An fMRI Investigation of the Neural Bases of Sequential Organization in Speech Production

Jason W. Bohland[1], Frank H. Guenther[1,2,3]

[1]Department of Cognitive and Neural Systems, Boston University. [2]Speech Communication Group, Research Labroratory of Electronics, Massachusetts Institute of Technology.

[3]Athinoula A. Martinos Center for Biomedical Imaging, Massachusetts General Hospital.
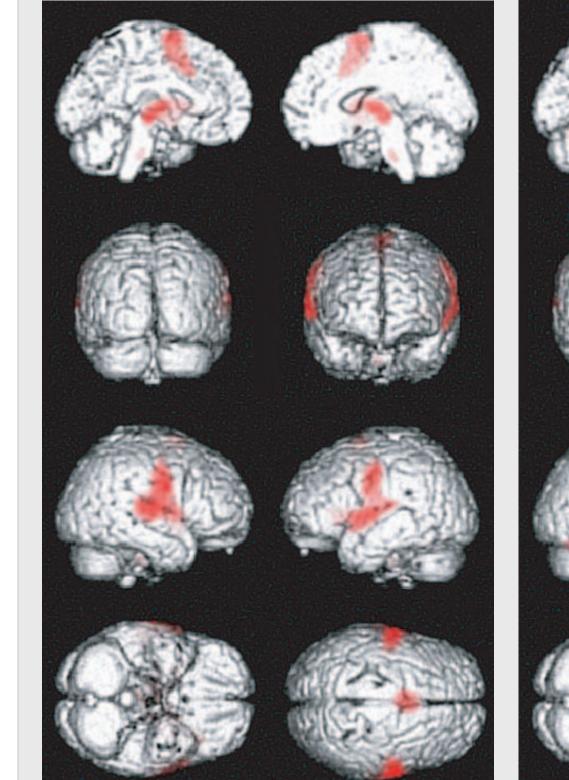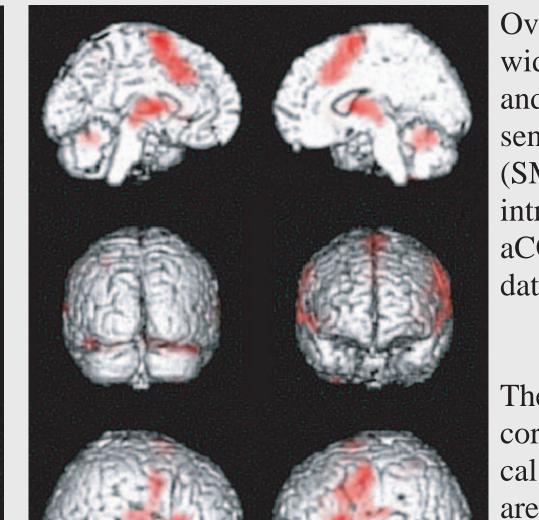
Introduction

Fluent speech requires phonemes and/or syllables to be arranged sequentially to form a coherent articulatory plan. The notion that representations for future speech sounds are activated in a serial order planning stage prior to execution was introduced by Lashley [1] and is supported by data including anticipatory coarticulation and speech error results. Lesion studies suggest that the medial premotor cortex and/or anterior peri-sylvian areas may constitute a cortical substrate for such planning (e.g. [2,3]).

We performed an fMRI experiment to elucidate the cortical and subcortical network responsible for speech motor sequencing. Specifically, we examined differences in brain activations during preparation and production of memory-guided non-lexical sequences of three syllables of varying complexity. We report on brain regions that showed differential activations across conditions, and suggest possible roles for these areas in the sequencing of syllables. Notable regions include the supplementary motor area, anterior insula and inferior frontal gyrus, the basal ganglia and thalamus, and the cerebellum.
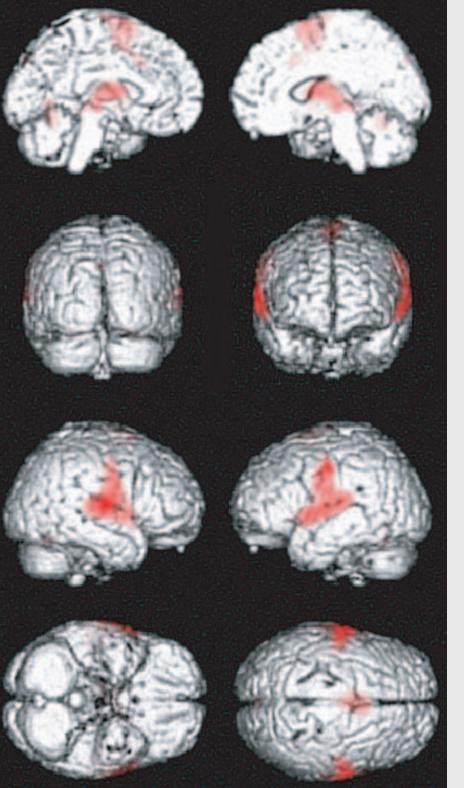
Methods

Stimuli

There were four stimulus types:

Simple sequences of simple syllables (S-syl,S-seq)	**ba-ba-ba**
Complex sequences of simple syllables (S-syl,C-seq)	**ba-ti-ku**
Simple sequences of complex syllables (C-syl,S-seq)	**stra-stra-stra**
Complex sequences of complex syllables (C-syl,C-seq)	**stra-kla-stri**

Each stimulus was presented visually, then removed from the projection screen. Subjects were instructed to vocalize the most recent sequence upon receiving a GO signal after a short random duration. In some trials, the GO signal did not arrive (NOGO trials). The baseline condition was visually presented sequences of x's with no speaking task.
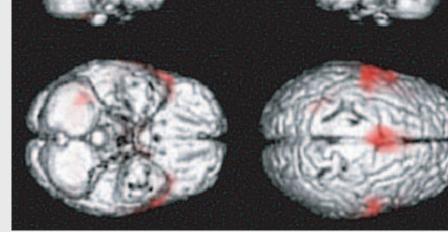
Details

- 13 neurologically normal right-handed English speakers
- Siemens 3T Trio Scanner
- Subjects performed 2-3 approximately 18 minute runs, 80 stimuli per run, mean ISI ~14.25s
- Event-Triggered Design, 3 volumes per trial (TR=2.5s, 30 slices, 5mm slice thickness); minimizes susceptibility artifacts and allows for production in relative silence.

Data Analysis

- Data were analyzed using the SpeechLab Toolkit (http://speechlab.bu.edu), which integrates SPM2 [4], a region-of-interest (ROI) toolbox [5], and FreeSurfer [6] methods into a common object-oriented Matlab-based processing stream.

- Two types of analyses were performed:

Standard Analysis
- Image volumes were realigned, normalized into stereotactic space, smoothed using a 12mm FWHM gaussian kernel, and analyzed using a random-effects analysis in SPM2.

ROI Analysis
- Freesurfer was used to create accurate cortical surface reconstructions from structural scans, and to perform automated cortical parcellation [7] according to a custom parcellation system for speech studies [8].
- Data were smoothed using a 12mm FWHM gaussian kernel within ROIs and analyzed using a random-effects analysis.
- ROI analysis provides a more powerful method to assess activations in regions of interest in the face of large anatomical variability [5].

ROI Parcellation System

Results

Basic Contrasts

A. S-syl,S-seq - Baseline

B.C-syl, C-seq - Baseline

C. GO - NOGO

Overt production of sequences of syllables activated a wide bilateral cortical and subcortical network: Left and right precentral gyrus (vPMC, vMC) and somato-sensory cortices (vSSC), the medial premotor areas (SMAa, SMAp), auditory cortex (H, PO, PP, T), the intra-sylvian cortex and nearby frontal regions (aINS, aCO, pCO, FO, iFO, iFT), thalamus, putamen, caudate, and superior cerebellum.

The preparation condition activated much of the same cortical network to a lesser degree. The auditory cortical areas as well as motor and somatosensory face areas were far less active across the NOGO conditions. Superio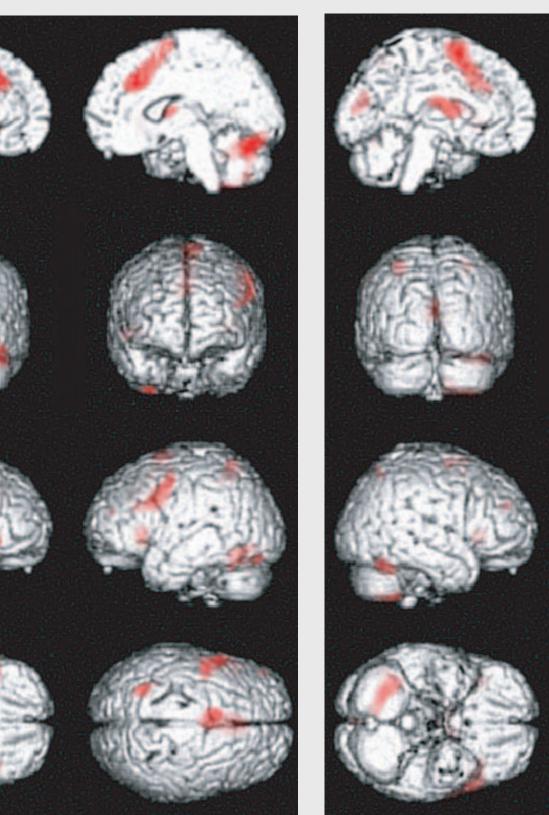r portions of the cerebellum, the basal ganglia, and the supplementary motor area also showed considerable increases of activity for overt production compared to preparation. The network of regions showing increased activation in the GO condition completely overlaps the areas found active for overt production of simple speech sounds [e.g. 9,10].
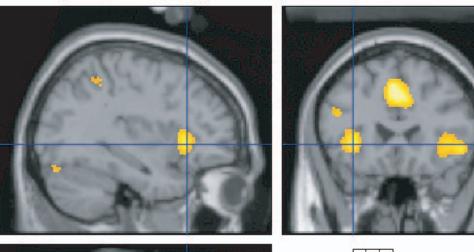
Sequential Content Contrasts

A C-seq - S-seq (GO condition)

B C-seq - S-seq (NOGO)

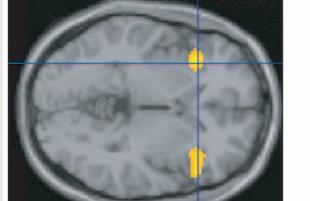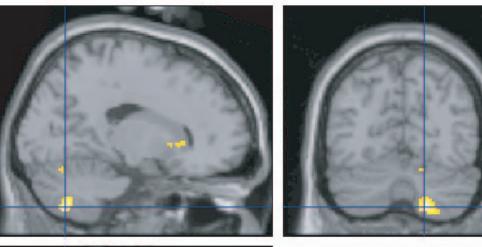C Peri-sylvian cortex

D Right Inferior Cerebellar Cortex

Additional sequential complexity (e.g. ra-ti-da vs. ra-ra-ra) yields additional activation in the aSMA, the left pre- and post-central gyri, superior parietal lobe, bilateral putamen, and superior cerebellum.
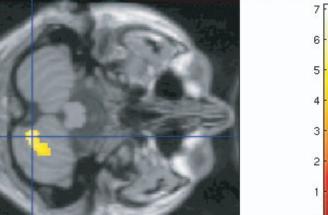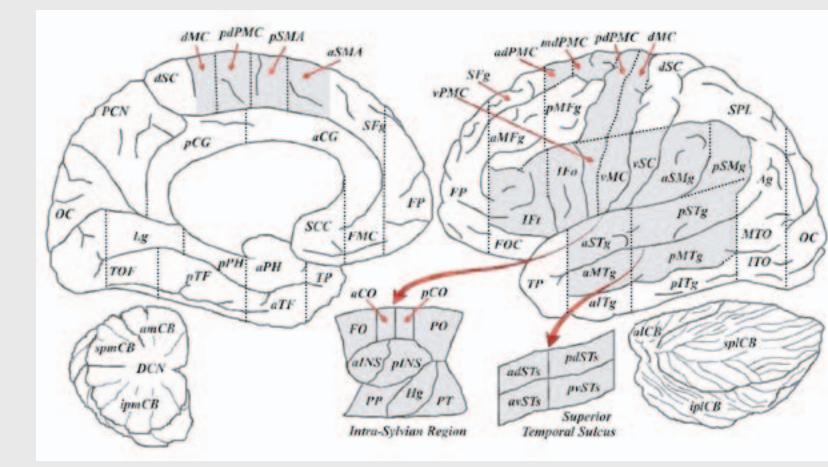
Panel (C) shows an additional locus of activation for production of complex sequences at the junction of the frontal operculum and anterior insula (c.f. [3,11,14]).

Panel (D) shows an area in the right hemisphere inferior cerebellar cortex that responds to complex sequences. This area is active in both preparation and production of complex sequences, regardless of syllable complexity.

Syllabic Content Contrasts

A Go Condition

B No Go Condition

Complex syllables activated the aSMA, the left pre-central gyrus, and the inferior frontal gyrus compared with simple syllables. Within the GO condition, there was additional superior cerebellar activation for complex syllables.

ROI Results

Effect sizes for selected cortical ROIs for various condition contrasts.

White bars show non-significant results
Green bars indicate $p < 0.05$
Yellow bars indicate $p < 0.01$
Red bars indicate $p < 0.001$

SEQ: complex-simple sequences
SYL: complex-simple syllables

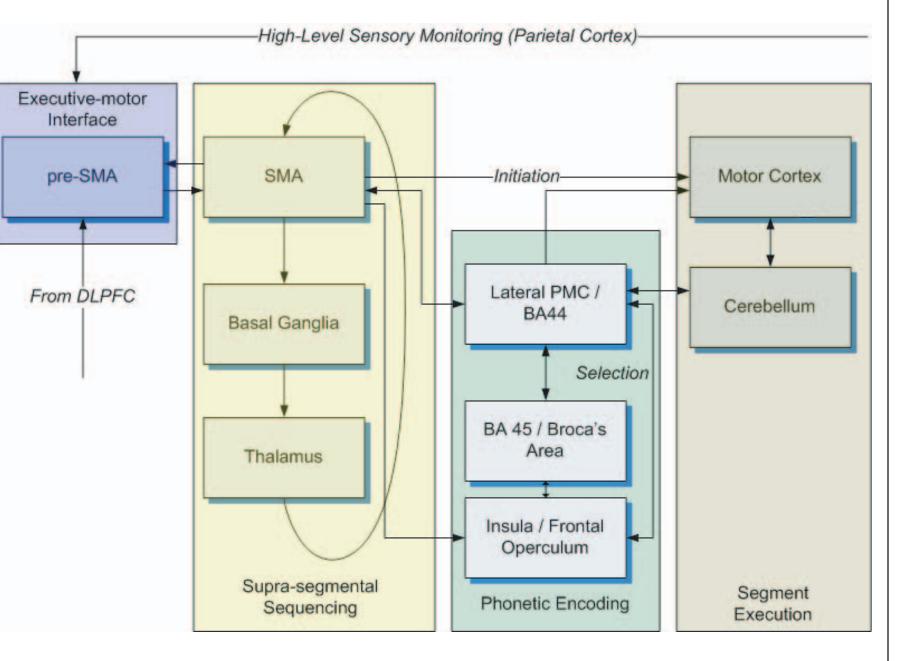Left Hemisphere   Right Hemisphere

Conclusions

- The anterior SMA showed the greatest sensitivity to content of sequences and is in a suitable position to serve as an interface between the production system and working memory.
- The posterior SMA was significantly more active during overt production, and may allow for initiation of motor commands for overt speech.
- The superior cerebellum was more active bilaterally during production than preparation, and more active for complex syllables than for simple syllables. This region may be used for feedforward control of well-learned syllables, and may be involved in coarticulation.
- The right inferior cerebellum became significantly active only for complex sequences. This area may be used in working memory or serial order representations.
- An area near the junction of the anterior insula and frontal operculum bilaterally showed differential activations depending on the complexity of sequences (see also [14]). While ROI results showed that these areas were significantly active even during preparation, the region was much more active during overt production, and somewhat more active in the left hemisphere.
These results are being used to guide the design of a more comprehensive version of the DIVA model of speech production [12,13] that includes biologically plausible representations of syllable sequencing (see diagram at right).

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