## Heschl's gyrus encoding of abstract speech cues in natural speech perception

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## INTRODUCTION

- Speech is a continuous, highly variable acoustic signa - The human brain effortlessly transforms this input into perceptually constant phonemic representations Vowels are distinguishable by F1 \& F2, but their values vary widely, with overlapping distributions, in connected speech Complicated by differences between speakers (vocal tract length) and within speaker (prosody, coarticulation)
The brain can normalize across these differences to generate single percepts for each vowel, but underlying neural computations are unknown
We performed direct intracranial recordings in Heschl's gyrus (HG) and planum temporale (PT) while 5 patients listened to natural speech
- High-gamma activity (HGA) was modulated by vowel ID - Using encoding models, we investigated which acoustic and linguistic vowel representations were encoded by HGA
Fundamental frequency (f0) and F1 normalized by f0 were encoded most consistently across HG \& PT


## METHODS

- HG \& PT recorded with sEEG while patients listened to 60 clips of natural speech (each $\sim 1 \mathrm{~min}$ clip followed by 2 questions to test comprehension)
- Speech annotated for phoneme identity, on/offsets
- Vowel fundamental frequency (f0) and formants F1-4 extracted (Praat) as the value at the vowel's midpoint


Figure 1. (A) Natural speech, annotations, and spectrogram, with Figure 1. (A) Natural speech, annotations, and spectrogram, with
fundamental freq. (f0) and formants (F1 \& F2) overlaid Single fundaes (midpoint, see markers) assigned to f0 \& F1-4 for every values (midpoint, see markers) assigned to f0 \& F1-4 for every
vowel. (B) HGA for a single electrode in left HG, recorded in patient P 1 . Blue portion: 500 ms window aligned to æ midpoint. (C) Topdown STP view and coronal slice of temporal lobe show electrode location from (B). (D) Formants were extracted across all clips; 2D gaussians fit to each vowel's distribution. Ellipses: 1 standard deviation. Points show the (F1, F2) location of each vowel from (A).

## METHODS

- HGA calculated (Hilbert transform) then extracted by aligning to each vowel's midpoint
- Sliding ANOVA used to identify electrodes modulated by vowel ID
- Is HG encoding vowel ID, formants, or something else?
- Encoding models built to predict HGA from acoustic \& phonetic features (see Table 1)
- Lasso regularization prevented overfitting and forced sparse feature selection
- Models evaluated by fraction of explained HGA variance ( $\mathrm{R}^{2}$ )
- Selected features were interpreted as being encoded in HGA

| Type | Features | Type | Features |
| :---: | :---: | :---: | :---: |
|  | F1/F3, F2/F3 [1] | Vowel ID | Binary [i, æ, ə, ...] |
|  | $\log (\mathrm{F} 2 / \mathrm{F} 1), \log (\mathrm{F} 3 / \mathrm{F} 1), \log (\mathrm{F} 4 / \mathrm{F} 1)[2]$ | Phonetic features | Height, front/back, rounded |
|  | $\log (\mathrm{F} 1 / \mathrm{f0}), \log (\mathrm{F} 2 / \mathrm{F} 1), \log (\mathrm{F3} / \mathrm{F} 2)[3]$ | Formants \& inverses | F1,..., F4; F1-1,..., $\mathrm{F}^{-1}$ |
|  | $\log (\mathrm{F} 1 / \mathrm{f0}), \log (\mathrm{F} 2 / \mathrm{F} 1), \log (\mathrm{F3} / \mathrm{F} 2)[4]$ | Fund. freq. \& inverses | f0, f0-1 |
|  | $\log \left(\mathrm{F} / \mathrm{F}^{*}\right), \log \left(\mathrm{F} 2 / \mathrm{F}^{*}\right), \log \left(\mathrm{F3} / \mathrm{F}^{*}\right)[5]$ | f0-norm. formants | F1/f0, F2/f0, F3/f0 |
|  | $\mathrm{F}^{*}=\operatorname{geomean}(\mathrm{F} 1, \mathrm{~F} 2, \mathrm{F3})$ | Acoustic props. | dB , duration |

Table 1. List of features included in the encoding model.

## RESULTS

Some electrodes show graded HGA responses (Fig. 2) that closely match vowel progression along F1-F2 diagonal (Fig. 1D). ANOVA F-stat shows time-dependent separability across all vowel IDs (not just the 5 exemplars in Fig. 2)
35/50 electrodes achieved ANOVA significance ( $\alpha=.01$, Bonf. corrected across all patients, channels, \& timepoints)
In 14 electrodes, encoding models could explain $>10 \%$ of HGA variance (Fig. 3)
Peak $R^{2}$ occurred at lags of 30 ms (3 elecs) or 40 ms (11)

| Patient | $\mathbf{1}$ | $\mathbf{2}$ | $\mathbf{3}$ | $\mathbf{4}$ | $\mathbf{5}$ |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Comprehension (\%) | 85 | 40 | 58 | 88 | 83 |
| Total number of electrodes | 6 | 11 | 15 | 7 | 11 |
| Significant ANOVA | 3 | 8 | 9 | 5 | 10 |
| Encoding model $\left(R^{2}>0.1\right)$ | 1 | 0 | 3 | 4 | 6 |

Table 2. Summary of results. Last 3 rows are electrode counts.


Figure 2. Mean HGA ( $\pm$ std err) Figure 2. Mean HGA ( $\pm$ std err)
from Fig. 1 electrode \& vowels. Graded HGA closely matches Graded HGA closely matches diagonal (Fig. 1D). F-statistics calculated via sliding ANOVA.

Figure 3. (A) Encoding model $R^{2}$ for 2 electrodes (mean $\pm$ std err across CV folds) . (B) $35 / 50$ elecs had significant HGA modulation by vowel ID (ANOVA); a subset of these were well-explained by encoding locations of significant elecs. Black elecs were significant via ANOVA but did not achieve the $\mathrm{R}^{2}$ cutoff.

## RESULTS

For each model, $\tilde{\beta}=|\beta| /$ sum $(|\beta|)$
f0 was most strongly encoded in HGA

- $13 / 14$ models: largest $\tilde{\beta}_{i}$ was $\tilde{\beta}_{1 / f 0}$ - $\tilde{\beta}_{f 0}+\tilde{\beta}_{1 / f 0}=0.63$ (mean across 14 models) F1/f0 was $2^{\text {nd }}$ most strongly encoded - 11 models: $2^{\text {nd }}$ or $3^{\text {rd }}$ largest feature - 12 models: $\tilde{\beta}_{\mathrm{F} 1 / \mathrm{f} 0}>\tilde{\beta}_{\mathrm{F} 1}+\tilde{\beta}_{1 / \mathrm{F} 1}$

Other encoded features:

- Duration

- Loudness (dB)

Figure 4. (A) Coeff magnitudes for each model were scaled to sum to 1 . Mean scaled coeff mag ( $\pm$ std dev) for top 5 features is shown. (B) For each model, scaled coeff mags were sorted, and the first N features that sum to 0.9 were kept. Bars represent the percent of total models
 (out of 14) that kept that feature.

## DISCUSSION

HGA on Heschl's gyrus is differentially activated across vowels during naturalistic listening conditions
At some sites, HGA encoded acoustic features

- Raw:
- Duration \& loudness (less perceptually relevant) - Fundamental frequency, $1^{\text {st }}$ formant (more relevant) - Normalized: formants normalized to f0
f0-normalized formants may be perceptually relevant for normalization across speakers or contexts (e.g. coarticulation) Limitations


## - Only 1 speaker

- Results are dependent on user-defined input features E.g. both fO \& $\mathrm{fO}^{-1}$ chosen in same models: in HGA~F(f0), F may be unknown
Only explored intrinsic cues; future work will also explore extrinsic contextual cues


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