate through the speech sensorimotor network as the error is recognized and processed, and ultimately induce a compensatory response. Third, we hypothesized that cortical responses to the perturbation during speaking would be correlated with compensation across subjects.

Download English Version:

https://daneshyari.com/en/article/6027854

Download Persian Version:

https://daneshyari.com/article/6027854

Daneshyari.com