Task-related differences in temporo-parietal cortical activation during human phonatory behaviors

Richard D. Andreatta [a,*], Joseph C. Stemple [a], Ashwini Joshi [a], Yang Jiang [b]

[a] Department of Rehabilitation Sciences, College of Health Sciences, University of Kentucky, Lexington, KY, USA
[b] Department of Behavioral Sciences, College of Medicine, University of Kentucky, Lexington, KY, USA

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ABSTRACT

Functional magnetic resonance imaging (fMRI) was used to investigate cortical activity related to differential control of the human phonatory system during a sentence production task. Our focus in this report was on activation of the temporo-parietal (TP) junctional region, suggested by recent models in speech production/perception to play a critical role between self-generated acoustic and associated somatosensory inputs related to the consequences of speech. Thirteen healthy participants produced multiple trials of phonetically balanced sentences during each of three performance conditions: "covert", "whisper" and "voice". An event-related, sparse sampling fMRI method was used to examine TP activity associated with sentence production during each condition. Results demonstrated differential responsiveness in the TP region bilaterally as a function of task conditions, with covert production generating the highest level of TP activation. These results suggest that the TP region is differentially responsive to phonation-specific production variables. Our finding that covert production instead of overt voicing resulted in the greatest activity in TP is consistent with recent reports demonstrating TP activation related to temporal ordering judgments and task-dependent memory use.

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Considering speech production involves respiratory, phonatory, resonance and articulatory subsystems working in dynamic coordination with audition, the role and contribution of each subsystem to the overall neural control of speech has yet to be disambiguated. The coordinated subsystems of speech production are in fact, experimentally divisible and amenable to individual analyses with limited confounding influence from remaining production components [26]. For those with interest in the neural substrate of human phonatory control, the ability to isolate the contribution of the larynx during speech may allow for a better understanding of the contribution of phonation-related neural activity during speech.

The laryngeal system has been described as a functional microcosm of the vocal tract [21] whose actions require substantial sensorimotor control and afferent monitoring to achieve the precise changes in pitch and intensity necessary during functional phonatory behaviors [3,22]. Low-threshold mechanoreceptive endings encode the dynamics of vocal fold behavior [1], providing critical movement-related somatosensory feedback that is in temporal register with acoustic feedback generated during phonation

[2,28,33]. In turn, the laryngeal motor control system is responsive to this barrage of sensory feedback during phonation.

Current theoretical models of speech production/perception (see [16,17]) suggest a critical role for comparative and integrative neural operations of sensorimotor and acoustic inputs during speech [5,16,17]. One cortical region suggested to play such a role is the zone in and around the temporo-parietal (TP) junction, a multimodal association area in the inferior parietal cortex, extending into the adjacent superior temporal gyrus. Geschwind [15] and Damasio and Damasio [11] implicated the involvement of the temporo-parietal region during speech as early as 1965 and 1980, respectively. More recently, Caplan et al. [6] found evidence among stroke patients for involvement of the posterior supramarginal gyrus and parietal operculum in acoustic–phonetic processing. Celsis et al. [7] identified the involvement of this same region in healthy volunteers asked to detect changes in phonological units during auditory tasks. The left posterior Sylvian fissure on the boundary of the parietal and temporal lobe has also shown evidence of auditory–motor responsivity and integration [19]. Hence, the TP region may form an important point of convergence for auditory and somatosensory inputs during speech production.

Given that the laryngeal system is the dominant source of sound during speech and that laryngeal control requires exquisite sensorimotor regulation, we consider the TP region to be a strong candidate to assess the effects of production conditions that manipulate acoustic output and sensorimotor regulation. We chose to

* Corresponding author at: Department of Rehabilitation Sciences, College of Health Sciences, University of Kentucky, 900 S. Limestone, Wethington 120-F, Lexington, KY 40536-0200, USA. Tel.: +1 859 218 0523.

E-mail address: richard.andreatta@uky.edu (R.D. Andreatta).

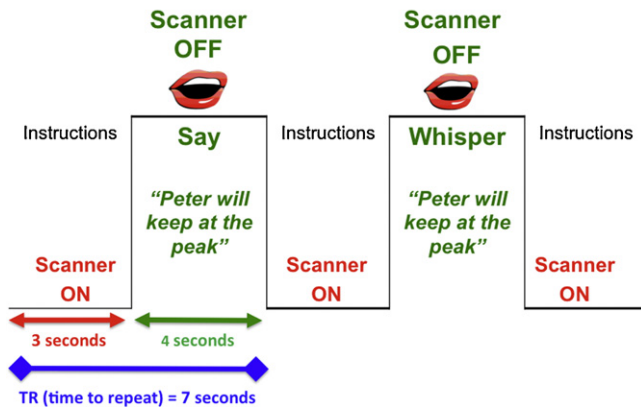## Event-Related Sparse Sampling Study Design

Fig. 1. Sparse sampling study paradigm.

focus our investigation on the TP region specifically because of its theoretical relevance to the integration of both acoustic and somatosensory inputs during speech [16,17]. The purpose of this report was to document changes in TP activity related to differential voluntary control of the phonatory system during a sentence production task under functional magnetic resonance imaging (fMRI). Manipulation of laryngeal-related acoustic and sensorimotor activity was achieved by requiring participants to overtly speak, whisper and covertly read a series of sentences during fMRI. It was hypothesized that TP activity would be sensitive to adjustments in the levels of laryngeal-related acoustic and sensorimotor activity during and across each of the production conditions for our sentence task.

Thirteen healthy, right-handed, native English speakers (4 male, 9 female), 22–57 years participated in the study. Participants had no history of neurological conditions or hearing loss. Participants underwent a videostroboscopic examination of the vocal folds prior to the fMRI procedure to ensure normal laryngeal structure and function. This study was approved by the Institutional Review Board at the University of Kentucky. All participants signed a written informed consent form prior to participation.

Participants performed multiple trials of six phonetically balanced sentences from the Consensus Auditory-Perceptual Evaluation of Voice (CAPE-V) [20] during each of three different performance conditions: "covert", "whisper" and "voice". Subjects were pre-trained on condition features and the meaning of instructions that would be visually provided in the scanner. Conditions were defined as: (1) "voice"—reading the sentence aloud at a normal and comfortable pitch and loudness, (2) "whisper"—reading the sentence aloud, yet with no voicing, and (3) "covert"—participants were instructed to read the sentences silently "in their heads" (as if reading aloud), without any speech-related movement or voicing. We confirmed that each participant understood our instructions by having each practice the three conditions outside of the scanner.

An event-related, sparse sampling fMRI design was used in this study to allow for the production of task conditions in the absence of gradient noise (Fig. 1) [31,32]. Participants received visual instructions for each trial projected onto a mirror on the head coil. A screen providing the condition cue for the upcoming trial was presented for 3 s. The next screen provided the target sentence and the participant was required to produce the sentence in either a covert, voiced or whispered manner. The sentence task occurred during the silent off-period of the sparse sampling sequence, a provision that reduced the potential for motion-related MR artifact [4]. Each trial period (scanner off) was jittered 3.5–4.5 s to better capture the hemodynamic response peak. Total subject time within the scanner was 35–40 min.

With the absence of gradient noise during task production, participants were capable of self-monitoring their sentence productions during the whisper and overt voicing conditions without the need for headphones. Participants were free to self-correct their speech. Participant's compliance with condition parameters was externally monitored by randomly sampling productions over the audio–visual interface within the scanner suite. Qualitatively, participants were compliant with all performance parameters.

Task conditions were designed to produce concurrent and graded sensorimotor and acoustic changes during sentence production. For the "voice" condition, phonation and articulatory acoustics were typical and contained all phonetic acoustic cues for all sound classes. For the "whisper" condition, the acoustic output was substantially degraded (no phonation, loss of voiced-consonant feature, added airstream turbulence). Lastly, the "covert" condition produced no acoustic output of any kind (laryngeal and/or supralaryngeal in origin). Overall, the production conditions can be viewed as existing on a continuum of laryngeal engagement, with the "voice" state at one end (most engaged) and the "covert" state at the other (least engaged). Acoustic features for the sentences produced under each condition were considered unique for each condition allowing for interpretation of TP activity related to both global acoustic features and peripheral sensorimotor performance. Commonalities across conditions related to language were subtracted using a comparative analysis between conditions, allowing us to identify any difference in cortical activity as a function of task demand.

Thirty trials for each condition of "covert", "whisper", and "voice" and 60 rest trials were distributed over three functional runs for each subject. Sentences were placed in an ABBA order, while the task conditions (including rest) were pseudo-randomized using a sequence provided by the Analysis of Functional Neuroimaging (AFNI) software [9]. All participants received the same order of trials to maintain task presentation consistency.

Movement artifact was minimized during signal acquisition by stabilizing the skull with memory-foam against the head coil, and using an event-related, sparse sampling approach. Scanner gradients were turned off during speech production and turned on for 3 s afterward during the visual instruction phase for the upcoming trial. Whole brain volumetric scans of blood oxygenation level dependent (BOLD) activity for the previous sentence production was collected during the scanner-on period. Head movement was not measured because of the methodology's strength in controlling for motion-related artifact. Functional data were T2* weighted echo-planar images. A single echo-planar imaging (EPI) volume was acquired with a TR = 7.0 s. A high-resolution, 3D anatomic image was acquired using a sagittal T1 weighted (MP-RAGE) sequence (TR = 2100 ms, TE = 2.93 ms, TI = 1100 ms, flip angle = 12°, FOV = 192 mm × 224 mm × 256 mm, with 1 mm isotropic voxels). The following parameters were applied during volume acquisition: TR = 2.5 s; TP = 156; TE = 30 ms; flip angle = 81°; 39 axial slices; 224 mm × 224 mm FOV (field of view); slice thickness = 3.5 mm; 64 × 64 matrix (yielding 3.5 mm × 3.5 mm × 3.5 mm voxels); bandwidth = 2056 Hz/Px.

Image processing and analyses was conducted using AFNI [10]. After pre-processing, structural 3D data were transformed into Talairach space using AFNI [10]. Following exclusion of the first few functional volumes due to T1 saturation effects, timing differences between slices due to acquisition order were adjusted with sync interpolation. fMRI data were motion adjusted to the image collected nearest in time to the structural image, and smoothed (4 mm FWHM). Each voxel was normalized within each functional run to yield activation measures expressed as "percent change" from baseline. For each subject, the voxel time series for each trial type ("covert", "whisper" and "voice") were estimated using AFNI. The general linear model for event-related fMRI was used to esti-

Table 1
Descriptive statistics for TP area and BA 4 for sentence production task ($N = 13$).

Area	Condition	Right		Left	
		Mean% BOLD signal change	S.D.	Mean% BOLD signal change	S.D.
TP	Whisper	0.811	0.705	0.881	0.681
	Voiced	1.100	0.577	1.18	0.644
	Covert	1.23	0.646	1.16	0.675
BA 4	Whisper	1.045	0.903	1.01	0.868
	Voiced	0.919	0.686	0.921	0.755
	Covert	0.873	0.759	0.893	0.815

mate the evoked hemodynamic delay for each trial type with no assumptions about the BOLD responses shape.

Brain regions of interest (ROI) were identified quantitatively using coordinate databases within AFNI (Talaraich–Tournoux). Each subject's structural brain image was put into the standardized space. Identical region masks were calculated by AFNI for the TP region and primary motor cortex (BA 4) and applied to all subjects to avoid subjectivity and bias from individual brain responses.

Averaged EPI activations were calculated for each condition in the selected voxels within the ROIs. All voxels were averaged within the ROIs for each time point, creating a single, spatially averaged time course for each trial type. The percent change in the BOLD signal for each condition was calculated in the ROIs for further analysis using AFNI. Second level analysis of percentage BOLD signal changes from each participant, as a random factor, was conducted. A two-factor repeated measures analysis of variance (RM-ANOVA) was conducted for percent BOLD signal change in TP and BA 4 for the sentence production conditions. Post hoc decomposition of the full model was conducted to identify significant simple main and comparison contrasts.

fMRI responses for the TP and BA 4 ROIs are reported for the sentence production conditions of "whisper", "voice" and "covert". BA 4 is being reported alongside the TP region to allow comparison and contrast of activity for a multimodal sensory area (TP) vs. a motor region (BA 4). For the TP area, bilateral activation was present during the sentence production tasks (Fig. 2), with "covert" sentence production evoking the largest mean activation, and "whisper" task conditions evoking the lowest percent change in cortical response (Table 1). Individual fMRI responses were similar to the group mean trend for 9 out of the 13 participants, suggesting a modestly consistent change in activation as a function of task/condition production.

In contrast to the trend noted in the TP region, the inverse trend in task-related cortical activation was found for BA 4 (whisper greater than voice, and voice greater than covert). The inverse trend in BA 4 was present bilaterally for the mean group and within individual data (Fig. 2A). The full model two-factor repeated measures ANOVA revealed a significant interaction between brain area and
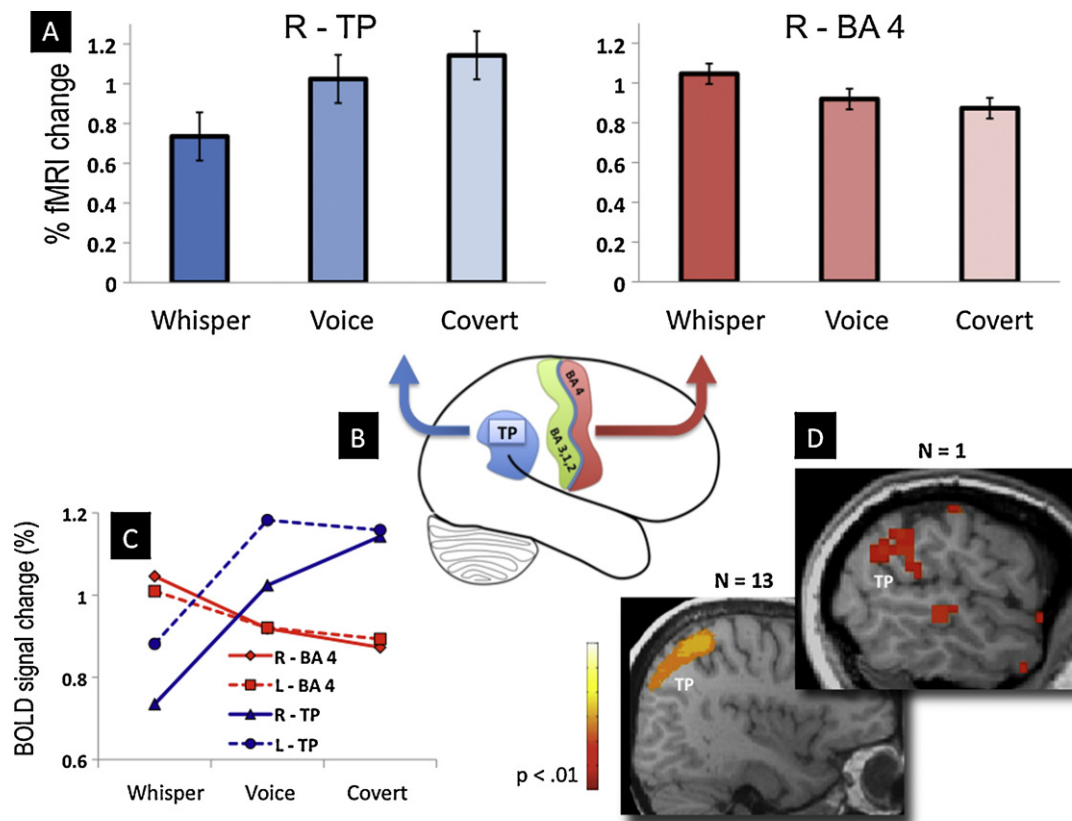
Fig. 2. (A) Bar graph for percent change in BOLD responses for right temporo-parietal (TP) region and right primary motor cortex (BA 4) for "whisper", "voice" and "covert" tasks. (B) Schematic representation of TP, BA 4 and primary somatosensory cortex (BA 1, 2 and 3). (C) Line graph for percent change in BOLD responses for right and left TP region and right and left BA 4 for "whisper", "voiced" and "covert" tasks. (D) BOLD activity for TP as the region of interest (ROI) for an individual participant ($N = 1$) and for all participants ($N = 13$).

Table 2
Full model RM-ANOVA with identified simple main and simple comparison effects.

Source	DF	Adjusted SS	Adjusted MS	Error DF	Error MS	F value	P-value
Full two factor RM-ANOVA							
Subject	12	41.085	3.423	36	0.827	4.14	<0.001[*]
Area	3	0.543	0.181	36	0.827	0.22	0.883
Subject × area	36	29.775	0.827				
Task	2	0.326	0.163	24	0.076	2.15	0.139
Area × task	6	1.877	0.312	72	0.0625	5.000	<0.001[*]
Subject × area × task	72	4.501	0.063				
Simple main effects							
Task at left TP	2	–	0.363	24	0.049	7.41	0.003[*]
Task at right TP	2	–	0.586	24	0.063	9.24	0.001[*]

Area	Task	DF	Adjusted SS	Adjusted MS	Error DF	Error MS	F value	P-value
Simple comparison effects								
L-	Whisper vs. voice	1	0.588	0.588	12	0.067	8.83	0.012[*]
TP	Whisper vs. covert	1	0.498	0.498	12	0.062	7.99	0.015[*]
R-	Whisper vs. voice	1	0.541	0.541	12	0.060	9.01	0.011[*]
TP	Whisper vs. covert	1	1.11	1.11	12	0.11	10.21	0.008[*]

[*] Statistical significant as $p = 0.0150$.

task condition (Table 2). Post hoc analysis (simple main and comparison effects) of the significant interaction revealed that within TP, significant differences were present in percent BOLD signal change between the whisper vs. voice and whisper vs. covert production conditions. The interaction effect can be seen in Fig. 2C as well as the significant pair-wise effects between task conditions within the TP. All other simple main and simple comparison effects were non-significant.

Our results have preliminarily shown that the temporo-parietal region responded differentially during whisper, voice and covert production of our sentence task. Generally, our data are consistent with previous reports such as Haslinger et al. [18] and Loucks et al. [25] who used fMRI to examine central laryngeal representations during vowel and syllable production respectively, reporting activation of the TP region. Our finding of a task/condition effect for the TP region suggests that this area is sensitive to changes in acoustic and sensorimotor performance factors during either covert or overt voice production.

Interestingly, covert production evoked the largest response in an area hypothesized to play a key role in somatosensory and acoustic association during speech [16]. Recent studies using auditory and visual modalities have indicated that the TP area is consistently engaged when memory use is strongly task dependent [8,13]. It has been postulated that sensory signals reaching the TP region may be filtered for task-relevance, allowing for full attention to re-living the task-related memory [8]. Given the memory requirements of having to read and produce a sentence silently in your mind, the strongest activation of the TP region during covert production is consistent with a memory-related function of this area.

An alternative, yet corresponding interpretation that may be applied to our results stems from a recent report by Davis et al. [12] demonstrating TP activity changes as a function of temporal ordering judgments of visual stimuli. In this report, bilateral TP activity increased substantially when subjects were required to make judgments regarding the temporal ordering of a visually presented sequence of stimuli vs. judgments about a stimuli's shape. The notion that TP regions are sensitive to temporal ordering decisions and are known to be sensitive to task-dependent memory use is consistent with our data. Since participants were required to imagine they were reading a sentence aloud, it is possible that they may have needed to envisage the temporal order of articulatory production features of the remembered words making up the sentences. This is an intriguing possibility and one that is amenable to direct testing.

In contrast to the TP region, the primary motor area (BA 4) responded strongest to the whisper condition, although no statistical differences were noted across our task conditions within BA 4. The non-significant finding for task condition within the primary motor cortex is of interest and somewhat unexpected given that the overall motor pattern across our task conditions differed in terms of vocal fold approximation, respiratory drive, and translaryngeal airflow/pressure regulation. As shown in Fig. 2, one can detect a slight trend whereby the whisper condition produced the highest degree of signal change, while the covert state produced the least.

The non-significant effect for task condition within BA 4 may be attributed to the large degree of individual variability noted and/or to the possible effects of sub-vocalizations specifically during the covert condition. Sub-vocalization activity may have resulted in low-level neuromotor drive to laryngeal muscles, a condition consistent with previous evidence of EMG activity produced during motor imagery of limb behaviors [23]. During covert speech experiments, sub-vocalizations are difficult to control since they are typically an unintentional and unconscious response to the task. If participants were sub-vocalizing during our covert sentence condition, greater levels of motor cortical activity could have resulted, thus obscuring any subtle task-related differences. Lastly, another possible explanation for the non-significant differences for condition within BA 4 may be attributed to the level of effort required for these different conditions, resulting in varying levels of task-related motor cortical excitability.

The results of this study in participants with normal voice are an important albeit preliminary step toward refining our understanding of the neural mechanisms underlying performance factors of human voice production. We have examined TP activation by requiring subjects to change their performance strategy during production of a common set of sentences. Future studies should assess fMRI response patterns of normal voice against those of participants with a variety of voice disorders. To date, the existing bulk of the imaging literature in voice disorders is confined to a few specific voice pathologies: spasmodic dysphonia, Parkinson's disease, and a single case report of idiopathic unilateral vocal fold paralysis [14,18,24,27,29,30]. Our central goal is to broaden the scope of neuroimaging studies to other voice pathologies, encompassing those that are managed by medical, surgical and behavioral means. Future studies should relate routine voice diagnostic behavioral measures (i.e. perceptual, acoustic, and aerodynamic) to brain imaging data to better understand the relationship between current clinical voice measures and the underlying neural events subserving disordered

voice. A clearer understanding of voice production, from central sensorimotor control to the contribution of the peripheral subsystems, will help to establish biomarkers and drive individually based treatment plans, leading to improved clinical outcomes in treatment seeking populations.

Acknowledgements

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