

Using ECoG to understand the
representation of vocal pitch in
humans

Ben Dichter, Jonathan Breshears,
Matthew Leonard, Claire Tang,
Edward Chang

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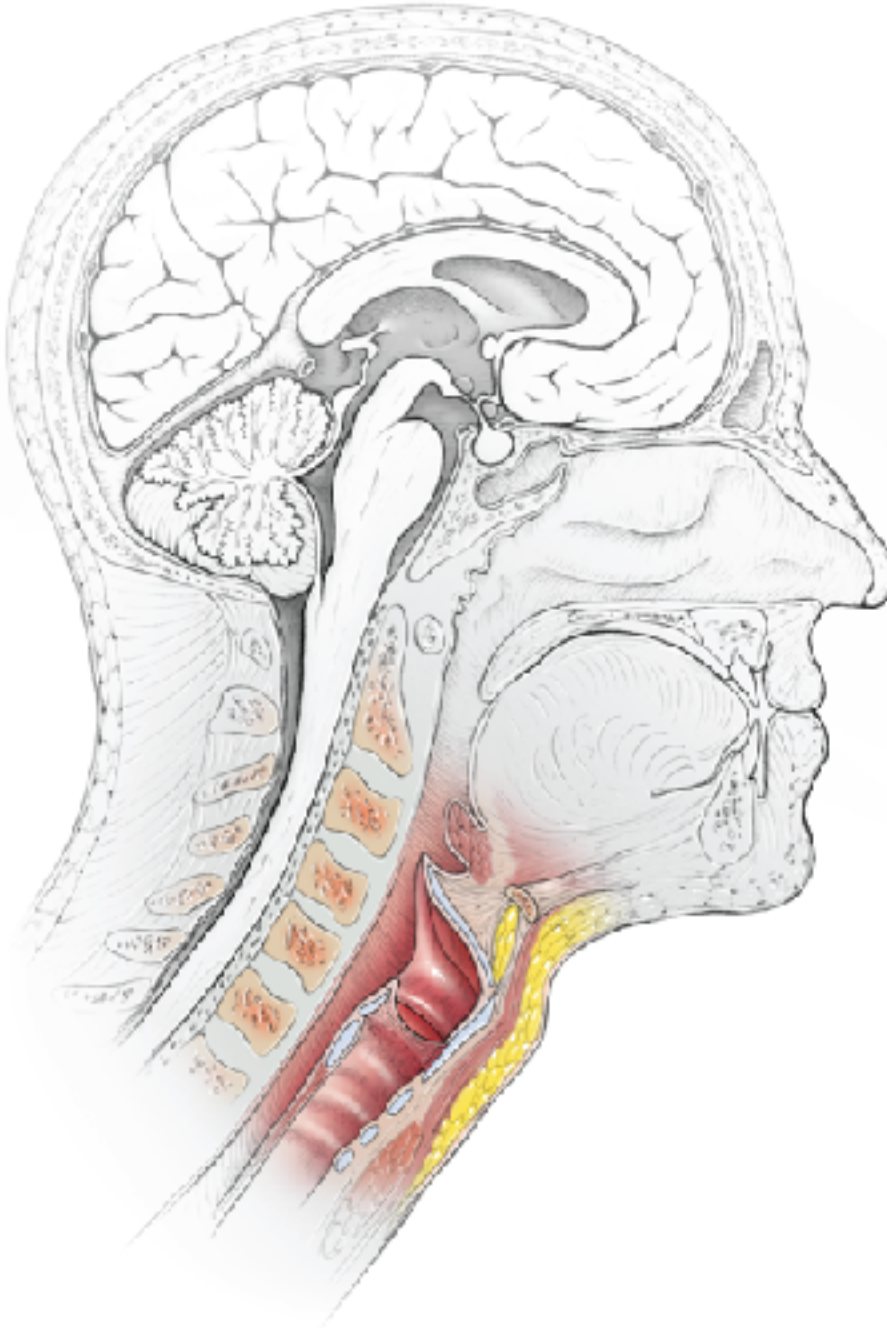
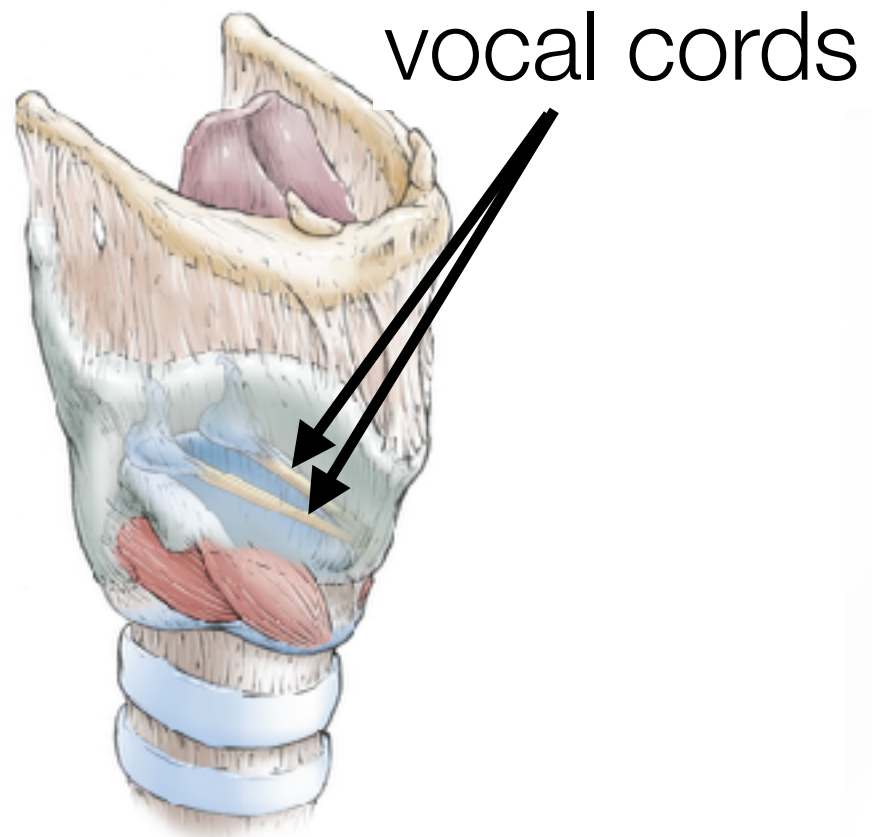
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 - Difference due to brain, not body (Fitch et al., 2016; Jurgens, 2002)

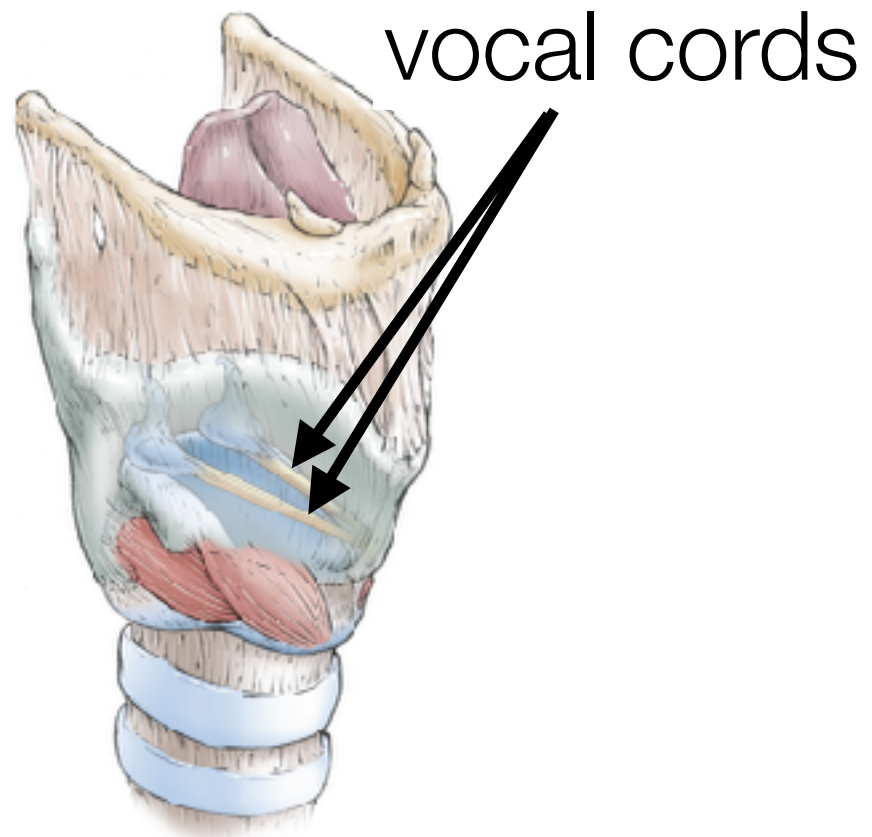
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- Humans have more **flexible control** than other primates
 - Difference due to brain, not body (Fitch et al., 2016; Jurgens, 2002)
 - Hypothesized to be a **key evolutionary step** toward speech (Brown et al., 2008; Pasinski, 2016; Hickok, 2016)

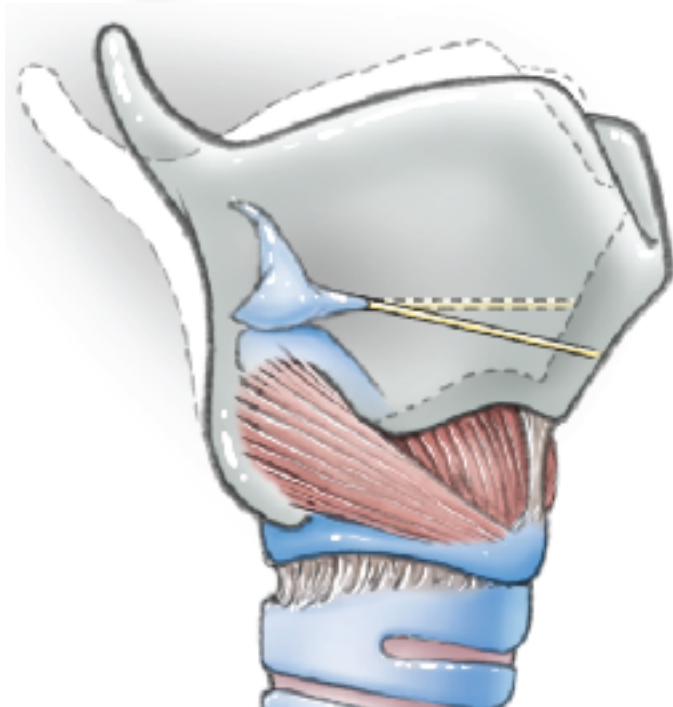
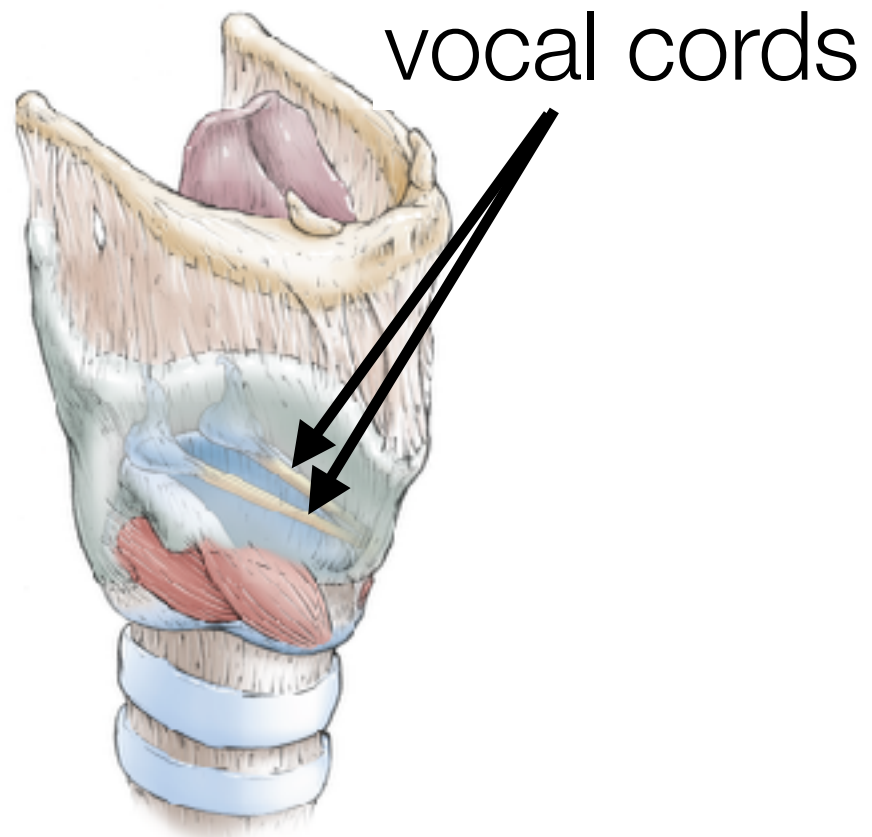
Pitch is controlled by the **larynx**



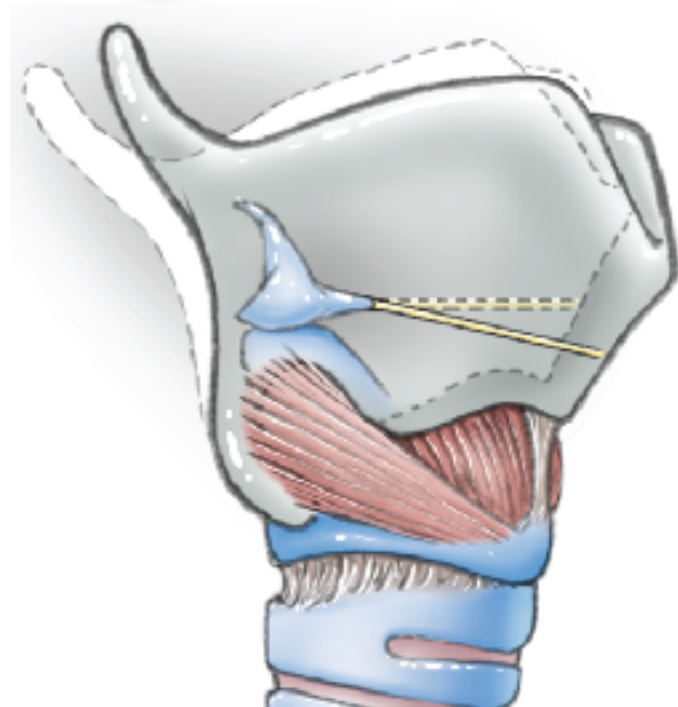
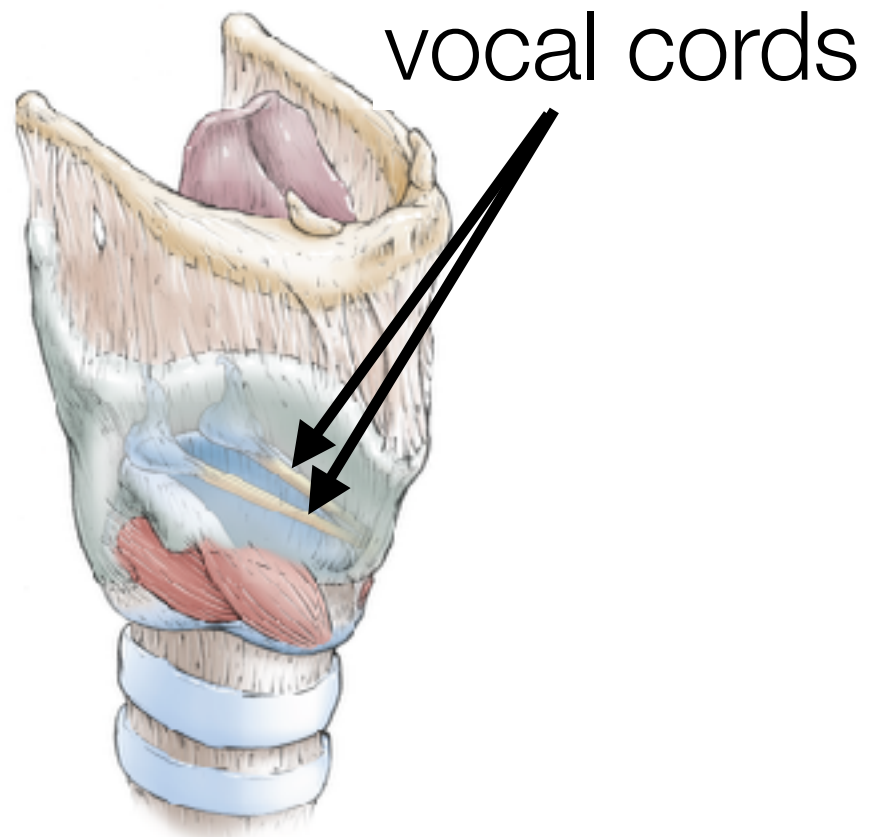
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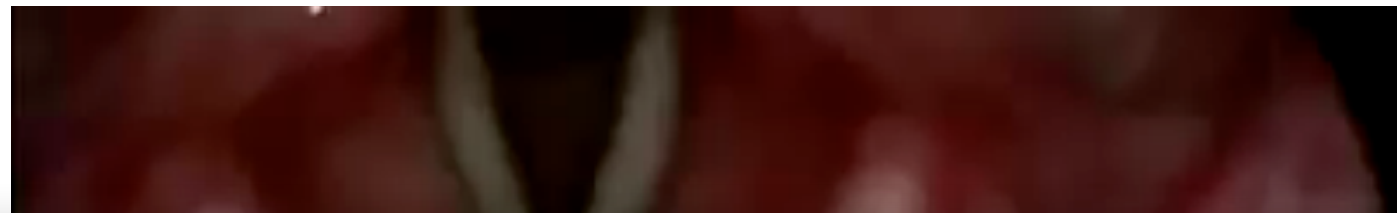
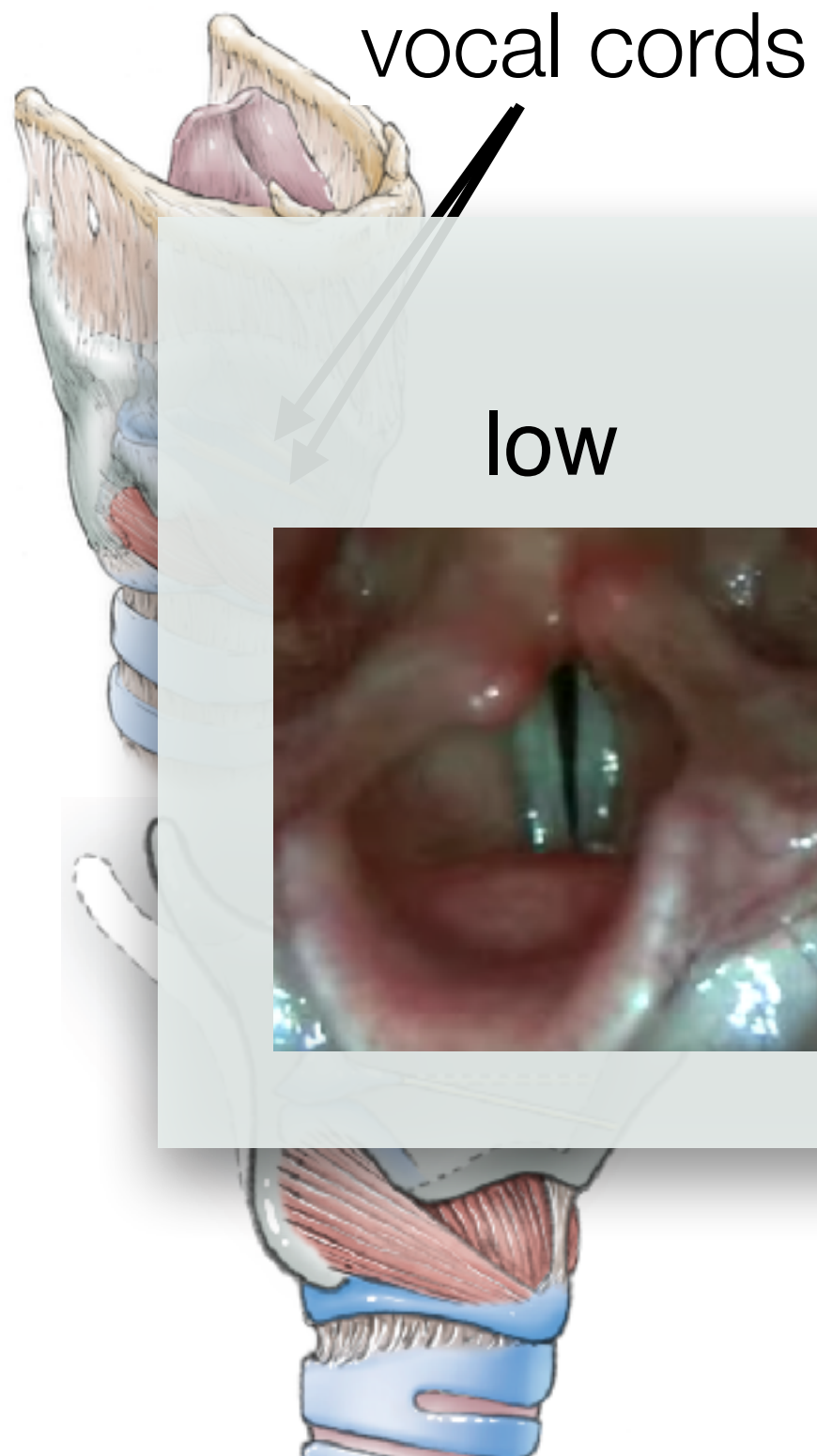
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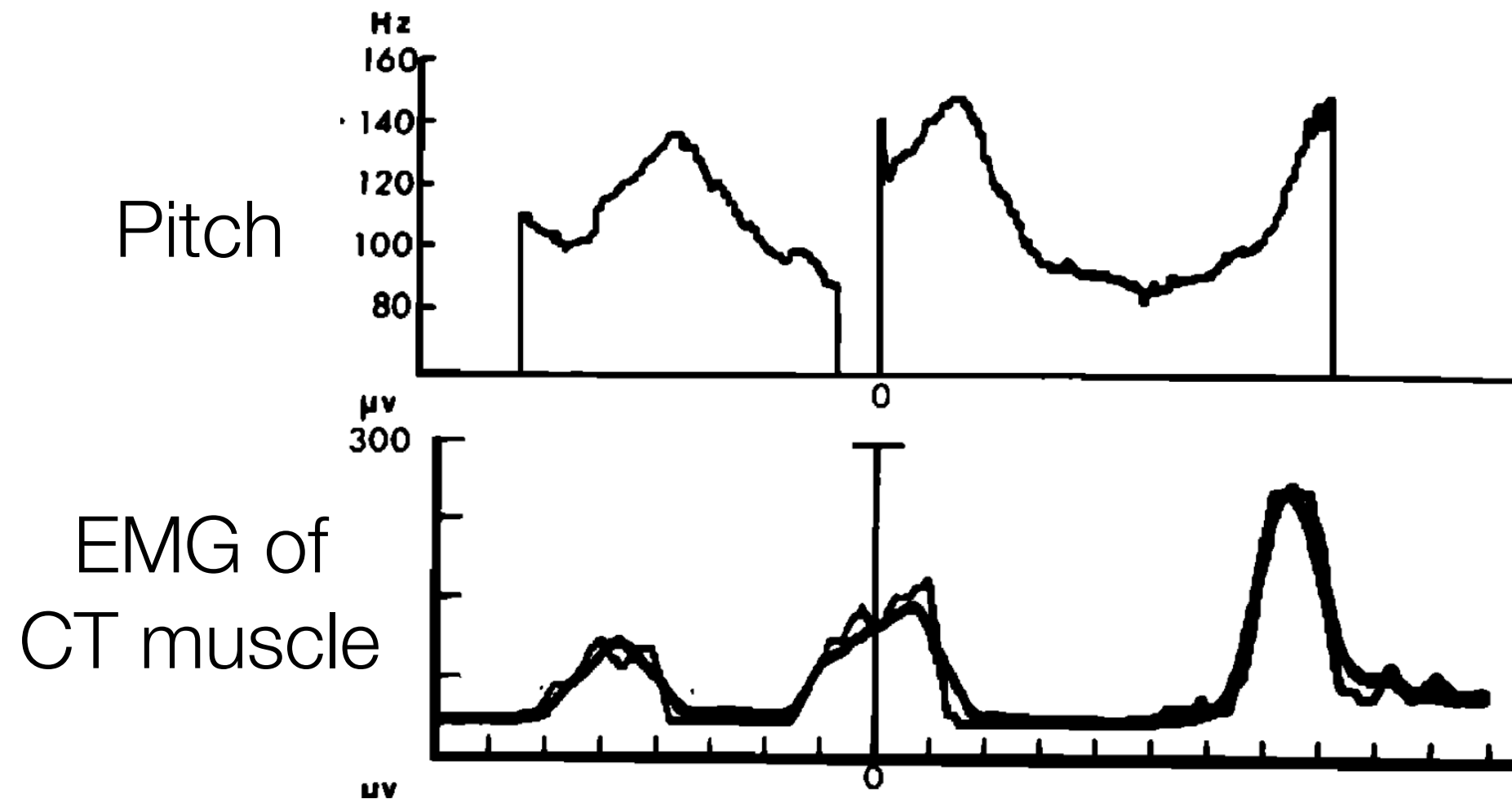
mid



high



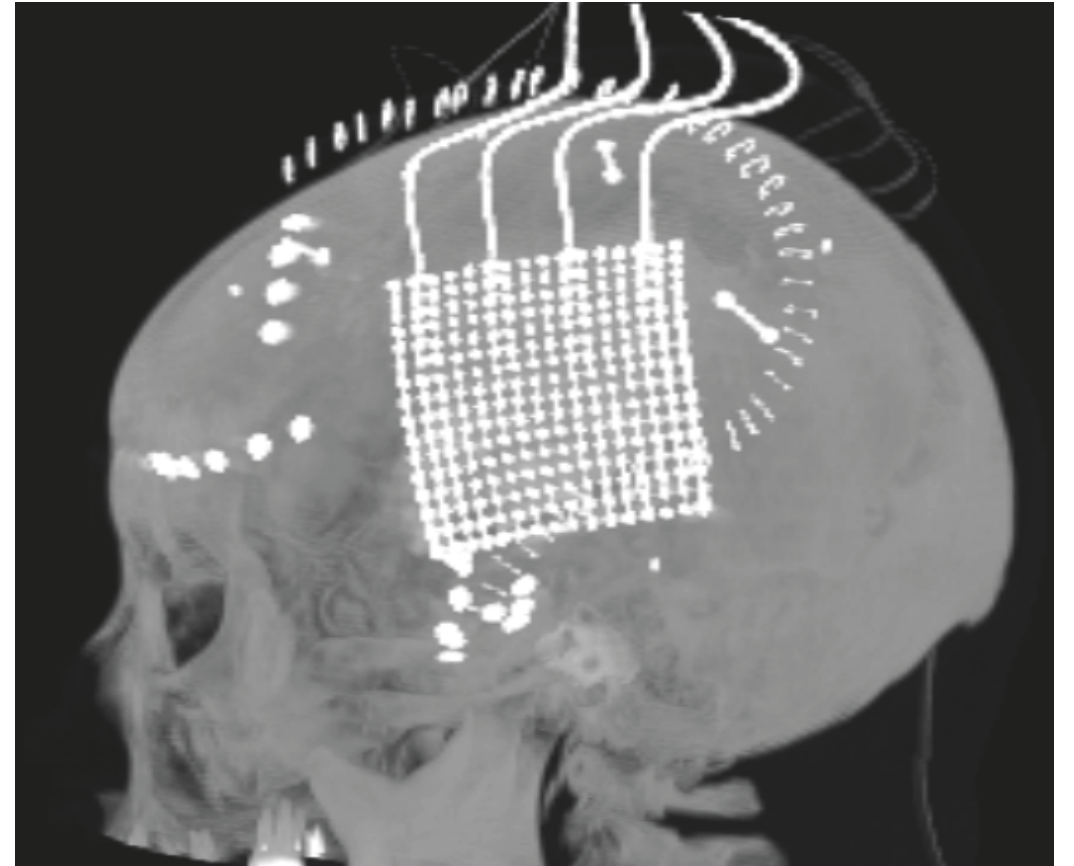
Muscular control of pitch



(Collier 1974)

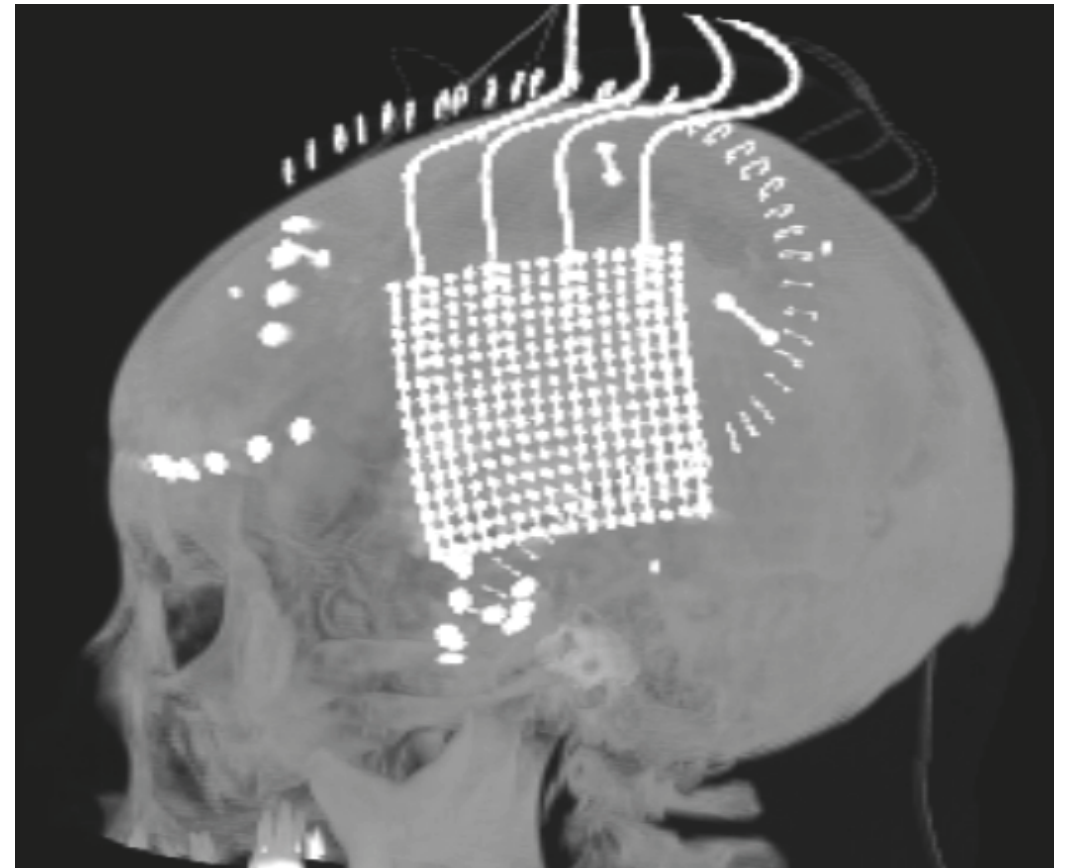
The cricothyroid (CT) muscle stretches the vocal folds and increases vocal pitch

Electrocorticography (ECoG)



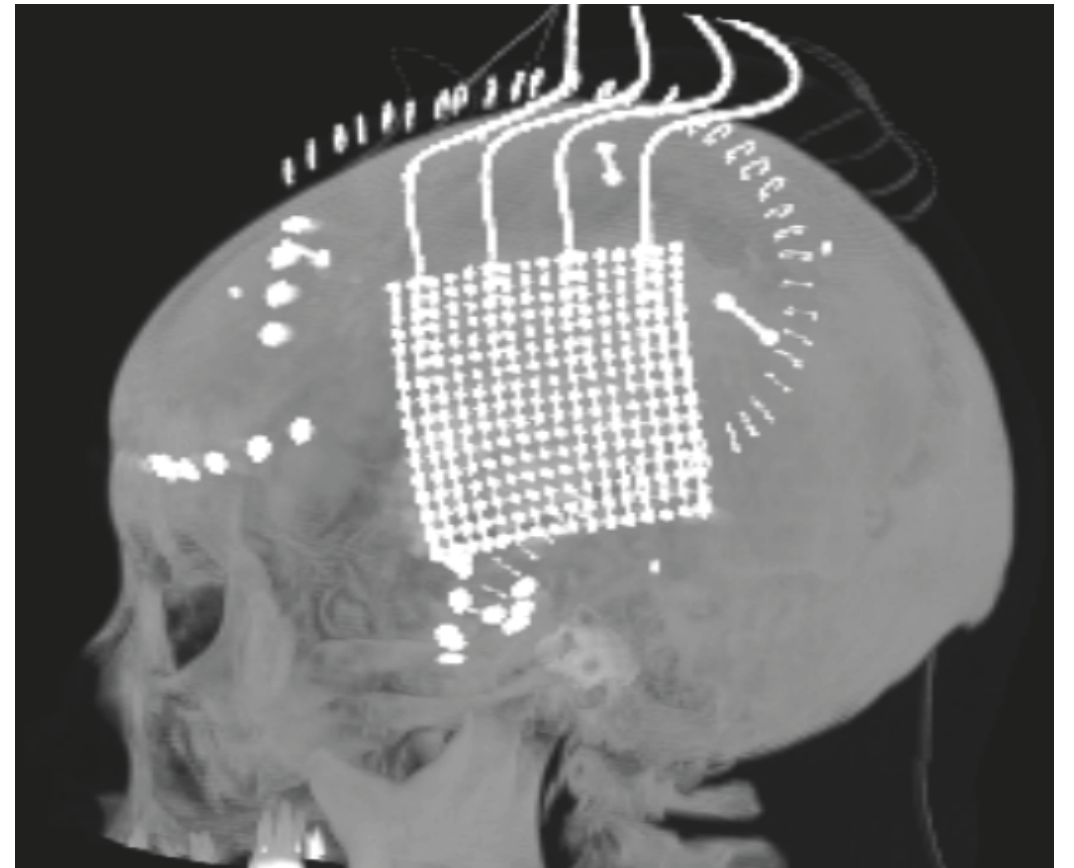
Electrocorticography (ECoG)

- Surgical treatment for epilepsy



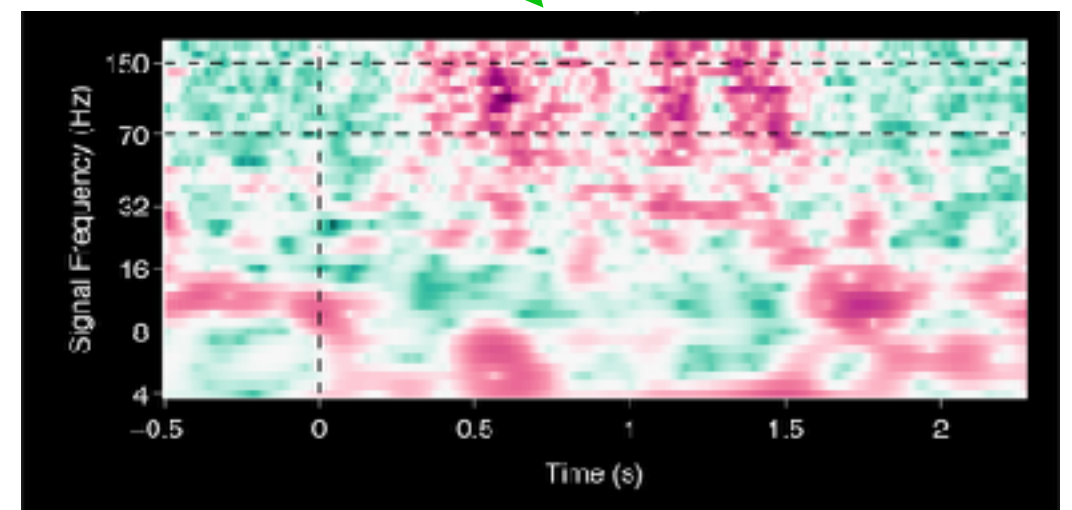
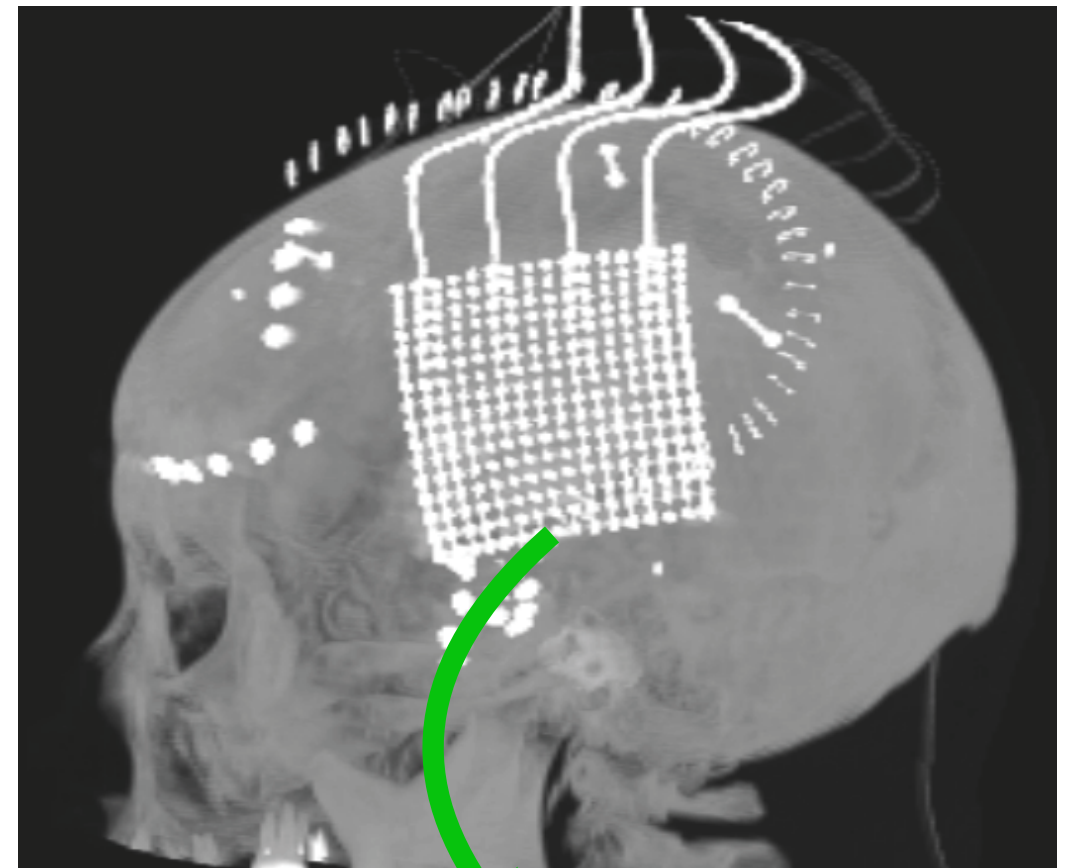
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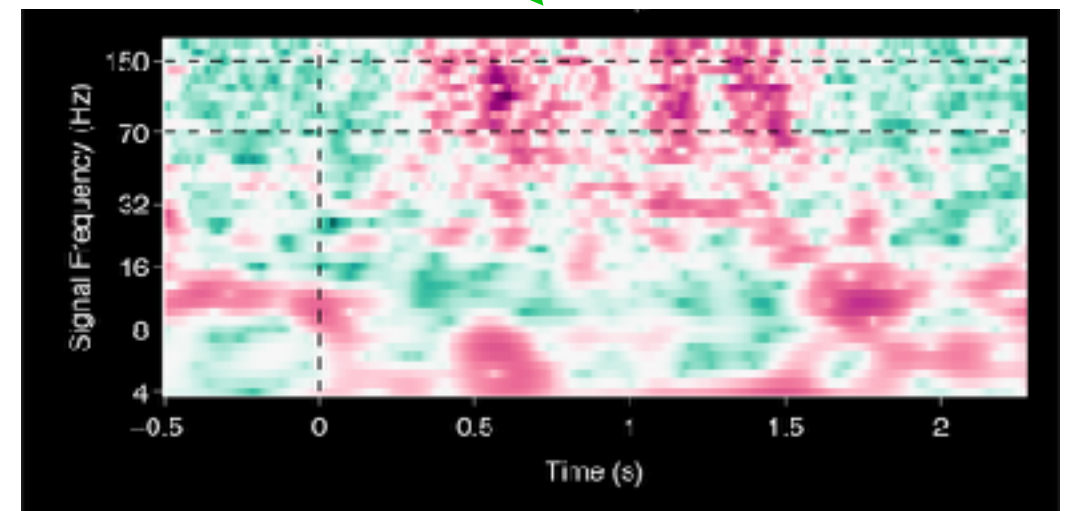
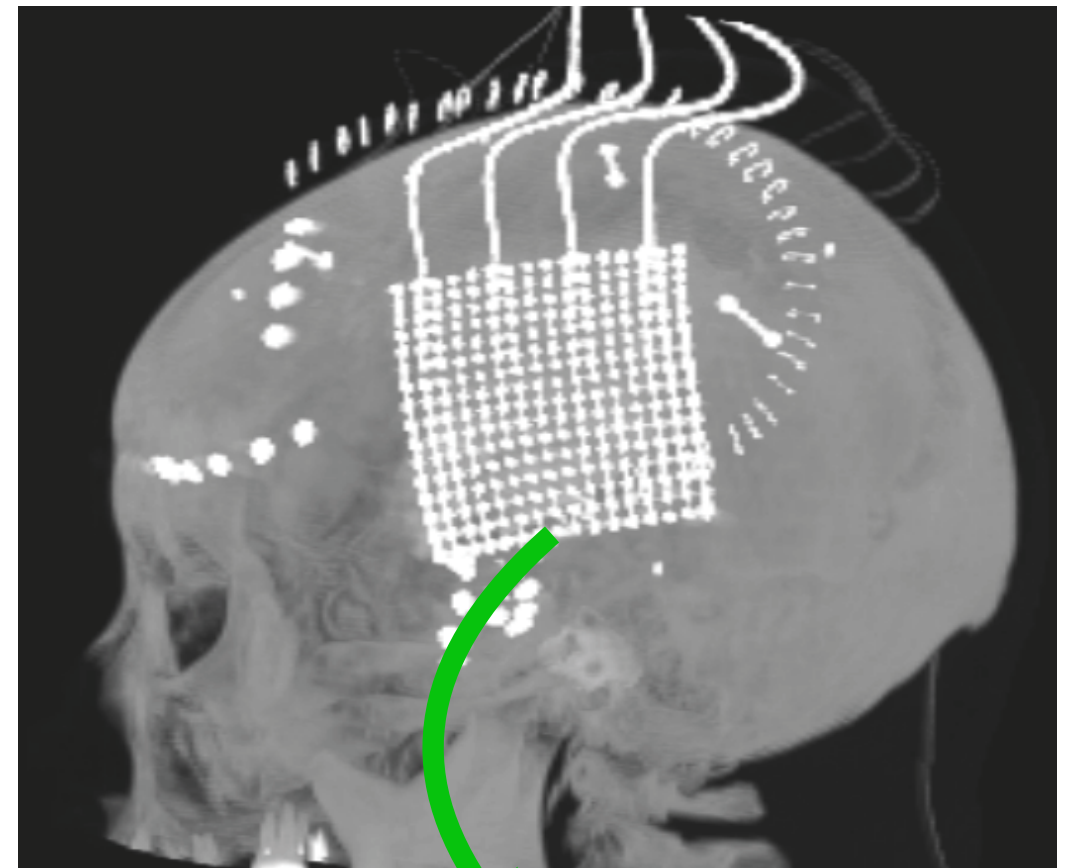
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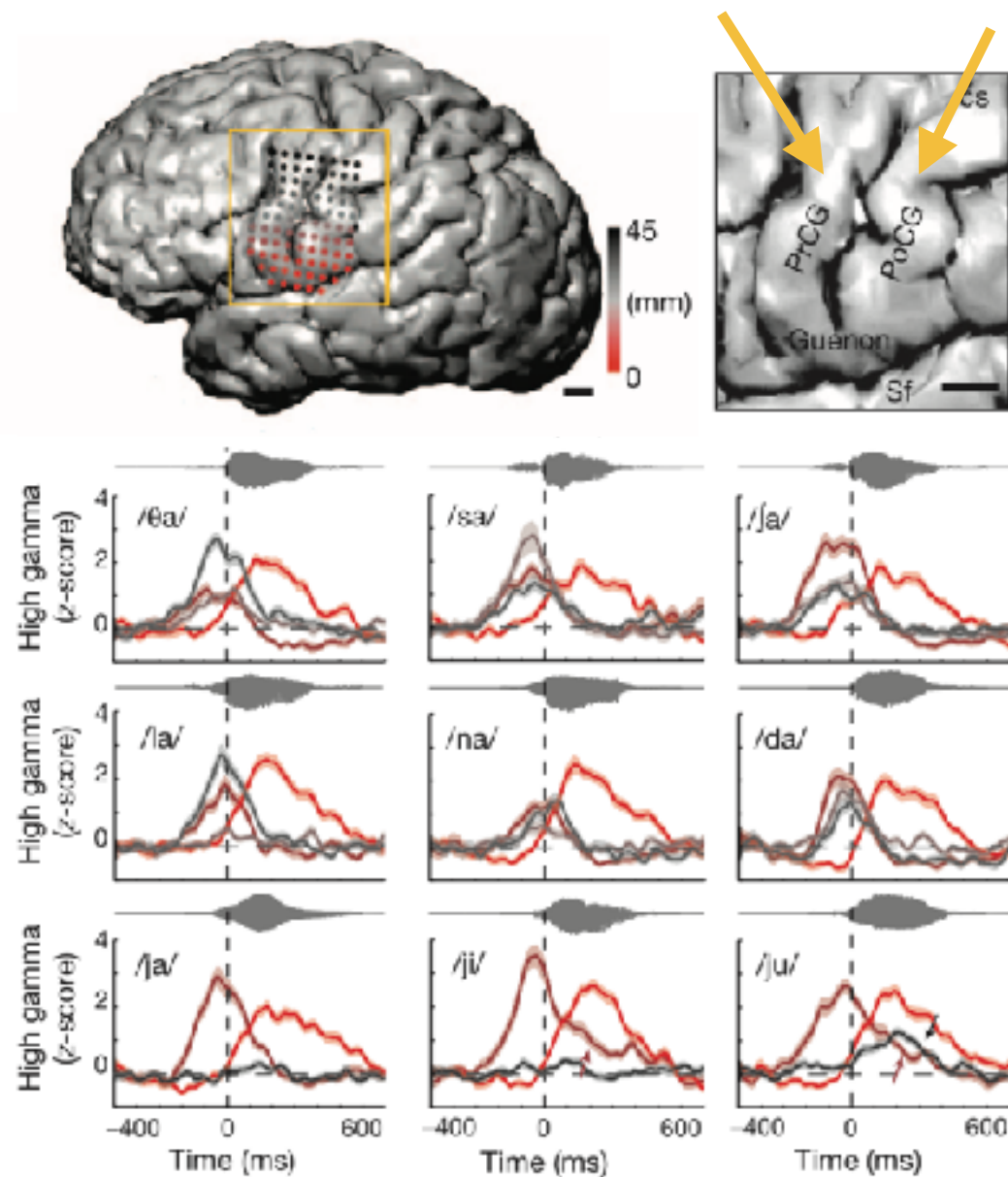
Electrocorticography (ECoG)

- Surgical treatment for epilepsy
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- Neural activity: amplitude in high gamma (70-150 Hz)
- Very good temporal resolution



Previous work: ECoG activity related to **articulators**

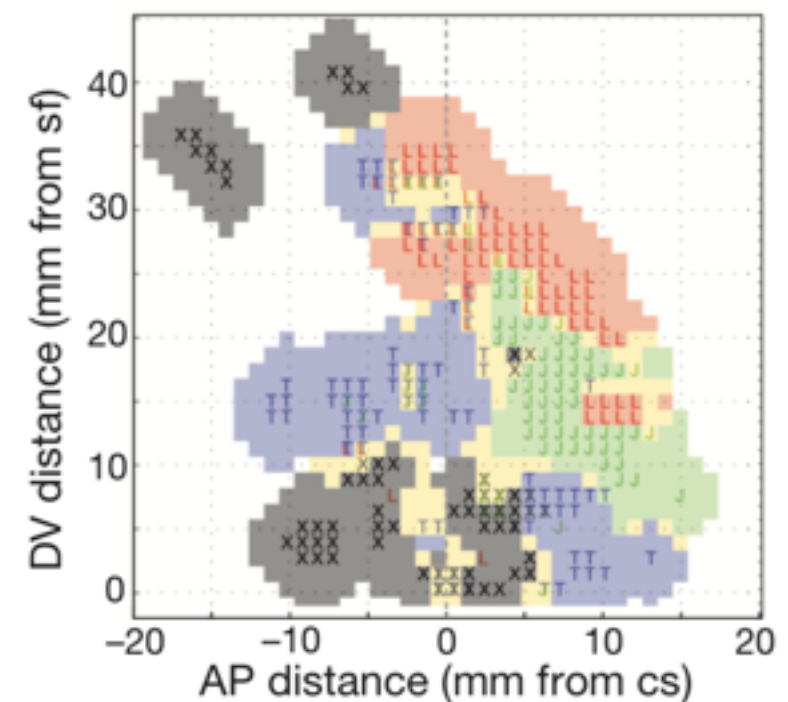
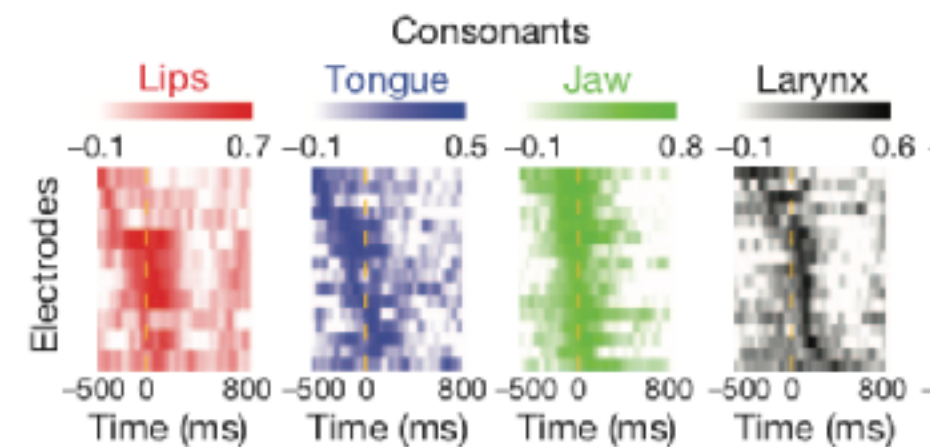
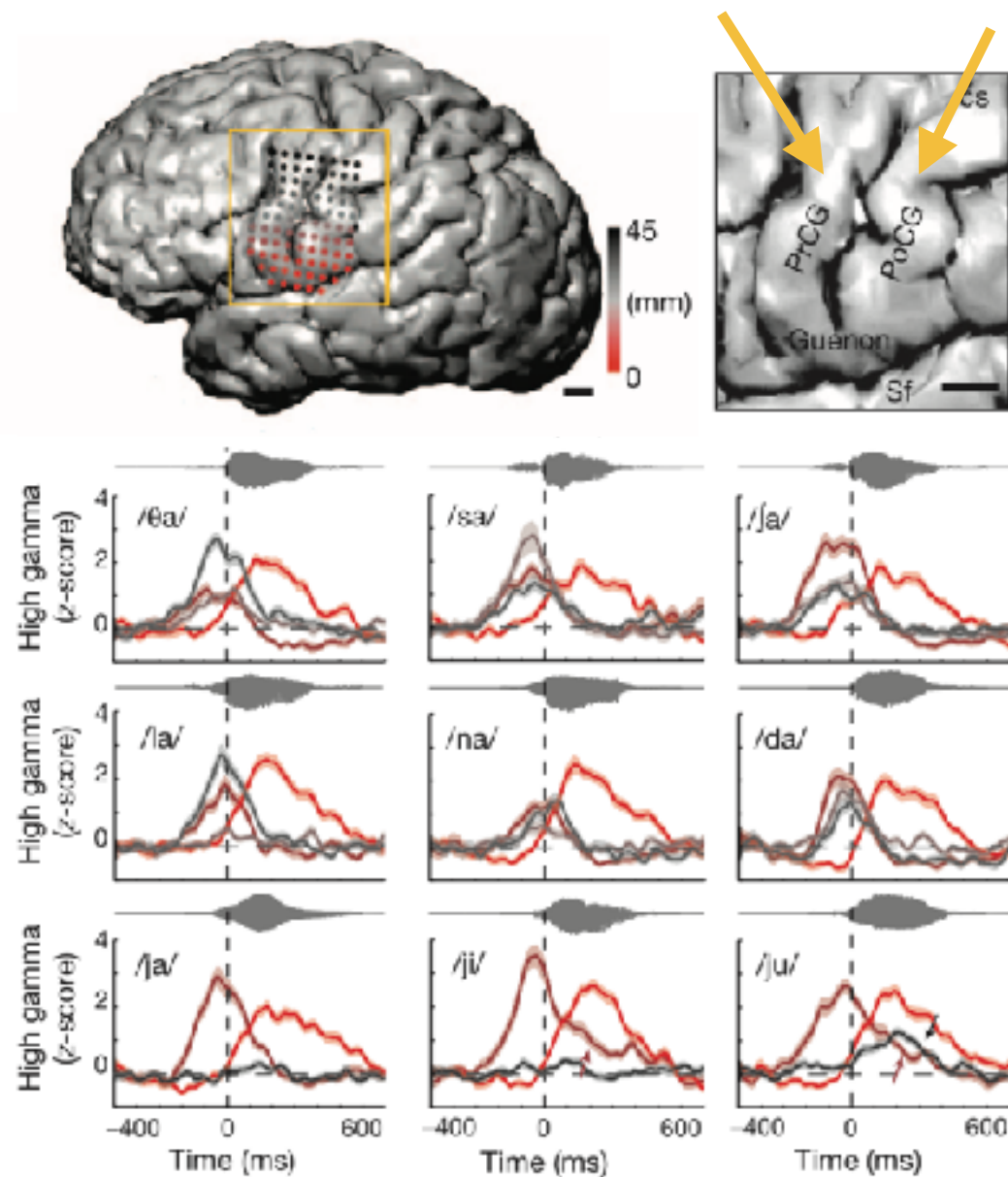
vSMC = M1 + S1



(Bouchard et al., *Nature*, 2015)

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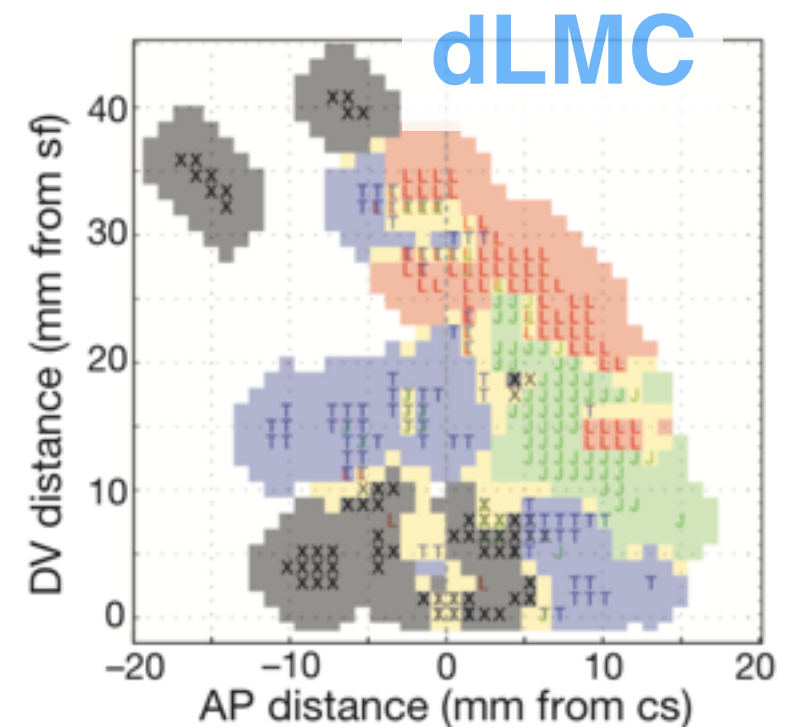
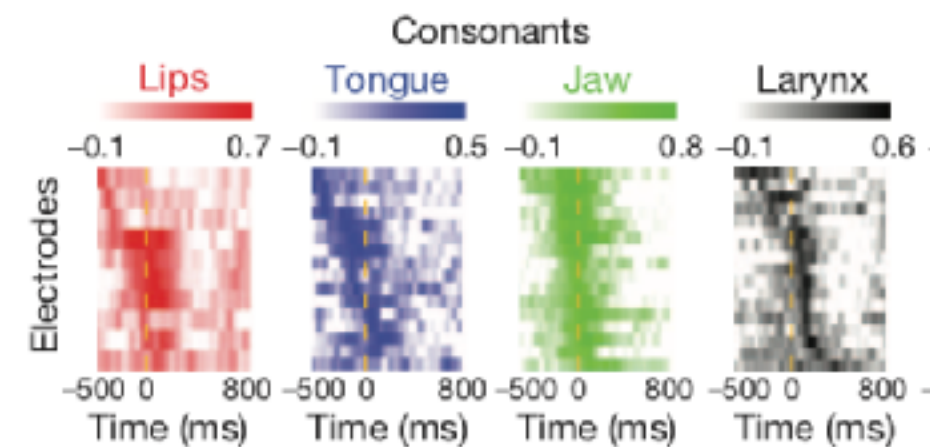
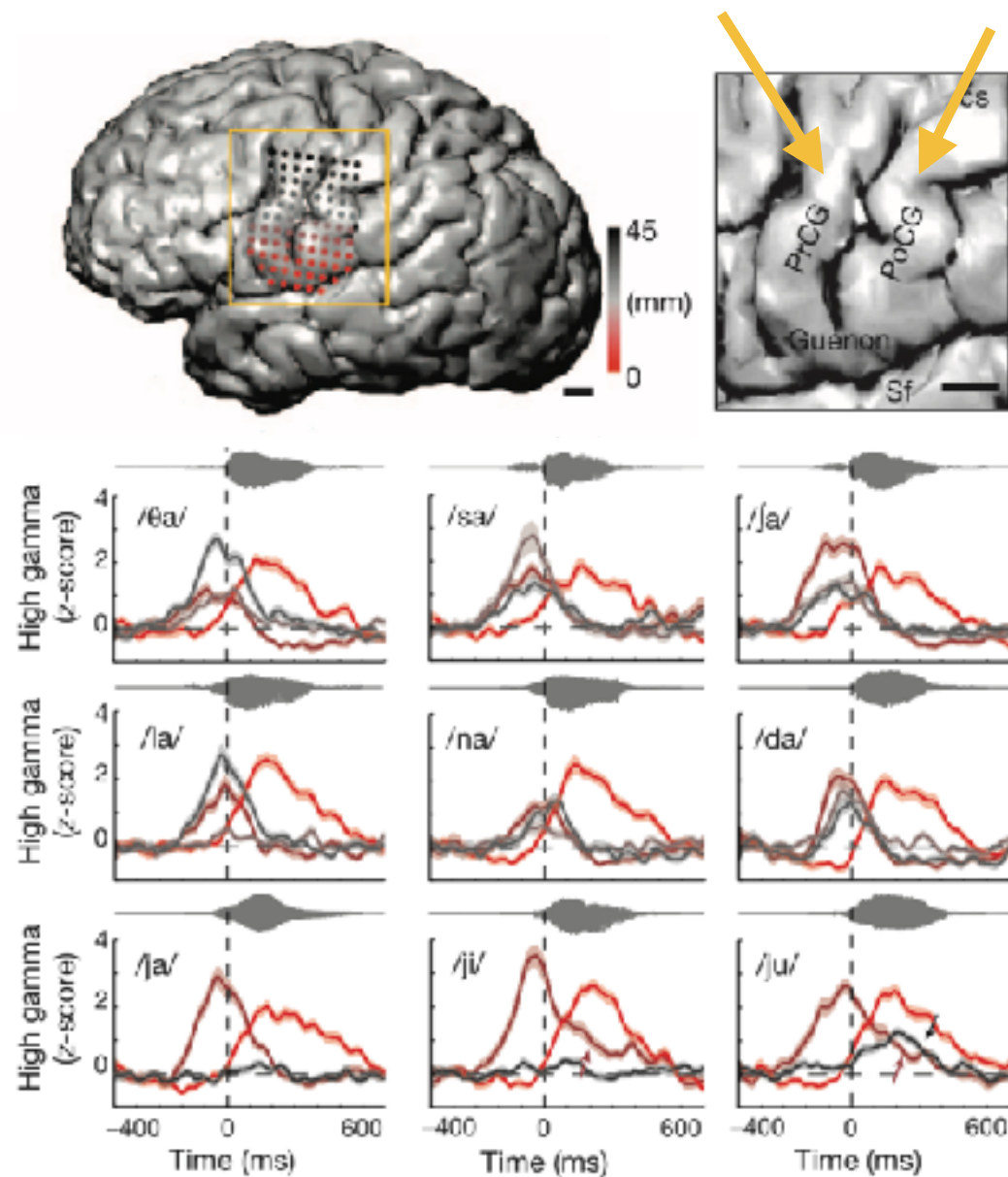
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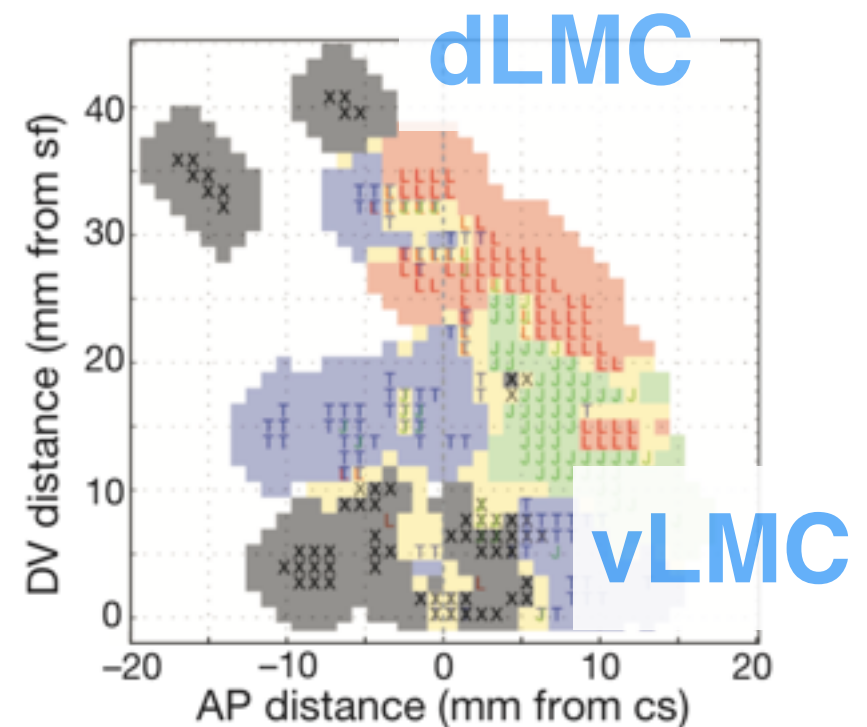
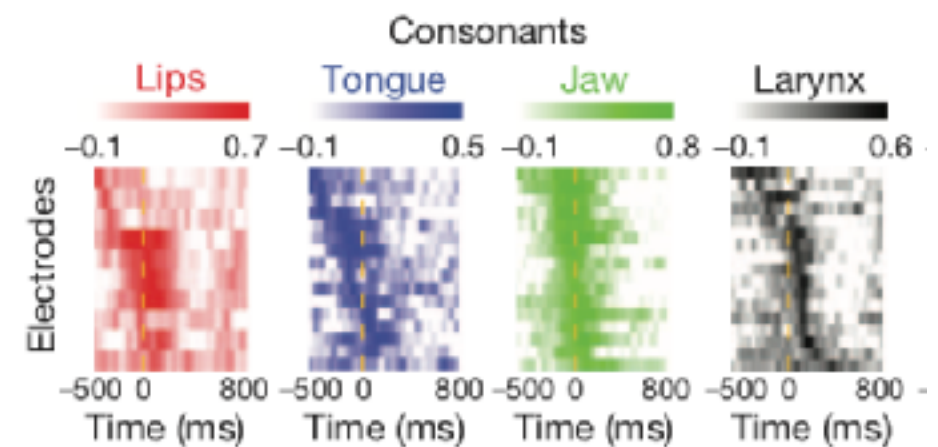
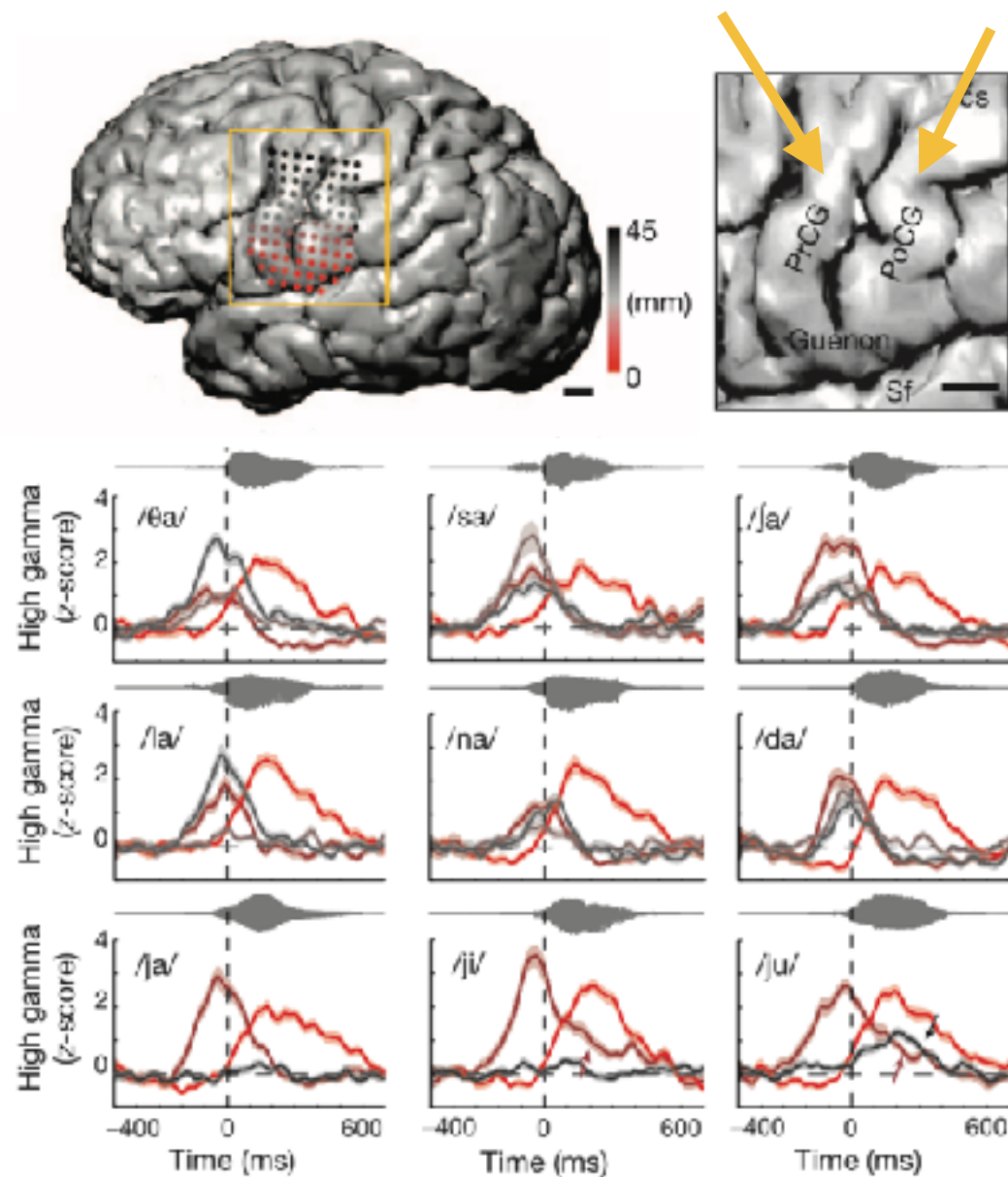
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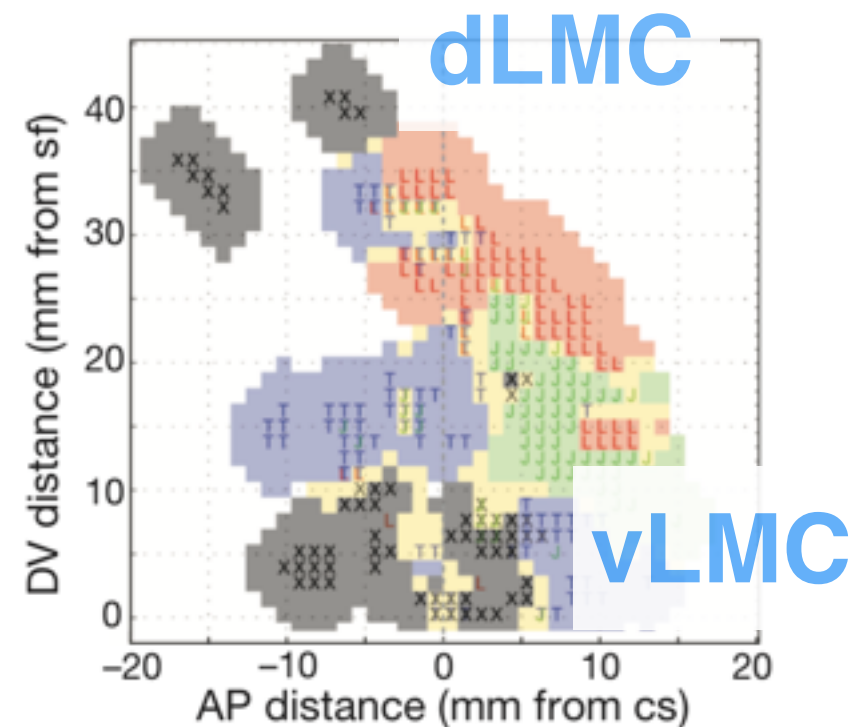
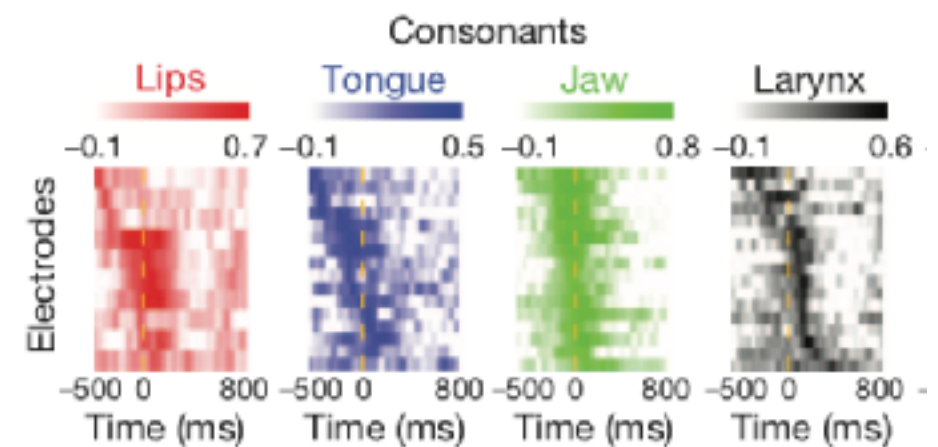
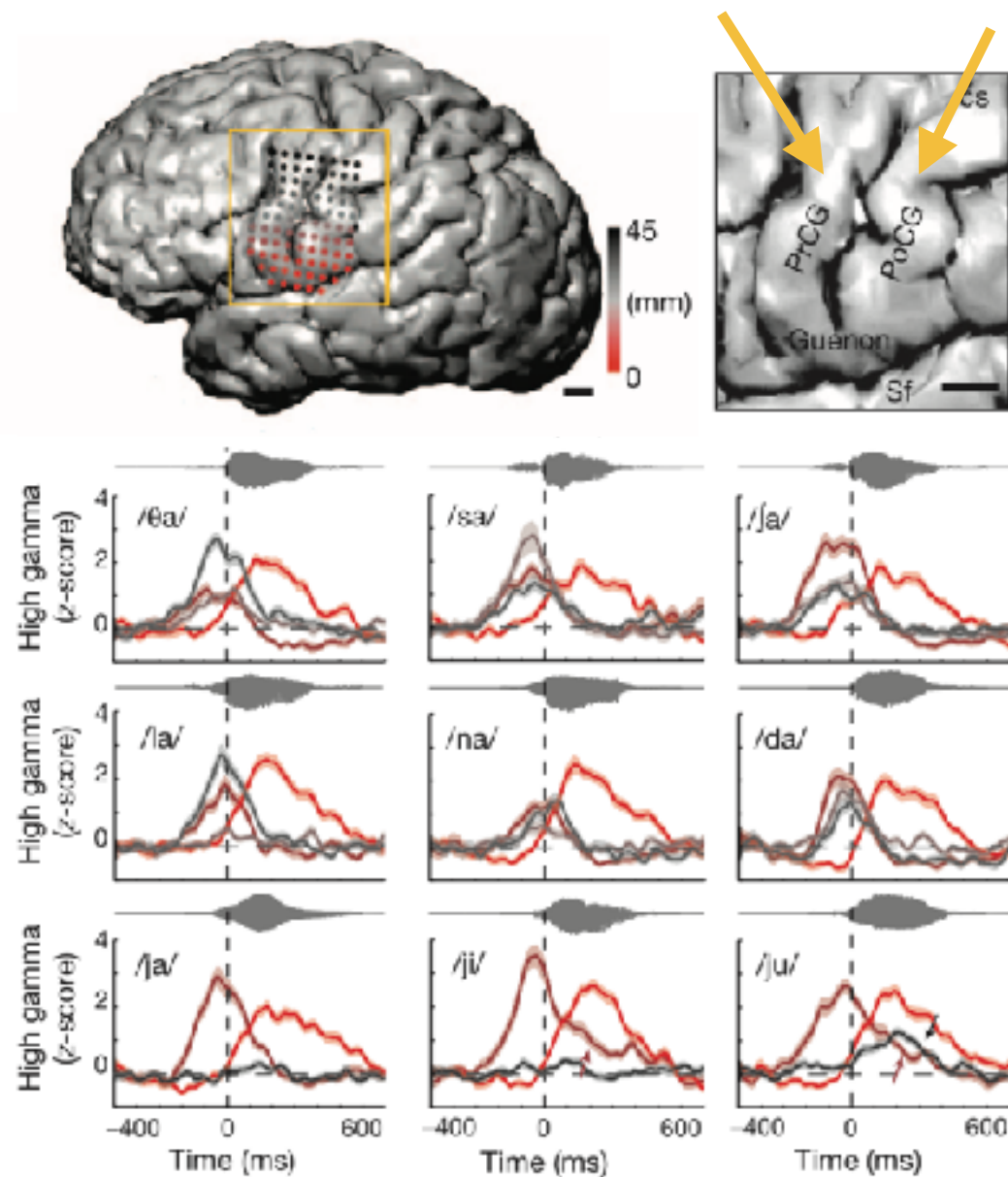
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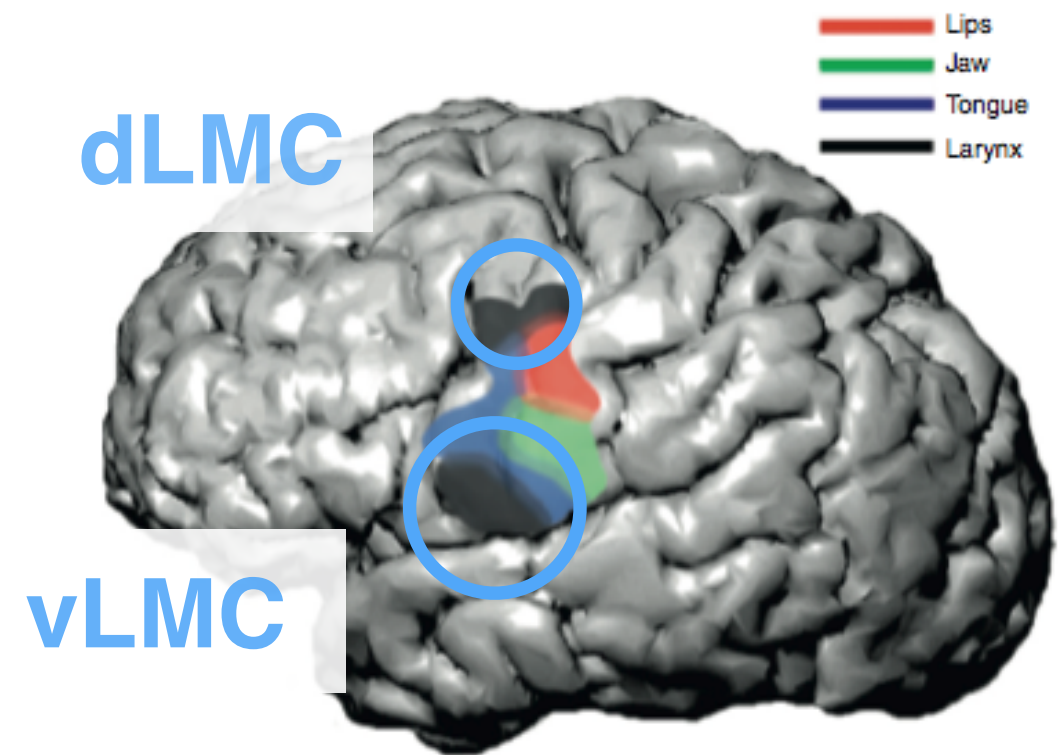
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Larynx is voicing only

(Bouchard et al., *Nature*, 2015)

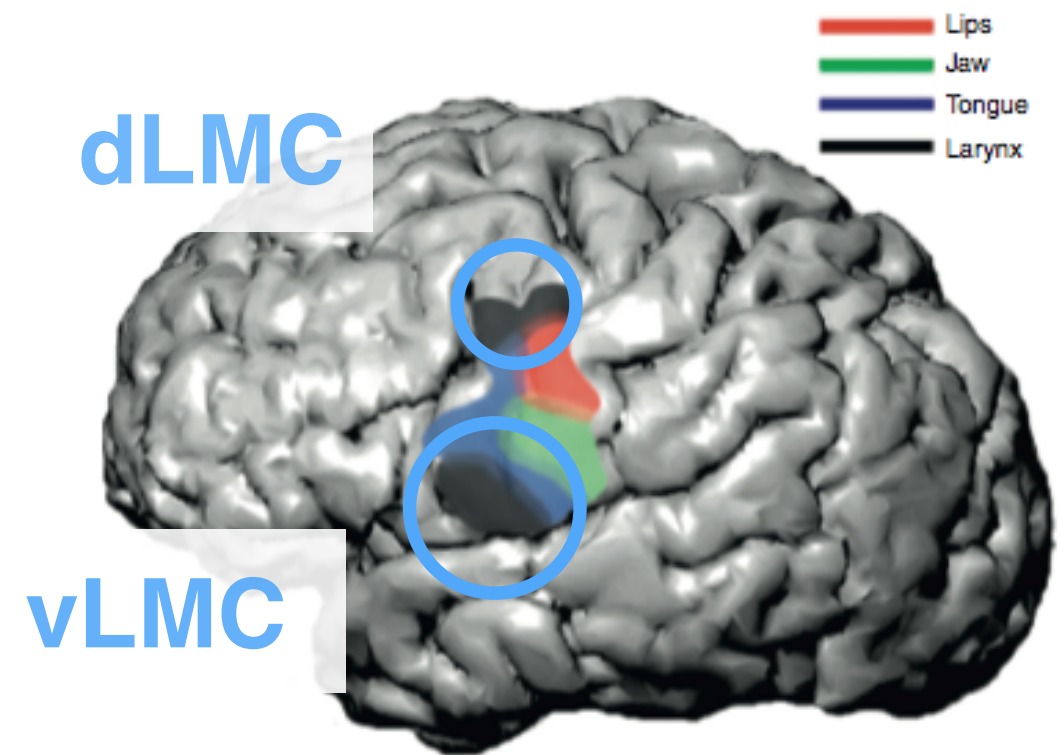
Cortical representation of larynx



Conant 2014 review

Cortical representation of larynx

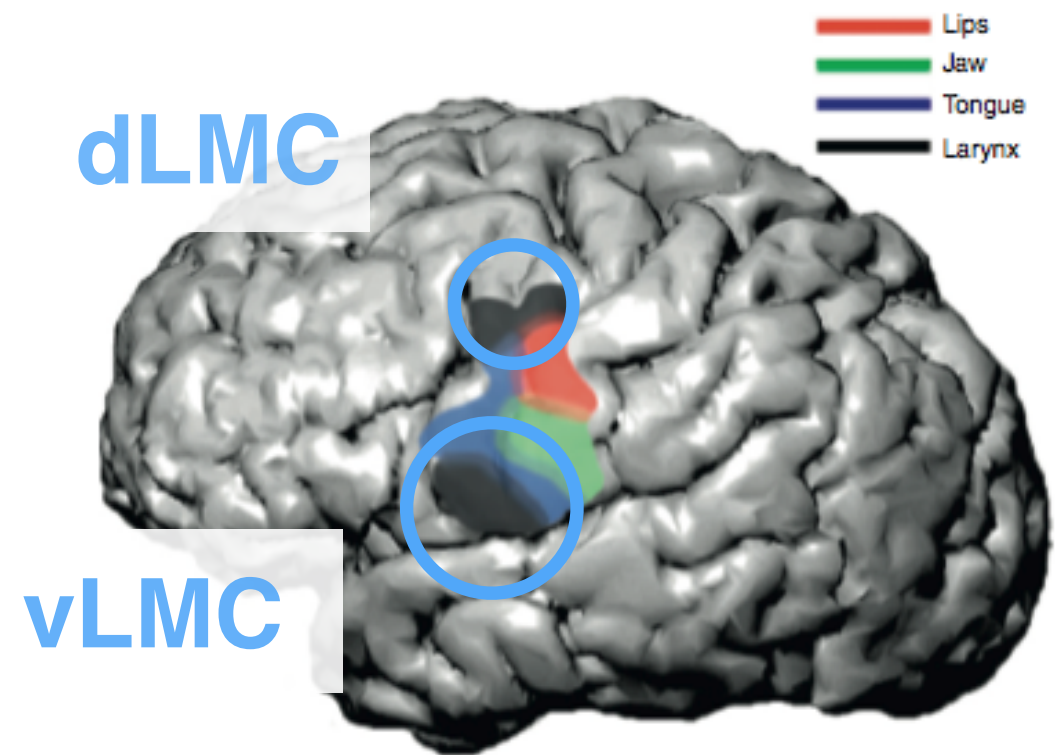
- dLMC and vLMC active in voicing



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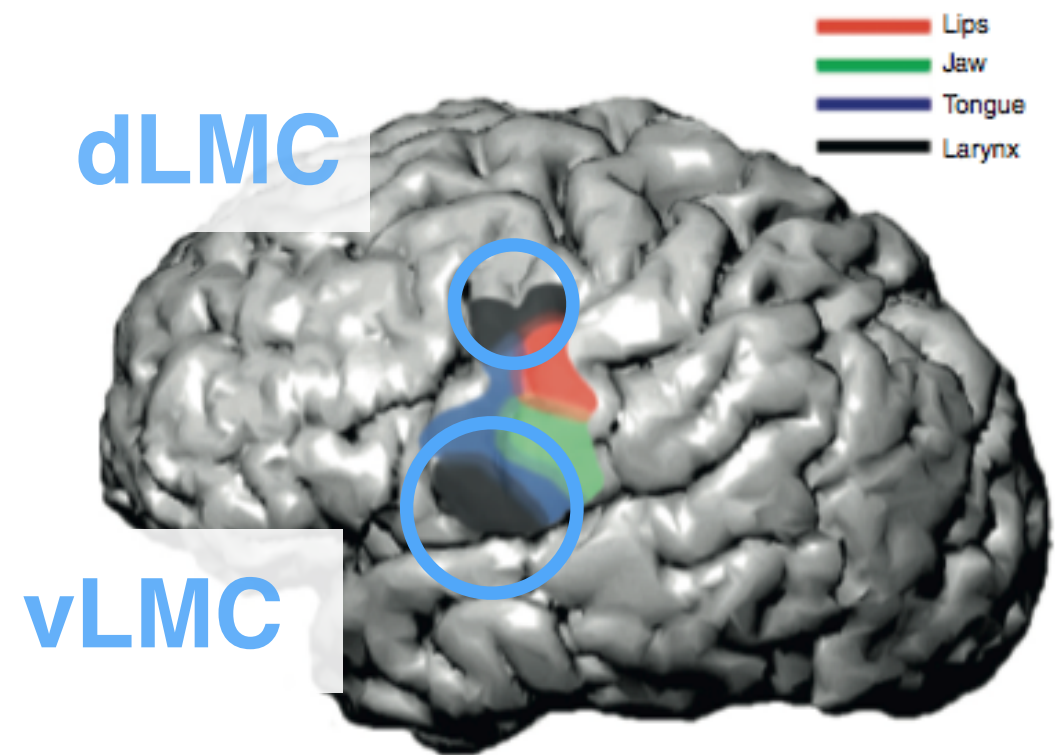
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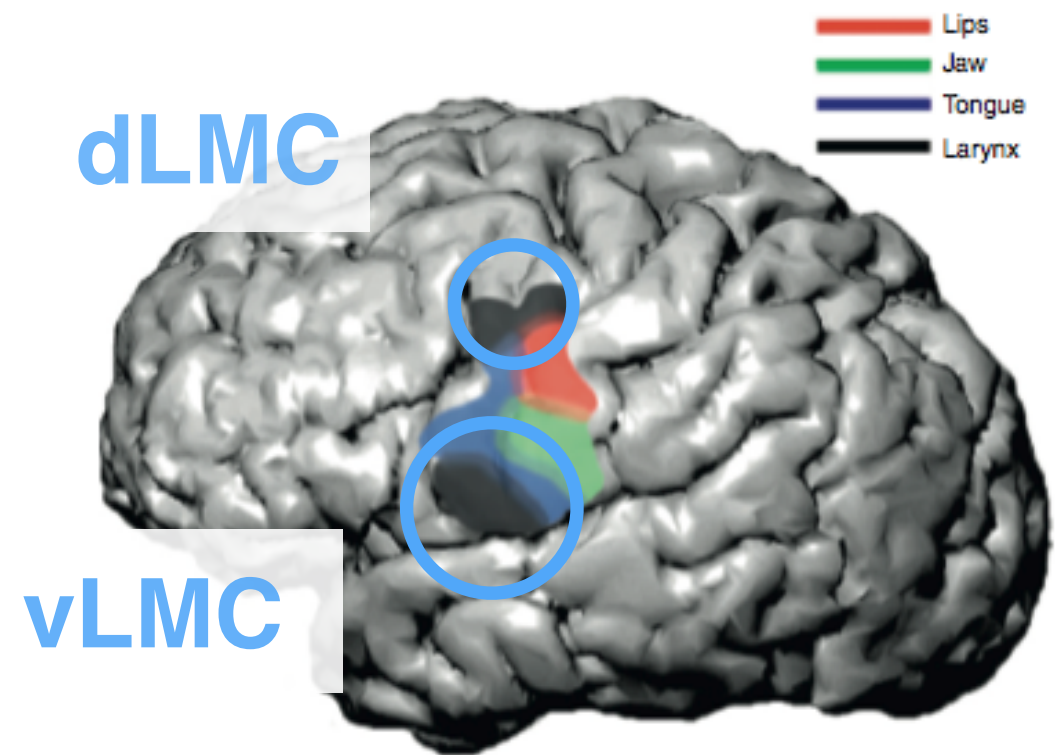
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Conant 2014 review

Cortical representation of larynx

- dLMC and vLMC active in voicing
- vLMC found in non-human primates but dLMC unique to humans among primates
- Tuning for pitch has not yet been identified
- We hypothesize that there is an explicit encoding of pitch in dLMC



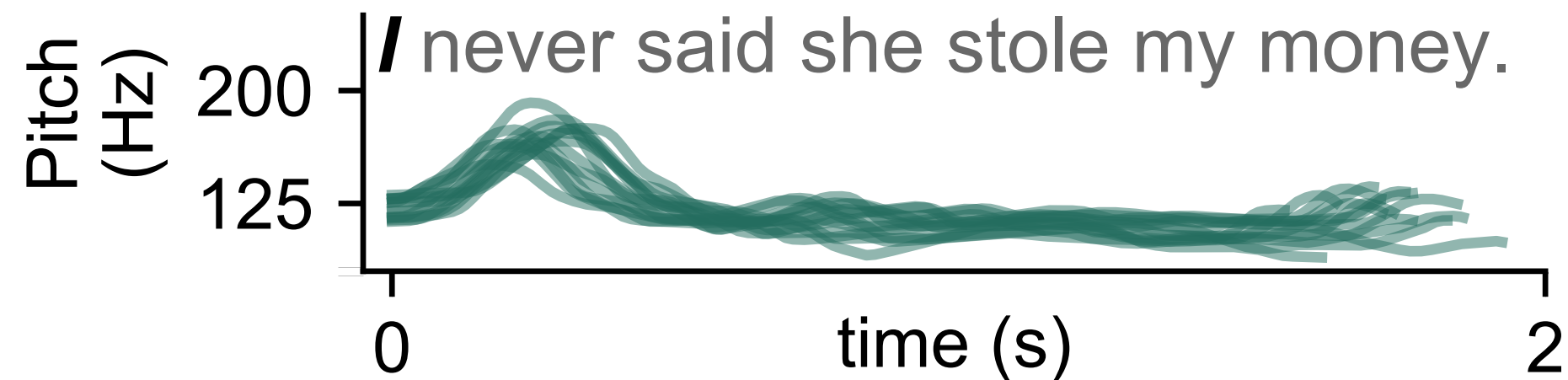
Conant 2014 review

Contrastive emphasis task: vocal pitch encoding

I never said she stole my money.

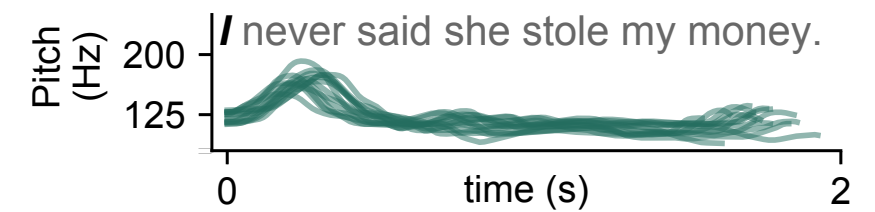
(Cell, *in press*)

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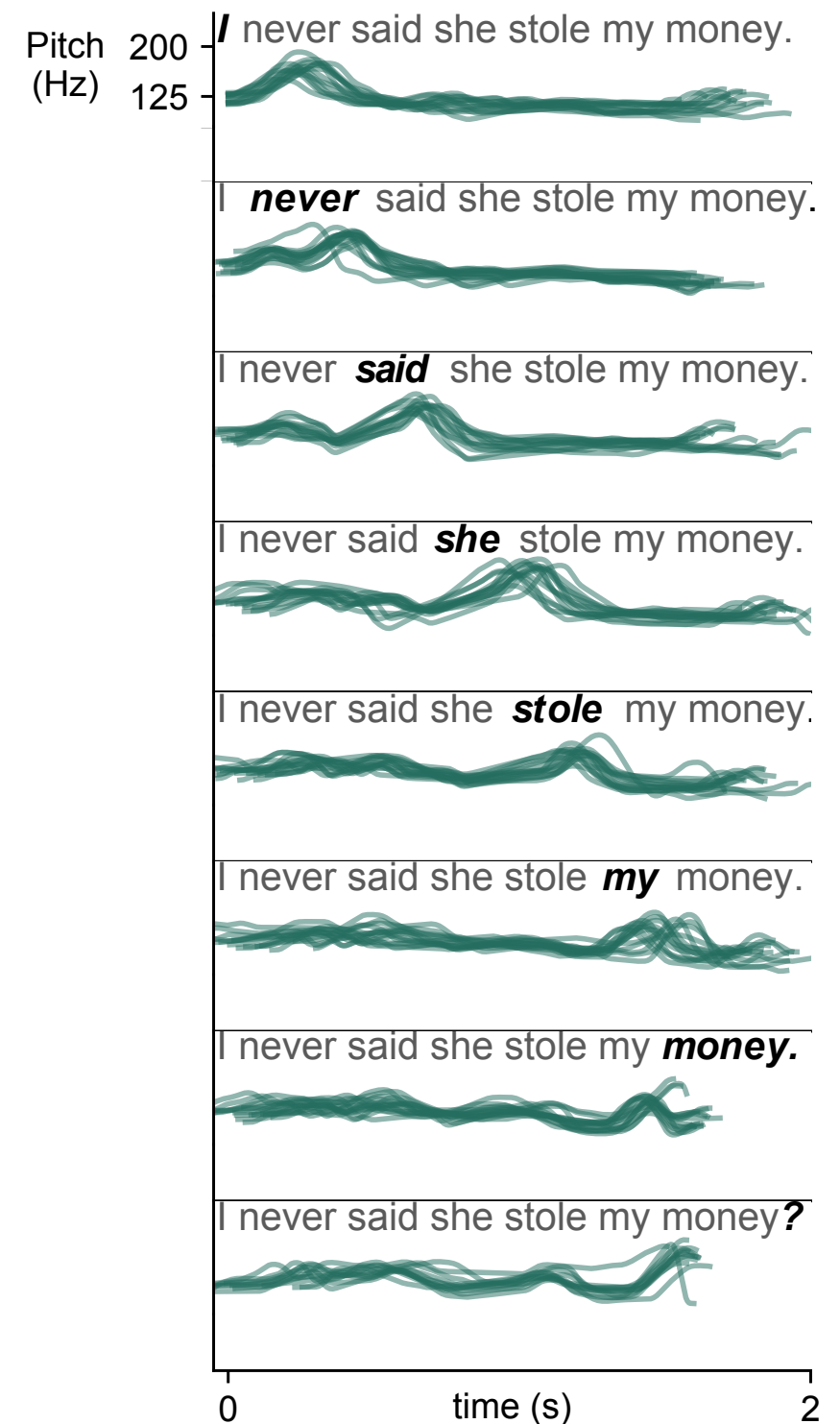
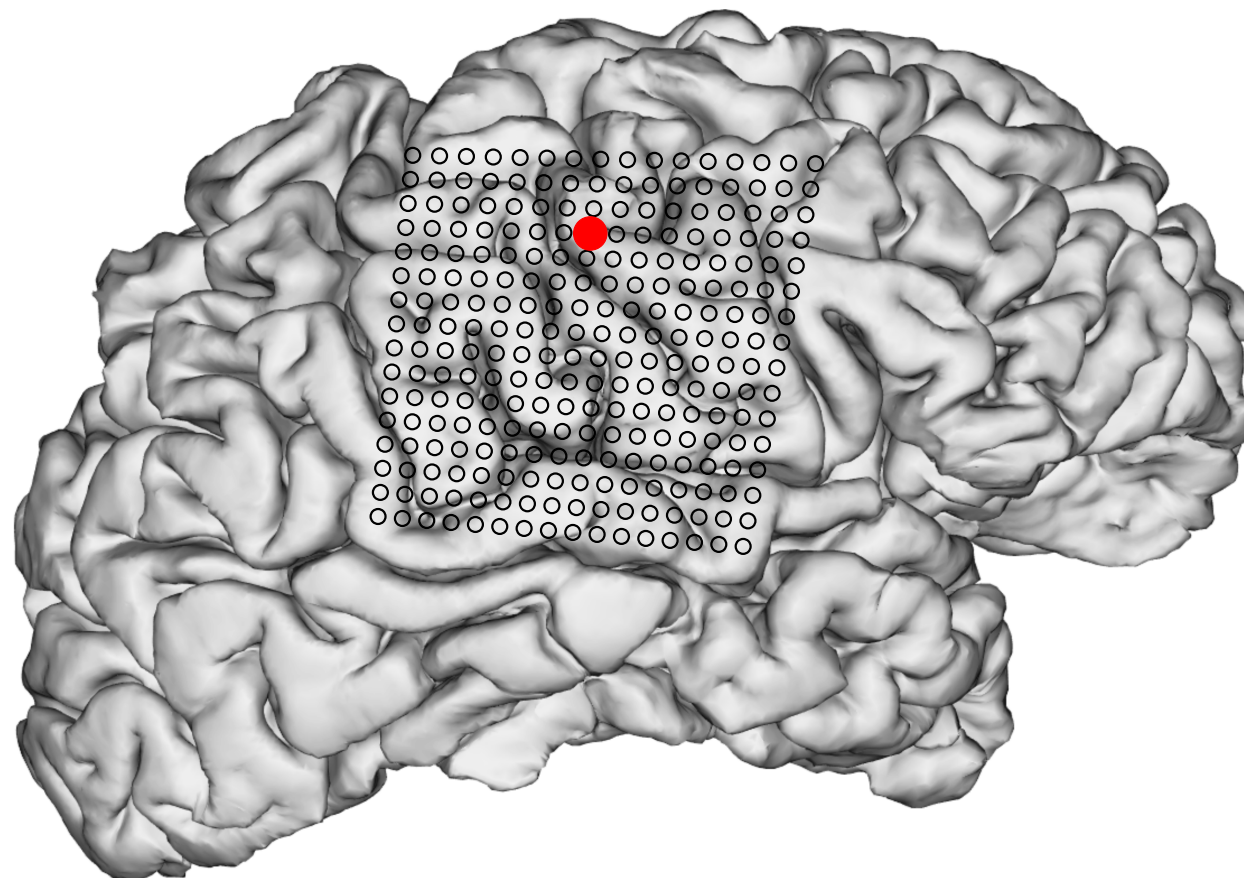
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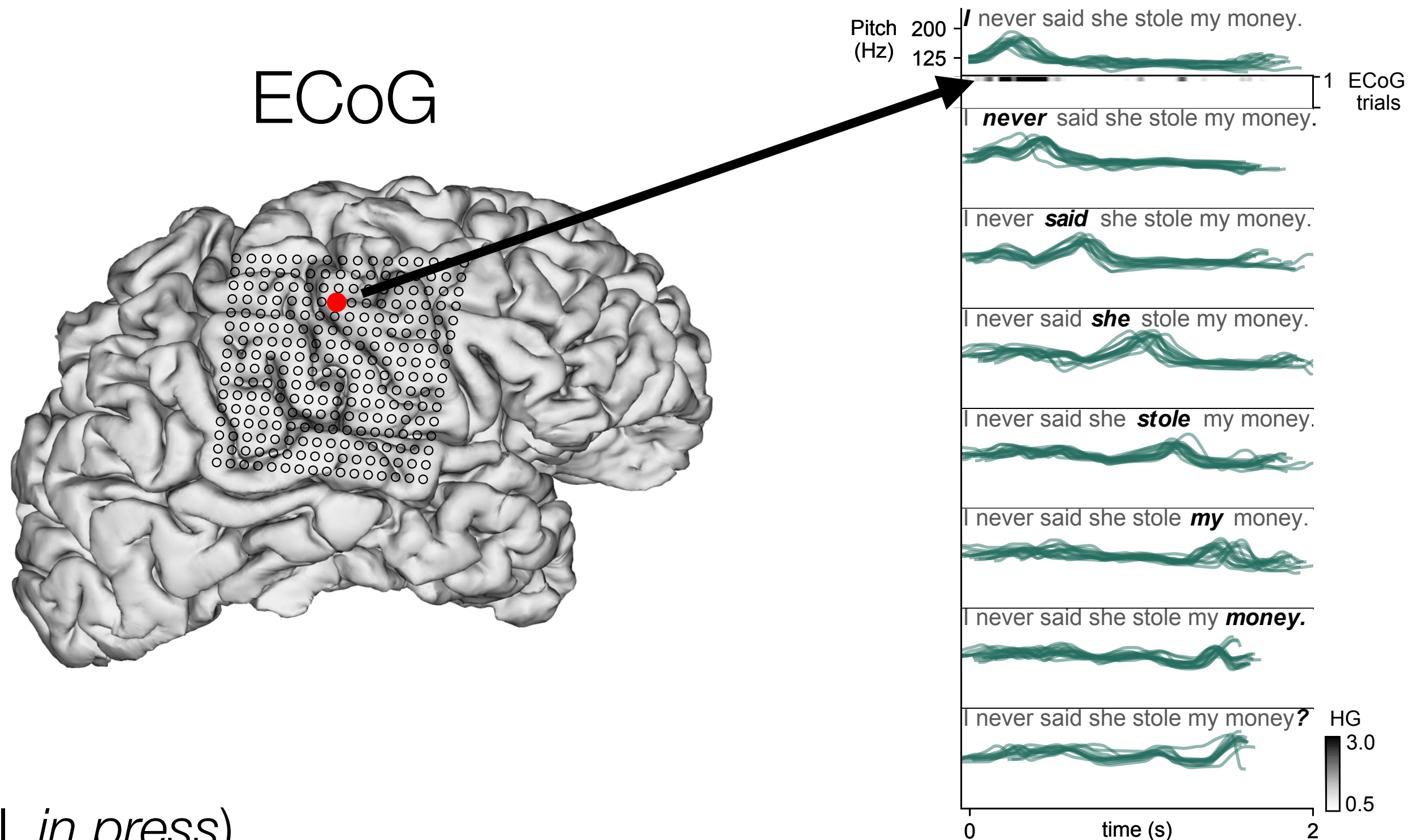
Contrastive emphasis task: vocal pitch encoding

ECoG



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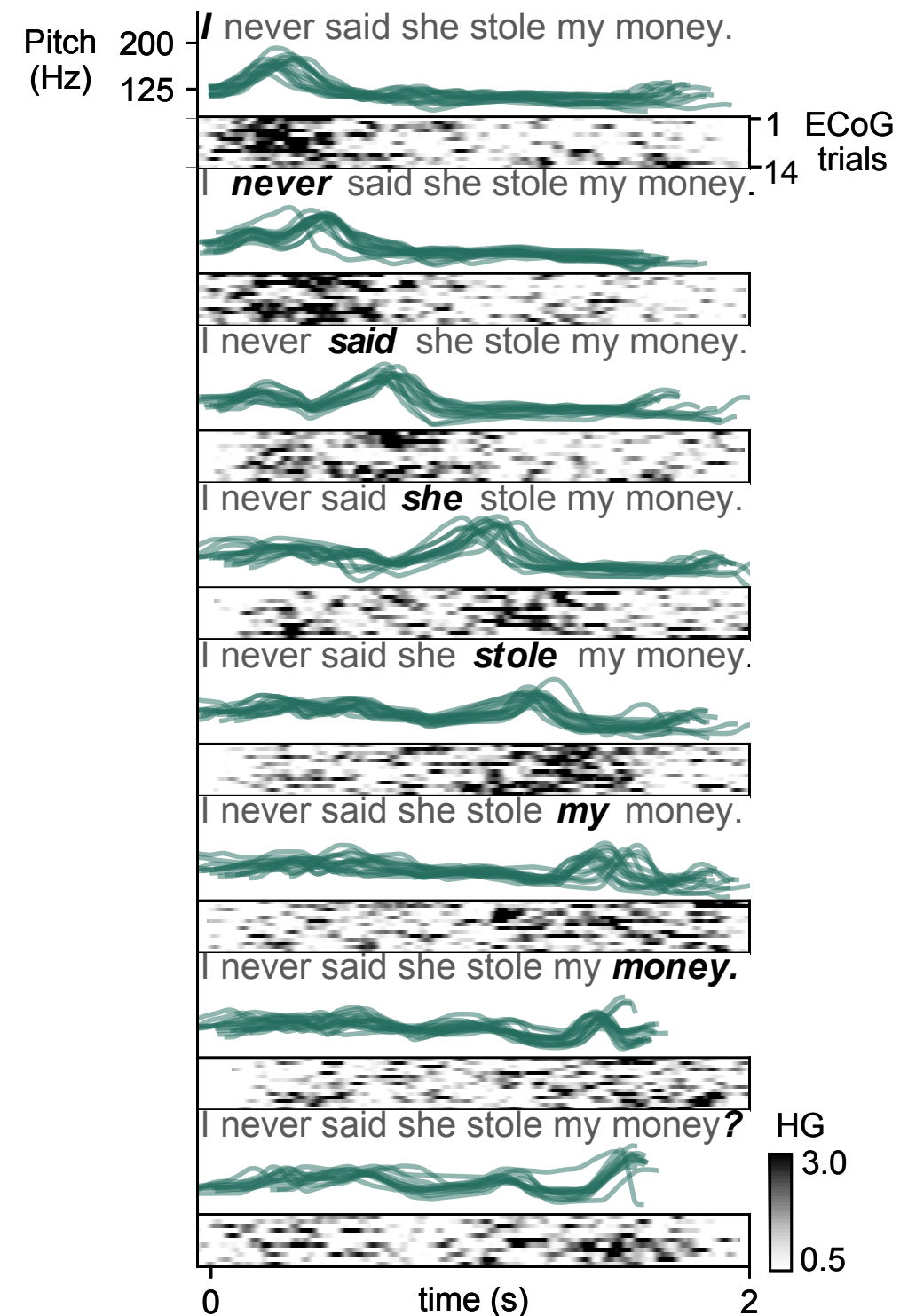
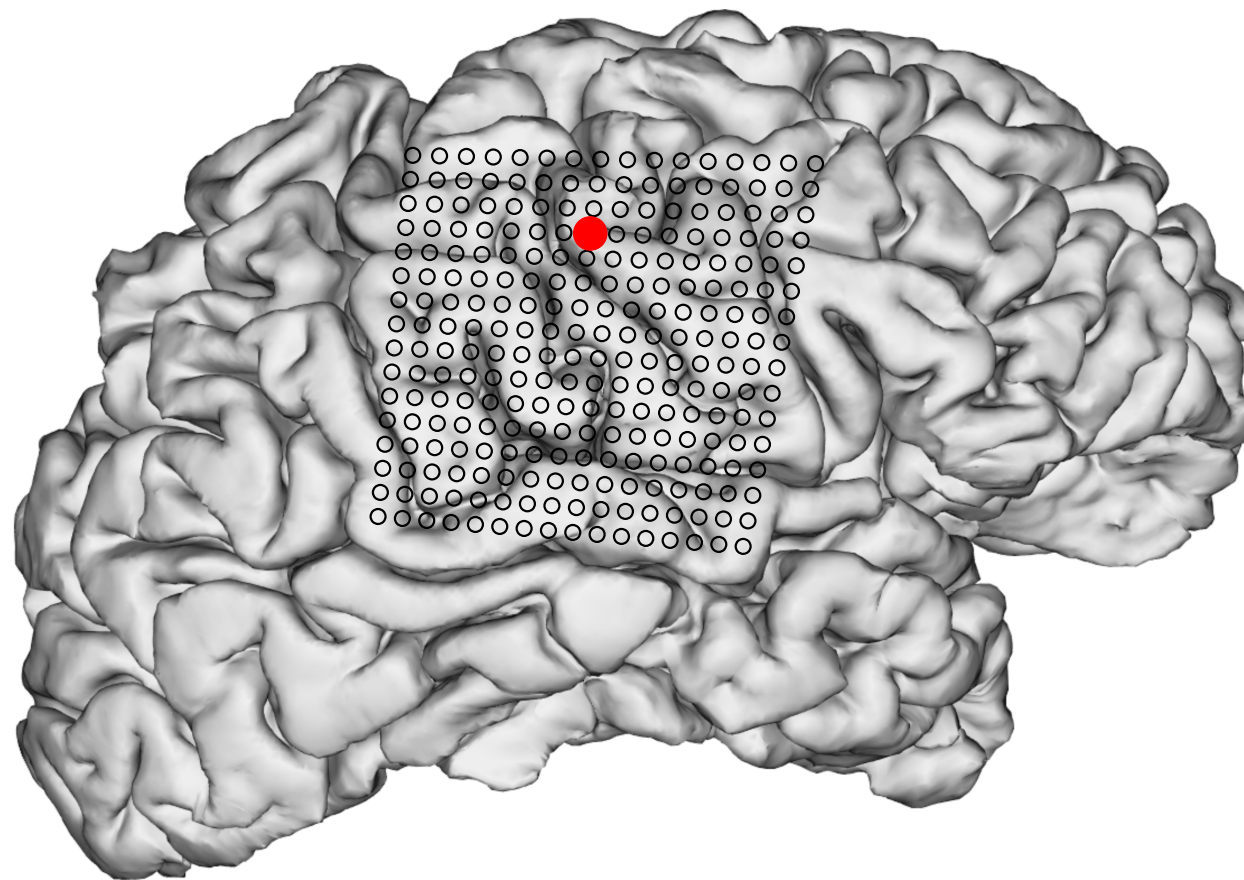
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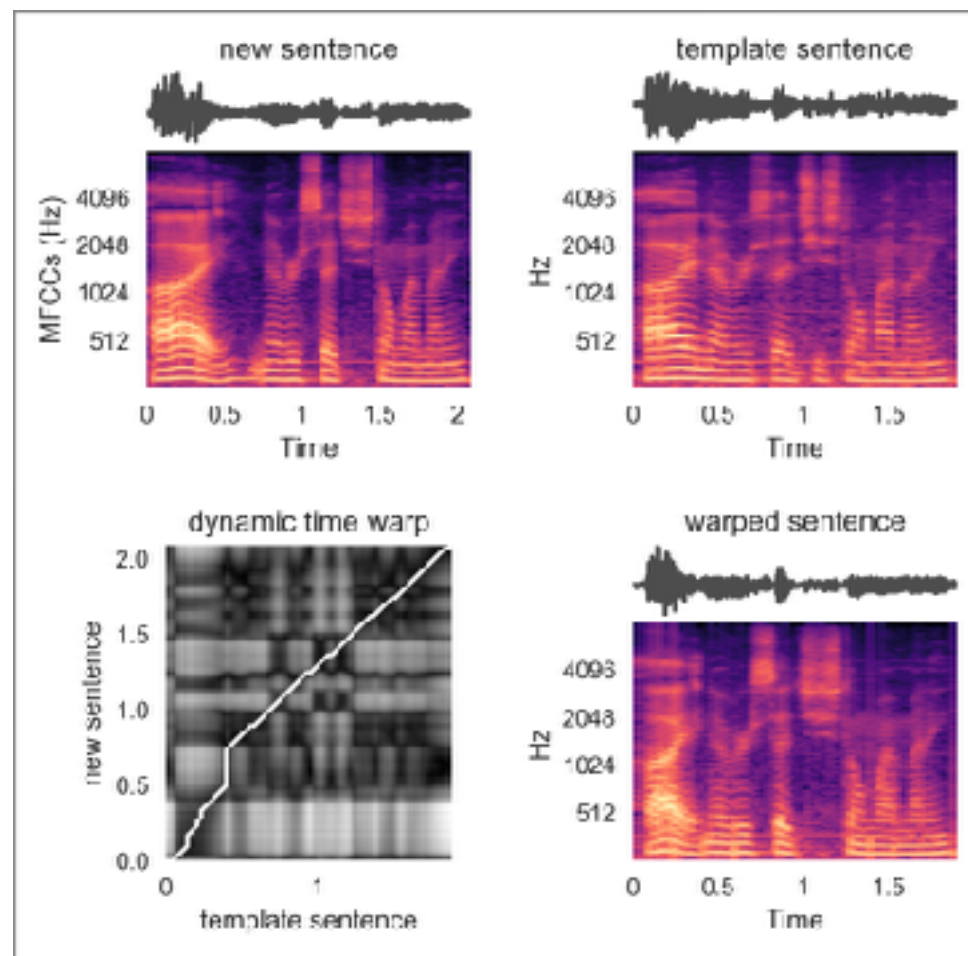
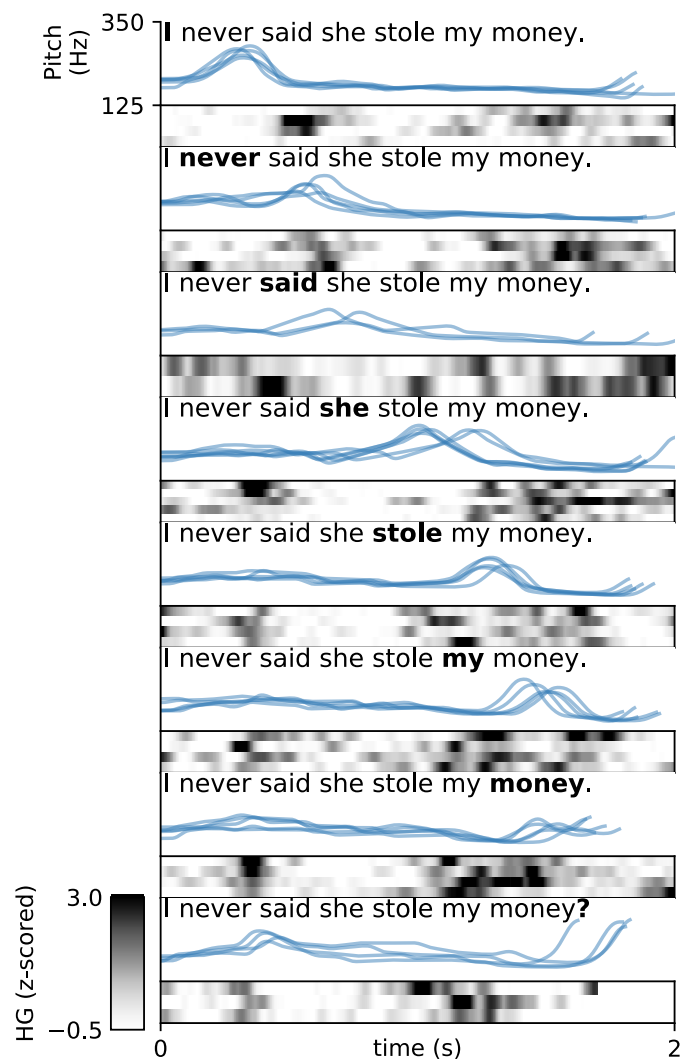
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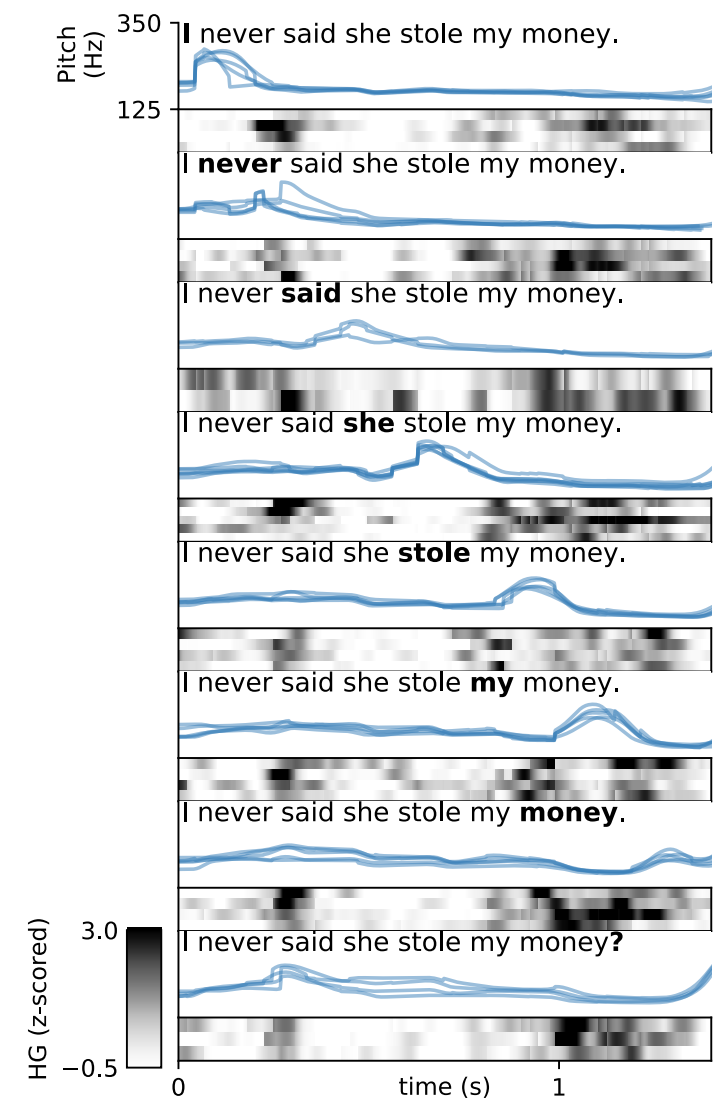
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Articulators: dynamic time warping

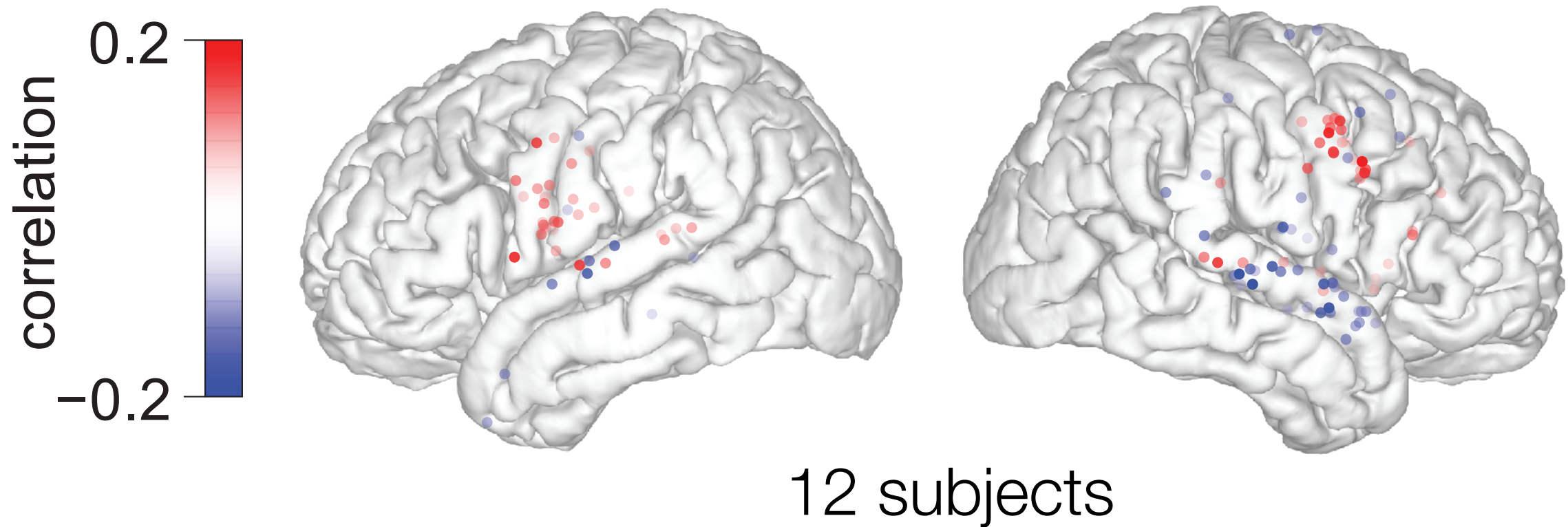
before warping



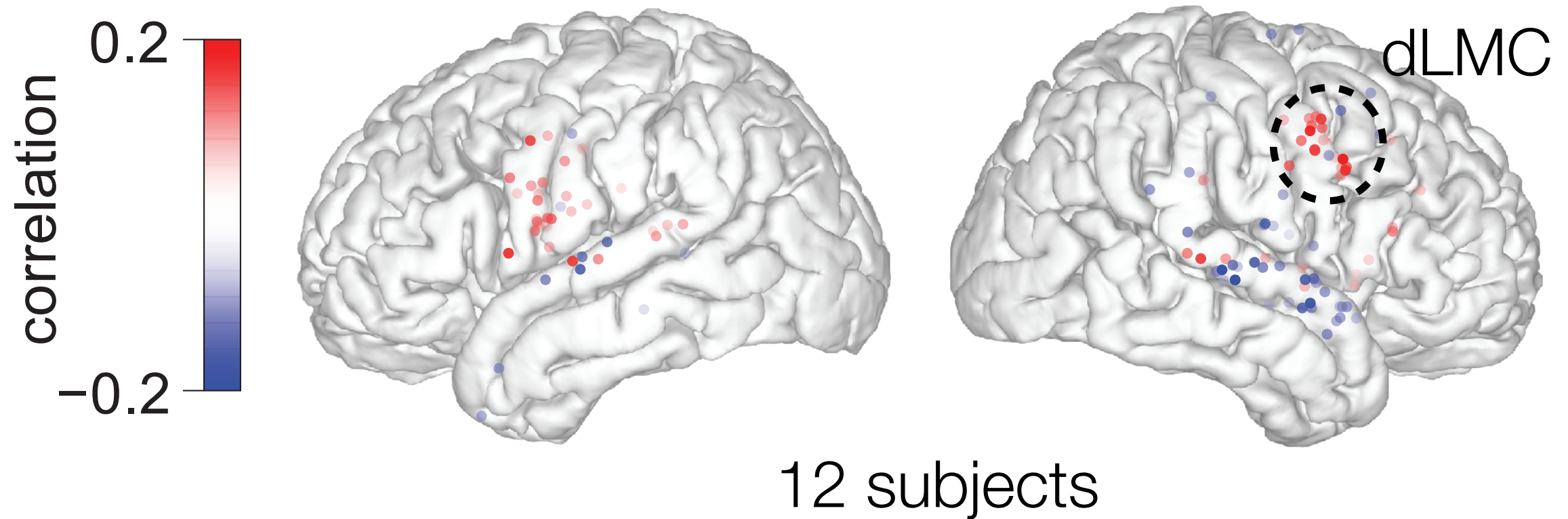
after warping



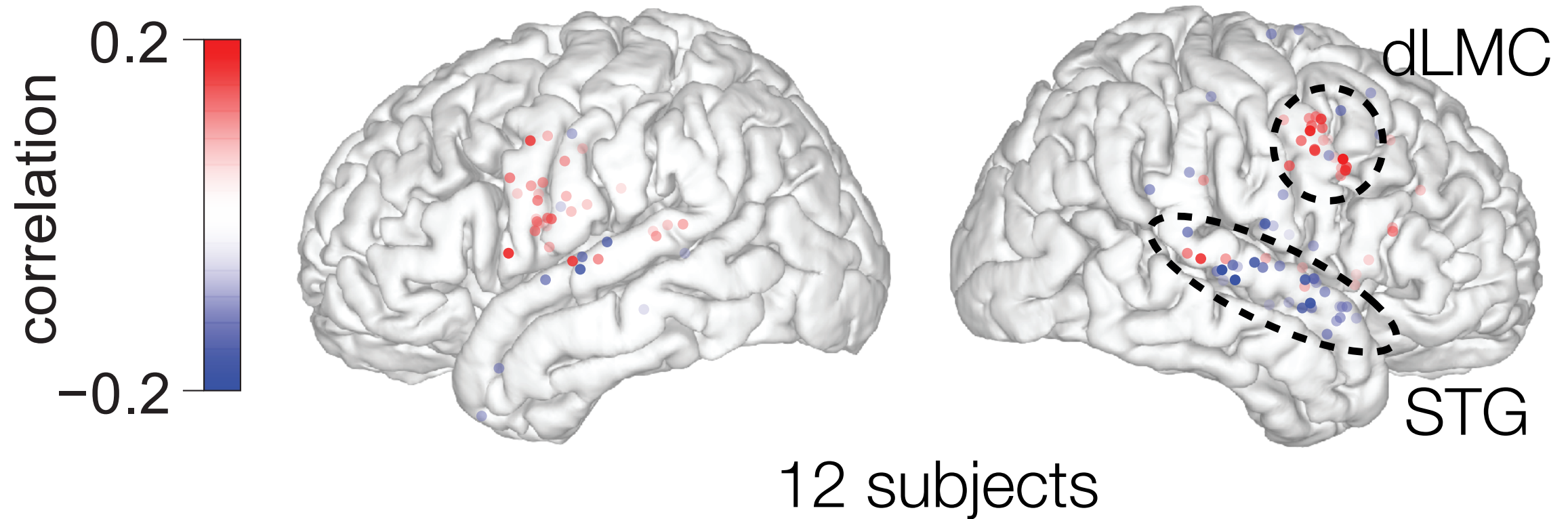
Pitch encoding in dLMC across subjects



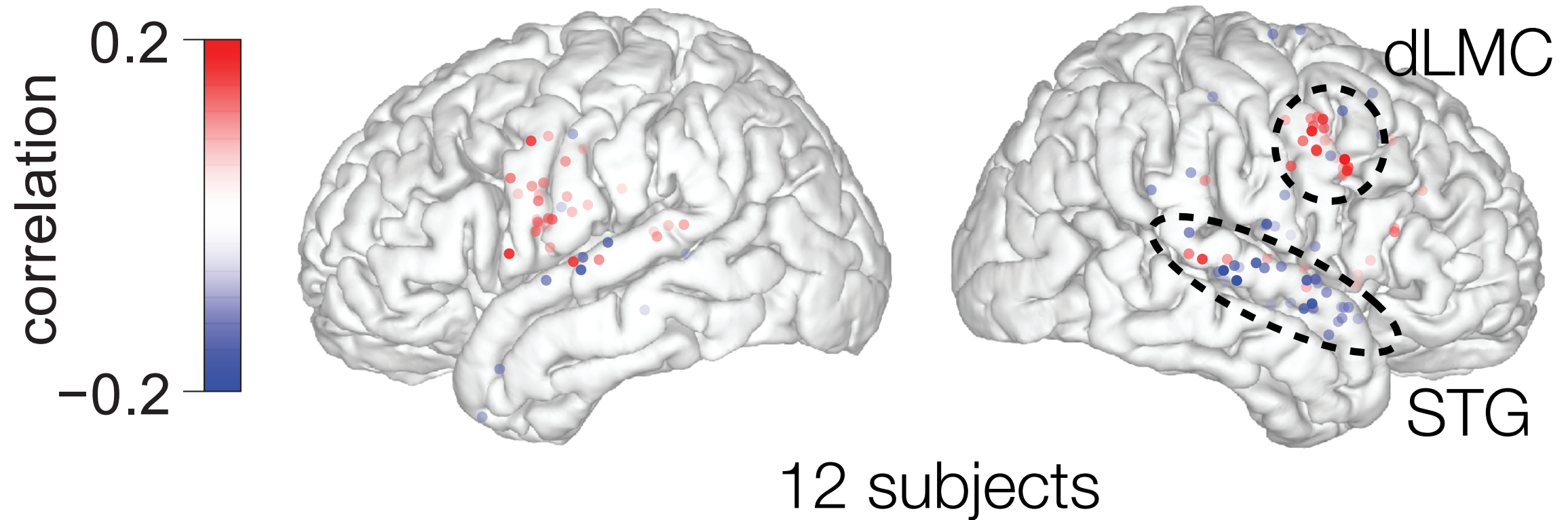
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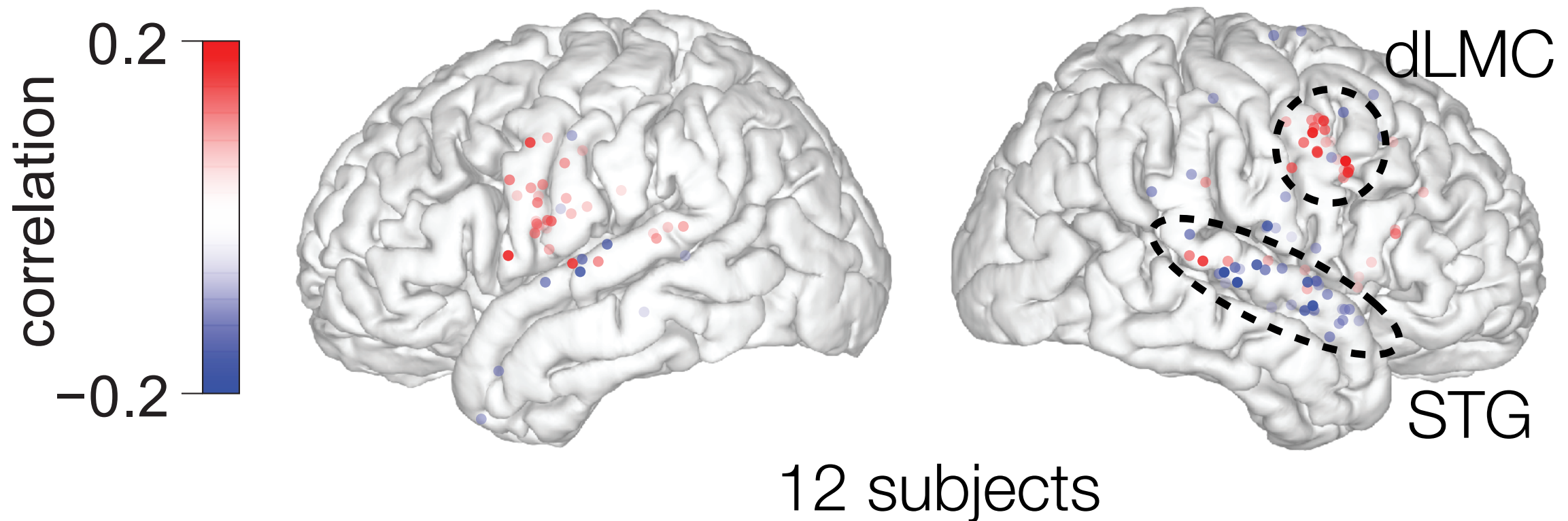


Pitch encoding in dLMC across subjects



Findings:

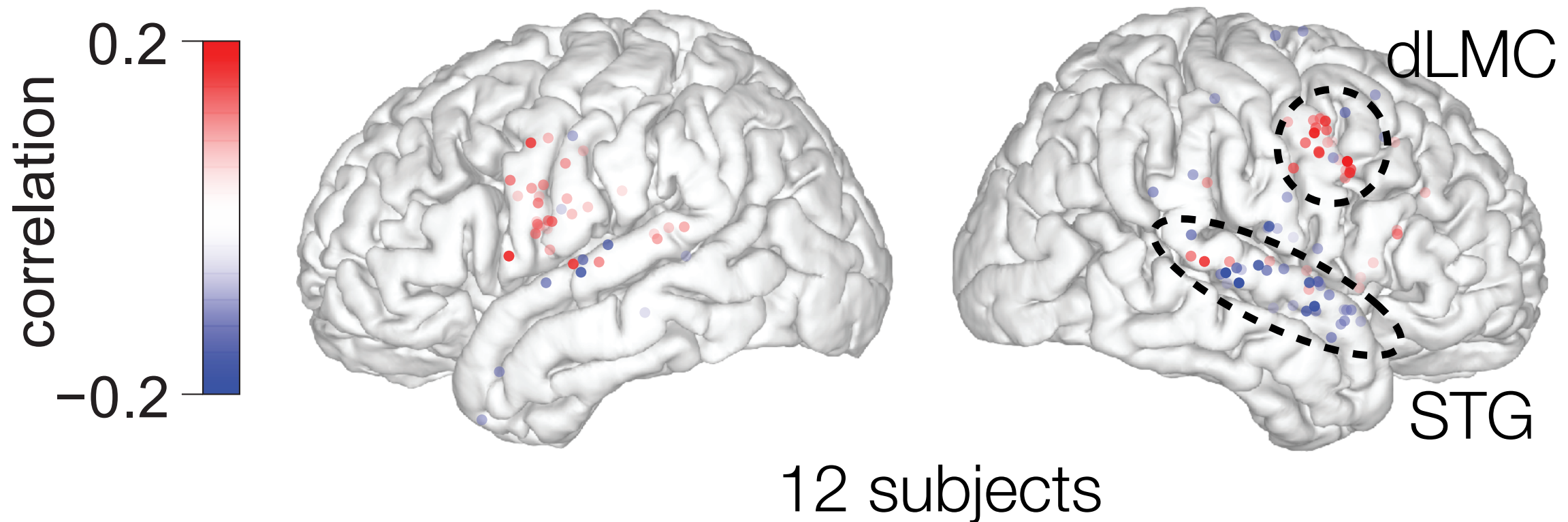
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Findings:

- In dLMC, higher pitch has higher activation

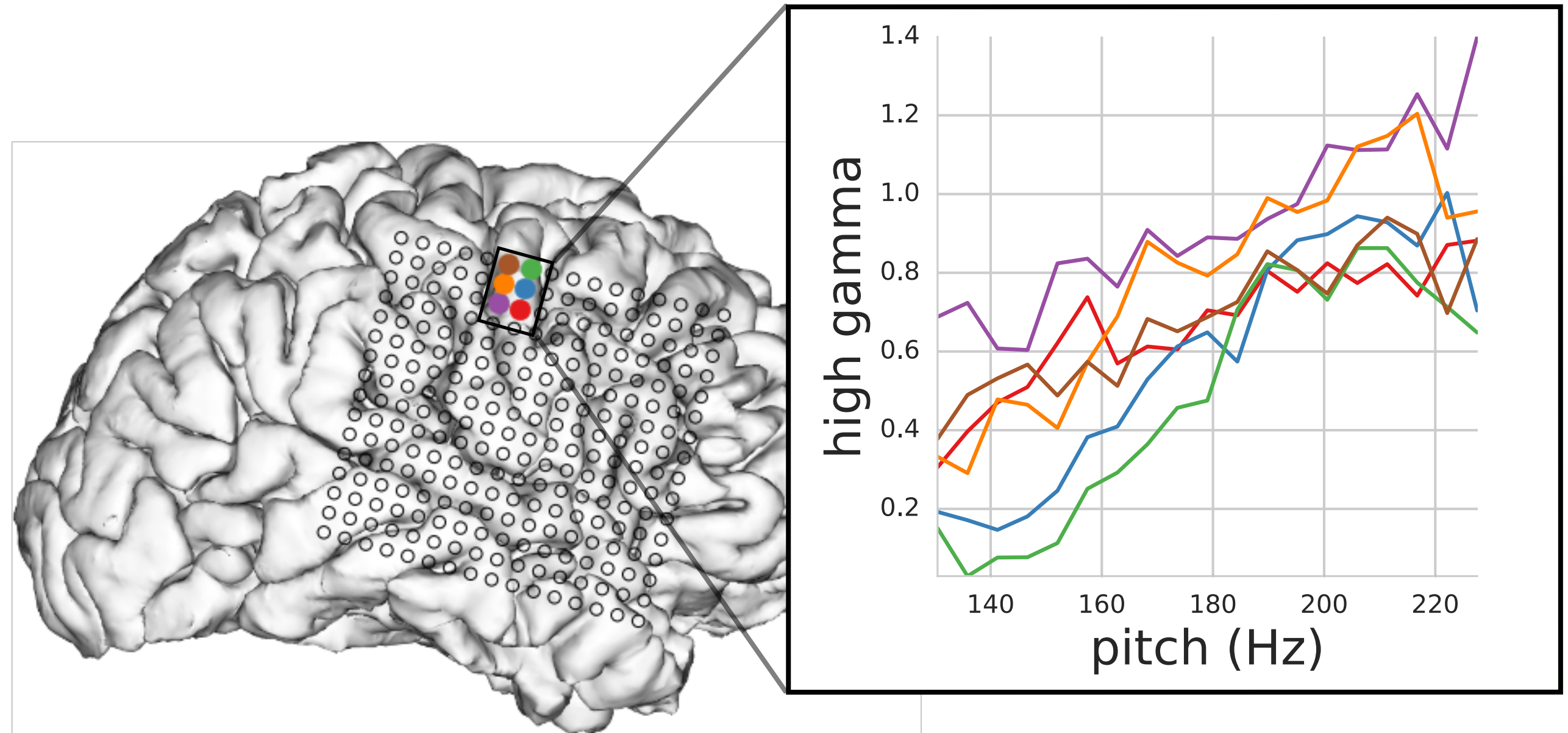
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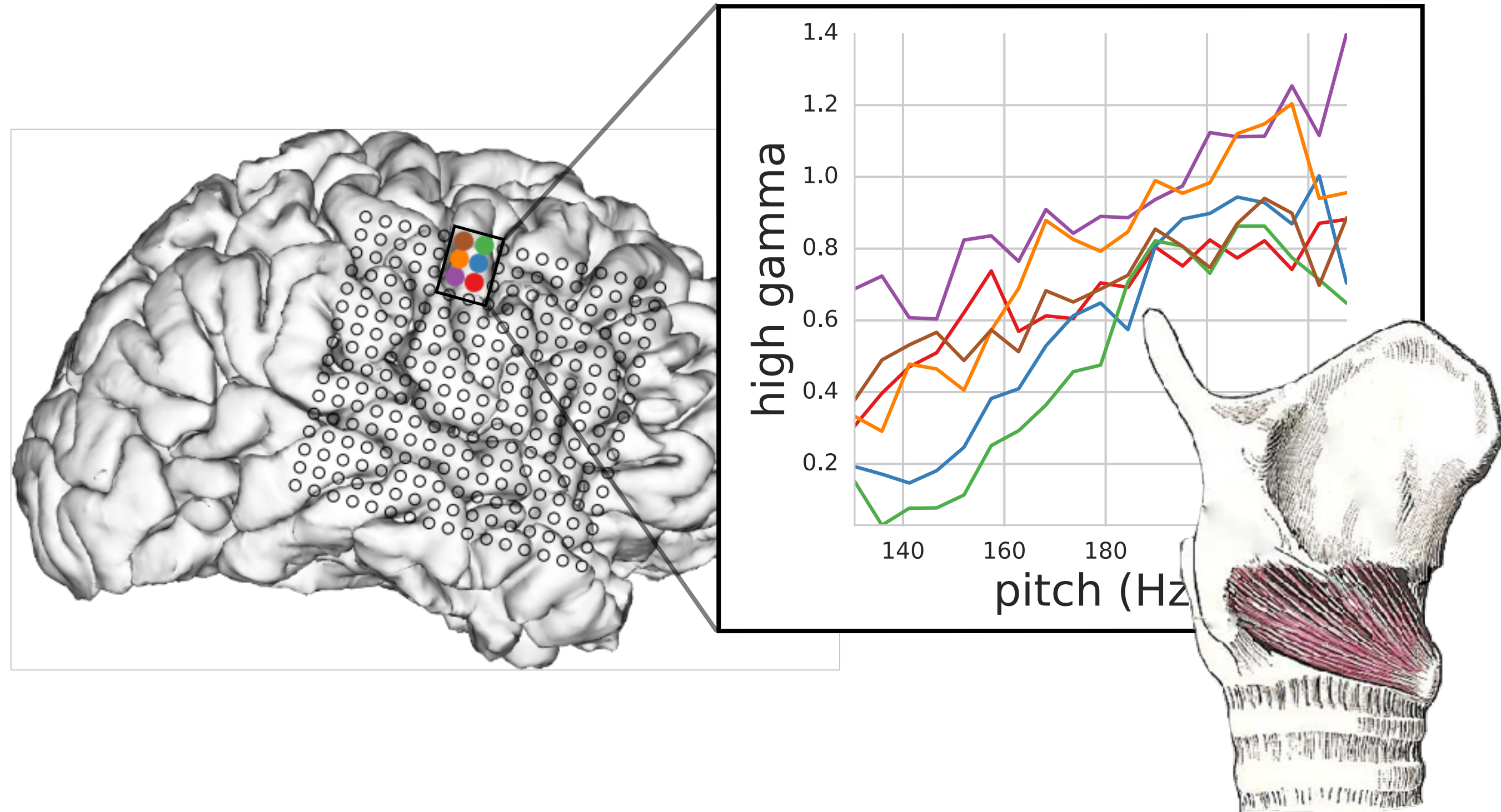
Findings:

- In dLMC, higher pitch has higher activation
- In the superior temporal gyrus, an auditory area, electrodes are split between preferring higher pitches and lower pitches

High gamma increases with pitch in dLMC

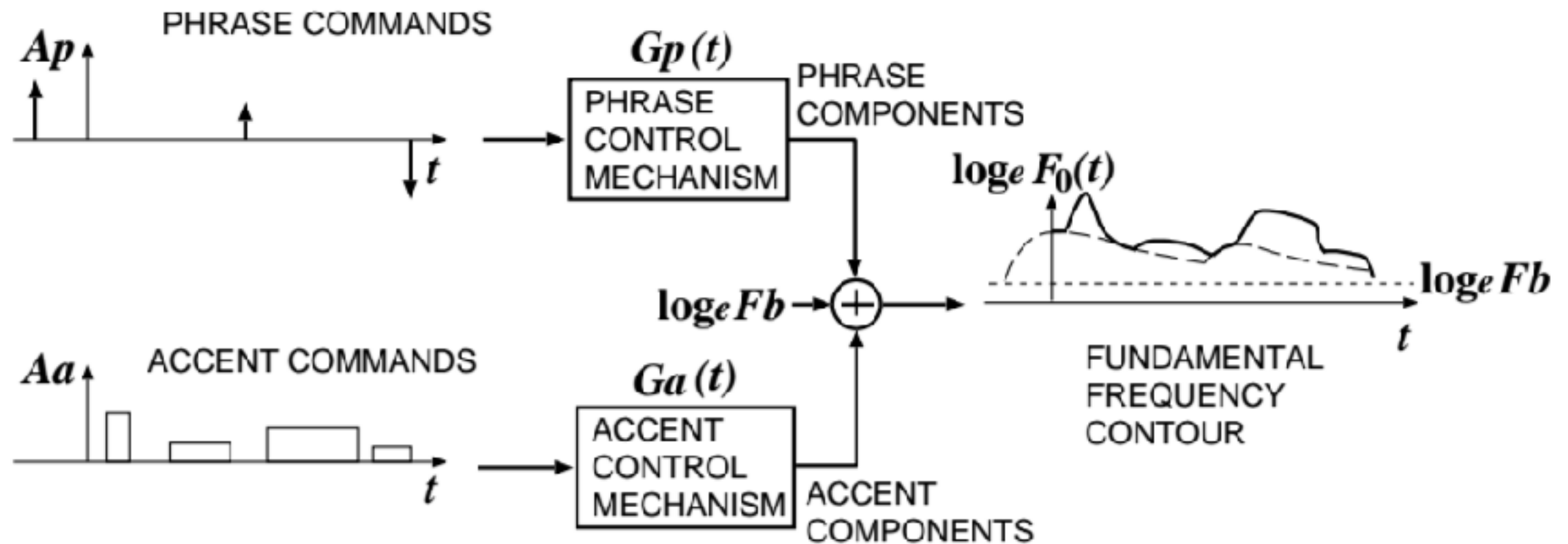


High gamma increases with pitch in dLMC



Encoding of Components of Prosody

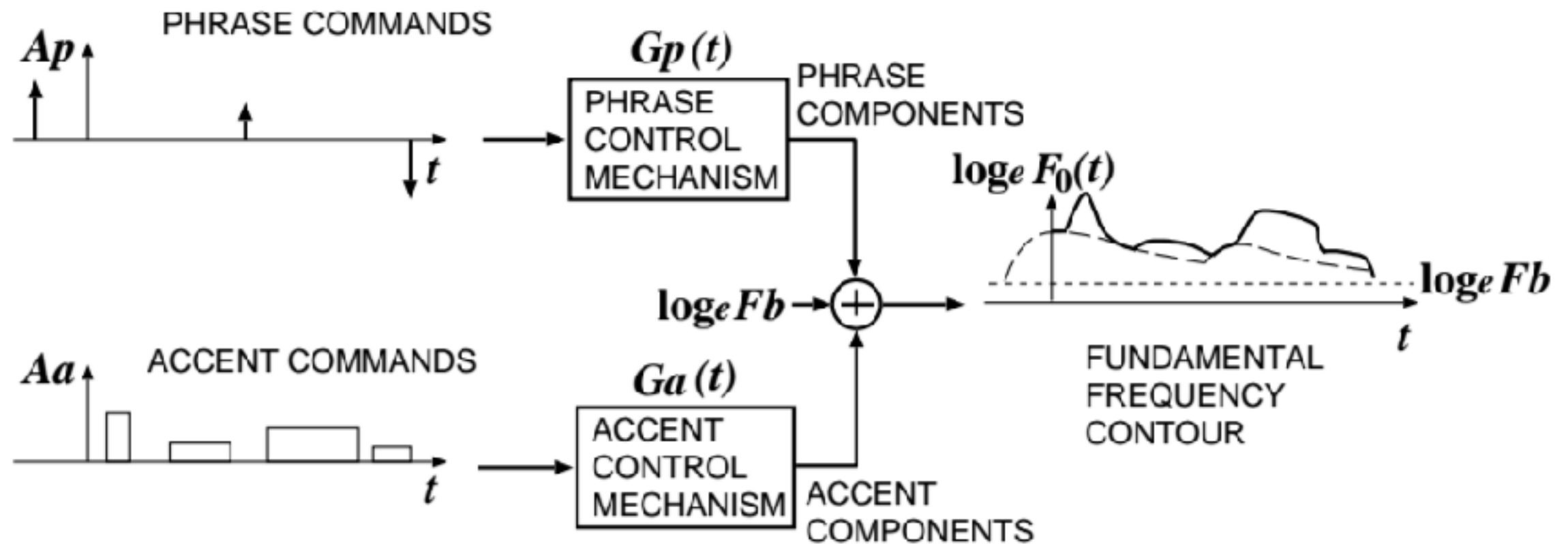
Fujisaki Model: a parsimonious explanation for pitch contours



(Fujisaki, Speech Prosody, 2004)

Encoding of Components of Prosody

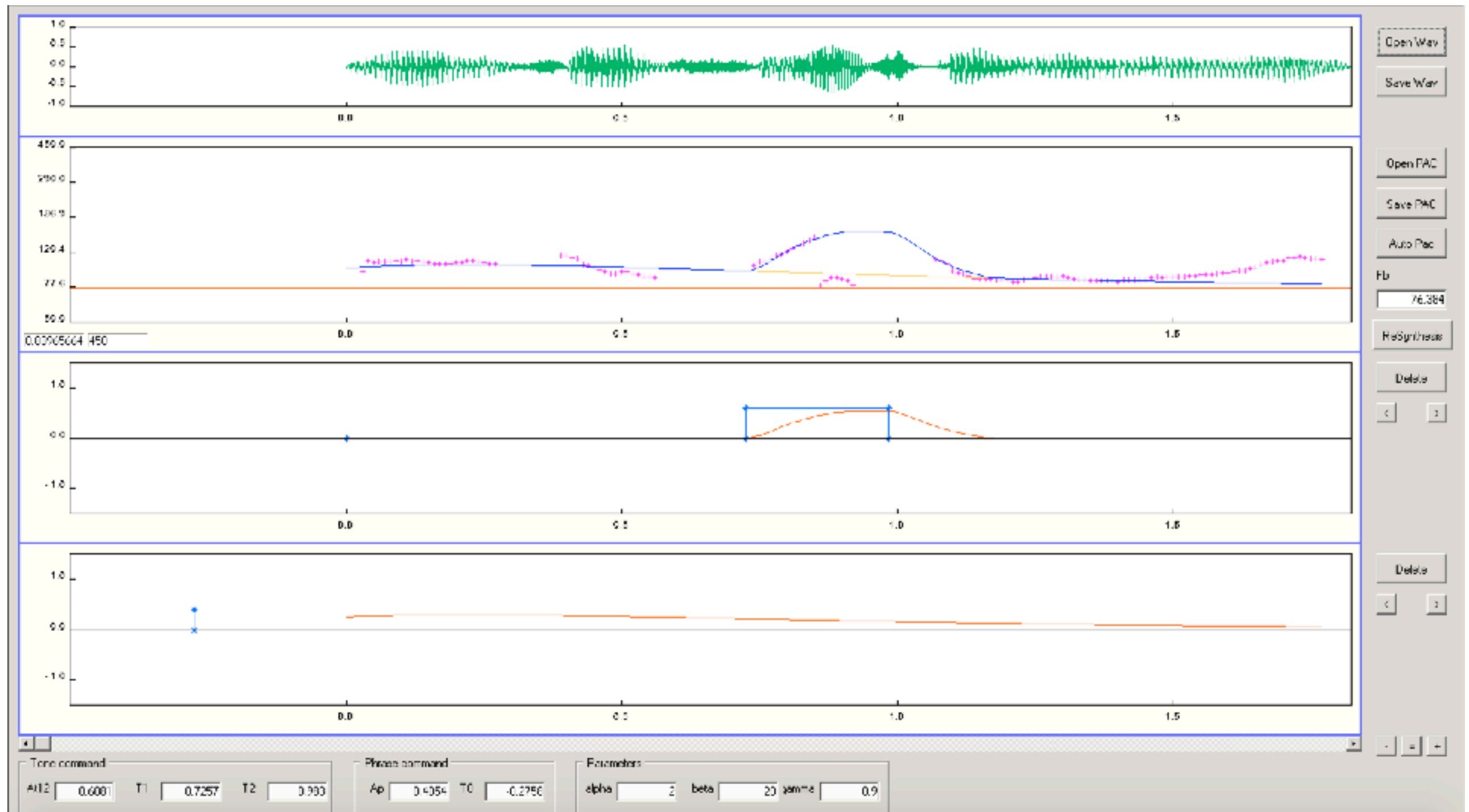
Fujisaki Model: a parsimonious explanation for pitch contours



Hypothesis: different components controlled separately

(Fujisaki, Speech Prosody, 2004)

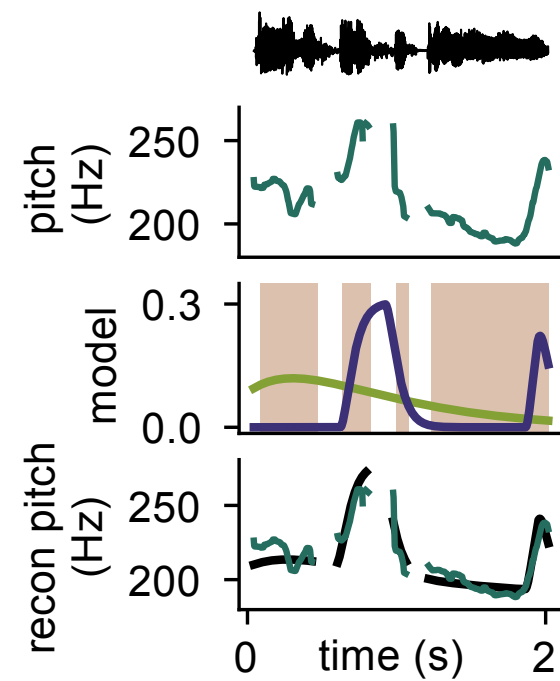
Fitting the Fujisaki model using FujiParaEditor



Written by Dr. Hansjörg Mixdorff

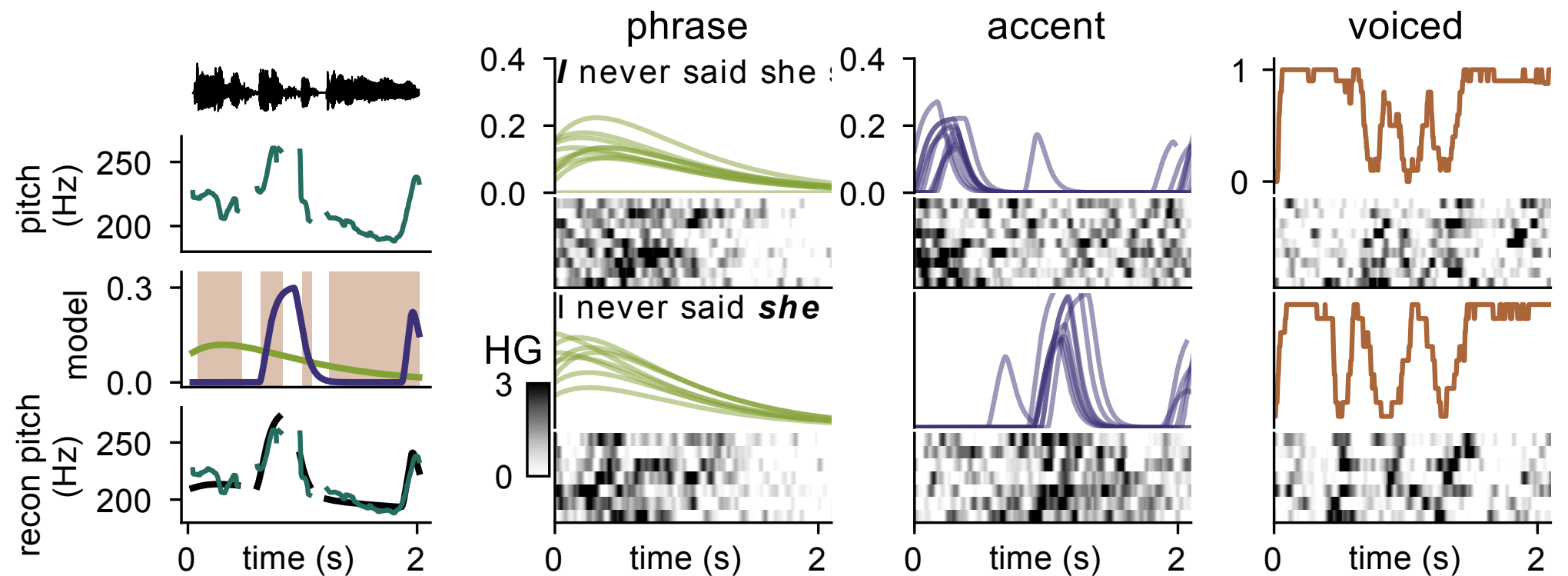
Encoding of Fujisaki components

phrase
accent
voicing



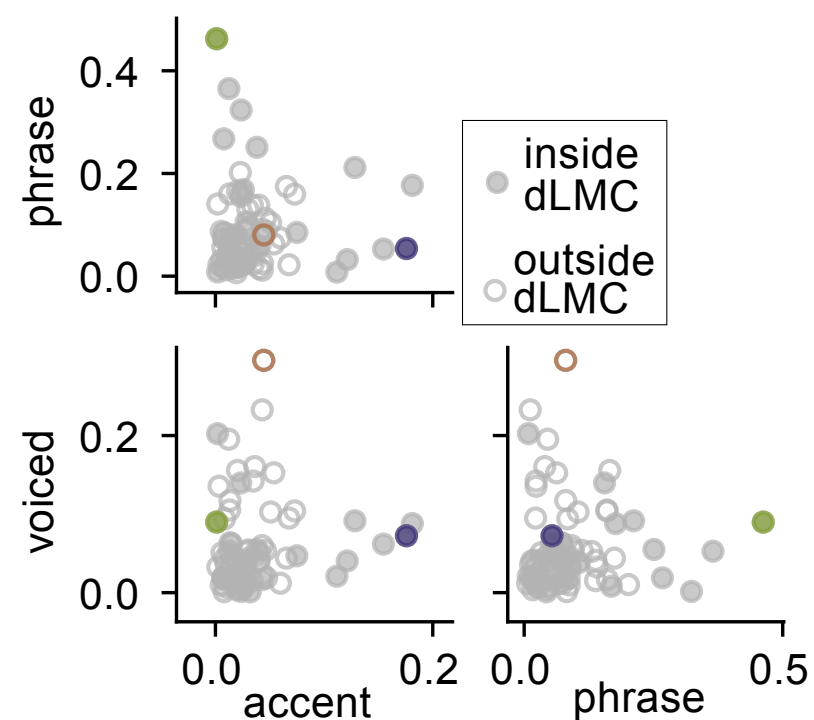
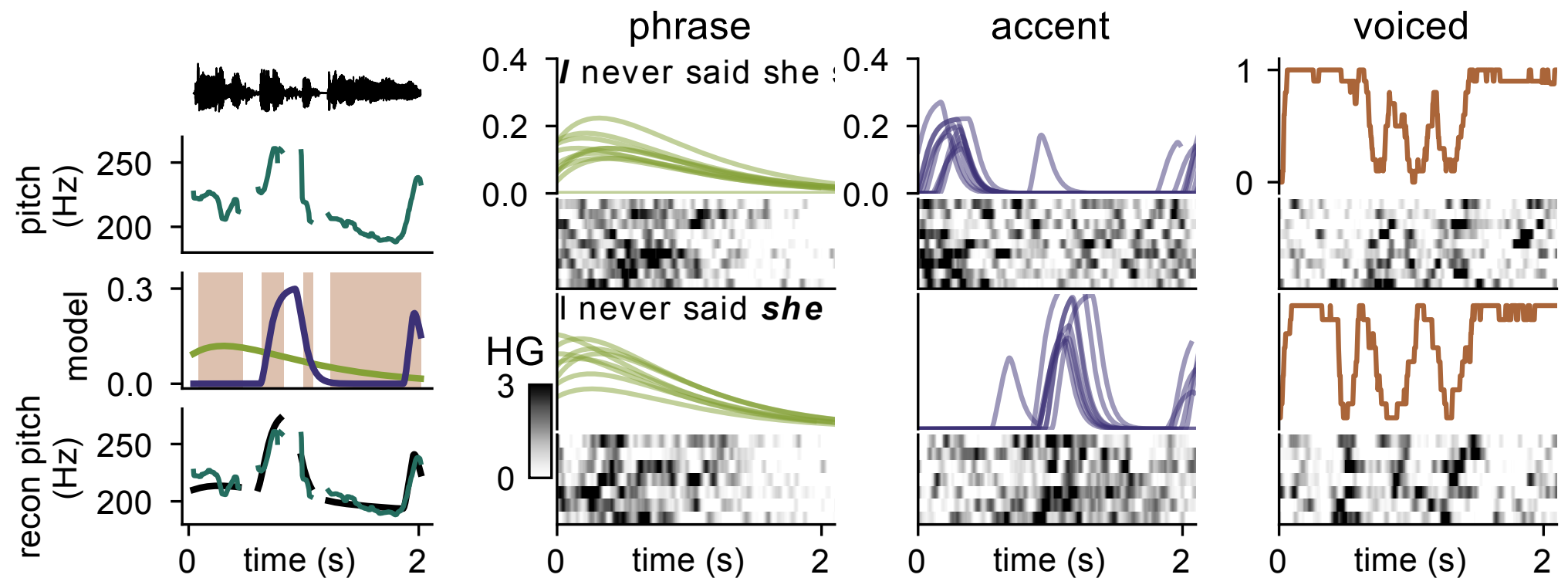
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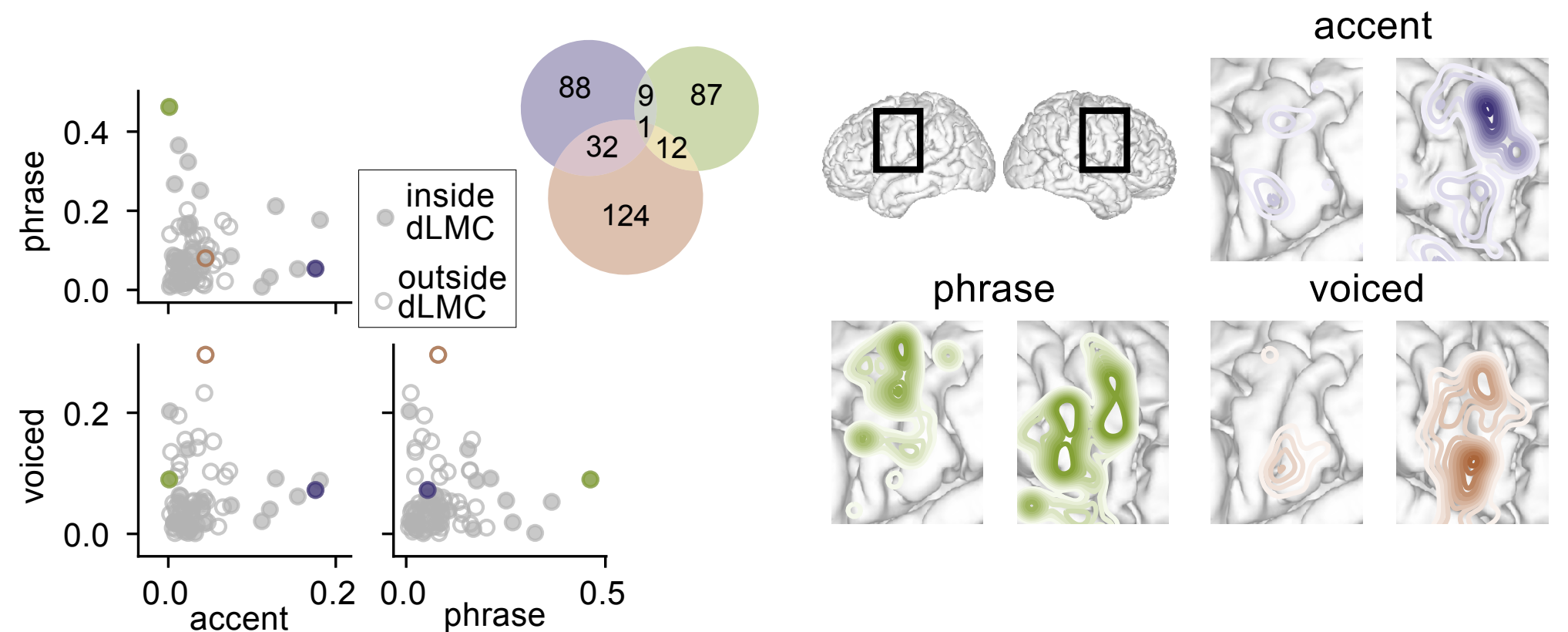
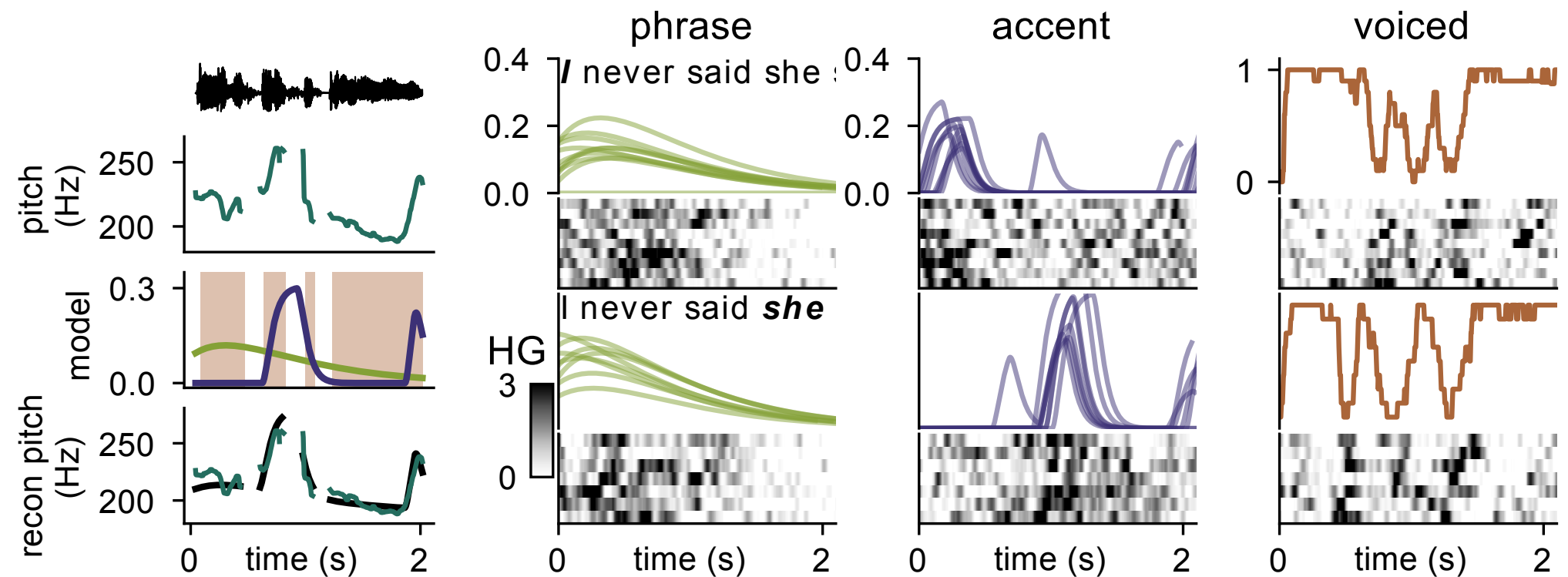
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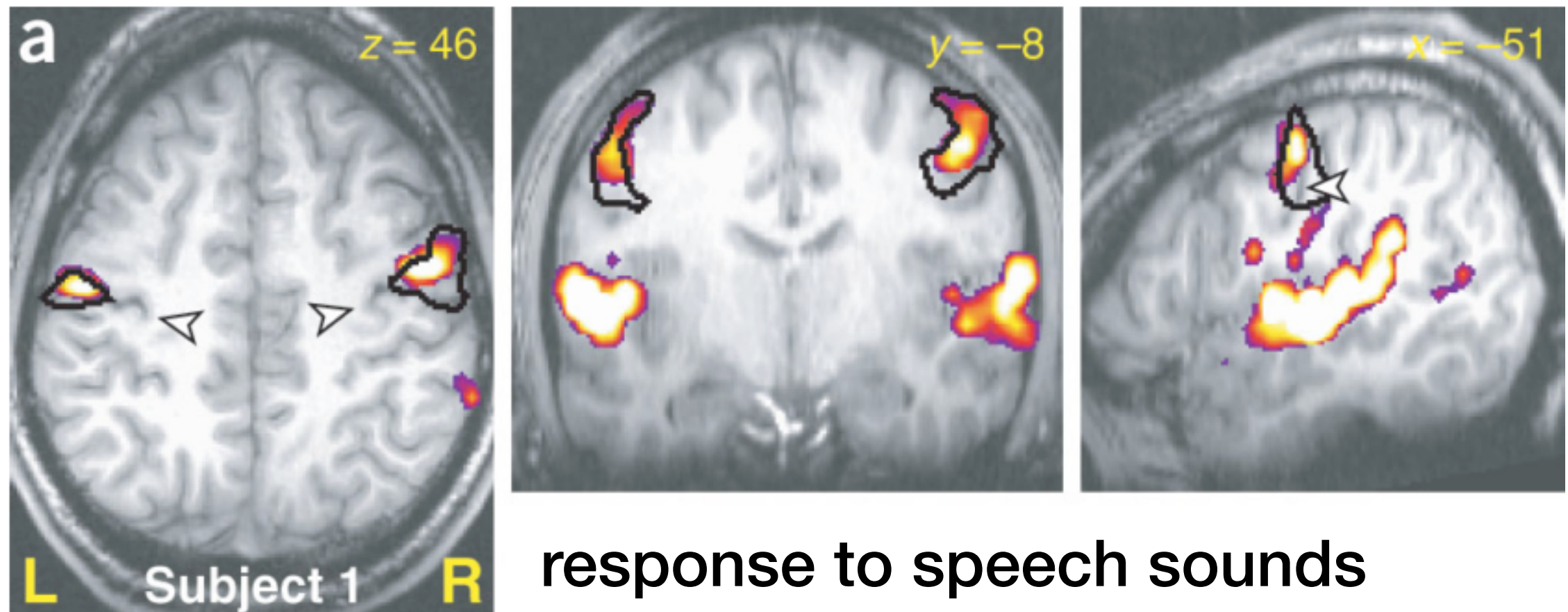


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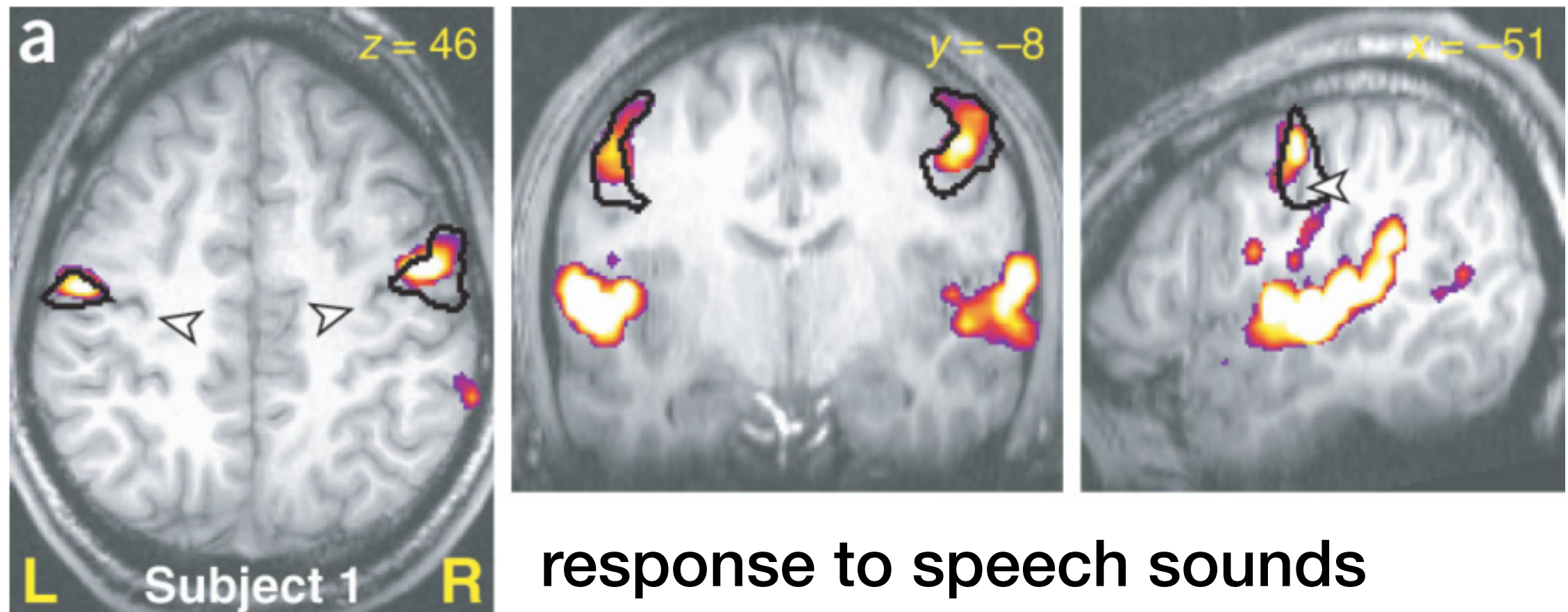


Auditory response M1



(Wilson et al. 2004)

Auditory response M1



(Wilson et al. 2004)

Does this area overlap with dLMC? Does it encode pitch?

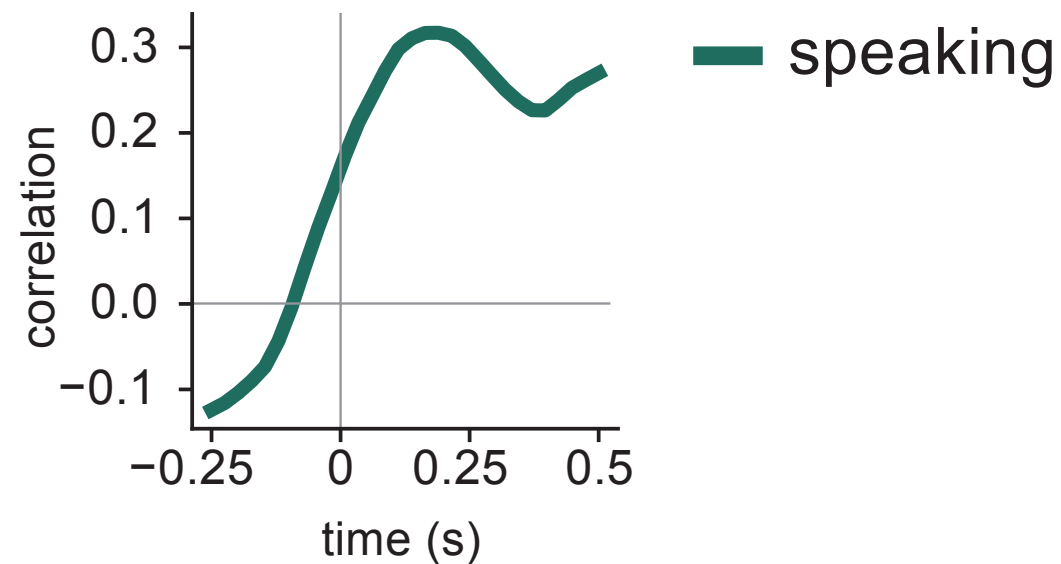
Auditory control: Playback

The recording of the task was played back to the subject

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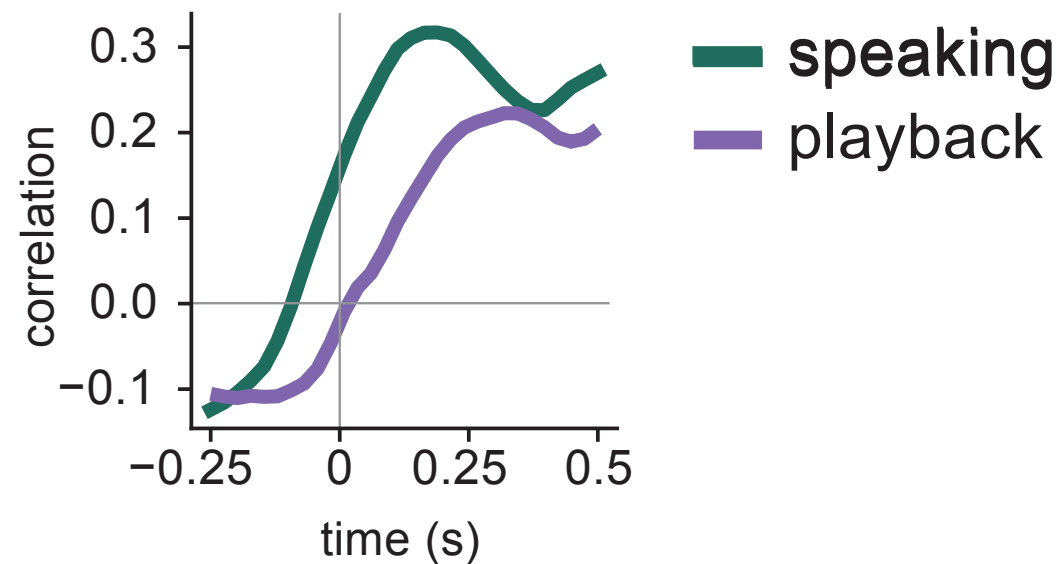
Cross-correlation
(example electrode)



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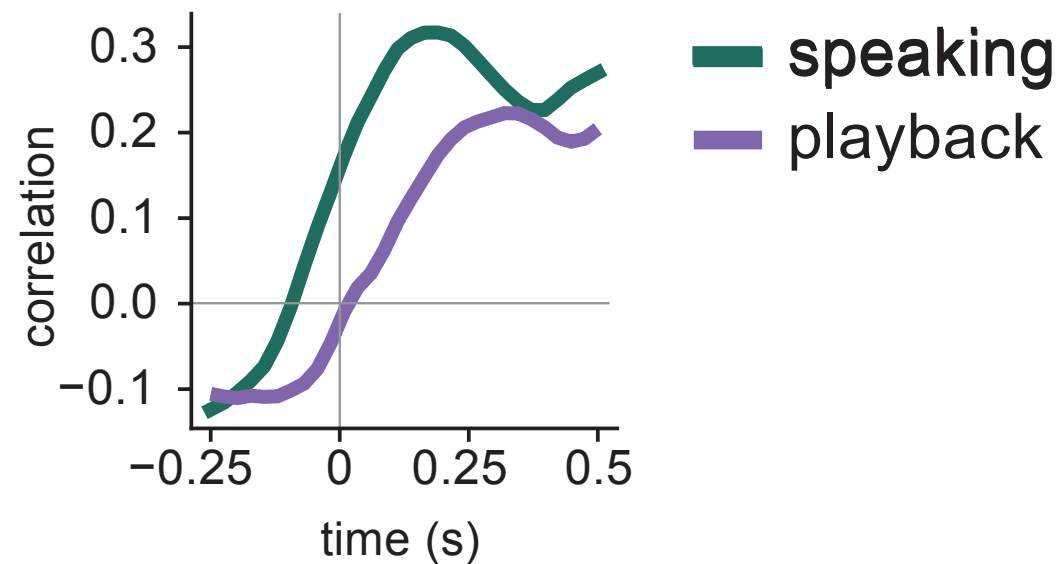
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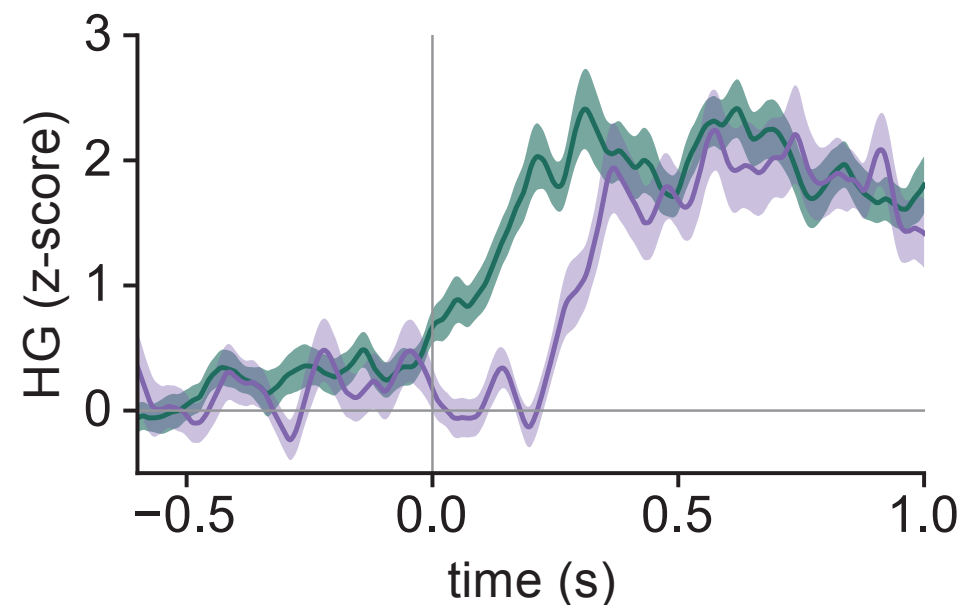
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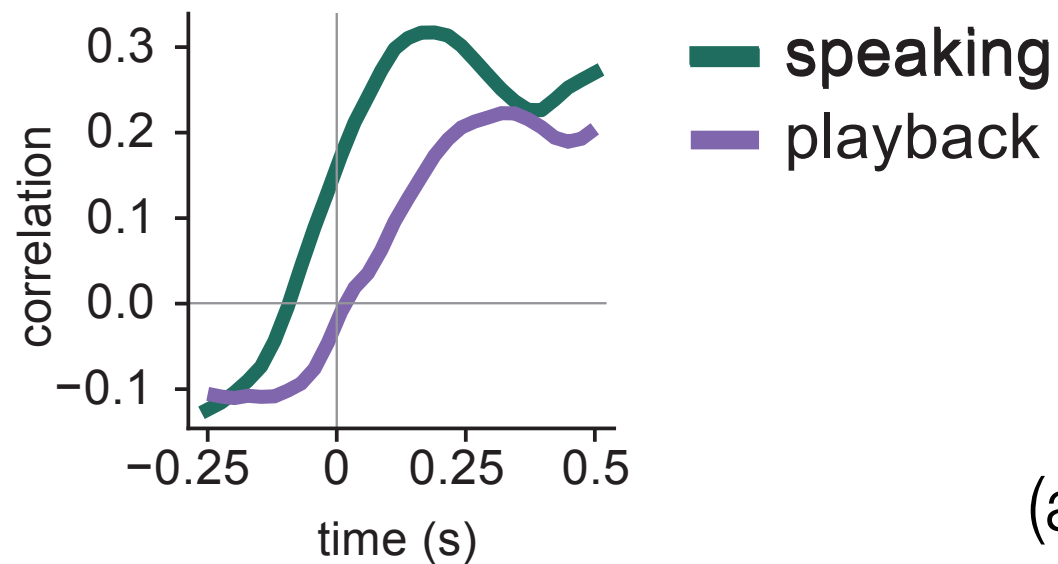
Onset delay
(example electrode)



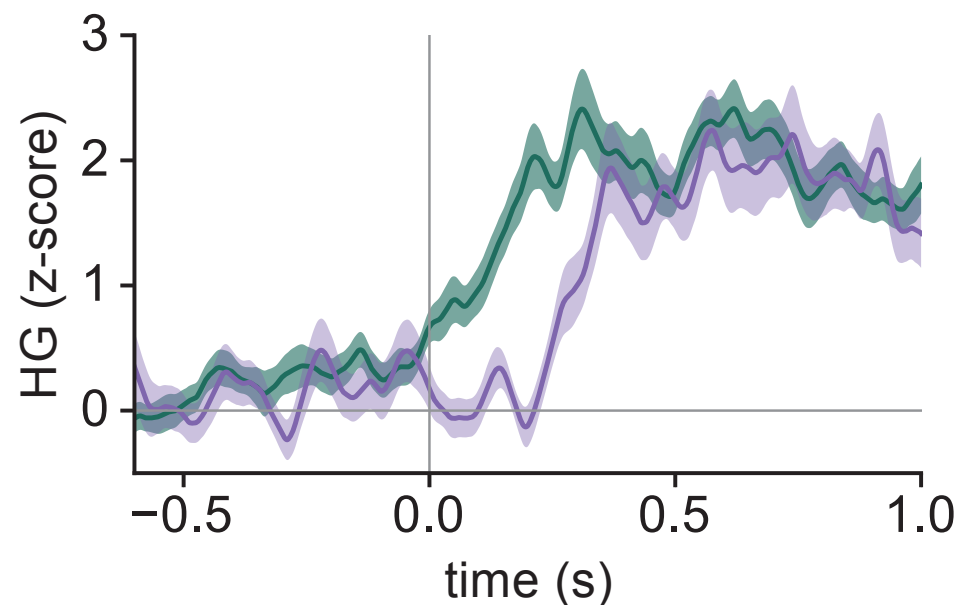
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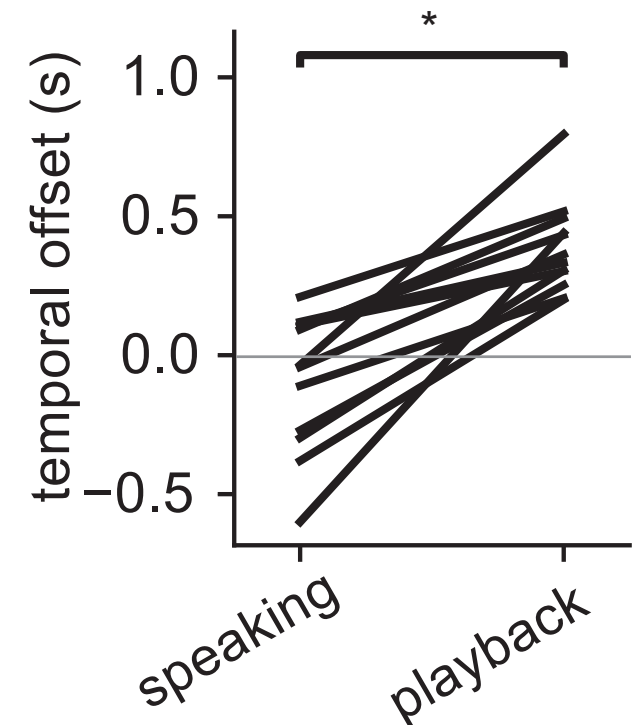
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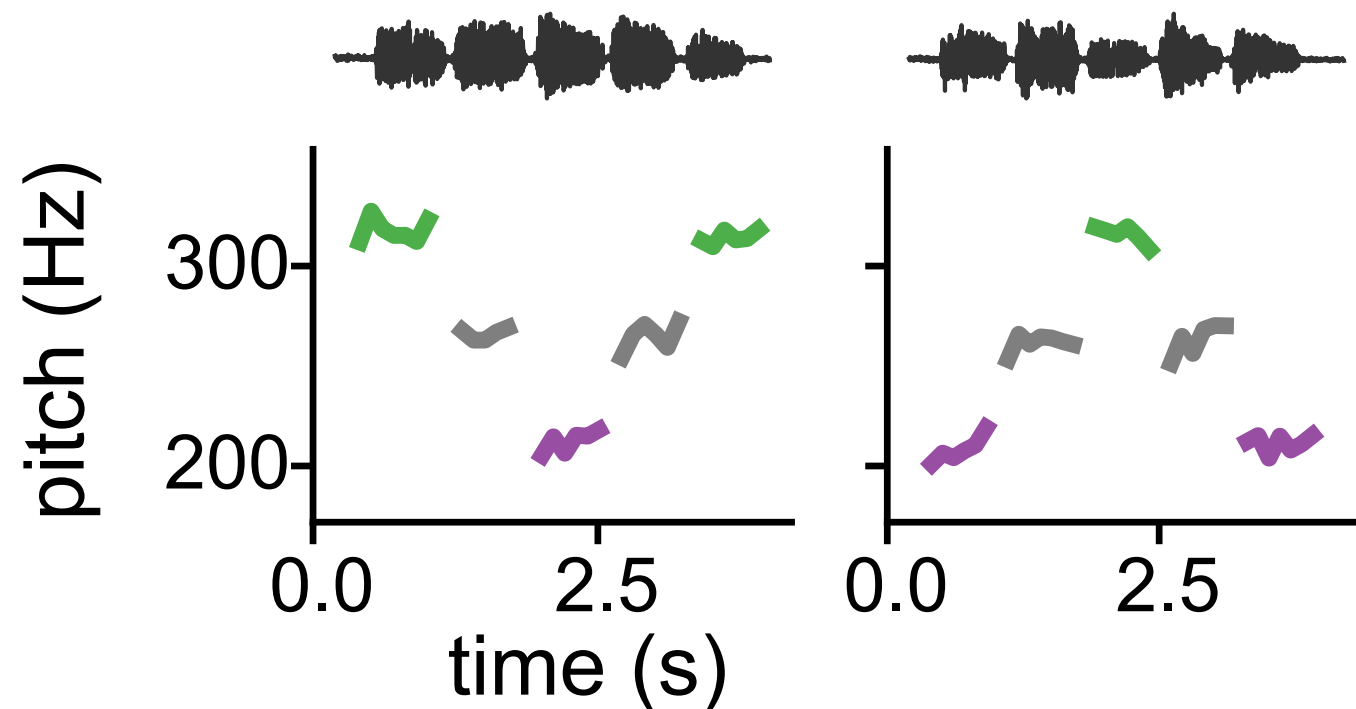
Onset delay
(all dLMC electrodes)



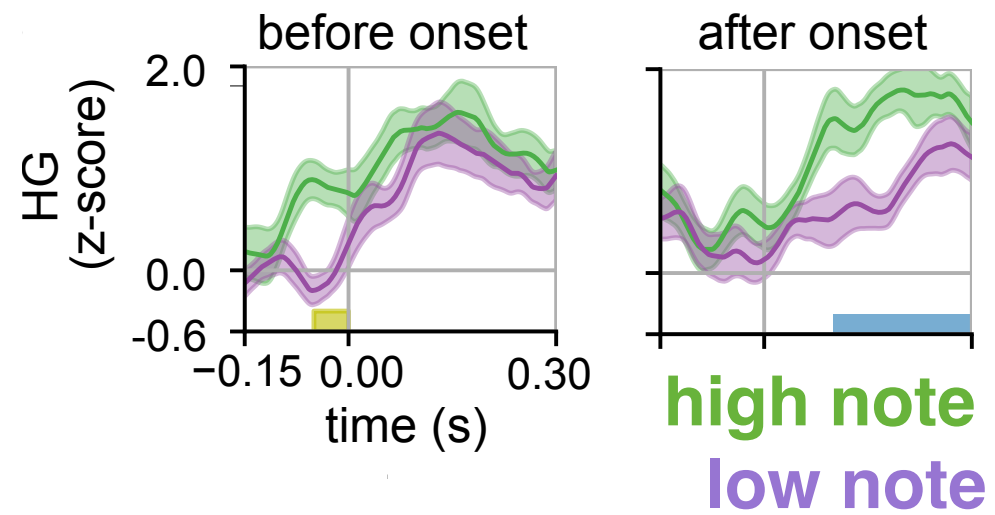
Pitch control during singing

Test whether laryngeal control is unique to speech

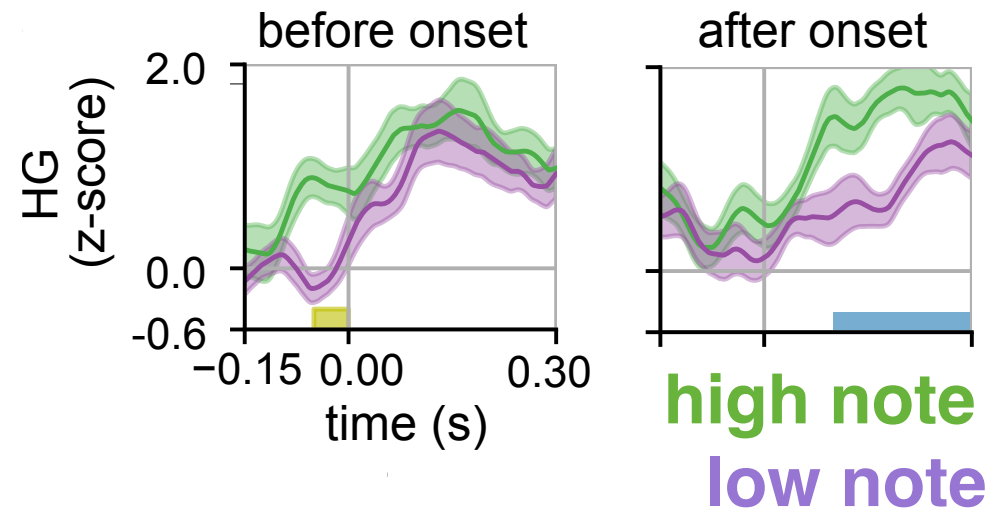
Task: Call-and-response singing task



Pitch control during singing

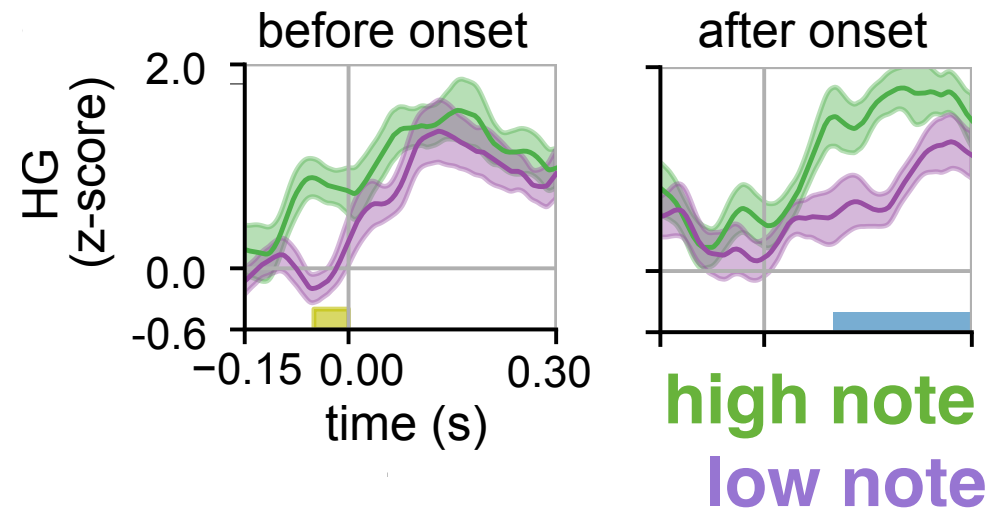


Pitch control during singing



Findings:

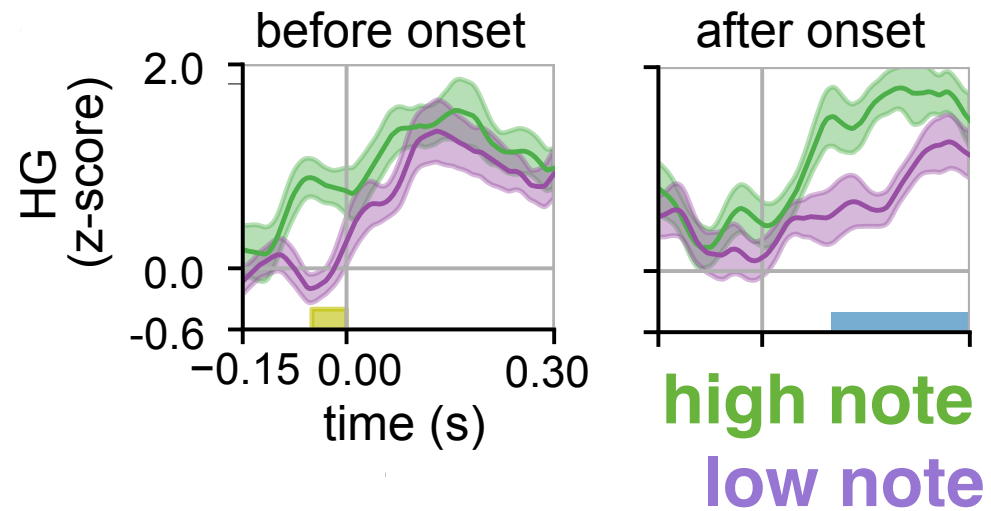
Pitch control during singing



Findings:

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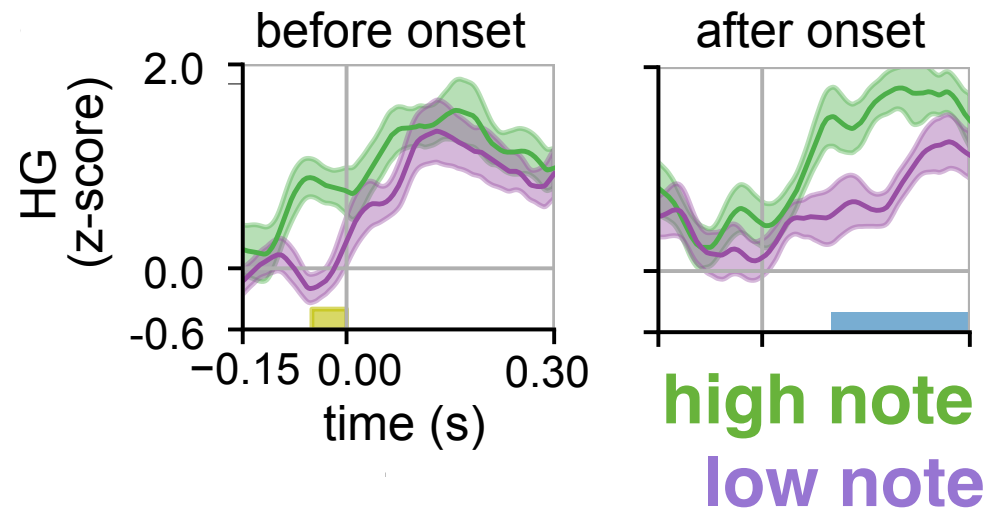
Pitch control during singing



Findings:

- Higher pitch has higher activation
- Representation starts before sound

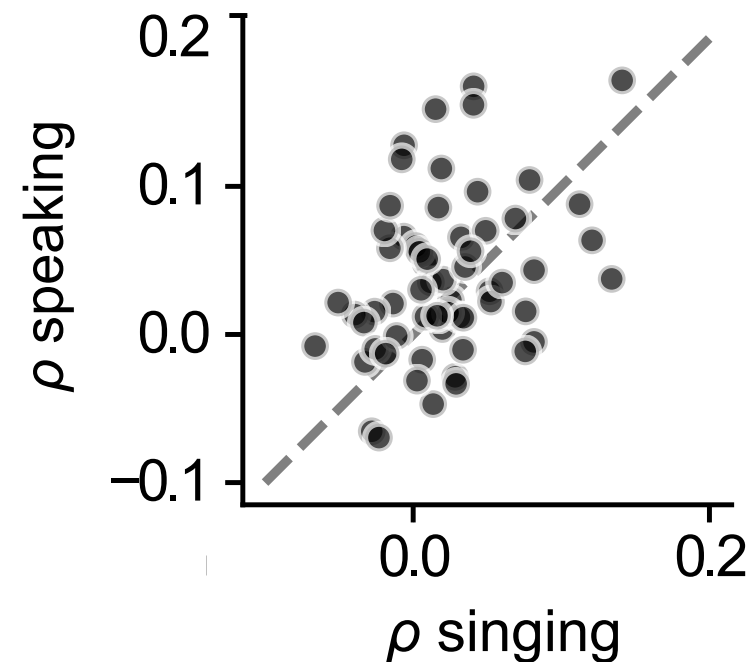
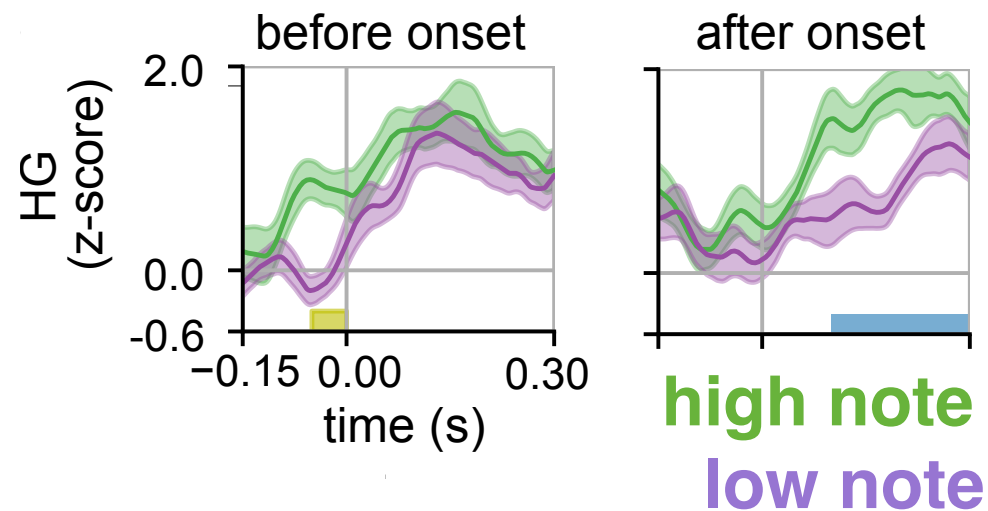
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- Correlated with pitch when speaking and singing
- Encodes fast pitch accents
- Control of pitch distinct from control of voicing

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- Correlated with pitch when speaking and singing
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But is it causal?

Cortical Stimulation

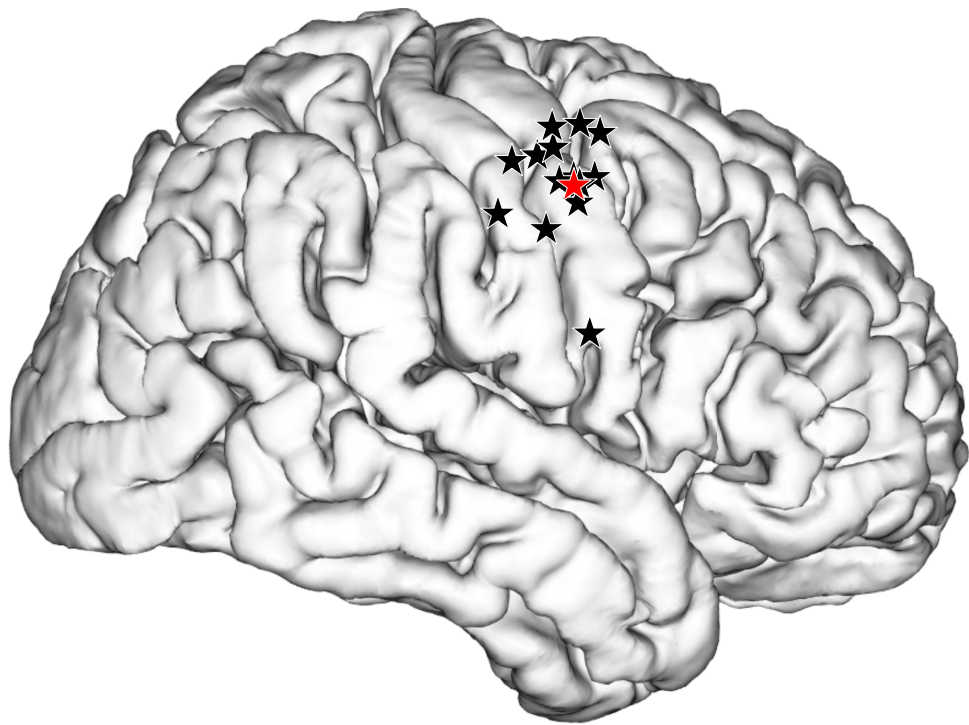
“Asleep”

Patient is asleep, with an endotracheal tube in the throat. The tube blocks any vocalizations, and has electrodes on the focal folds that measure contractions.

Cortical stimulation of dLMC evokes larynx response

Patients are anesthetized with electrodes placed on vocal chords

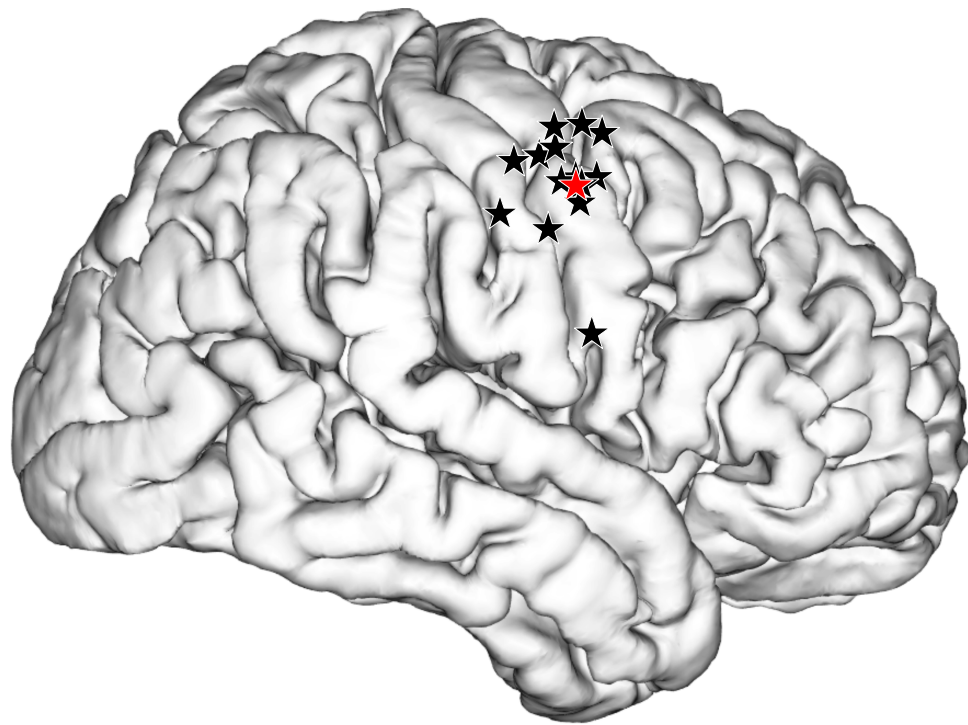
**Brain locations that made
larynx respond**



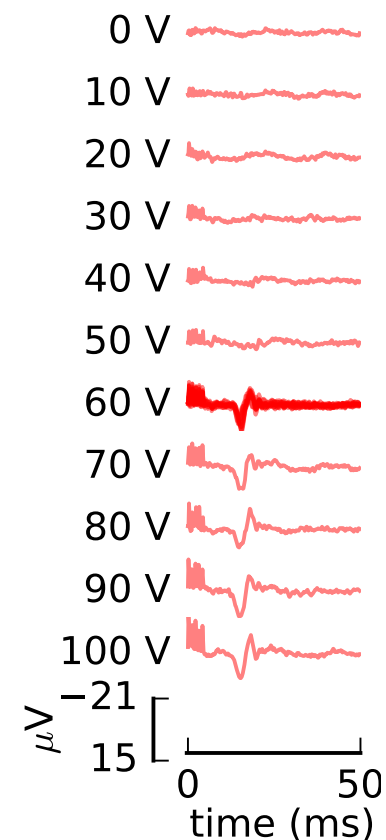
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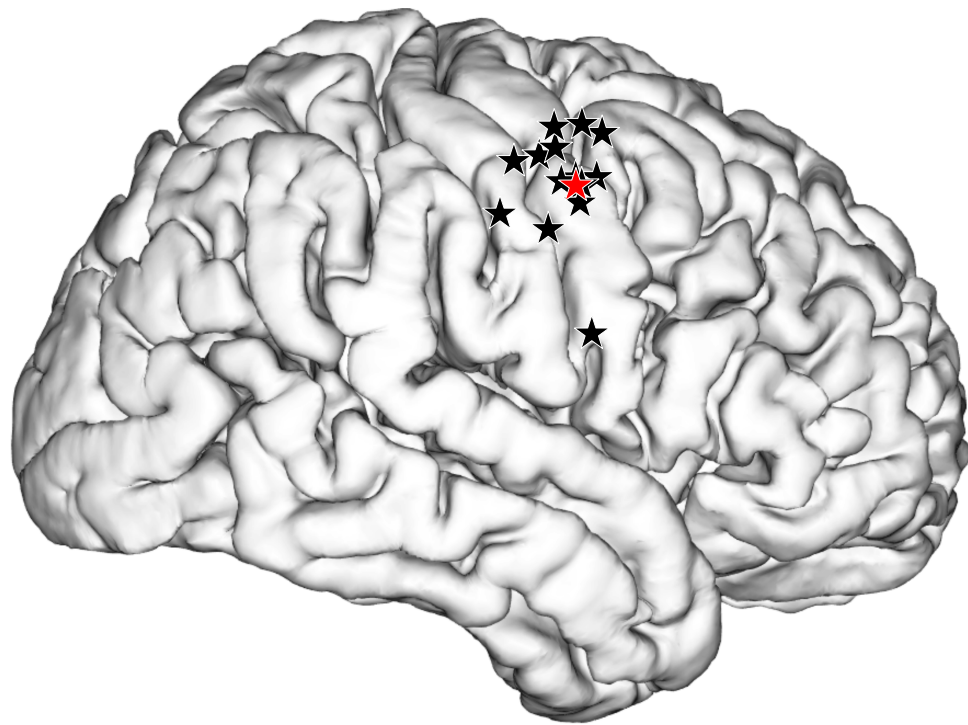
**larynx
response**



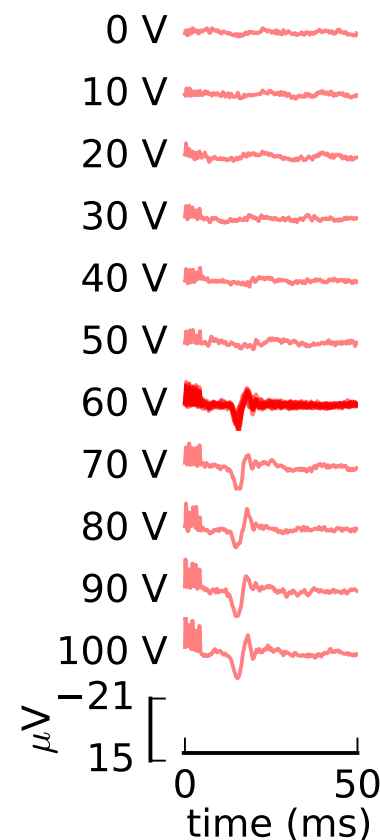
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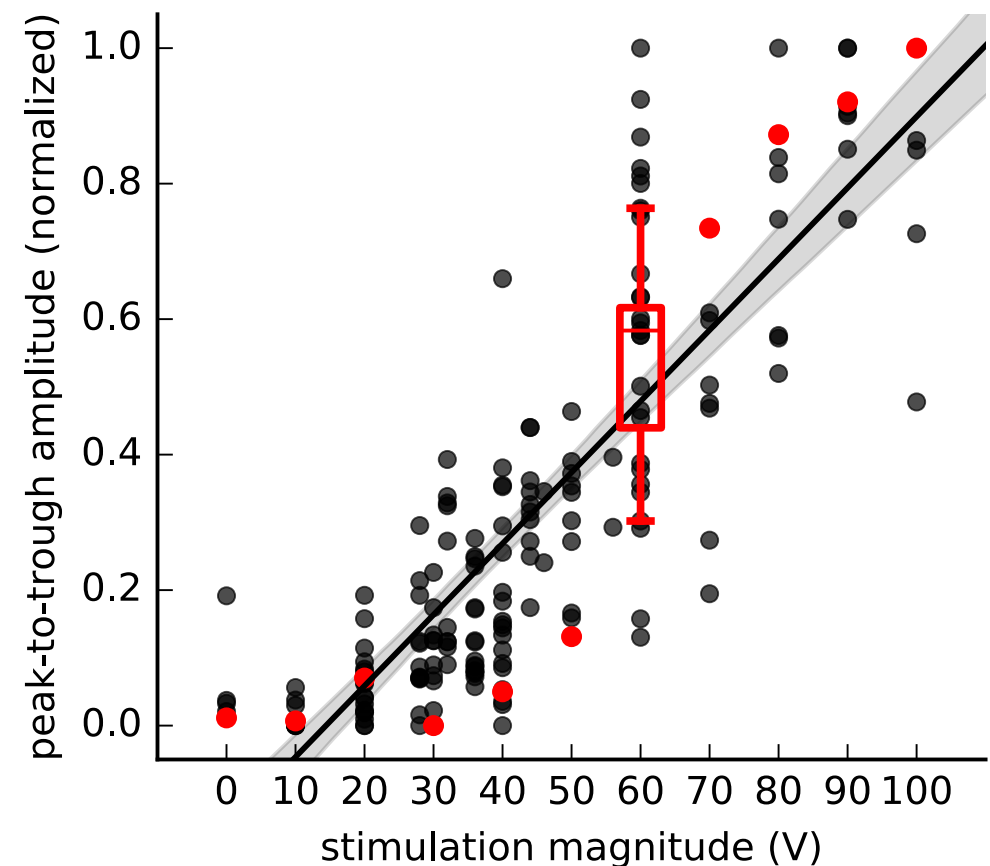
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**larynx
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**Stronger stimulation cause
stronger response**



Cortical Stimulation

“Asleep”

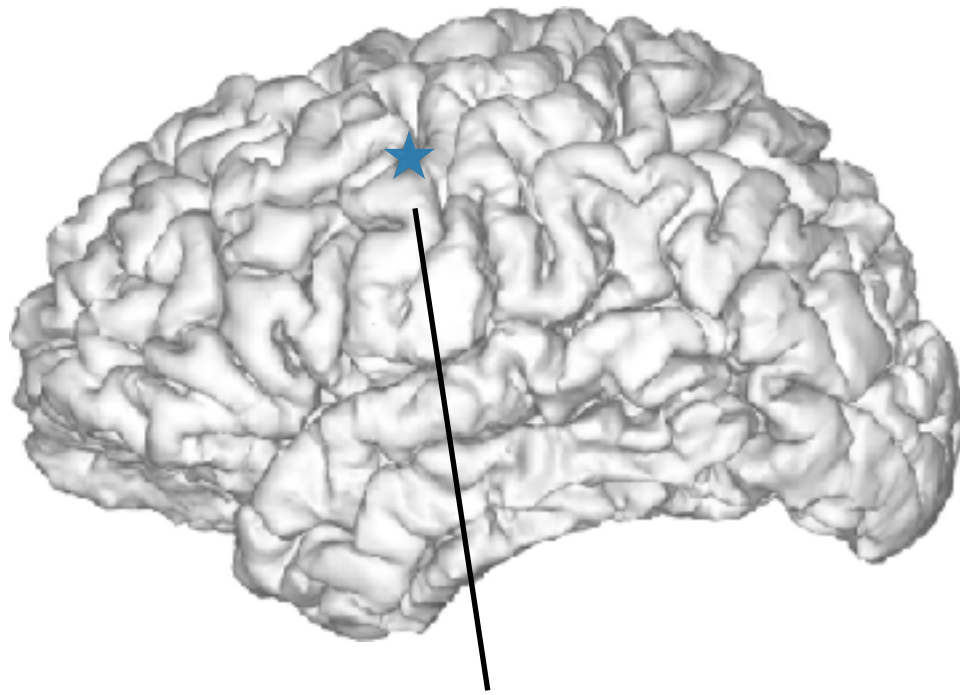
Patient is asleep, with an endotracheal tube in the throat. The tube blocks any vocalizations, and has electrodes on the focal folds that measure contractions.

**Stimulation evokes
laryngeal contraction**

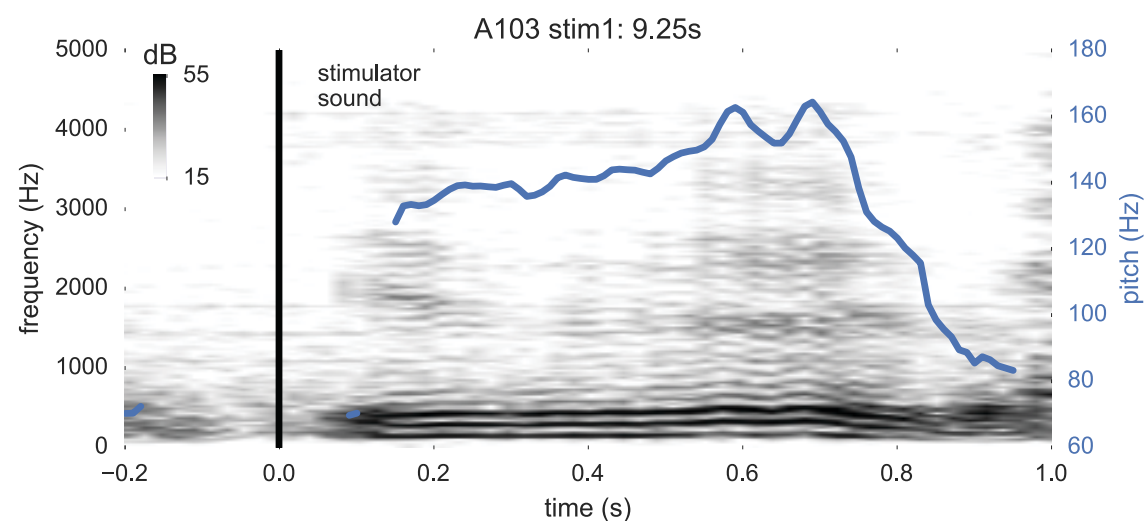
“Awake”

Patients are awake, doing simple tasks like counting and describing the experience of stimulation.

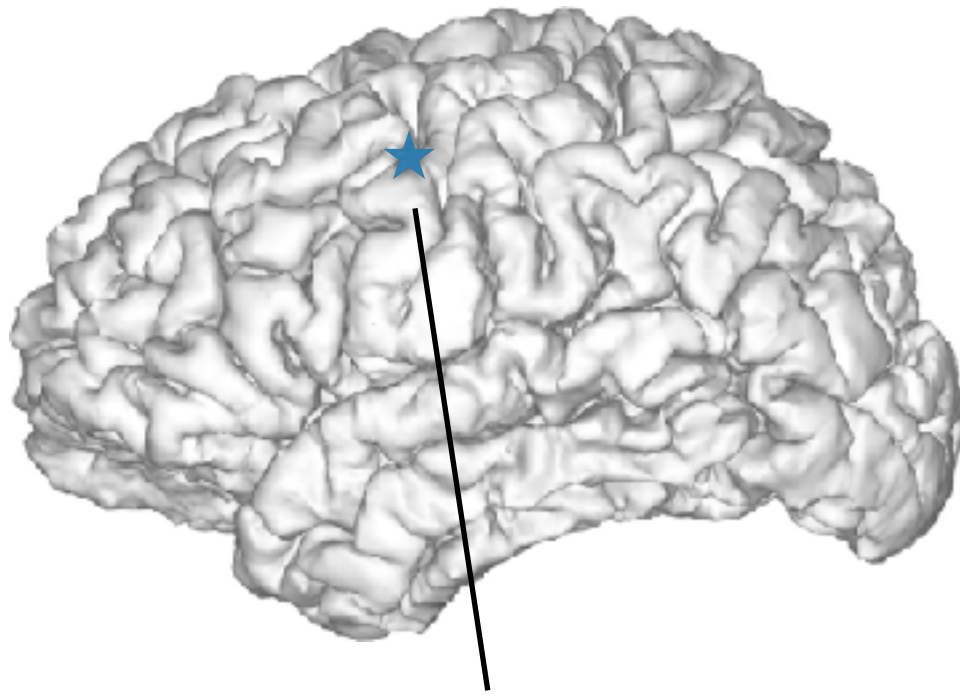
“Awake” dLMC stimulation **evokes vocalization** with varied acoustic structure



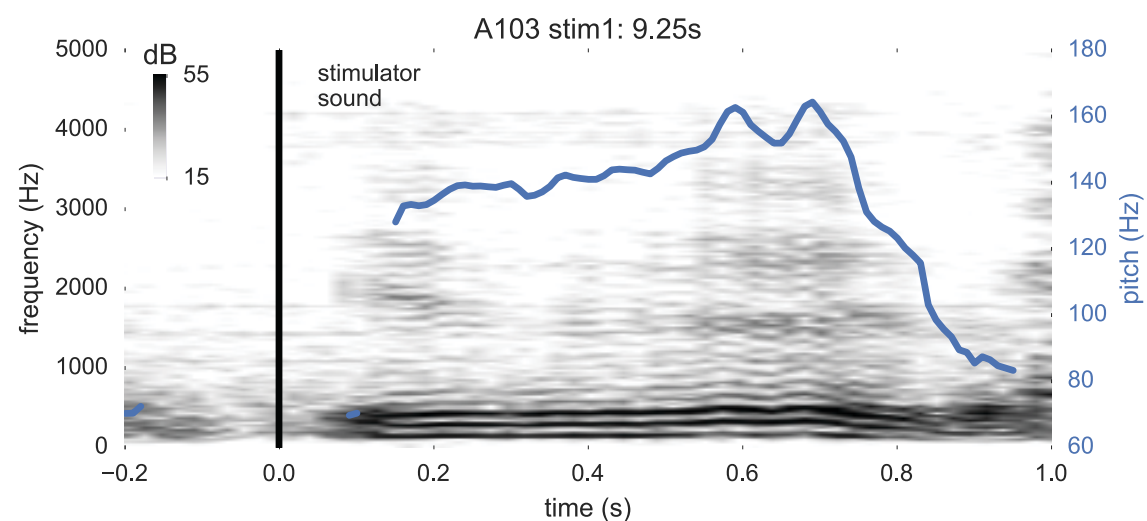
chest voice



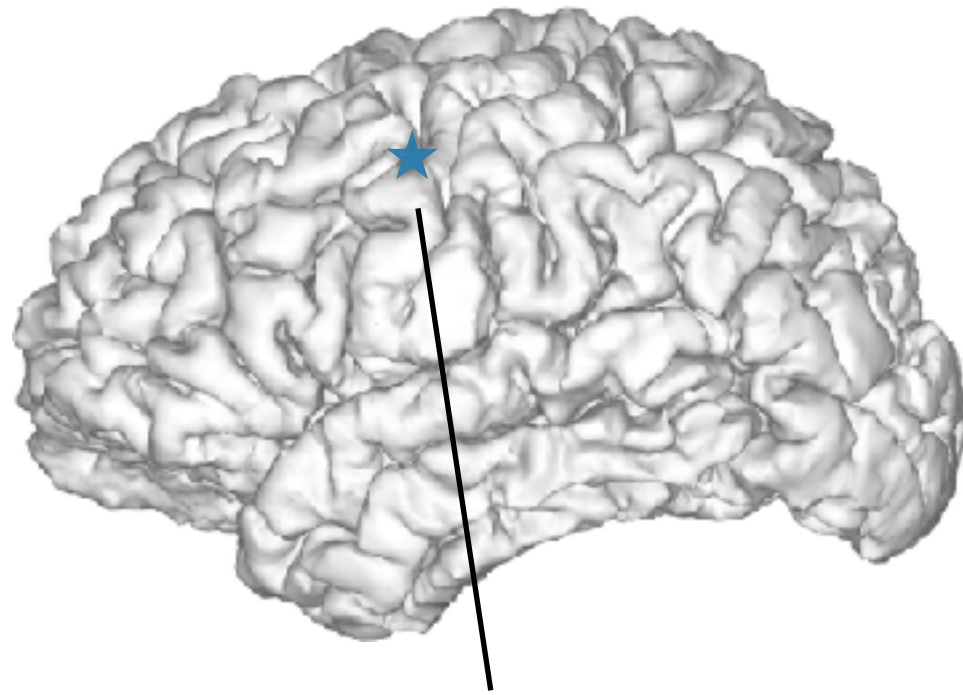
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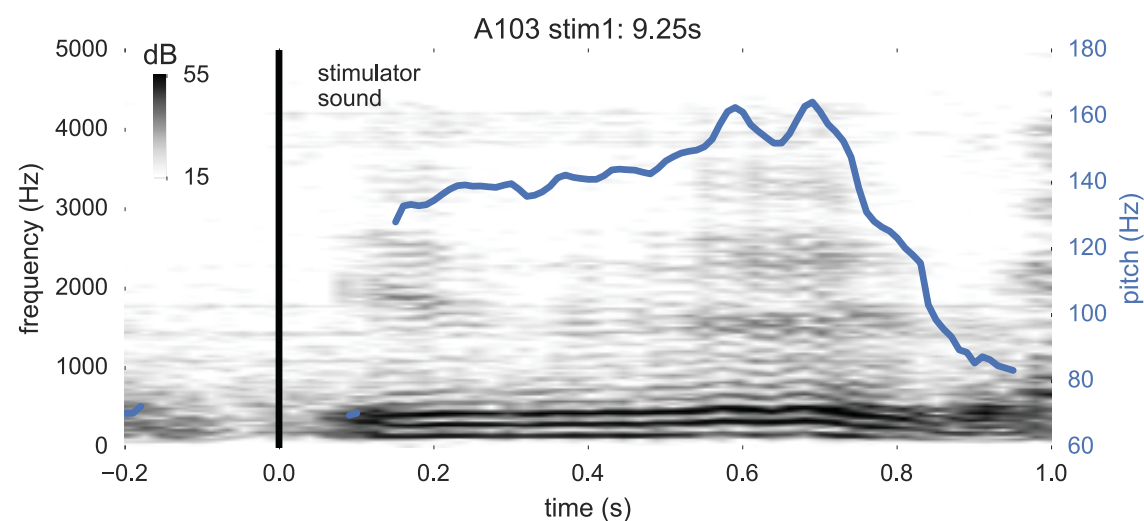
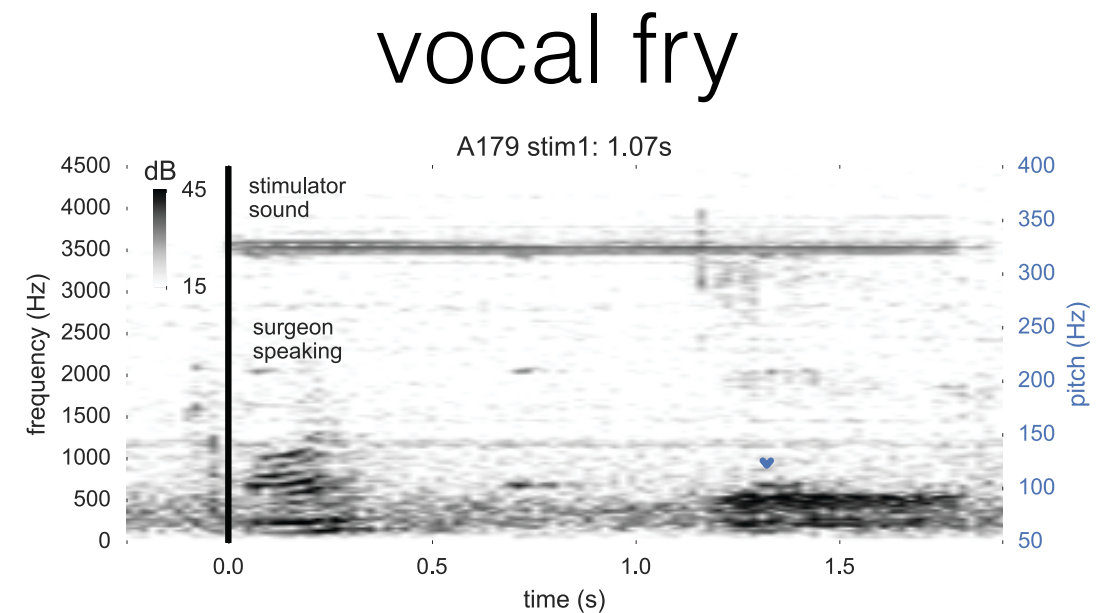
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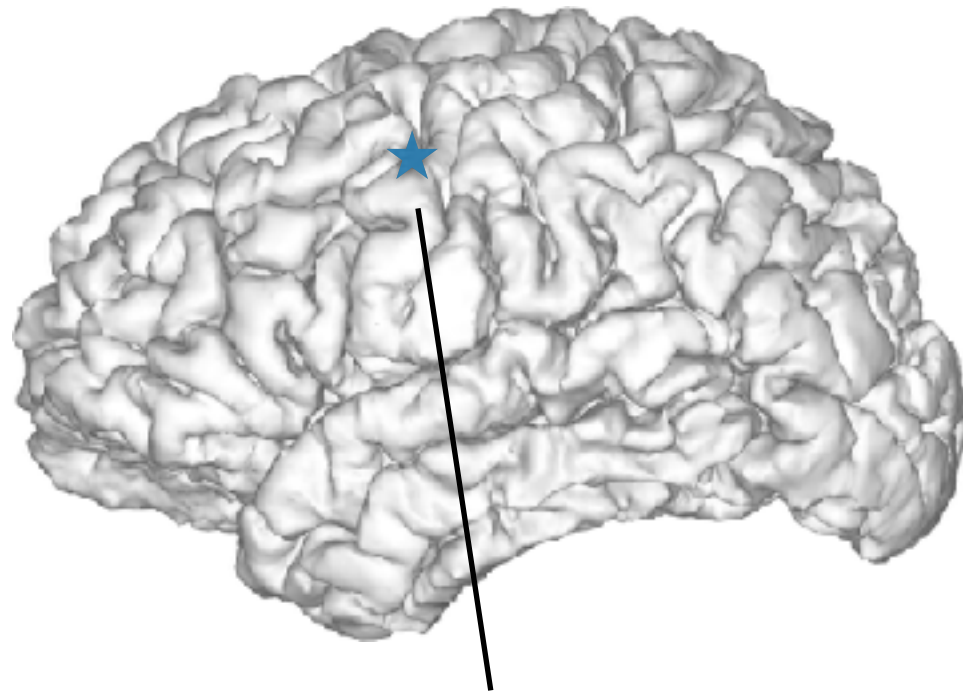
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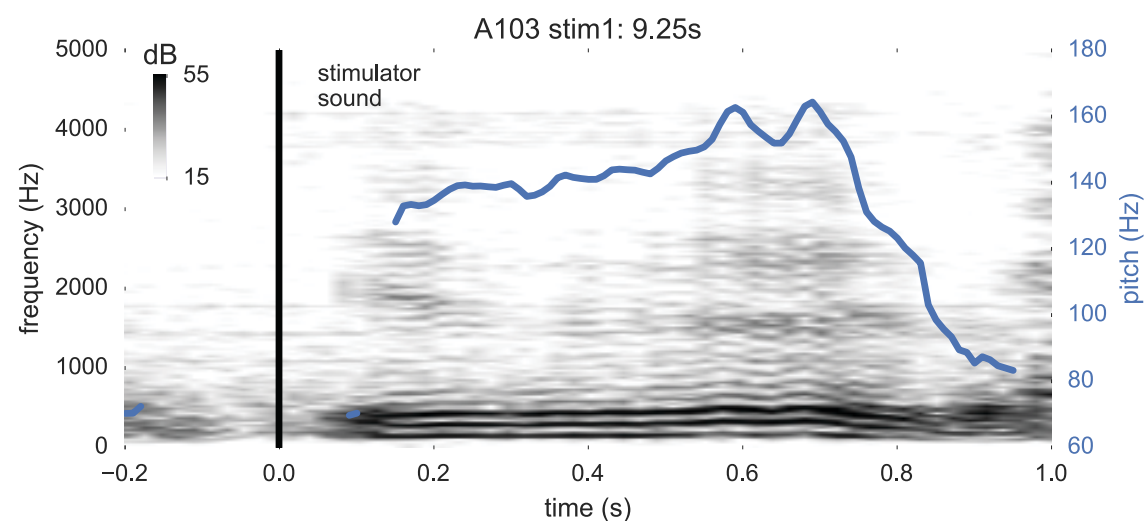
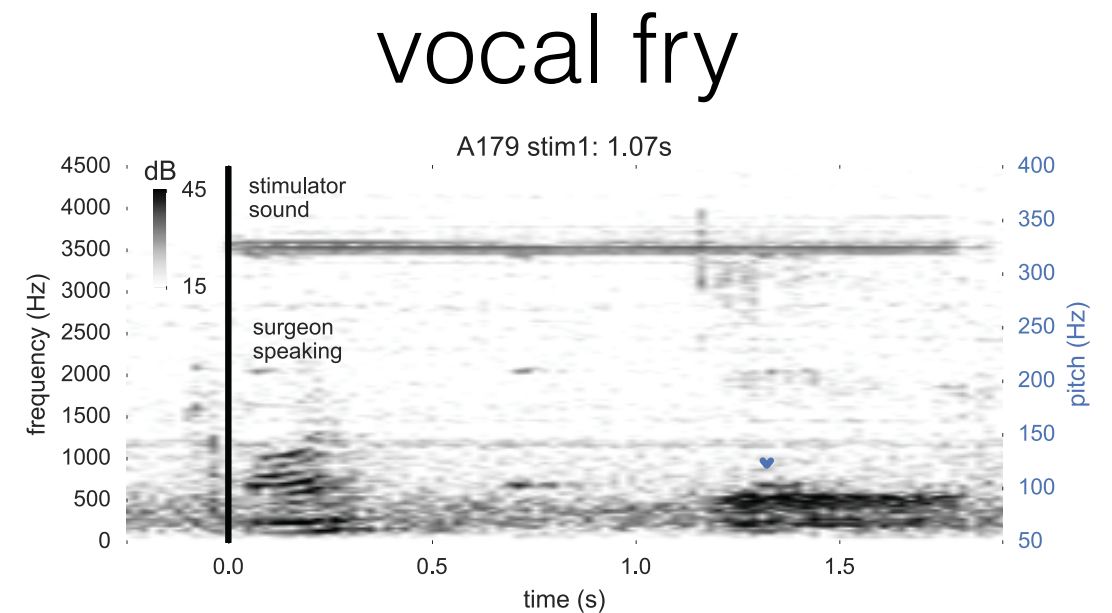
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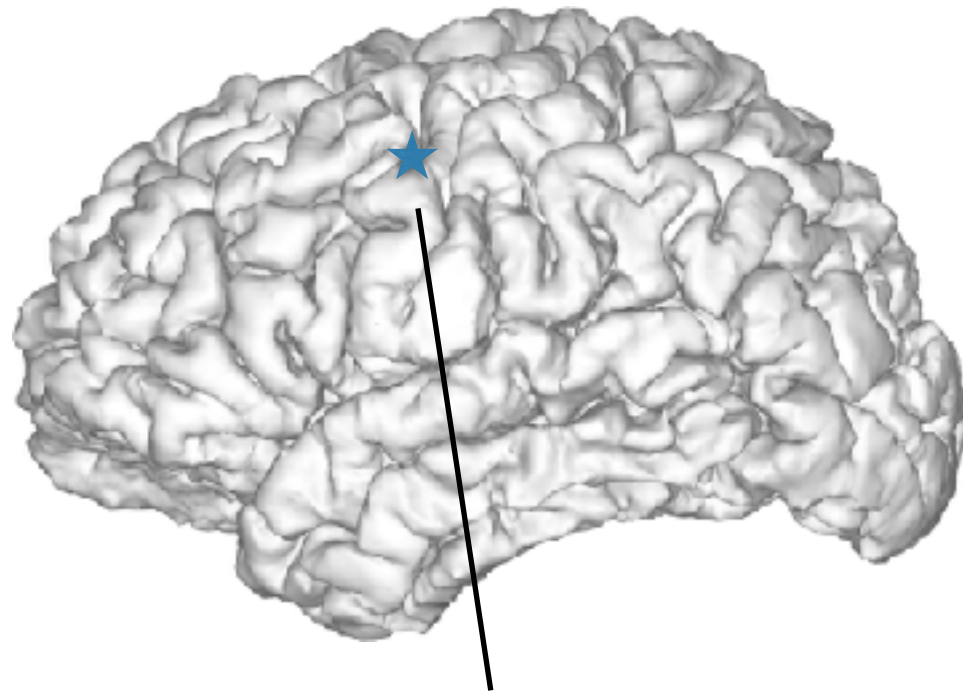
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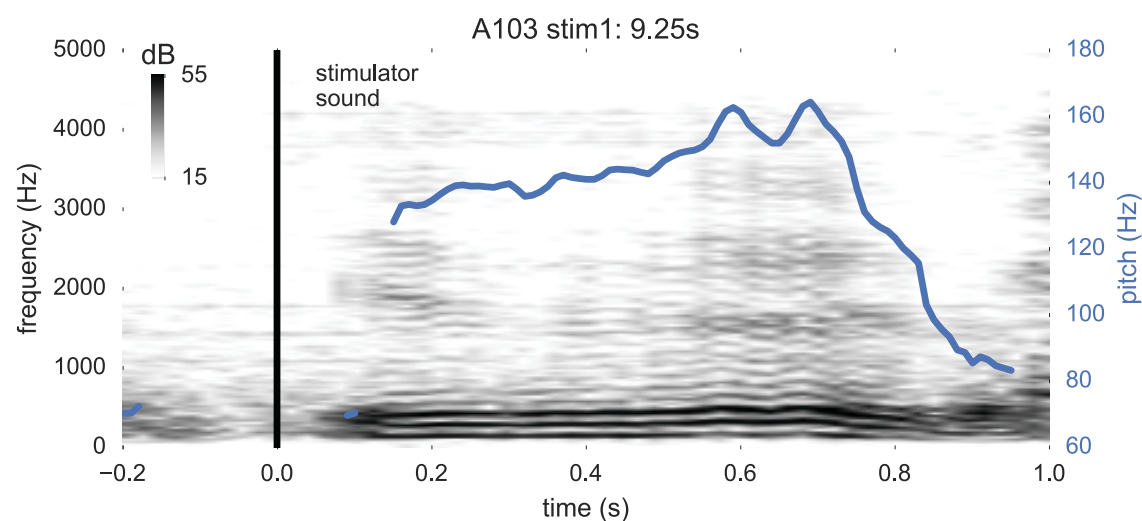
chest voice



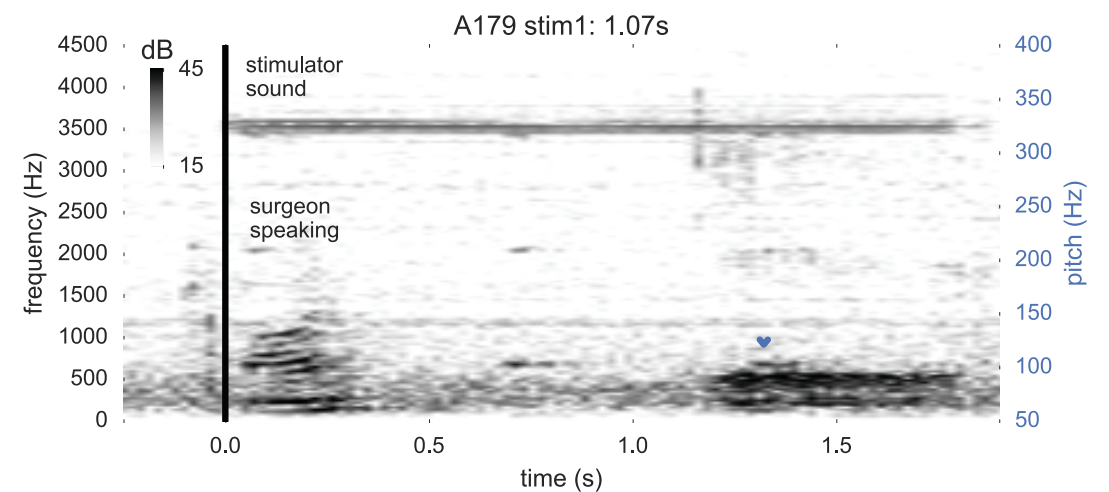
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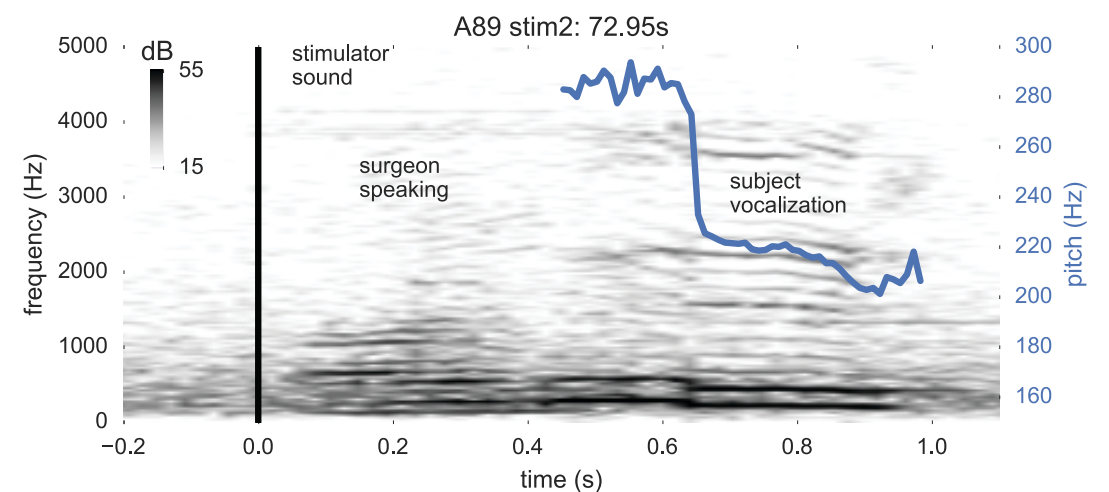
chest voice



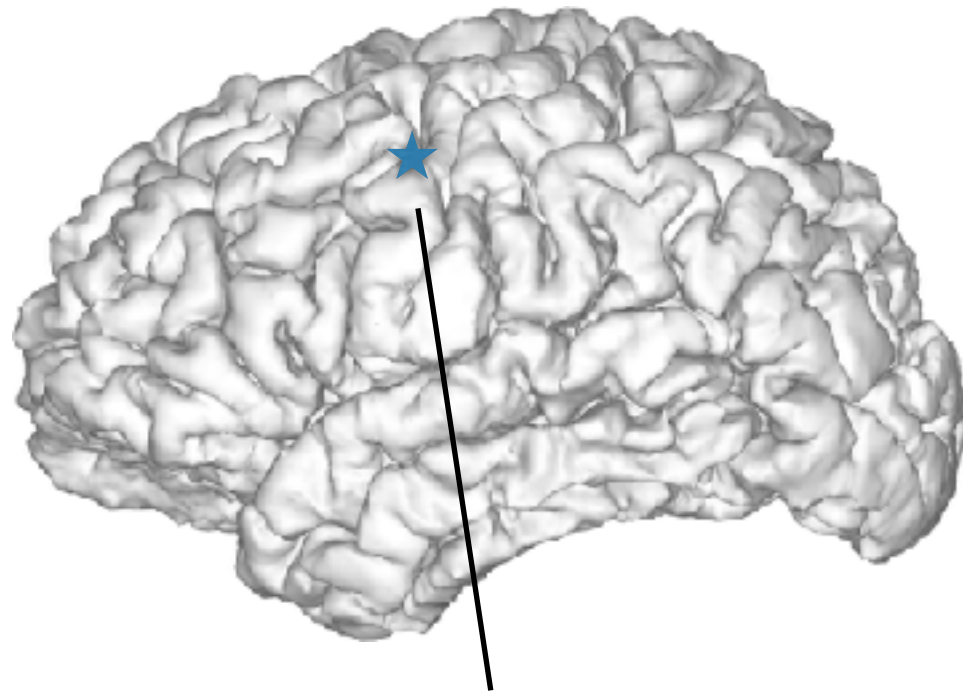
vocal fry



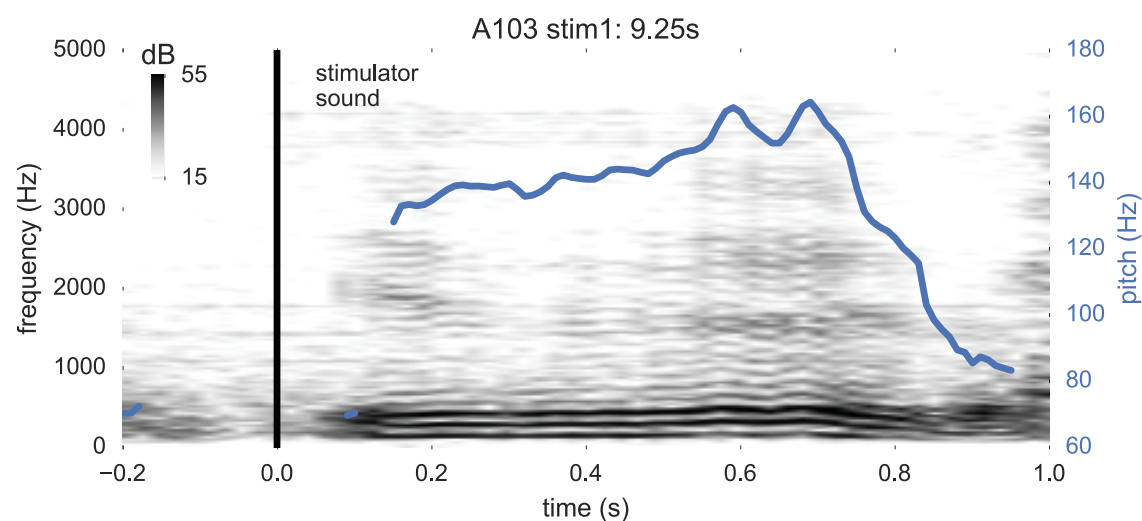
false alto



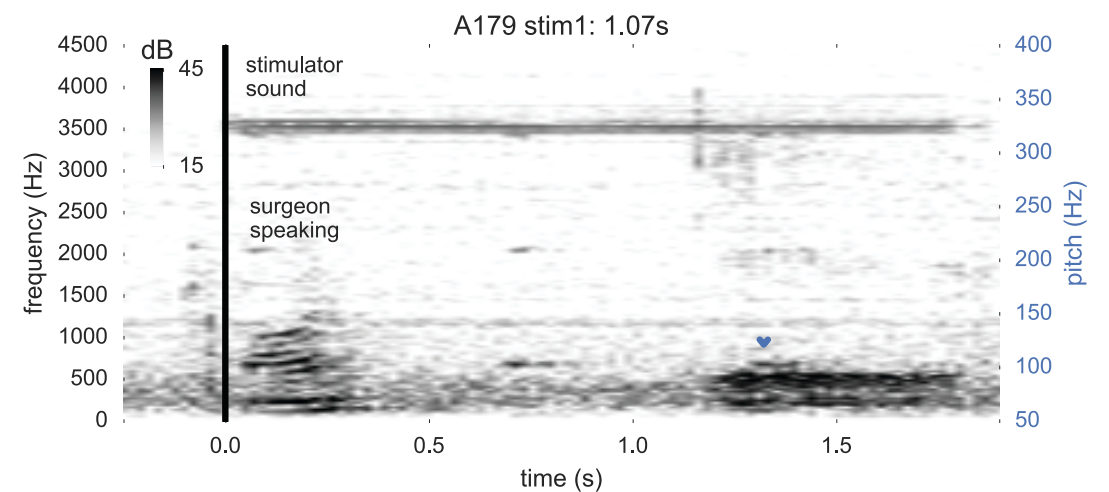
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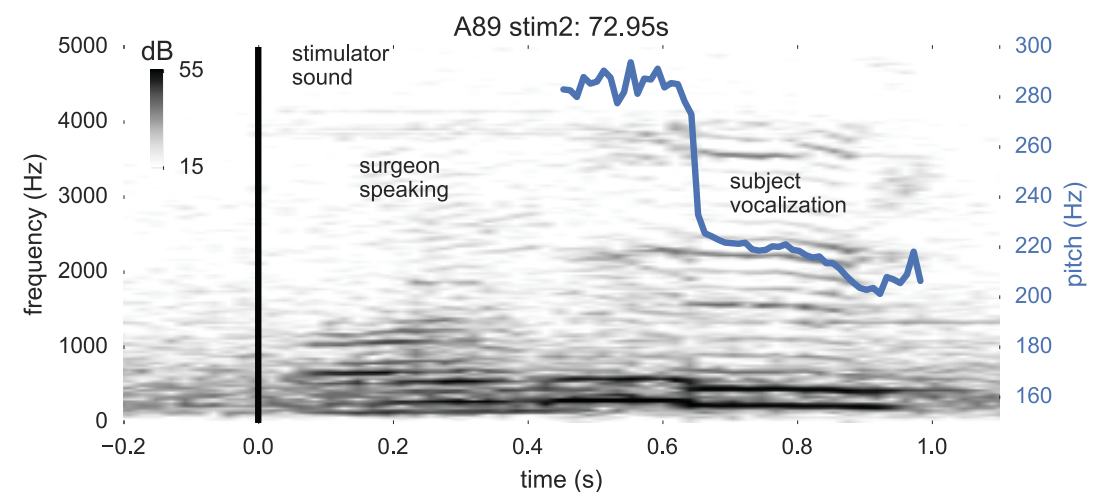
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vocal fry



false alto



Results

The dLMC is a sensorimotor speech area that encodes pitch

Auditory

- Responds to acoustic stimuli and represents vocal pitch

Motor

- Correlated with pitch when speaking and singing
- Monotonically increases with pitch
- Cortical stimulation evokes vocalizations and a graded laryngeal motor response

Role of sensorimotor representation

Role of sensorimotor representation

Two possibilities:

Role of sensorimotor representation

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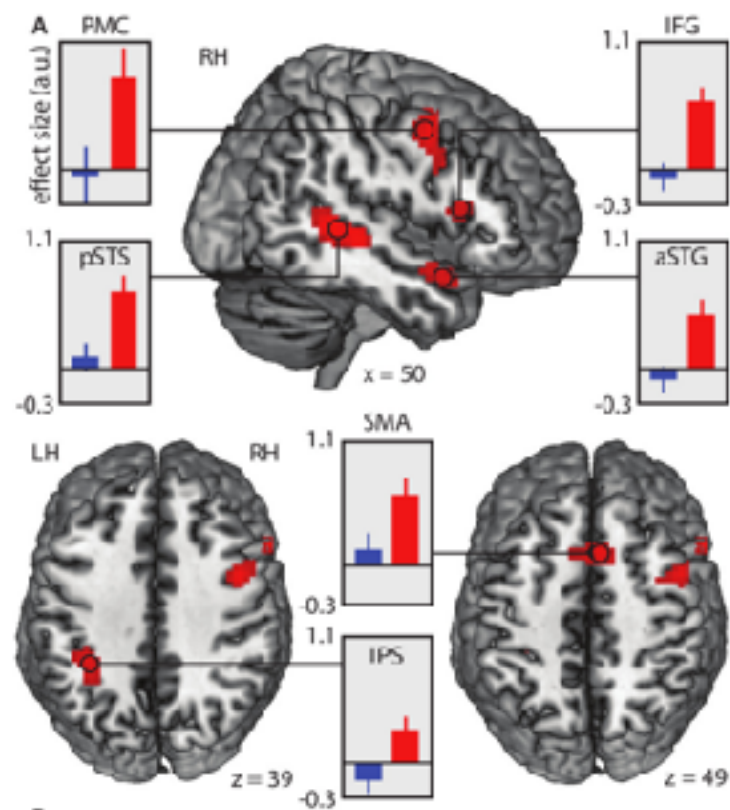
1. Motor theory of speech perception

Role of sensorimotor representation

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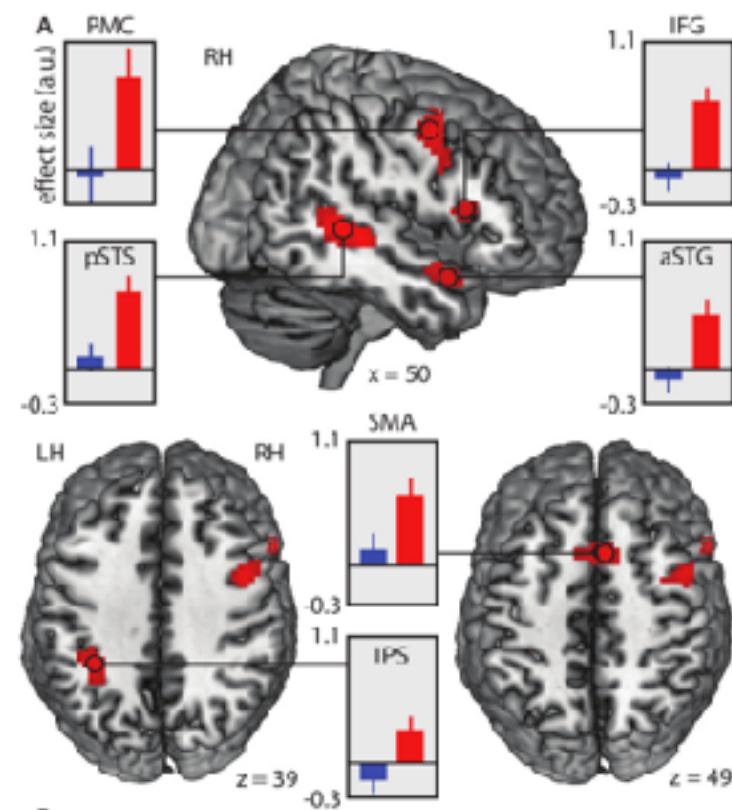
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Evidence for motor theory in dLMC



(Sammler et al. 2015)

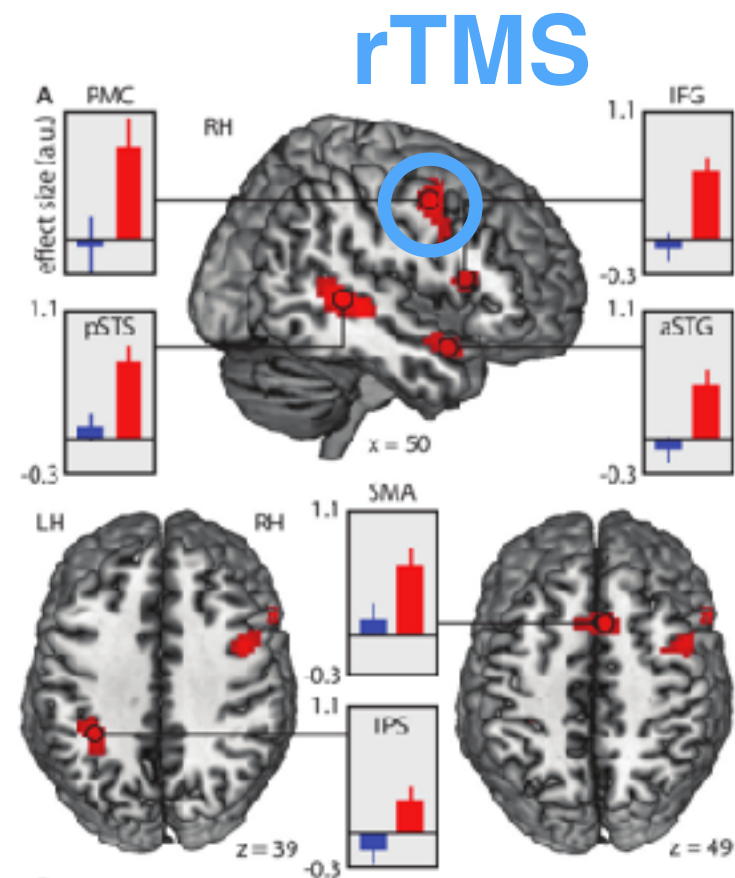
Evidence for motor theory in dLMC



- The right PMC is more active when focusing on pitch

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Evidence for motor theory in dLMC



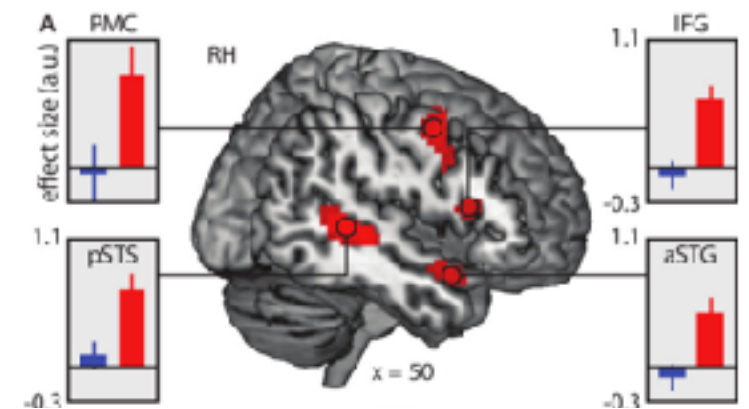
- The right PMc is more active when focusing on pitch
- rTMS over right PMc worsens pitch discrimination but not phoneme discrimination

(Sammler et al. 2015)

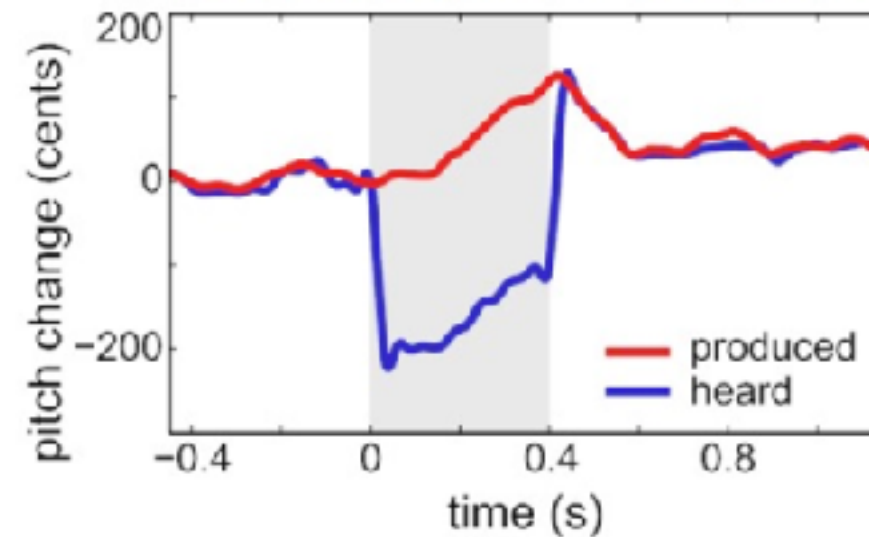
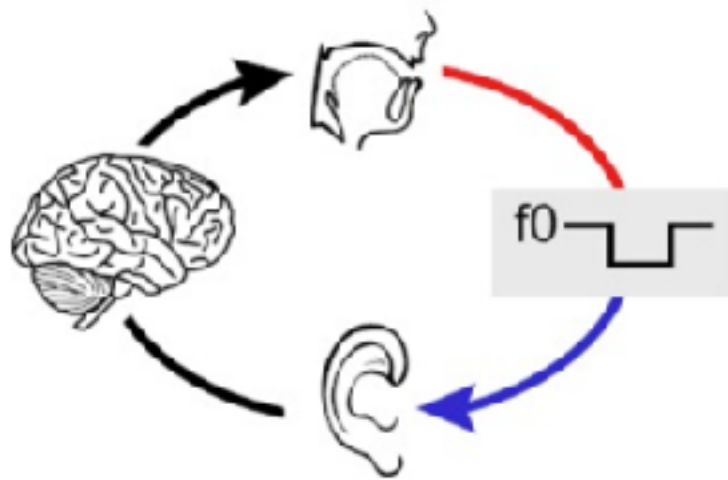
Role of sensorimotor representation

Two possibilities:

1. Motor theory of speech perception
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2. Feedback control
 - Why passive listening response?
Seems wasteful.

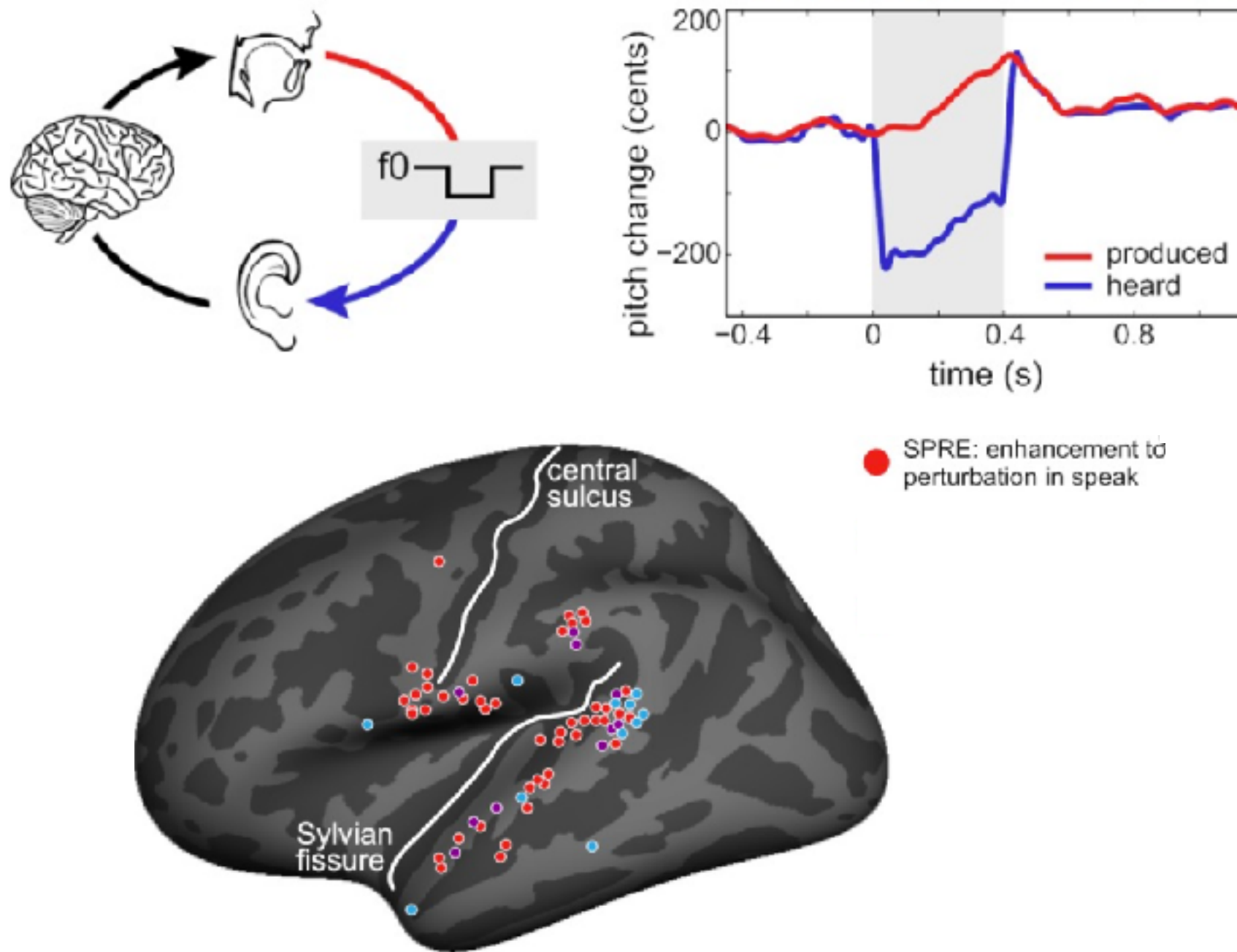


Sensorimotor role: evidence for feedback control in vLMC, not dLMC



(Chang, Niziolek et al. 2013)

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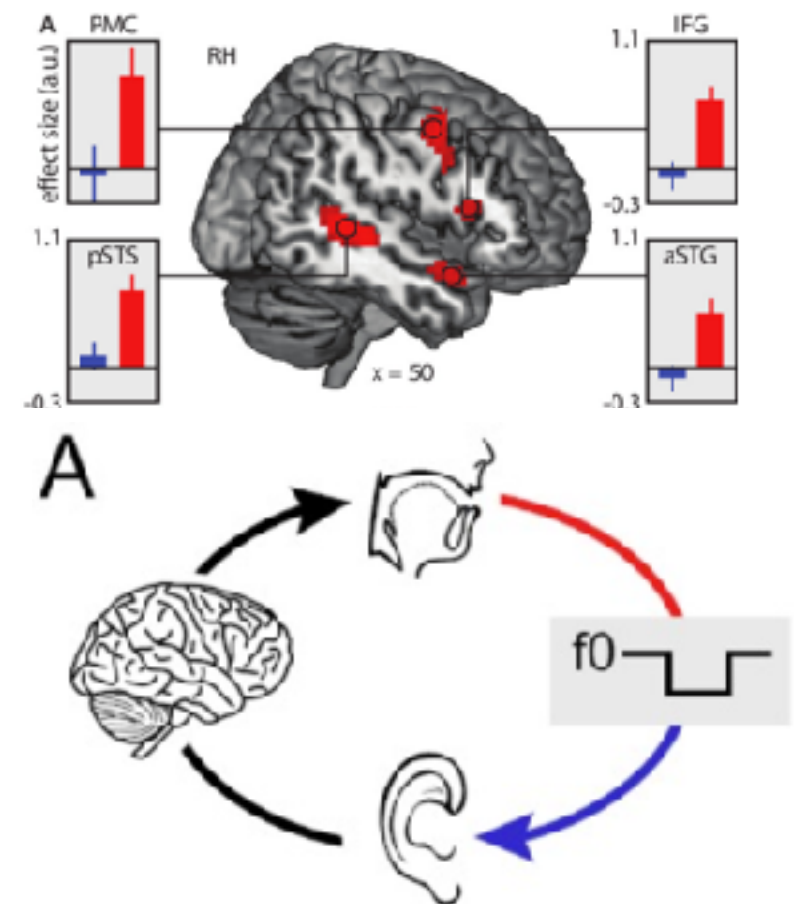


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Role of sensorimotor representation

Two possibilities:

1. Motor theory of speech perception
 - Specifically for voice/pitch control
2. Feedback control
 - Why passive listening response? Seems wasteful.



Either way, merging of motor and auditory pitch representation could be key to development of speech

Estimating produced vocal pitch from brain activity

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Some people are locked in and unable to move at all

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With a speech prosthetic we could be able to record their intended speech and provide an alternate way for them to to **communicate**

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With a speech prosthetic we could be able to record their intended speech and provide an alternate way for them to to **communicate**

So how well could we **infer prosody**?

Estimating produced vocal pitch from brain activity: Kalman Filter

$$\begin{aligned} \mathbf{x}_{t+1} &= \mathbf{A}\mathbf{x}_t + \mathbf{w}_t & \mathbf{w}_\bullet &\sim \mathcal{N}(0, \mathbf{Q}) \\ y_t &= \mathbf{C}\mathbf{x}_t + v_t & v_\bullet &\sim \mathcal{N}(0, \mathbf{R}) \end{aligned}$$

x: pitch

y: neural activity

t: time

w, v: noise

Estimating produced vocal pitch from brain activity: Kalman Filter

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models neural encoding of pitch

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Estimating produced vocal pitch from brain activity: Kalman Filter

models dynamics of pitch

$$\begin{array}{l} \overbrace{x_{t+1} = Ax_t + w_t} \\ y_t = Cx_t + v_t \\ \underbrace{\hspace{10em}} \end{array} \quad \begin{array}{l} w_{\bullet} \sim \mathcal{N}(0, Q) \\ v_{\bullet} \sim \mathcal{N}(0, R) \end{array}$$

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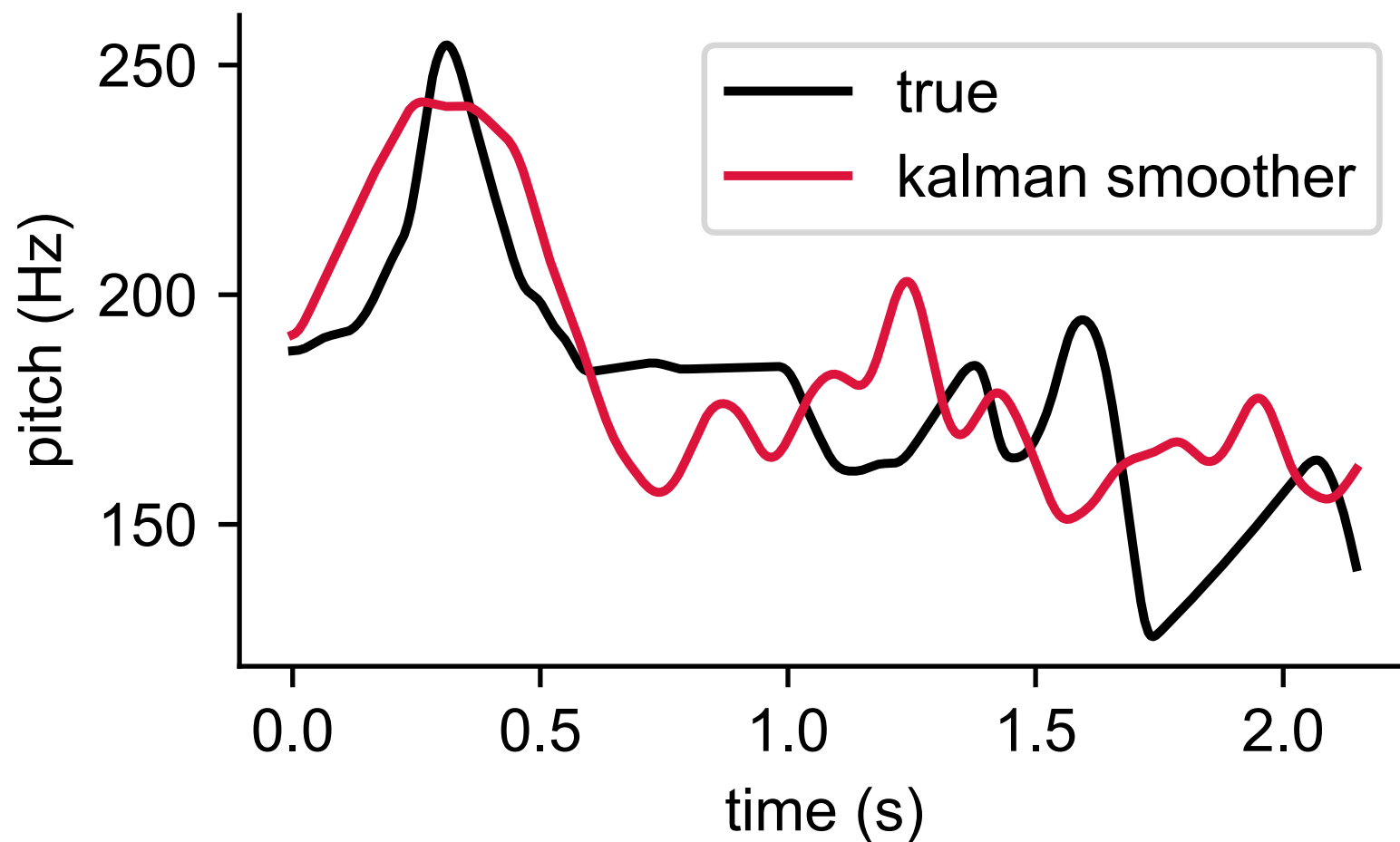
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Estimating produced vocal pitch from brain activity: Kalman Filter

example sentence



models dynamics of pitch

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models neural encoding of pitch

correlation across
held out sentences = 0.7

Estimating **word of emphasis** directly

Linear Discriminant Analysis

$$y|w = i \sim \mathcal{N}(\mu_i, \Sigma)$$

Estimating **word of emphasis** directly

Linear Discriminant Analysis

neural activity



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Estimating **word of emphasis** directly

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word of emphasis

Estimating **word of emphasis** directly

Linear Discriminant Analysis

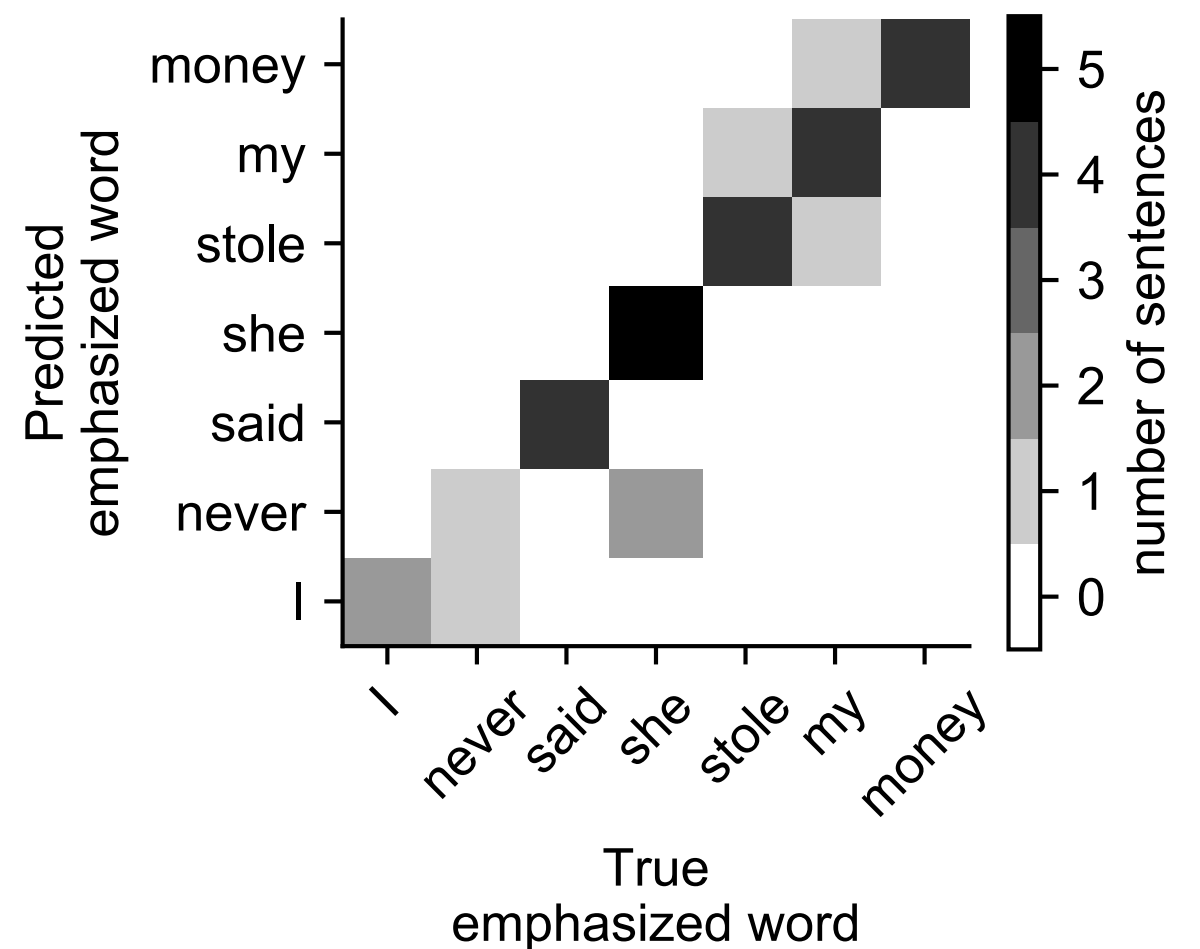
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$$y|w = i \sim \mathcal{N}(\mu_i, \Sigma)$$

word of emphasis

Classification Accuracy (80%)



The Chang Lab

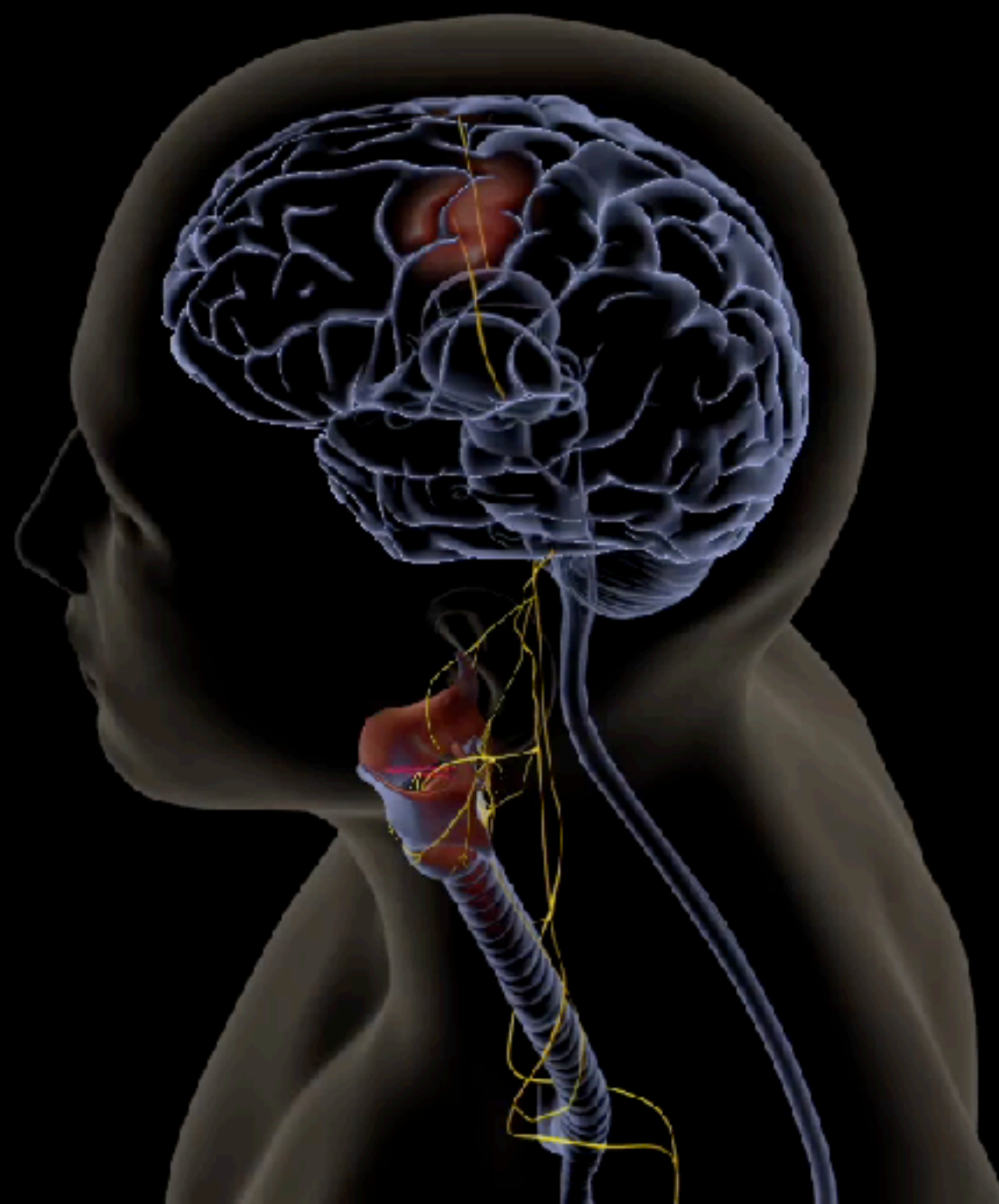


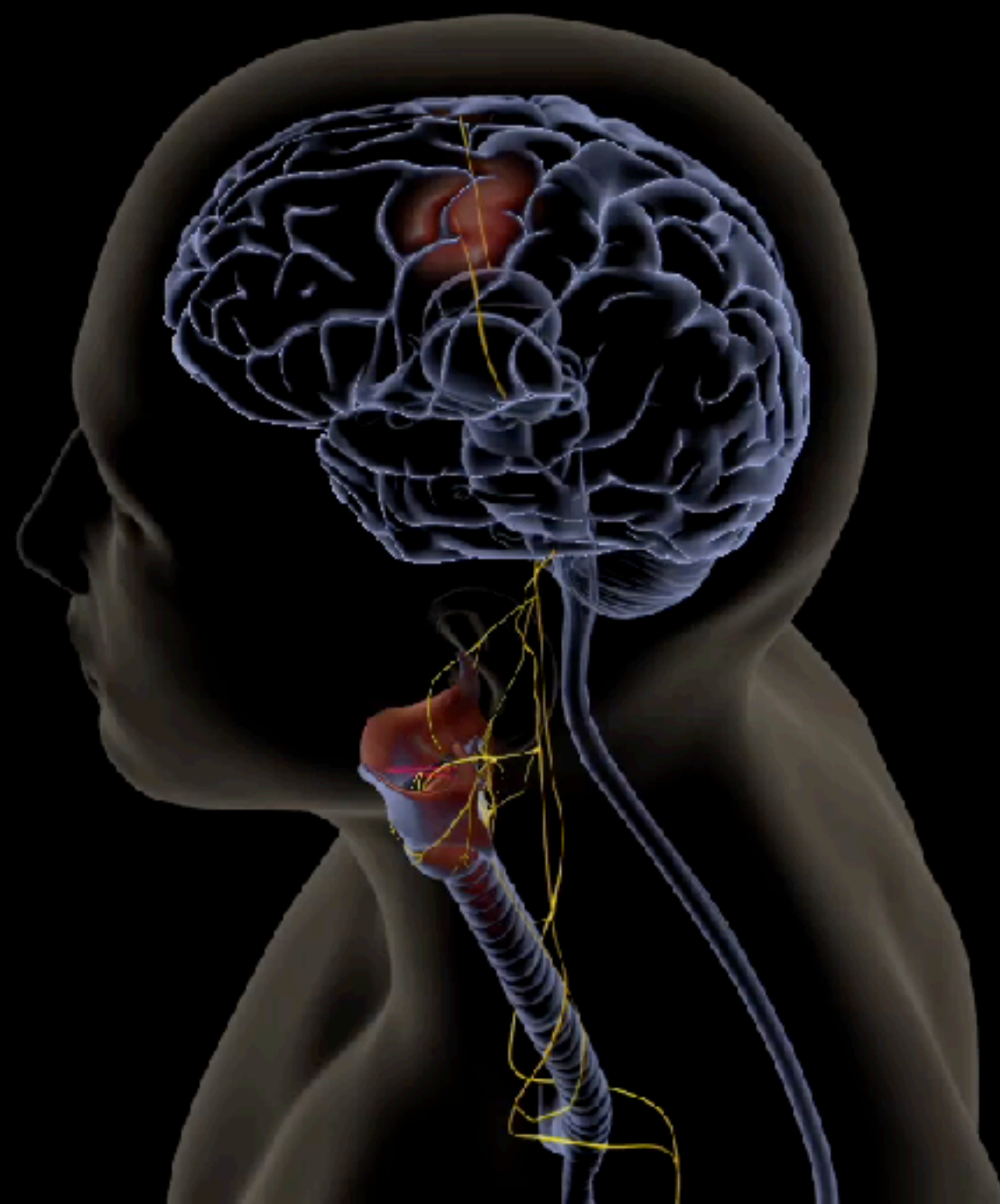
Jonathan
Breshears

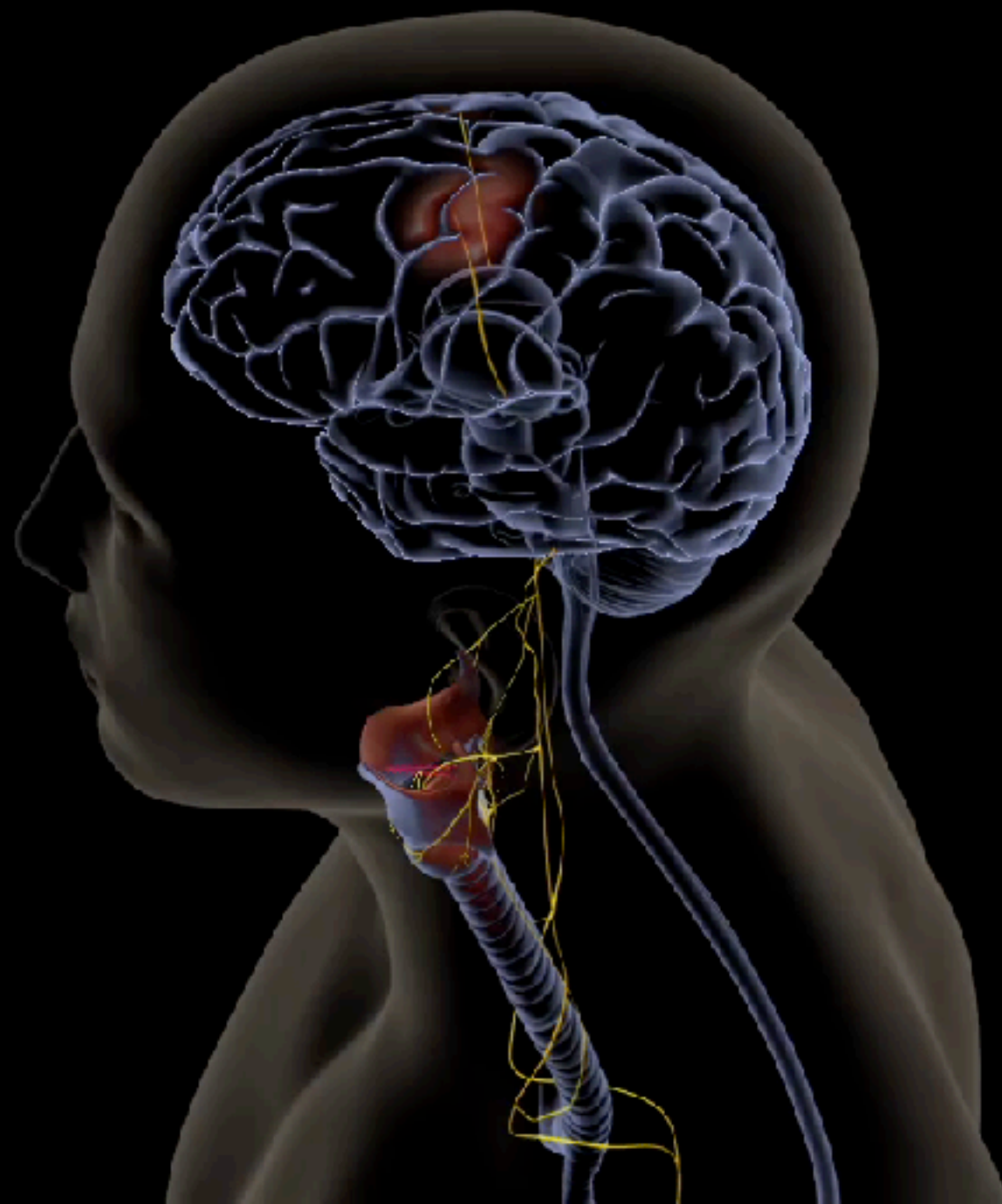


Matt Leonard





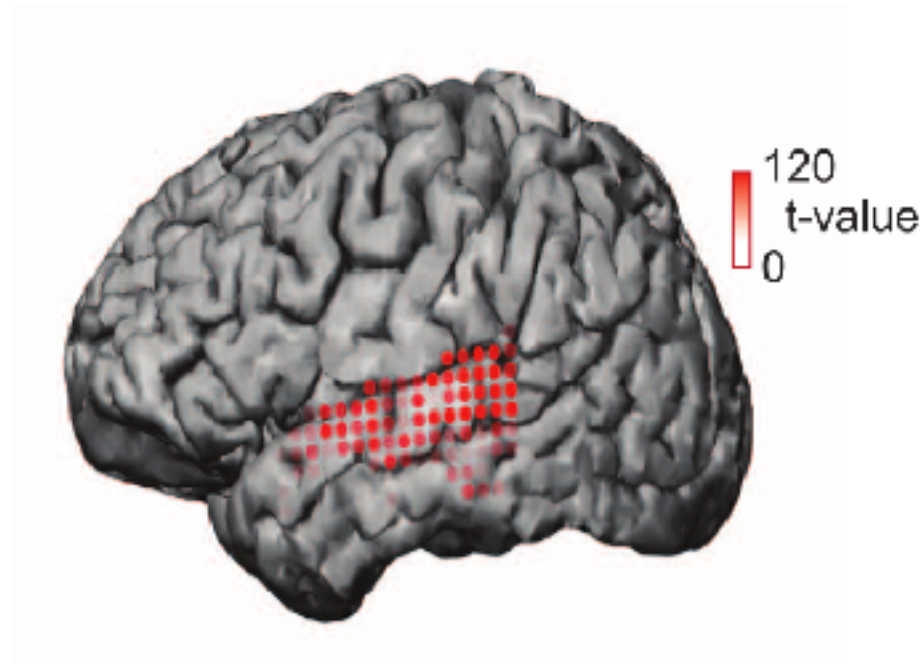




Questions?

Previous work: ECoG activity related to **speech sounds**

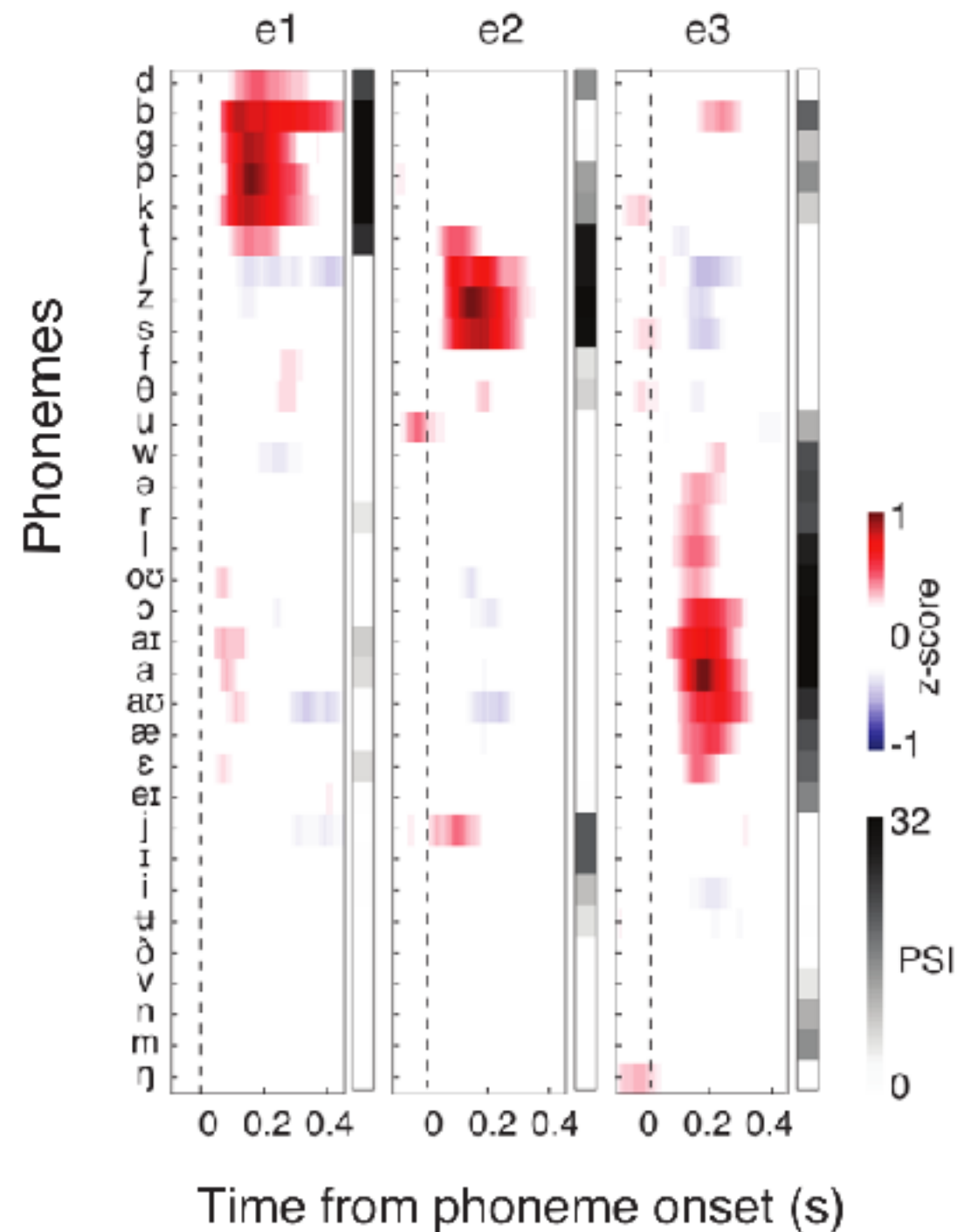
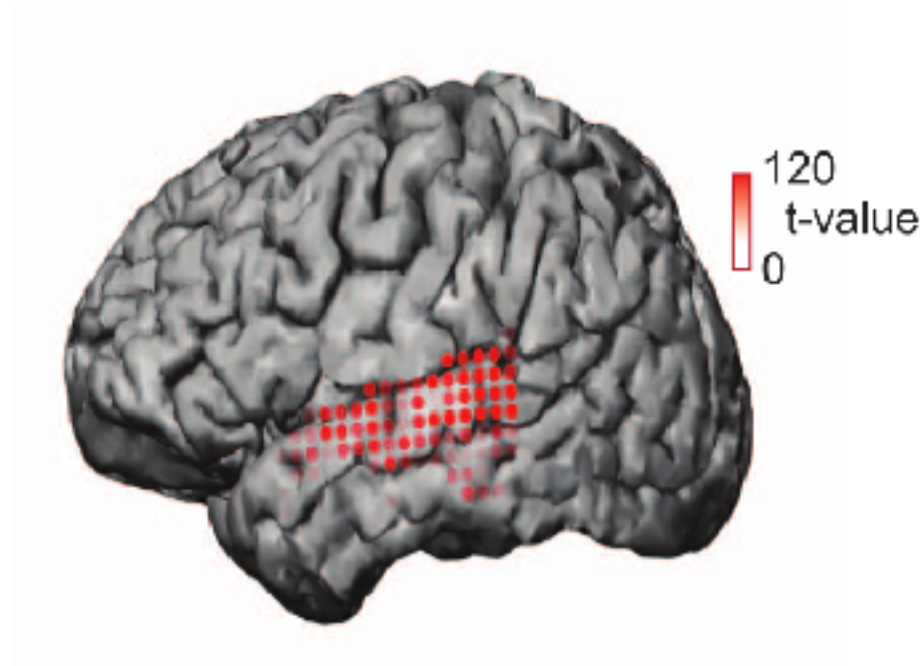
Task: Passive listening to continuous speech corpus (which is phonetically transcribed)



(Mesgarani et al., *Science*, 2014)

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Cortical Representation of pitch **perception**

(Claire Tang et al.,
Science 2017)

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1. How is intonation represented in non-primary auditory cortex on the STG?

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1. How is intonation represented in non-primary auditory cortex on the STG?
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Cortical Representation of pitch **perception**

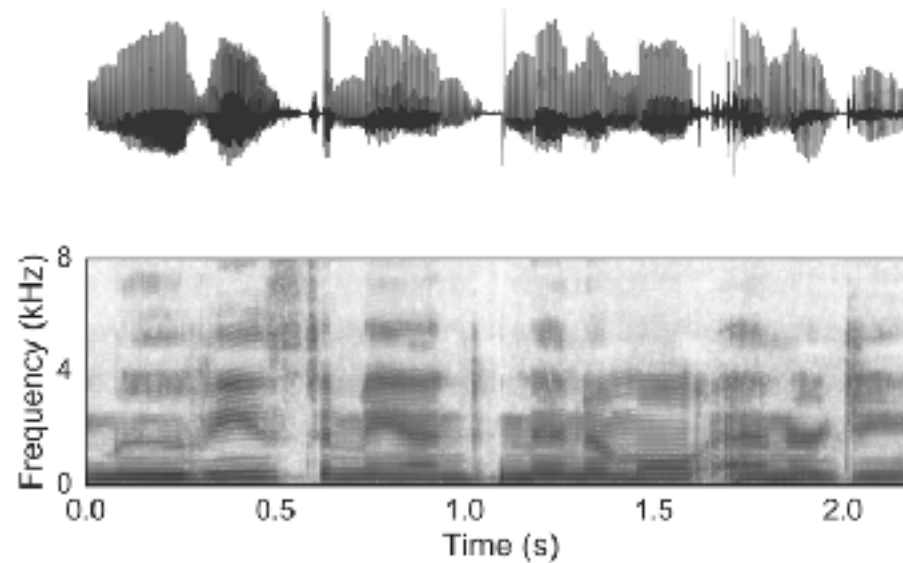
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 - Absolute vs. relative pitch?
- (Claire Tang et al.,
Science 2017)

Stimuli

- designed to vary intonation, phonetic content, and speaker independently.

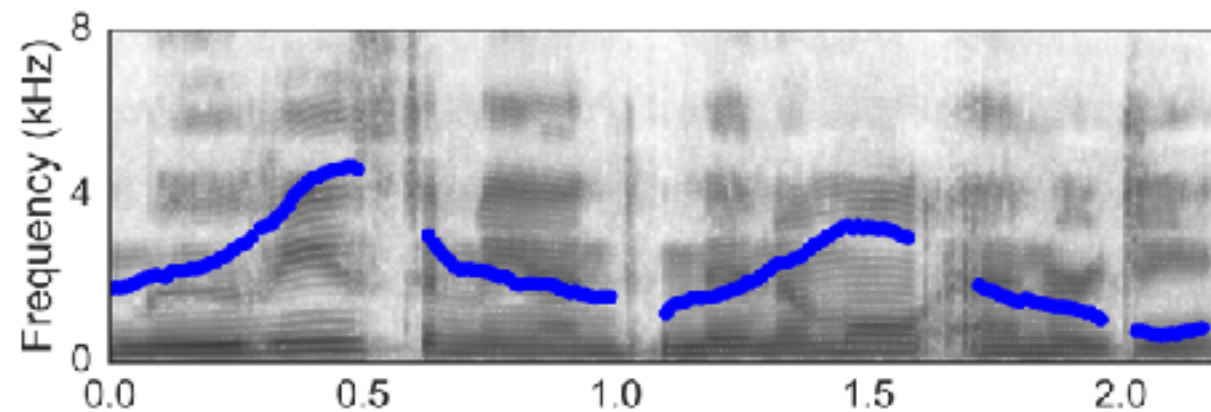
4 intonation contours x 4 sentences x 3 speakers

Four intonation conditions have distinct pitch contours and linguistic meaning

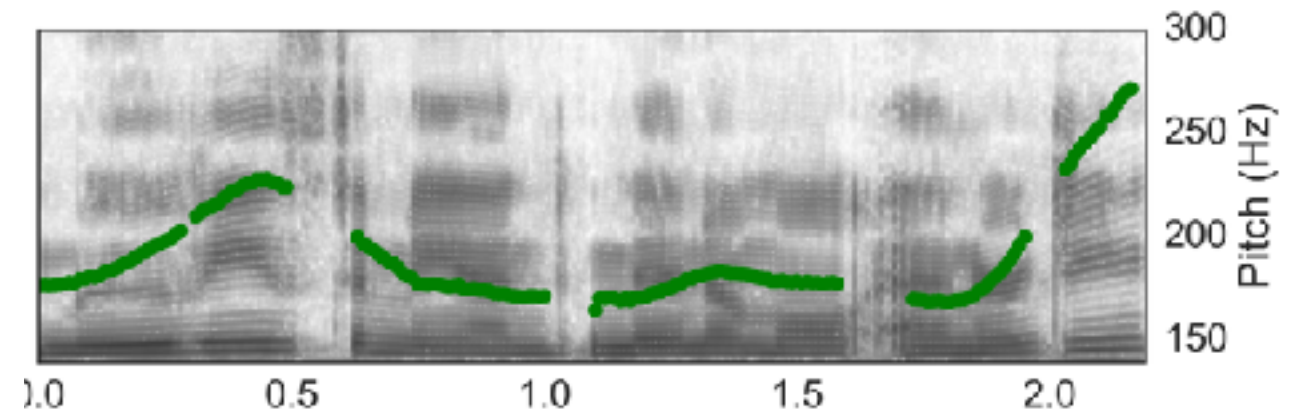


Neutral

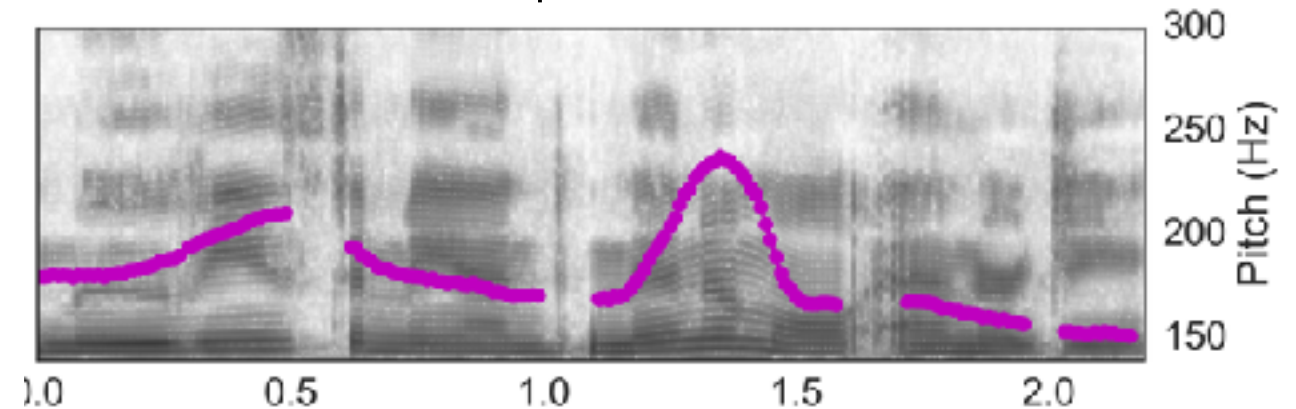
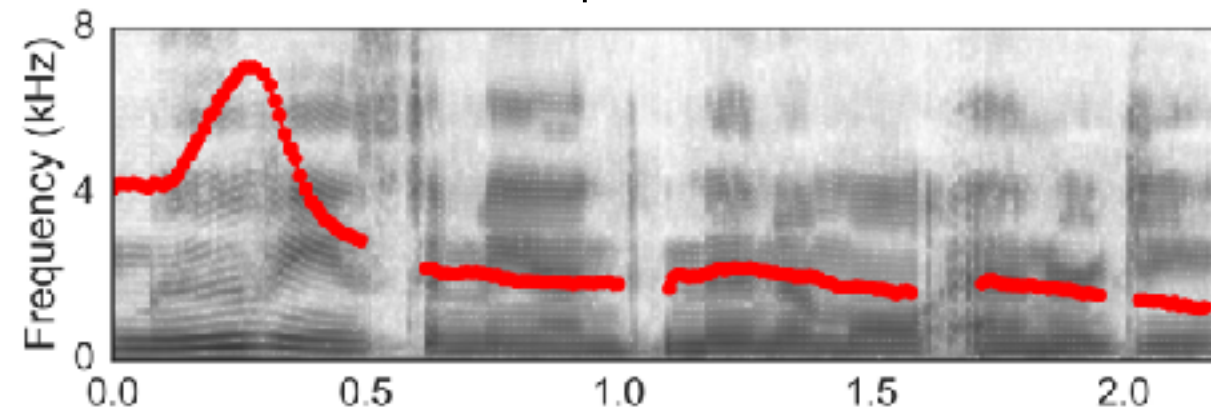
Question



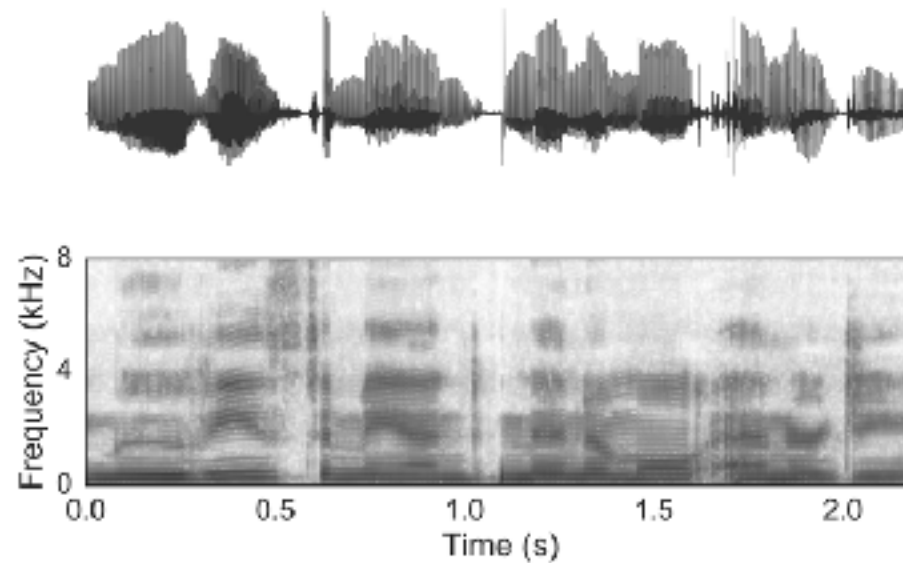
Emphasis 1



Emphasis 3

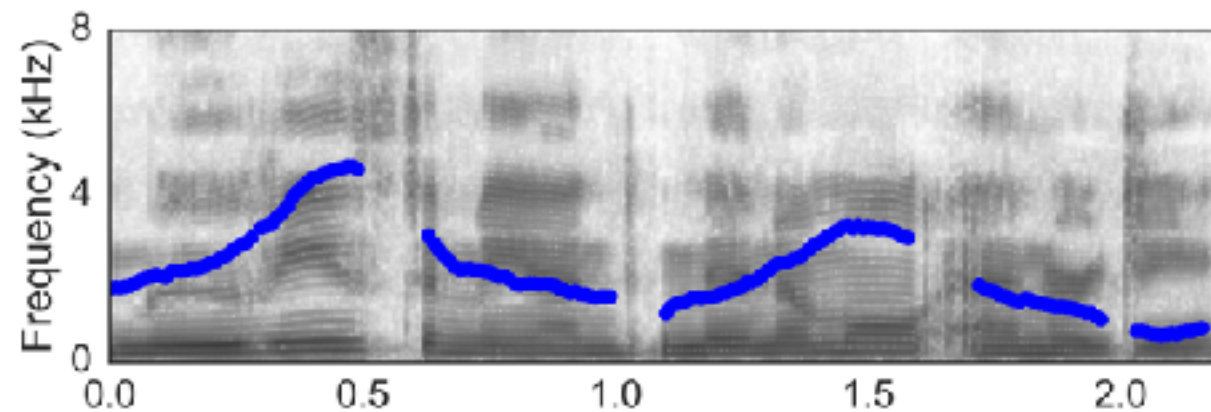


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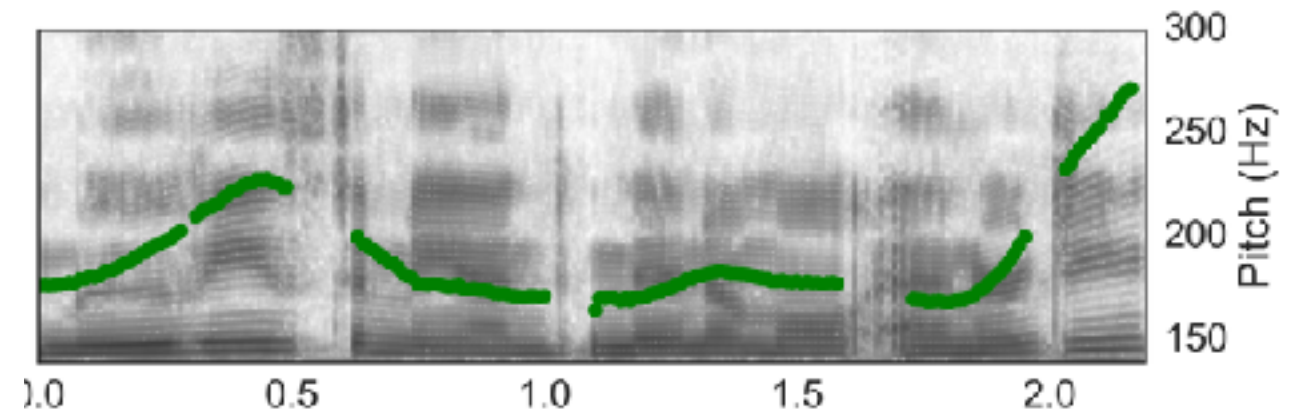


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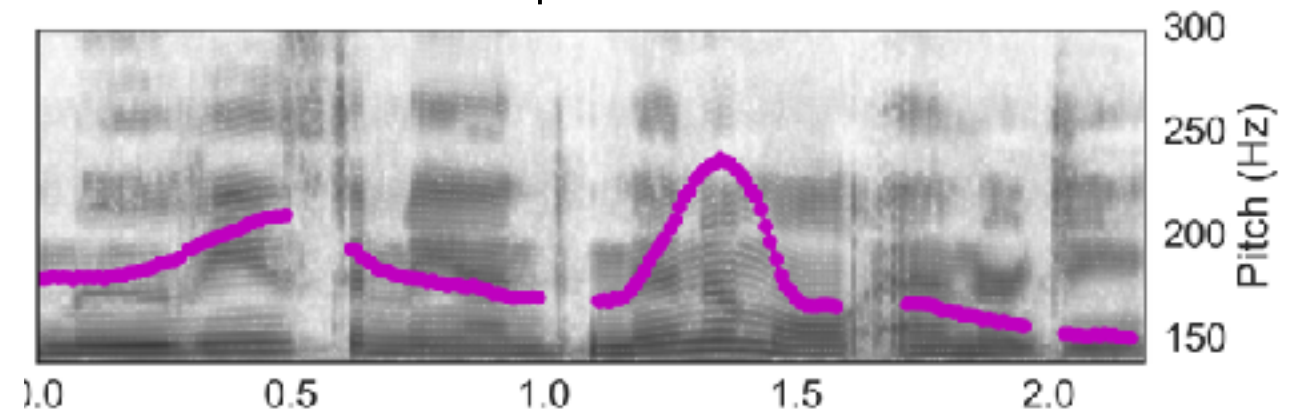
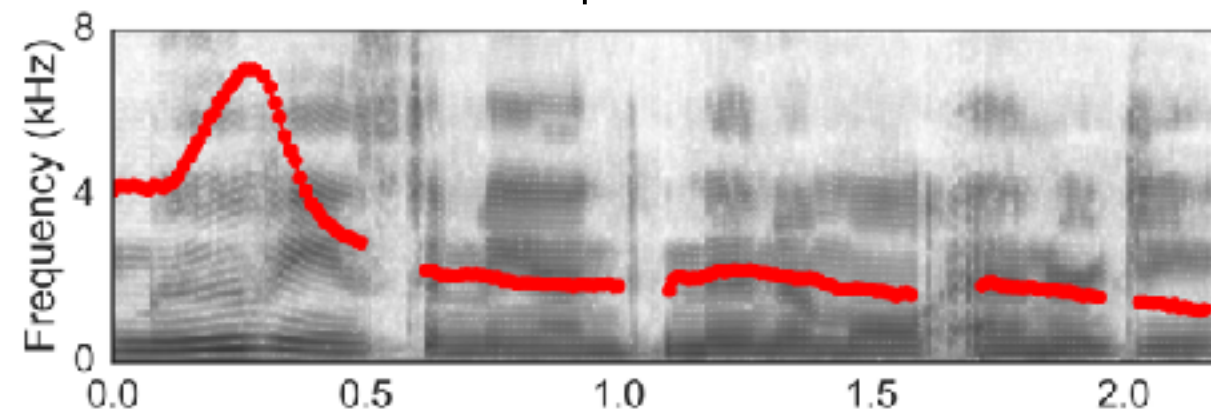
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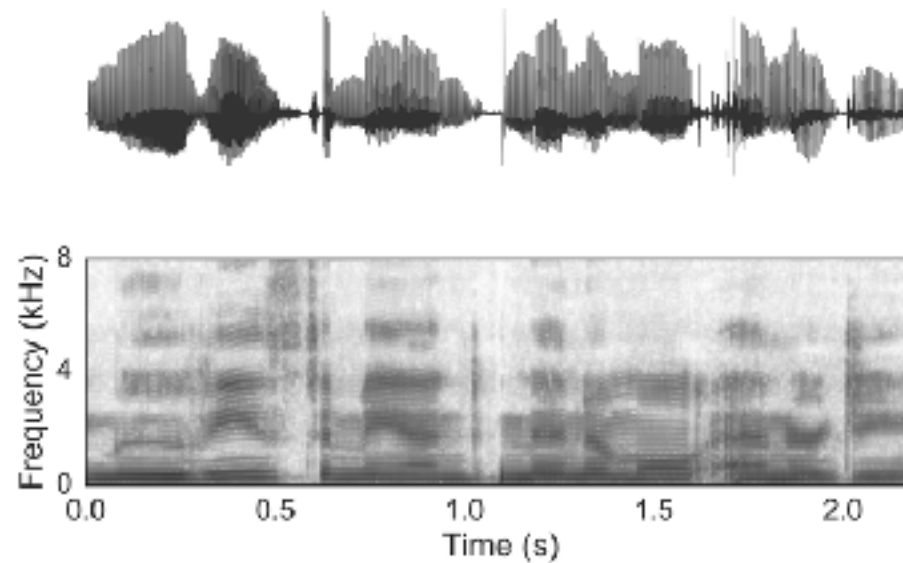
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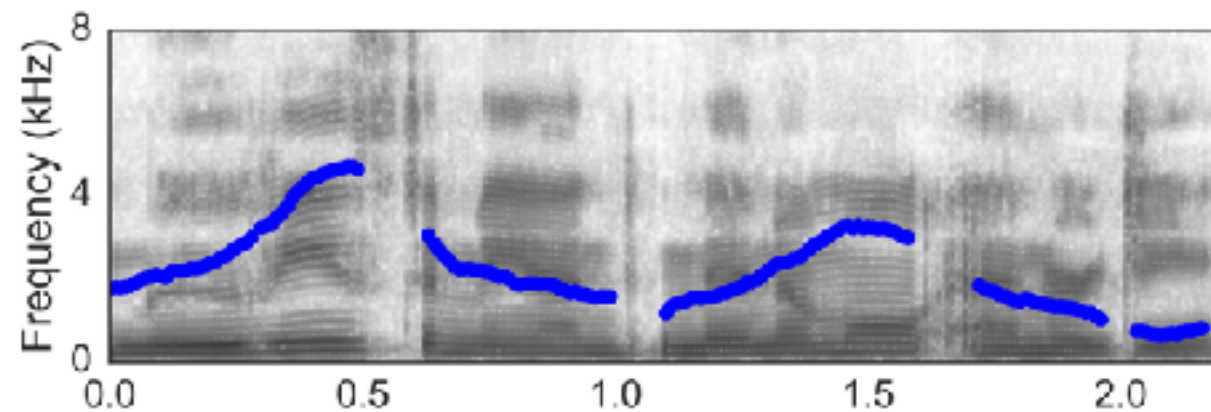


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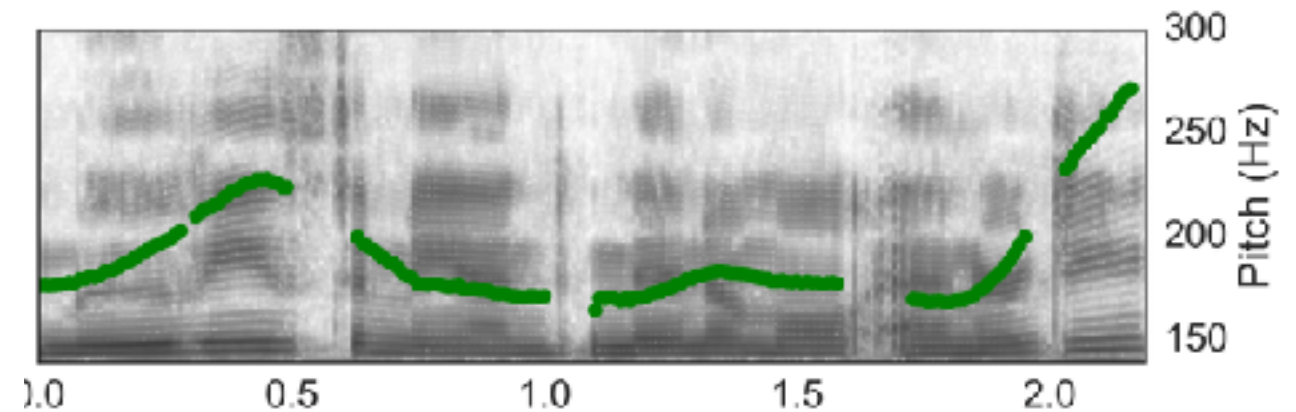


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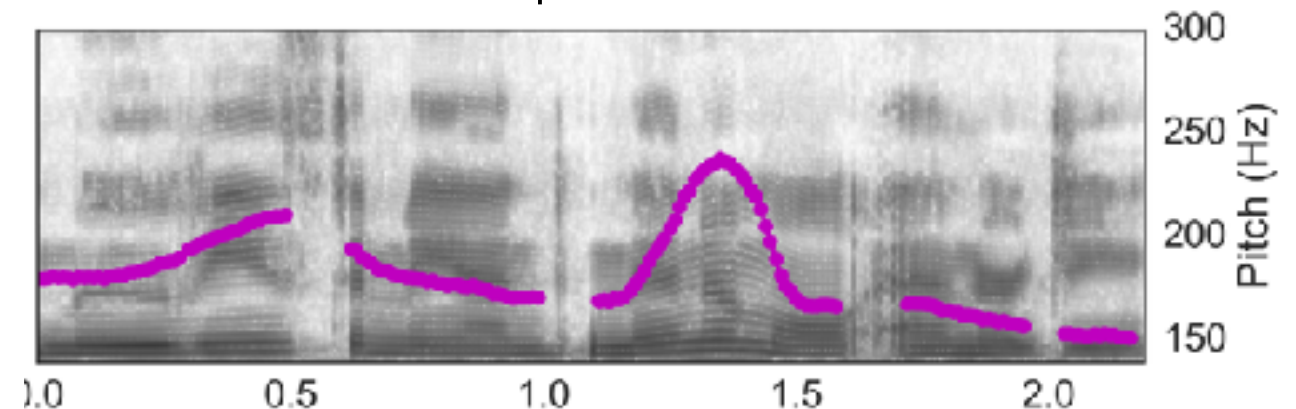
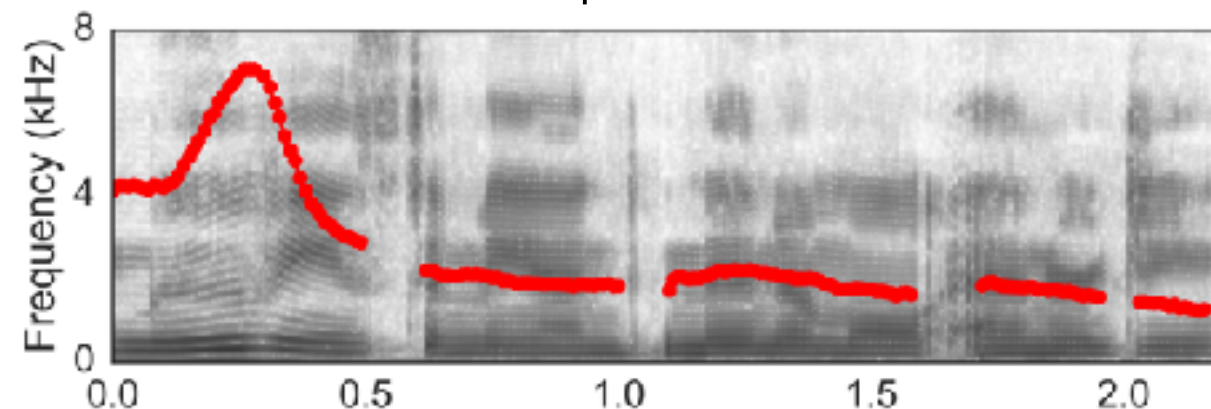
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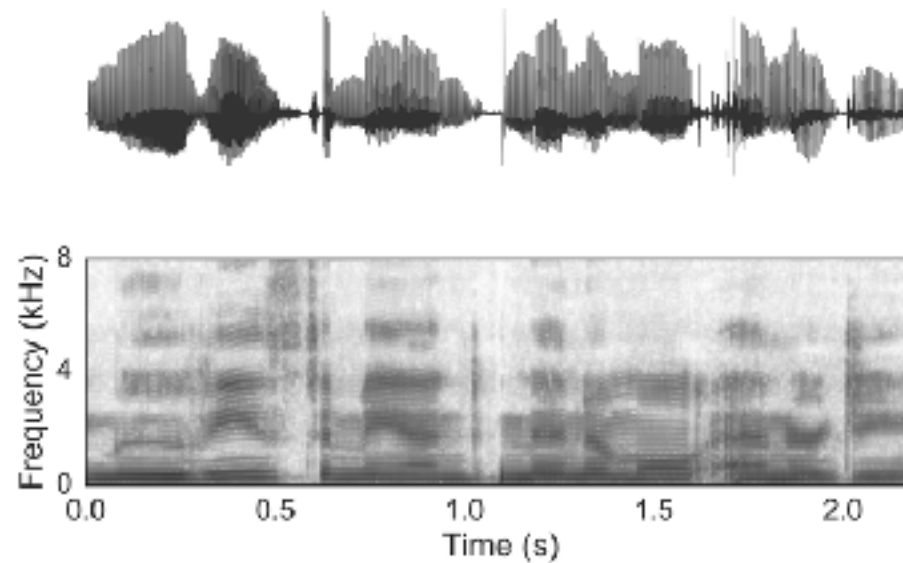
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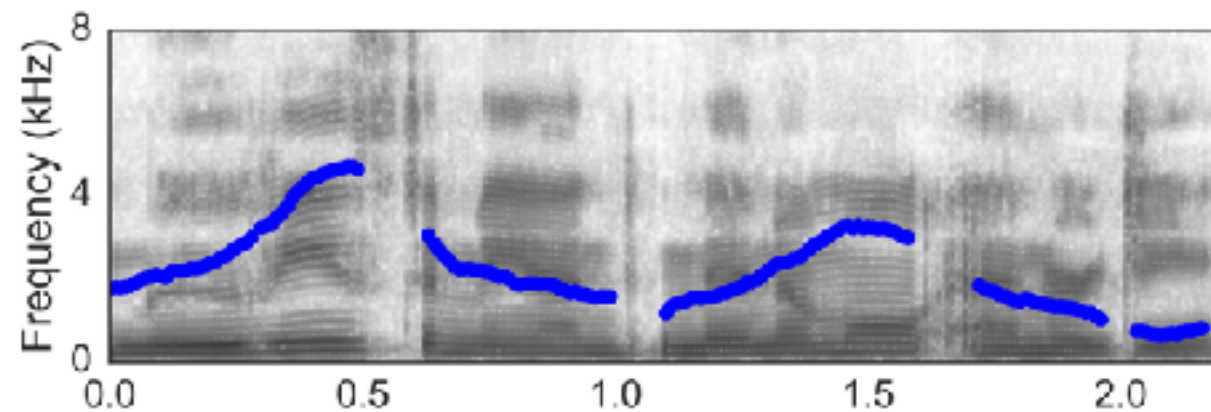


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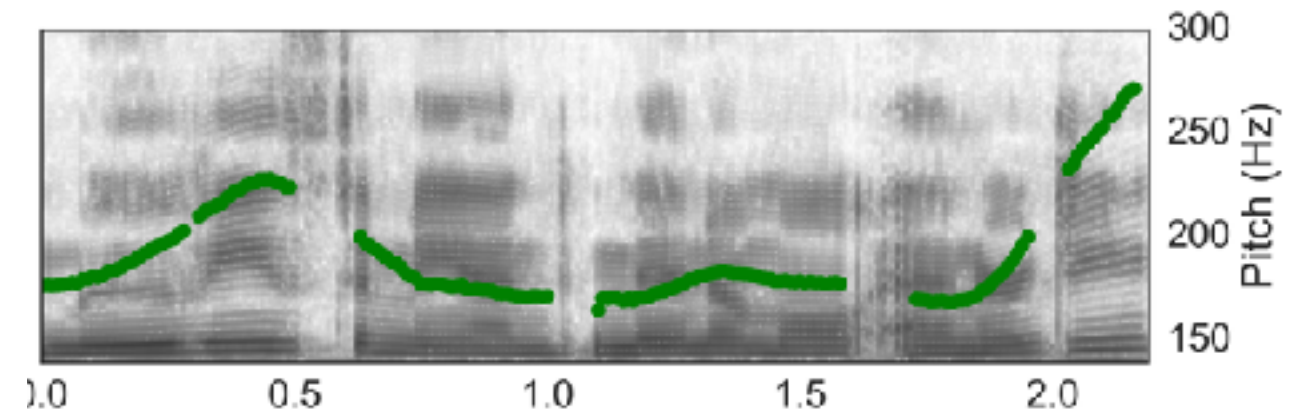


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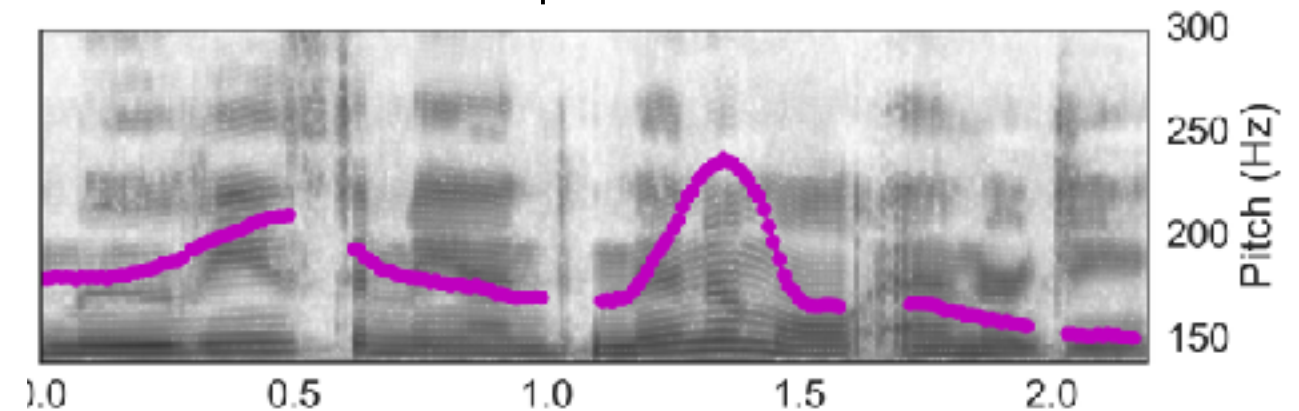
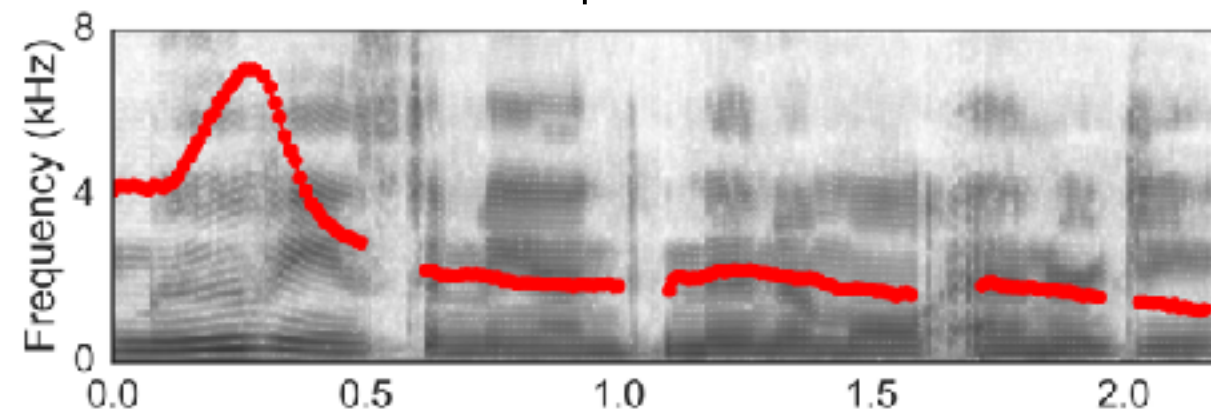
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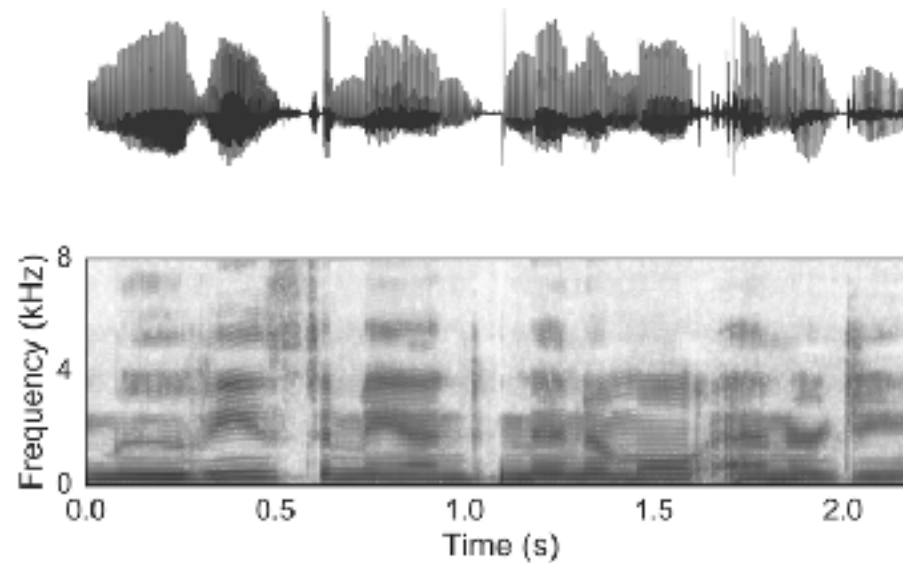
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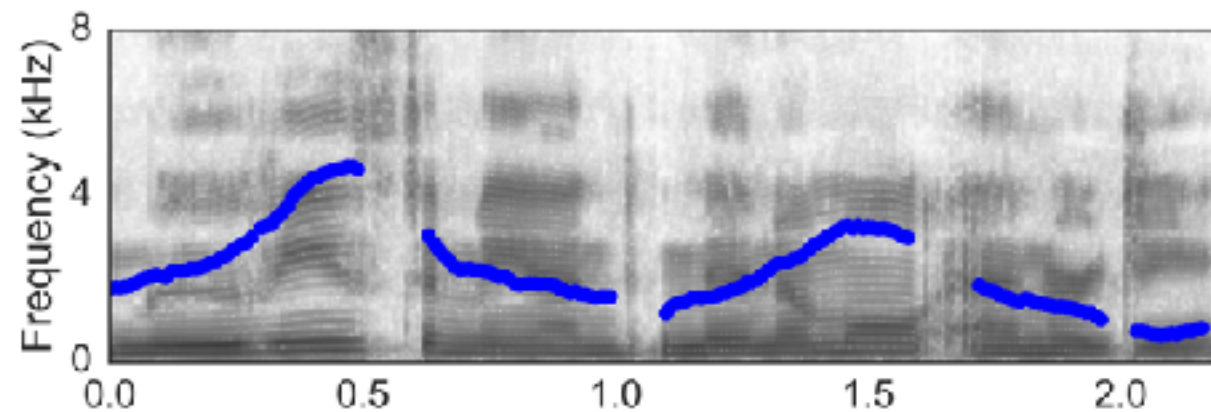


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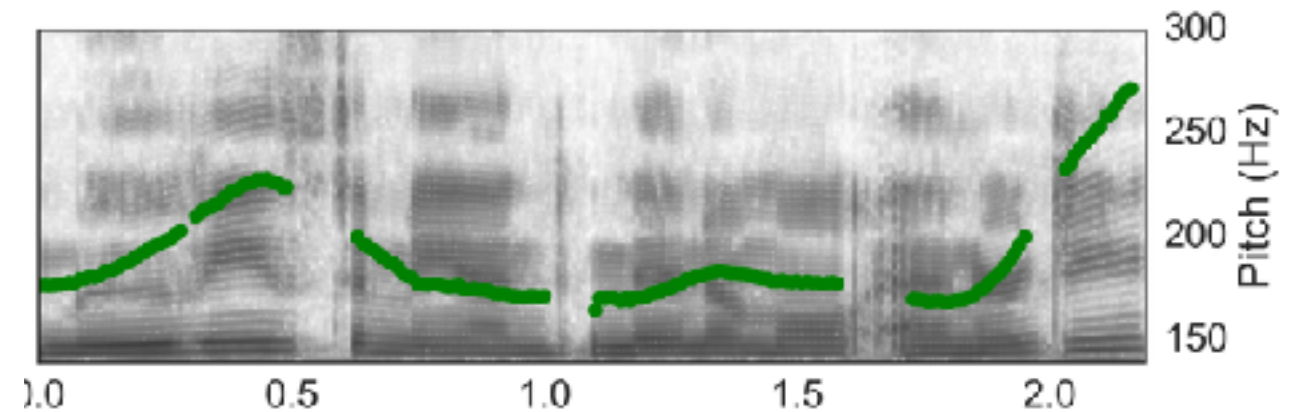


Neutral

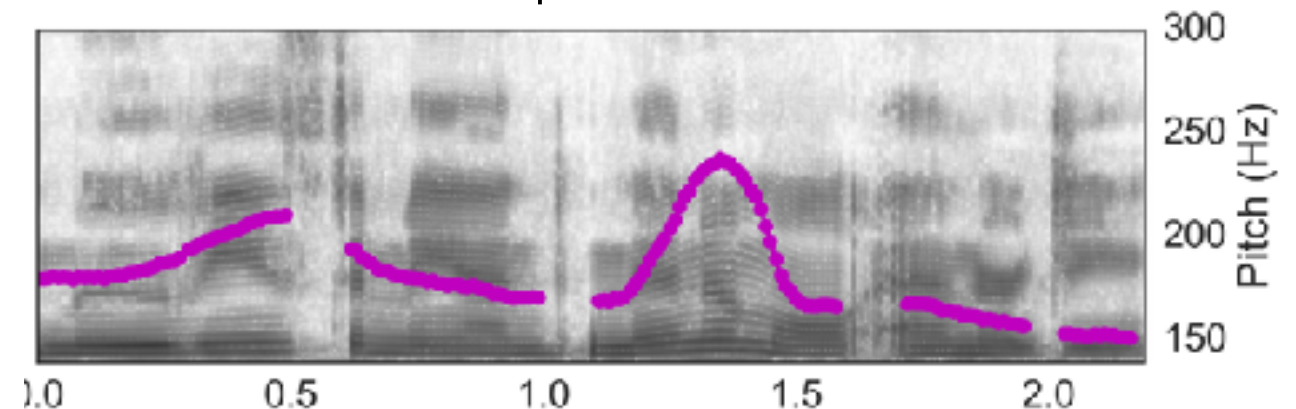
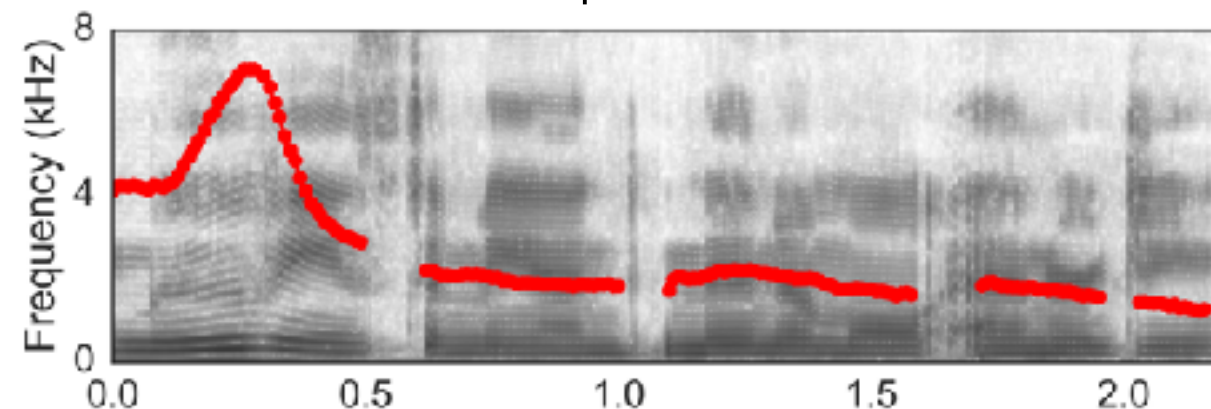
Question



Emphasis 1

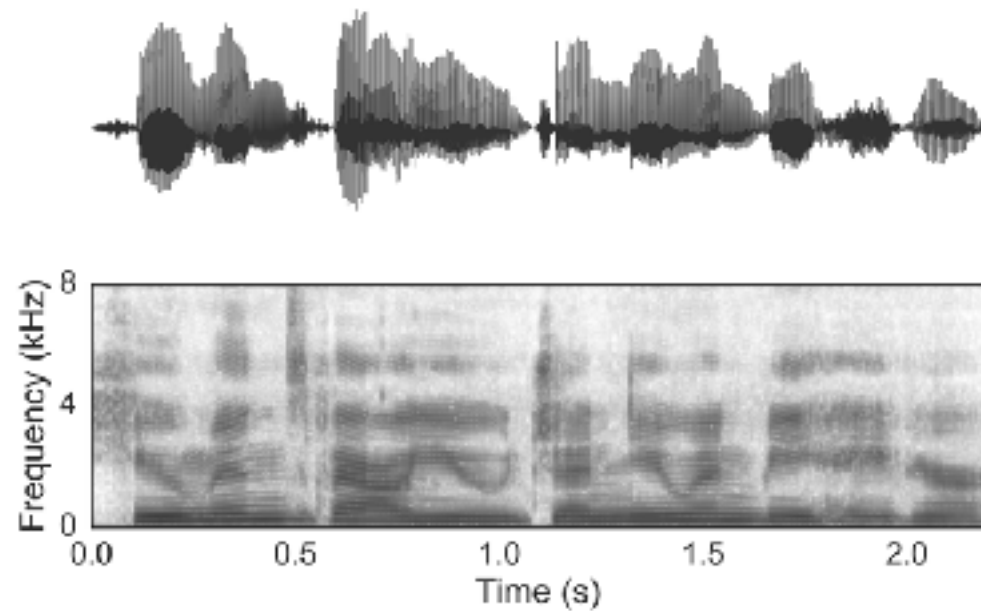


Emphasis 3

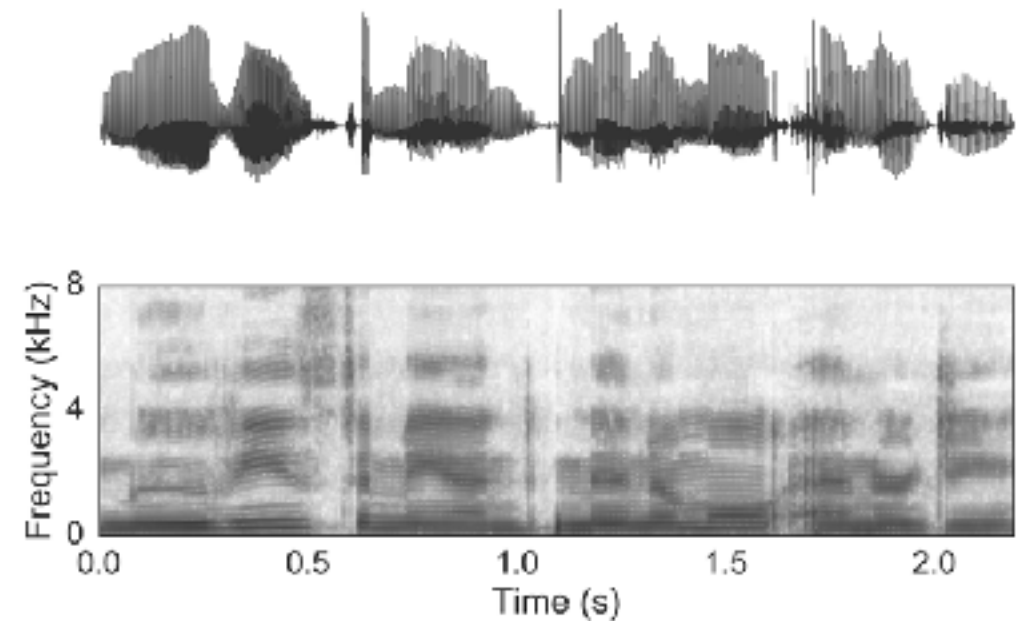


Four phonetically distinct sentences duration-matched by syllable and RMS intensity normalized

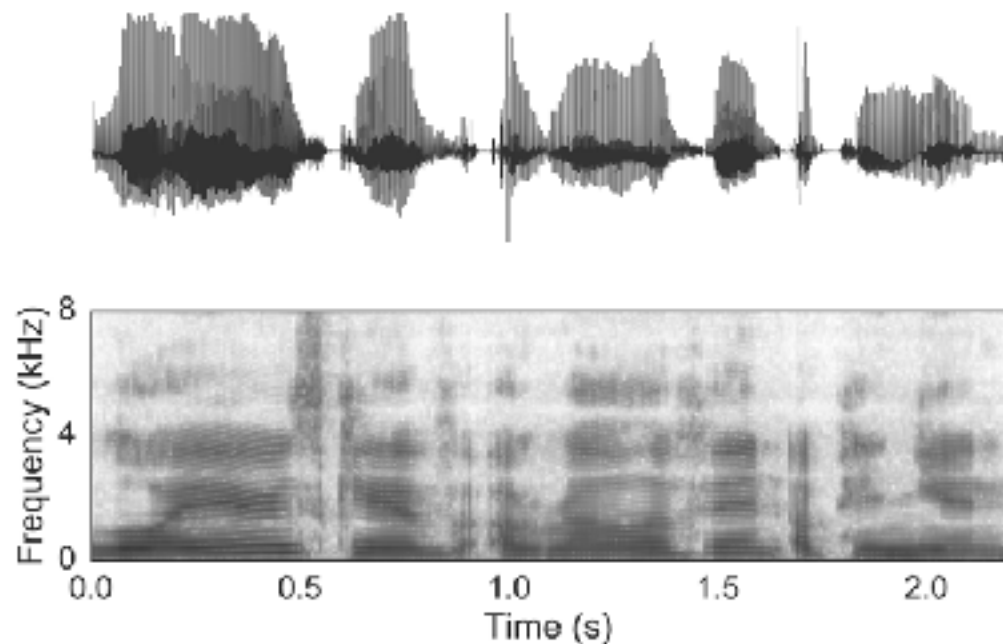
Humans value genuine behavior



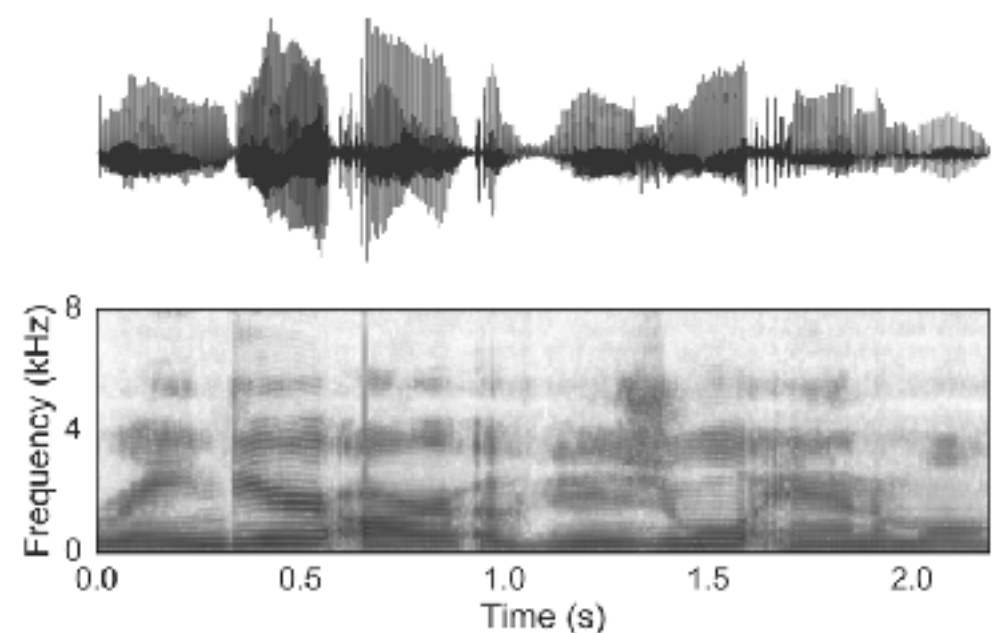
Movies demand minimal energy



Lawyers give a relevant opinion

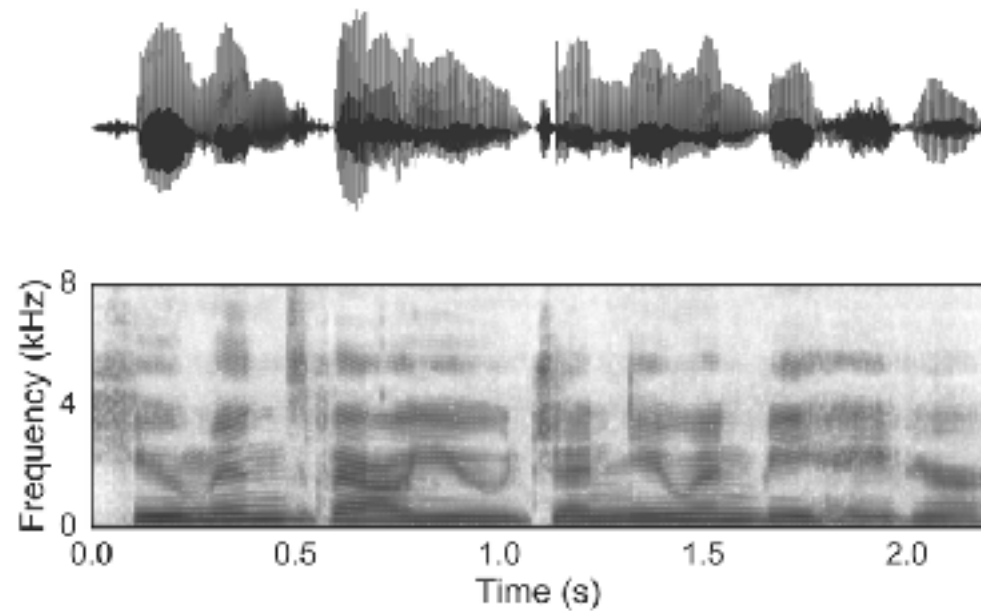


Reindeer are a visual animal

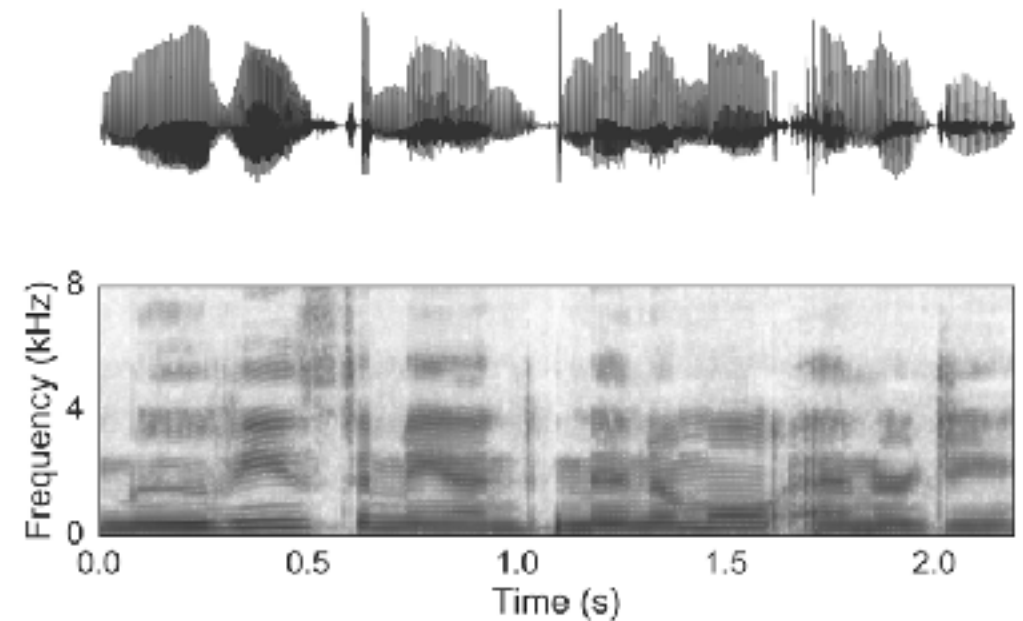


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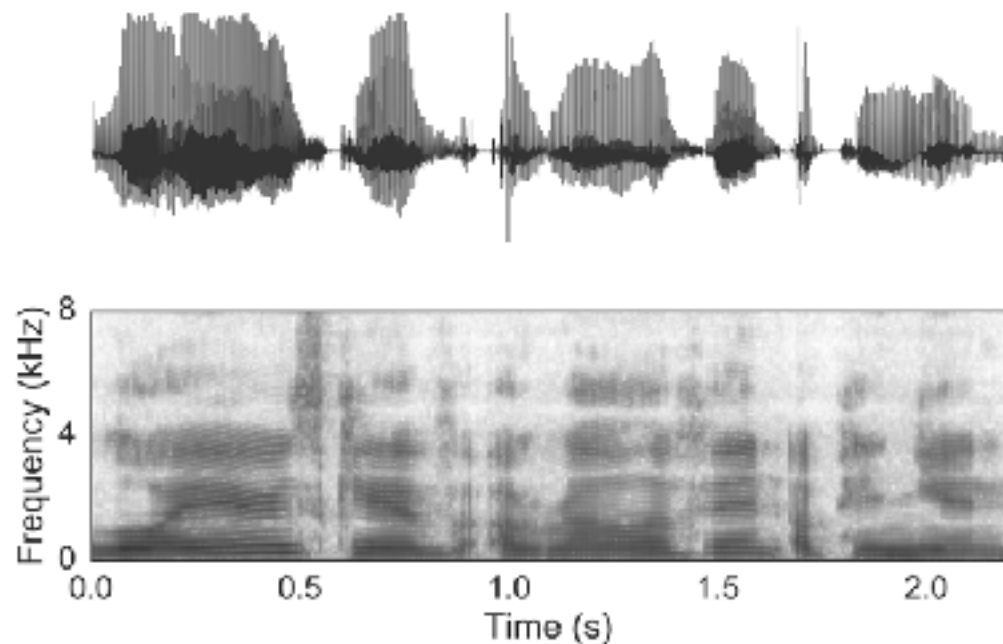
Humans value genuine behavior



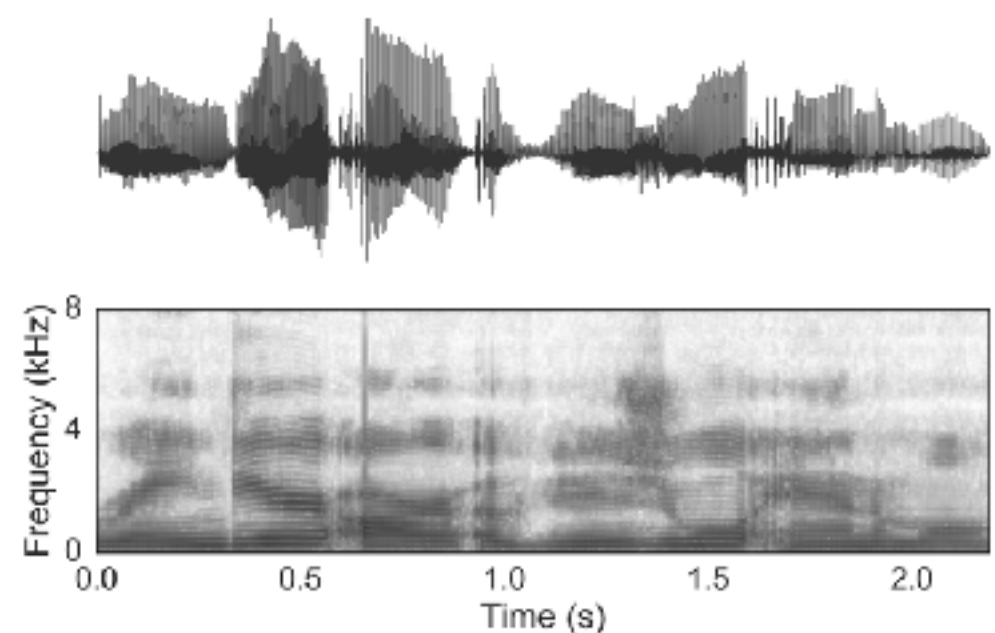
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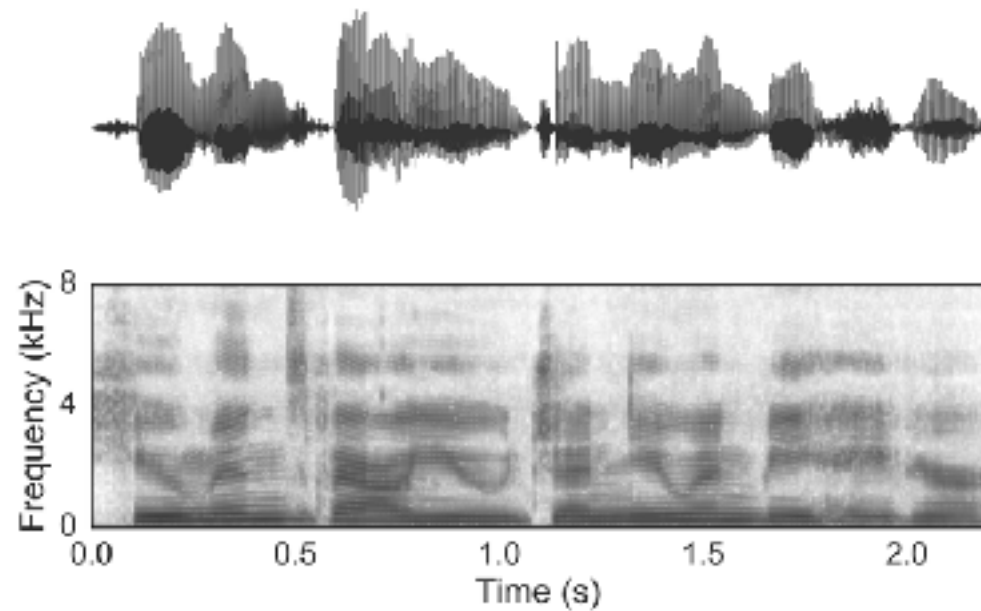


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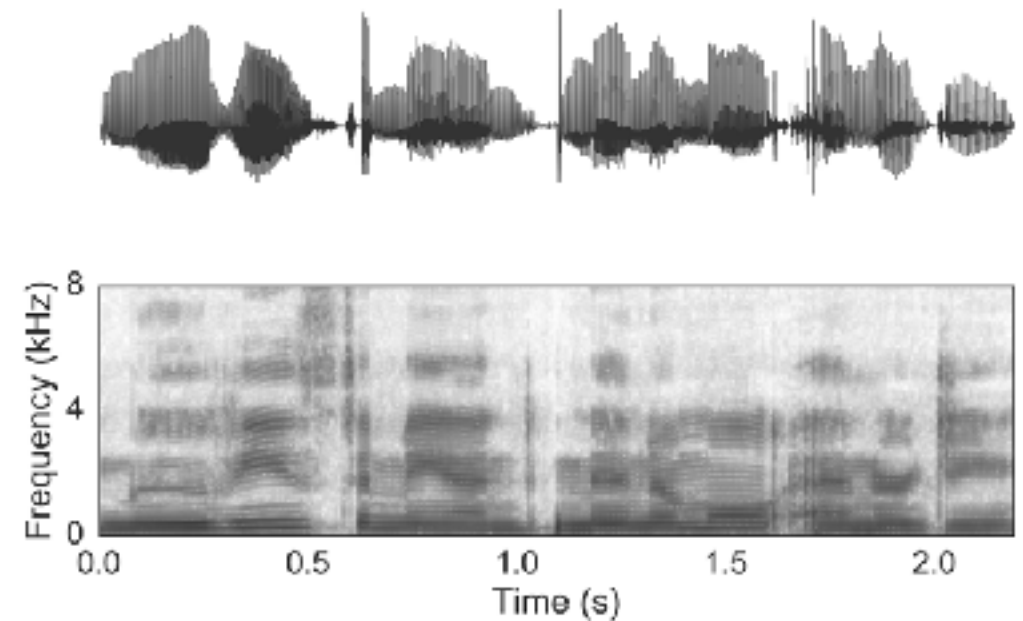


Four phonetically distinct sentences duration-matched by syllable and RMS intensity normalized

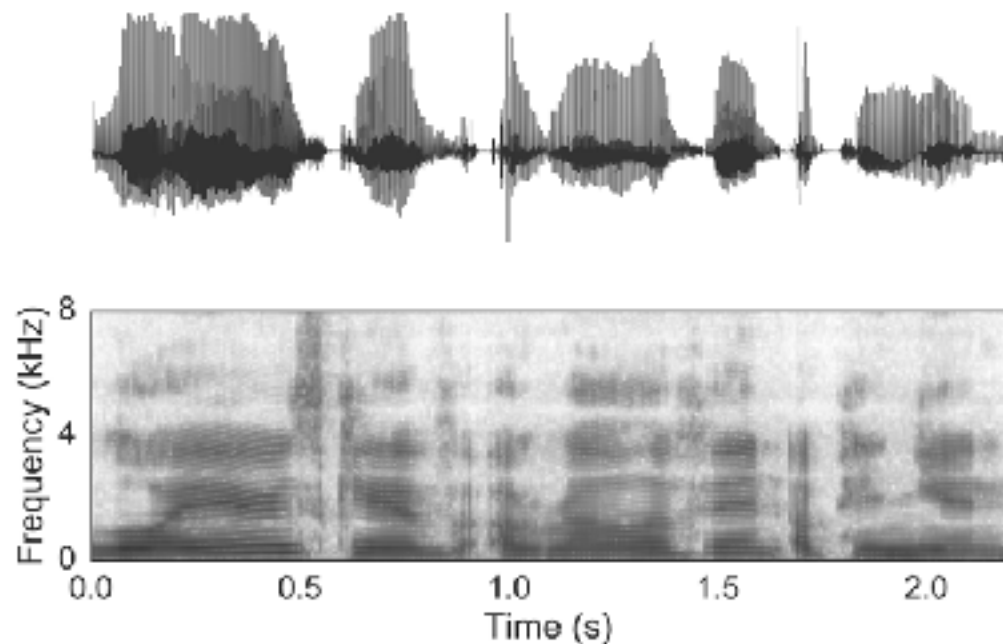
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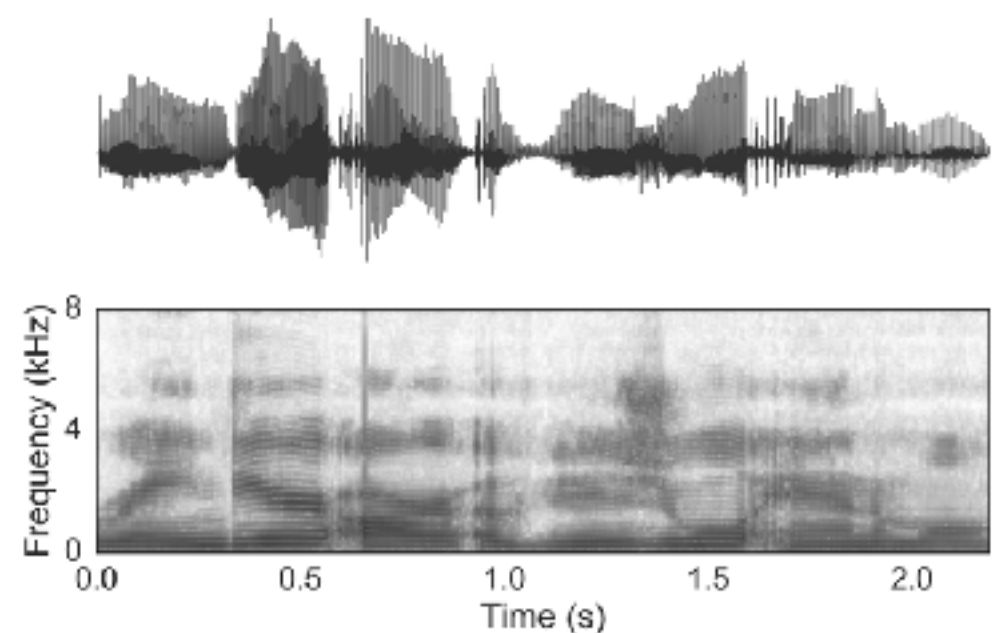
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Lawyers give a relevant opinion

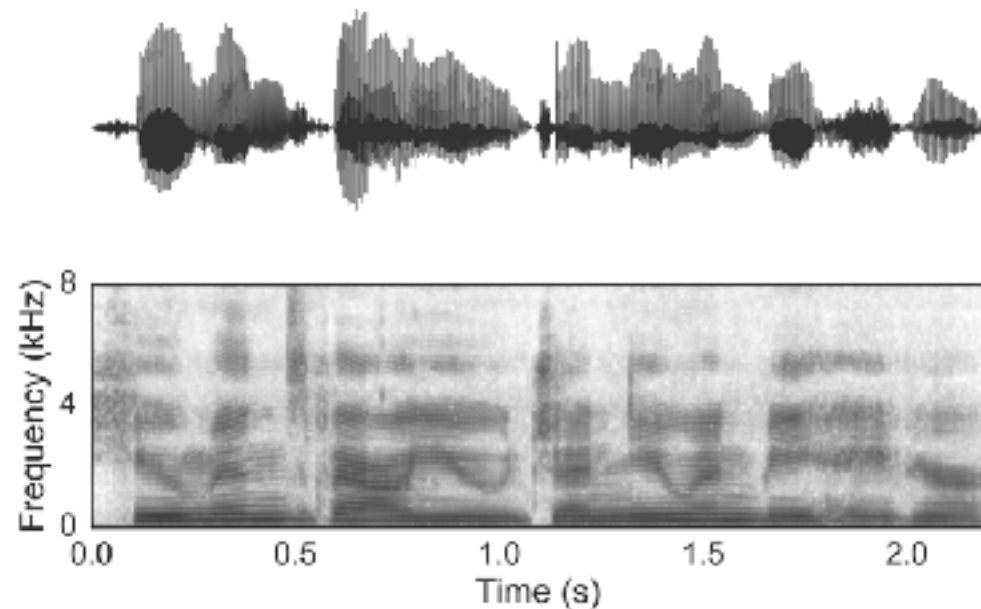


Reindeer are a visual animal

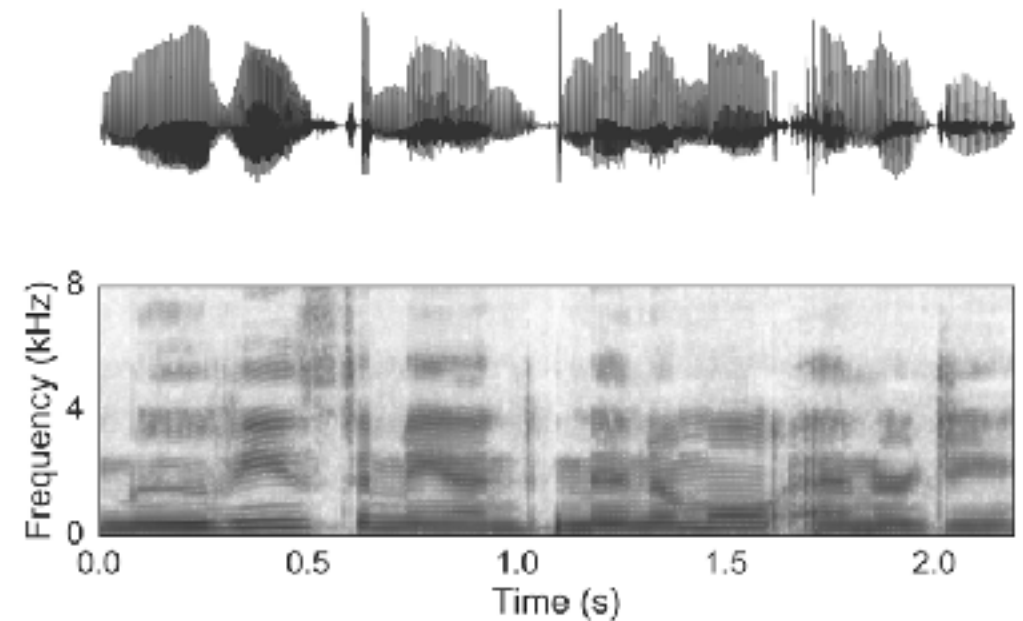


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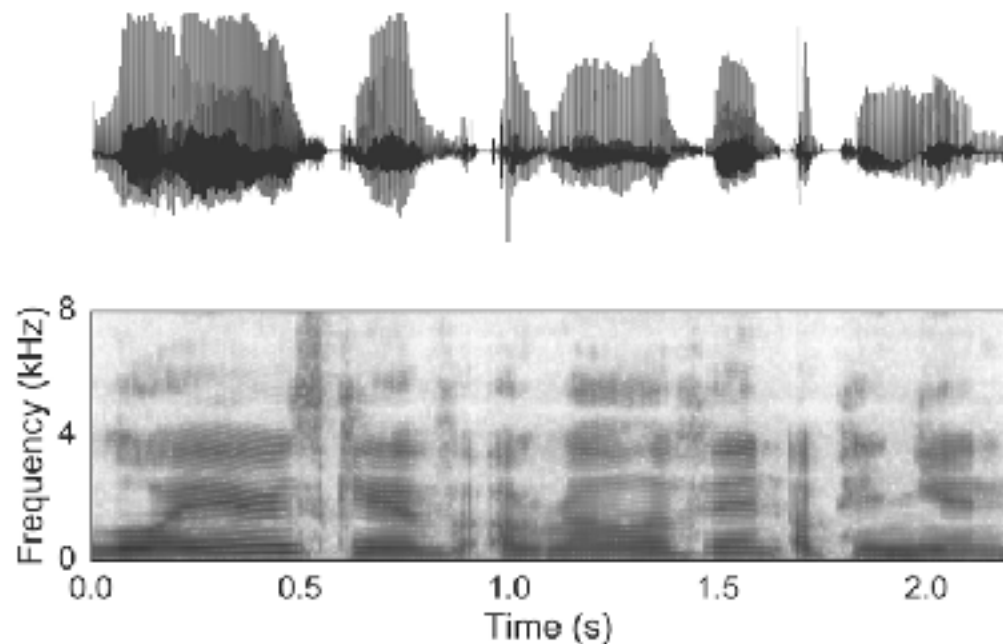
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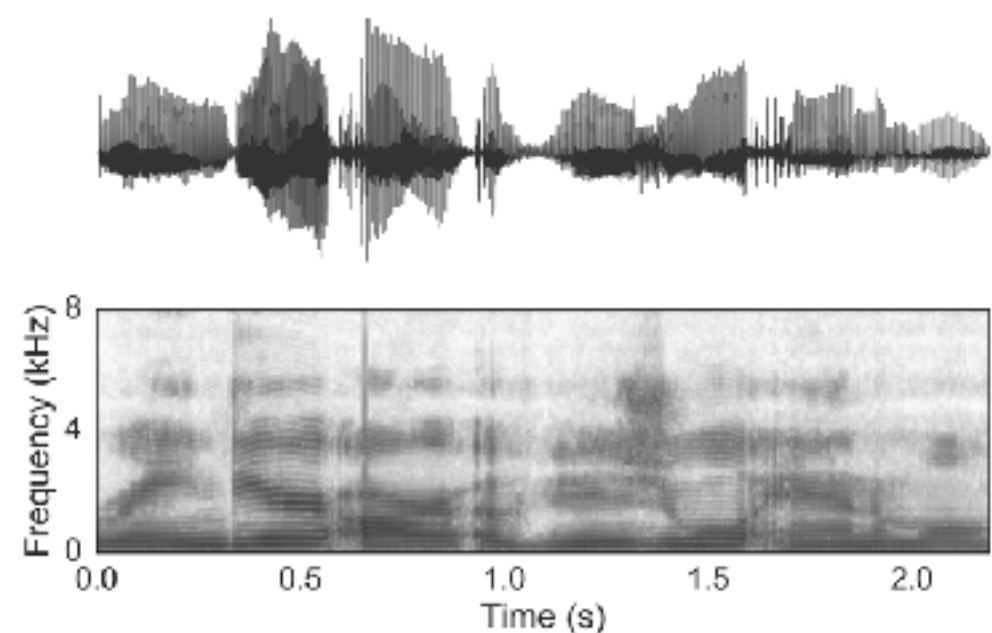
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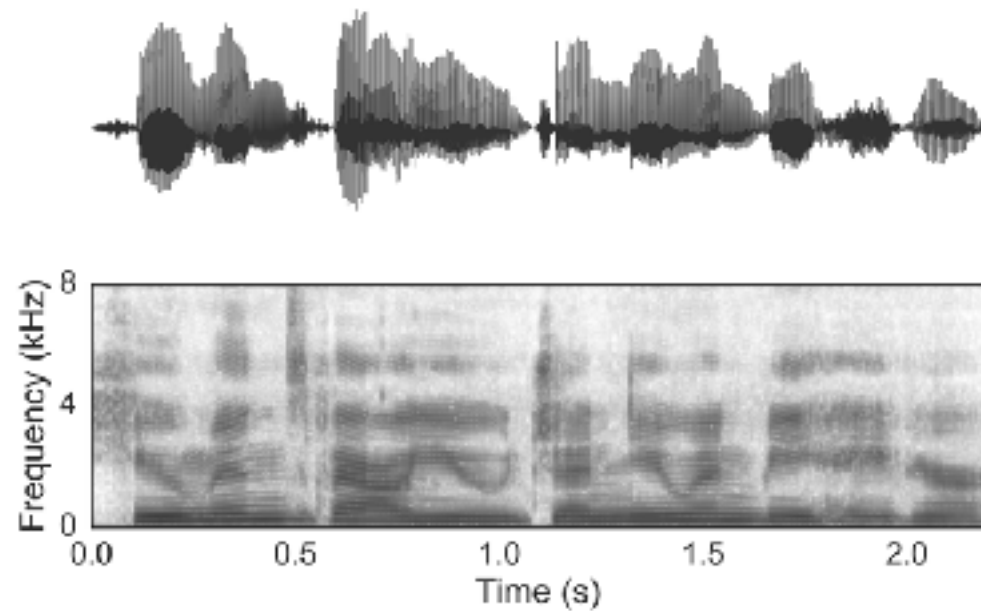


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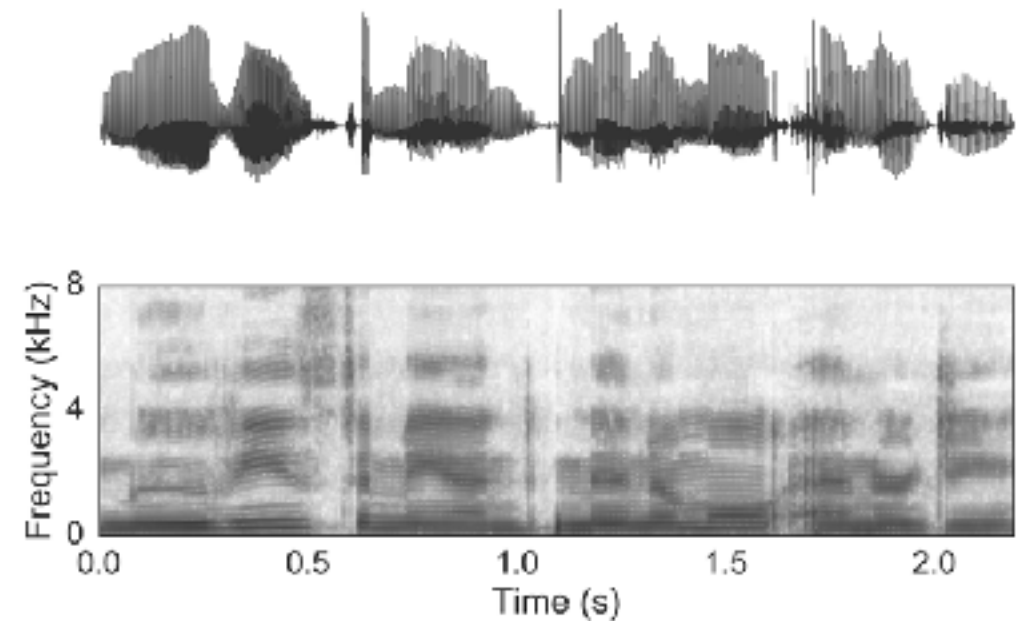


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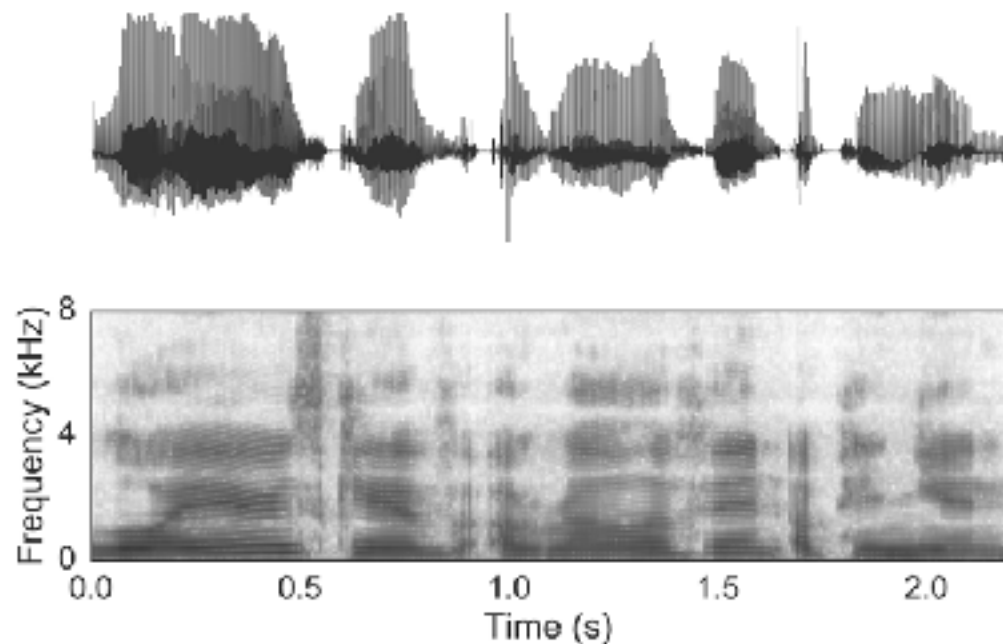
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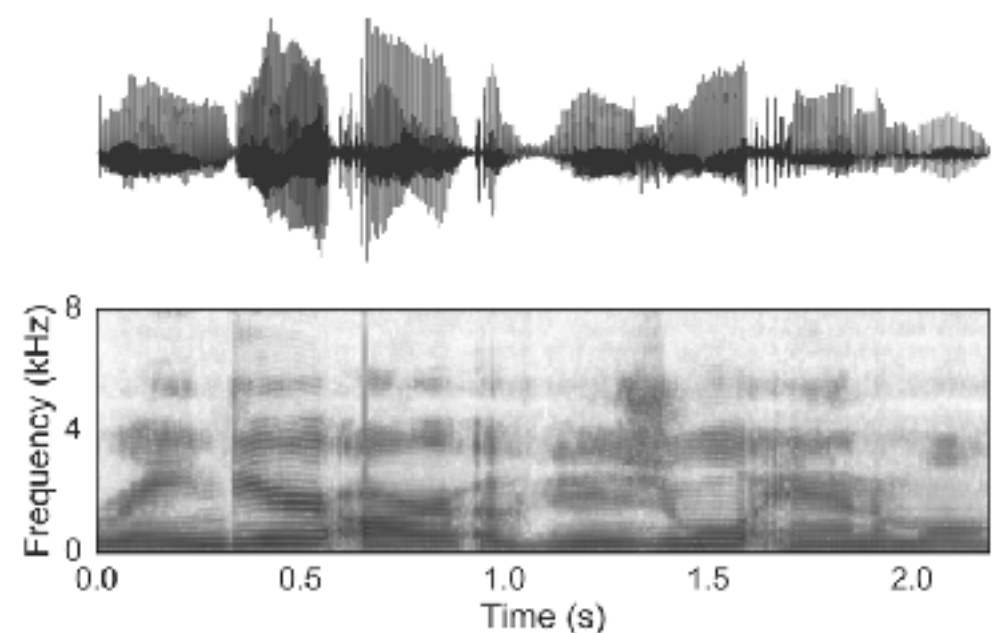
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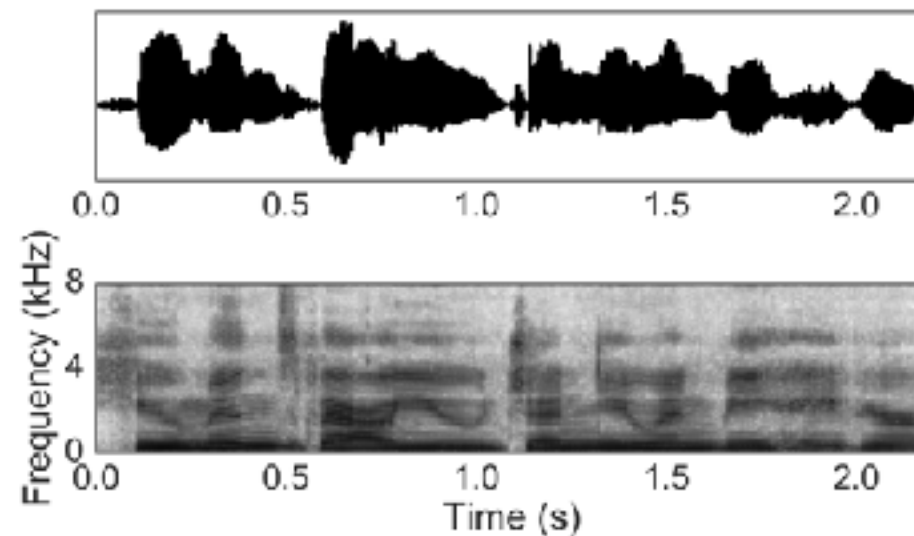
Lawyers give a relevant opinion



Reindeer are a visual animal



Different speakers synthesized with two pitch levels and two formant levels

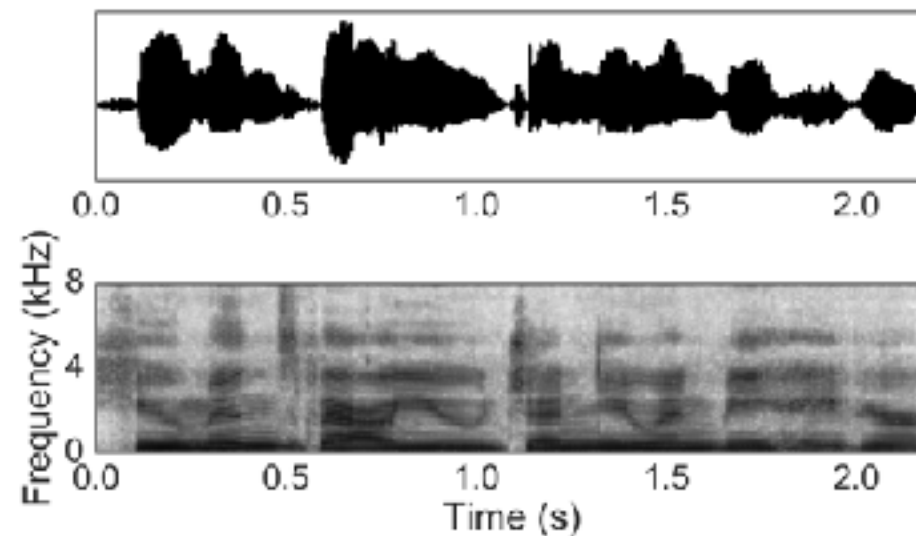


Low pitch +
Low formants

High pitch +
Low formants

High pitch +
High formants

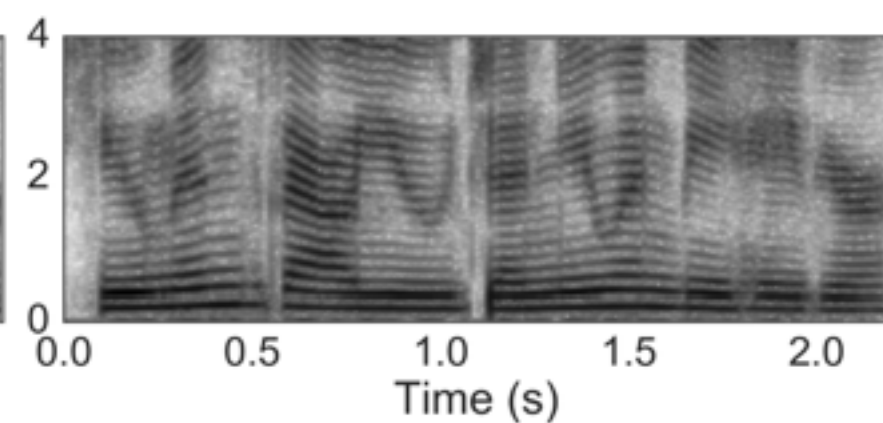
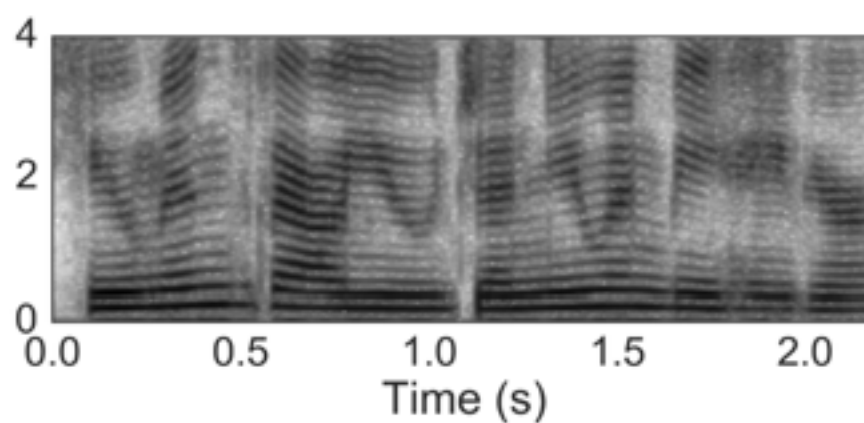
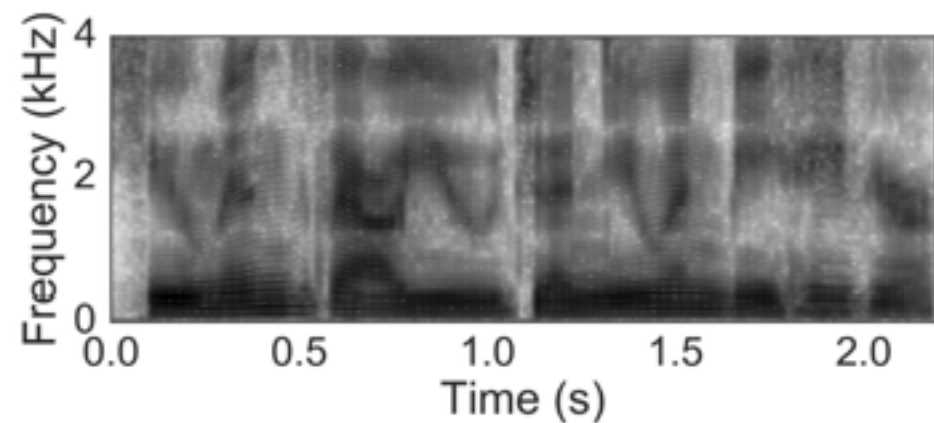
Different speakers synthesized with two pitch levels and two formant levels



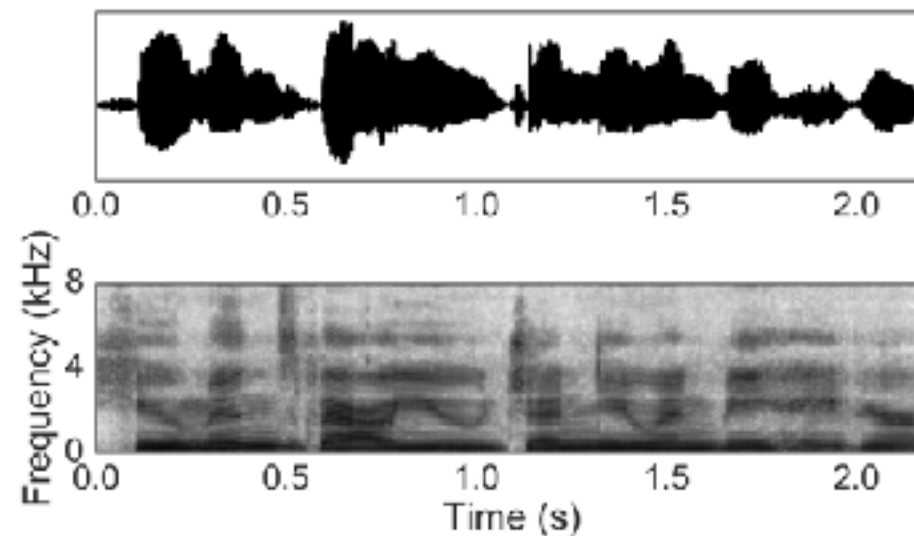
Low pitch +
Low formants

High pitch +
Low formants

High pitch +
High formants



Different speakers synthesized with two pitch levels and two formant levels



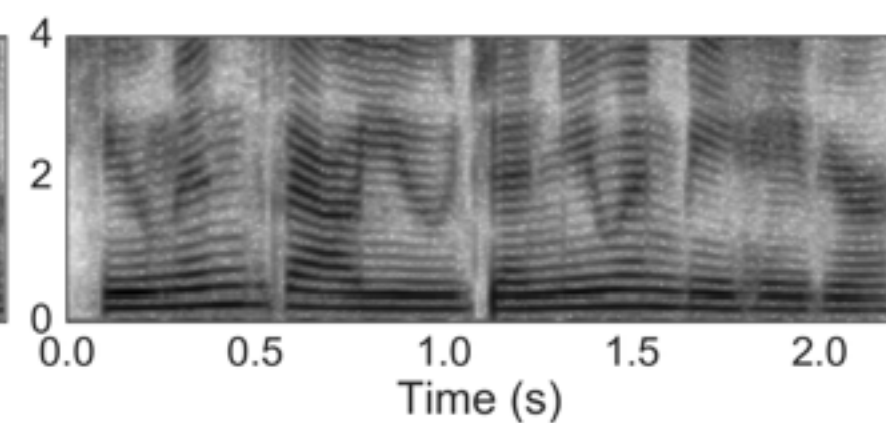
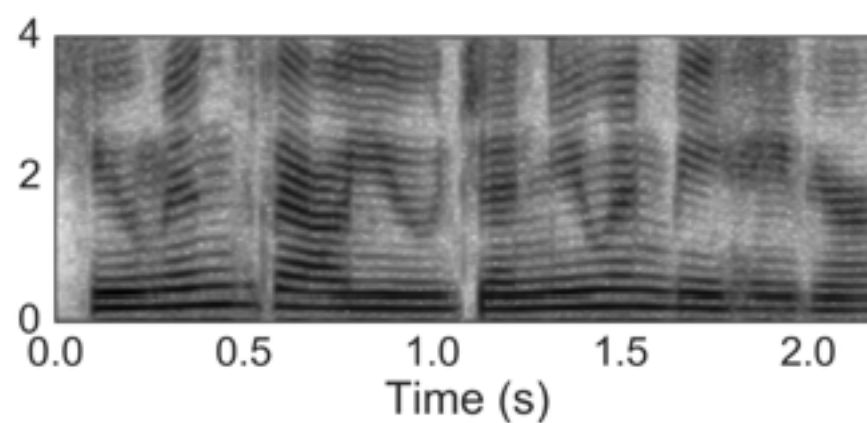
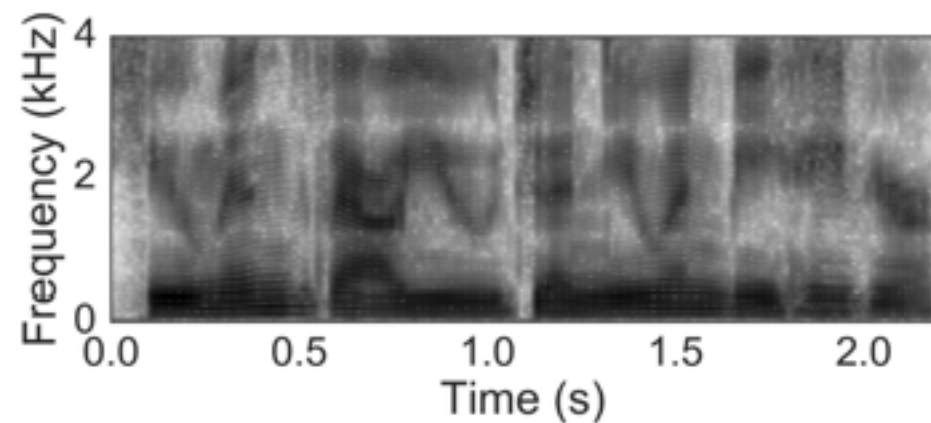
Low pitch +
Low formants



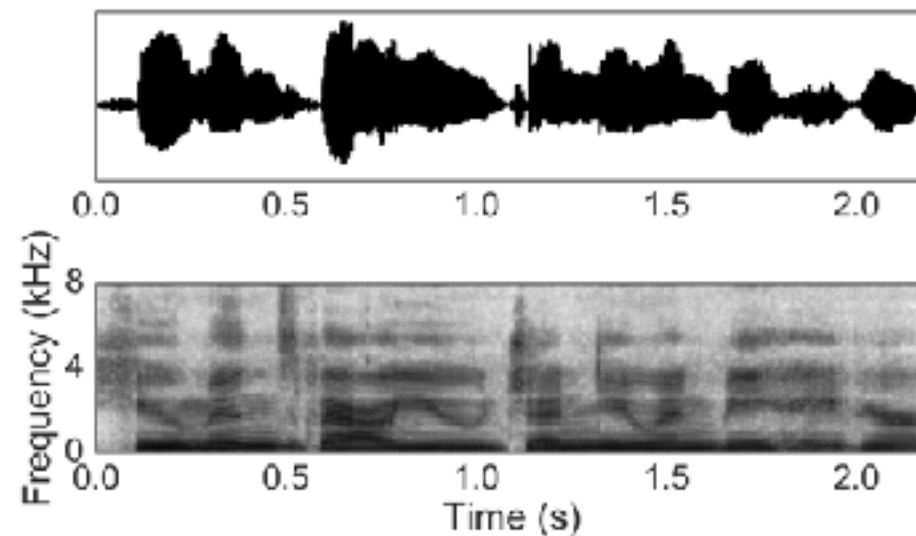
High pitch +
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High pitch +
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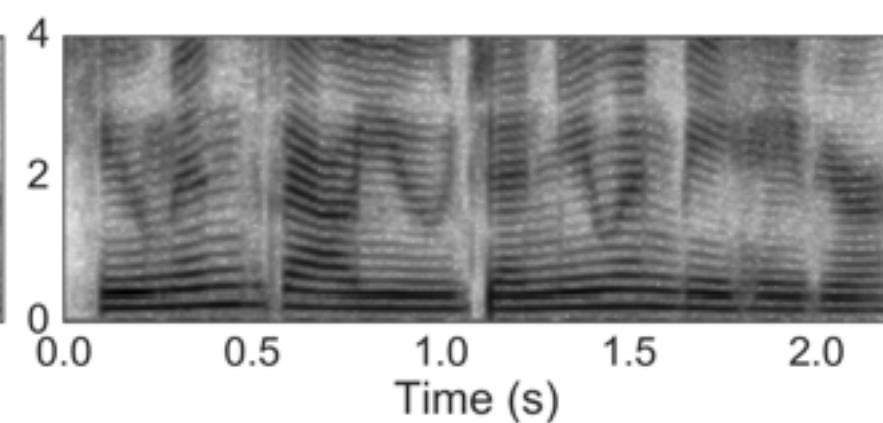
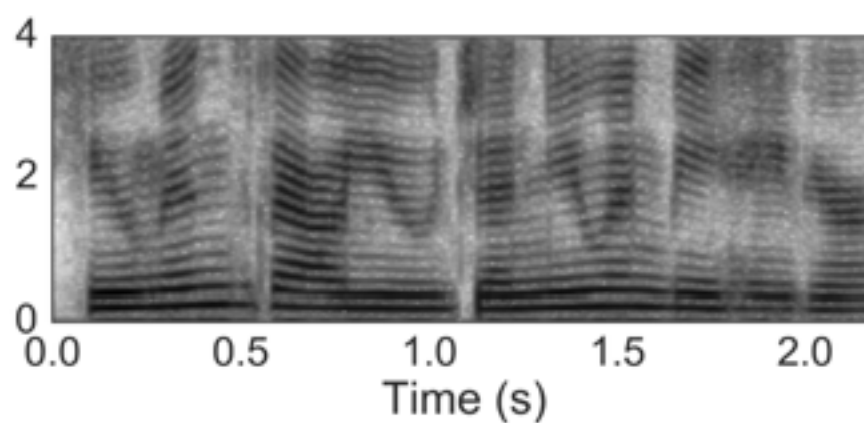
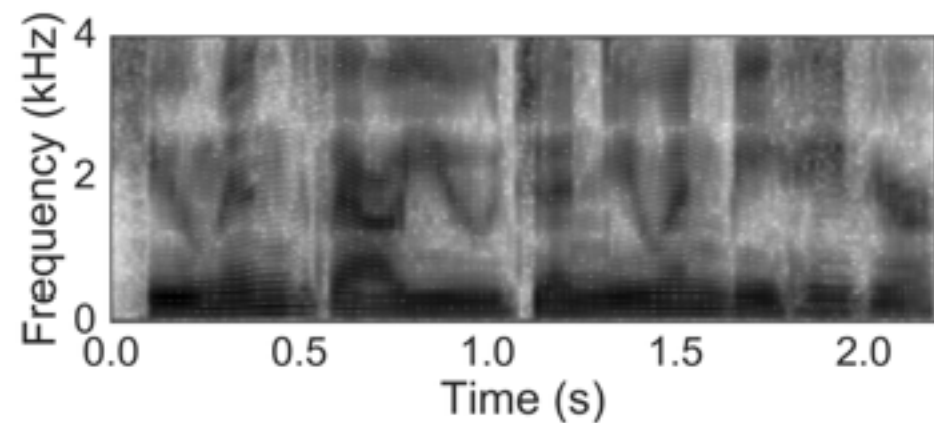
Different speakers synthesized with two pitch levels and two formant levels



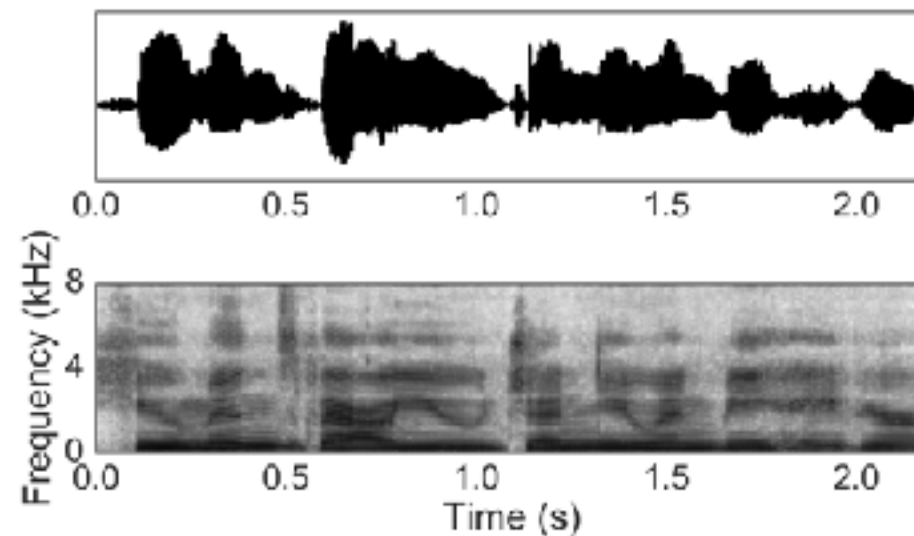
Low pitch +
Low formants

High pitch +
Low formants

High pitch +
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Different speakers synthesized with two pitch levels and two formant levels



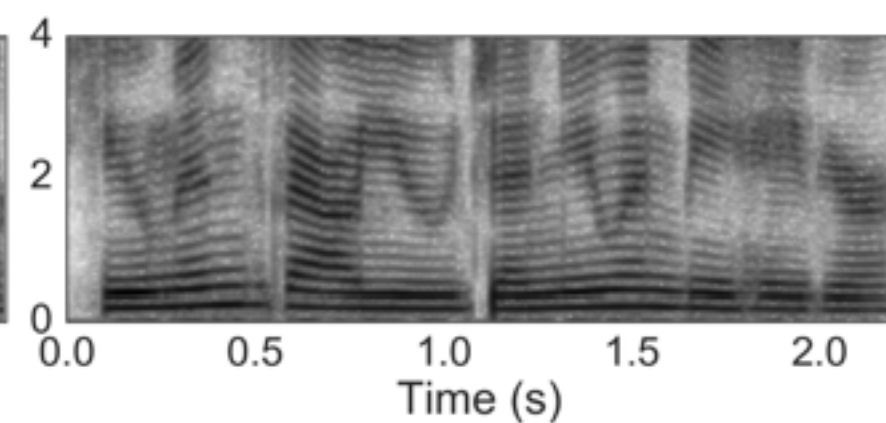
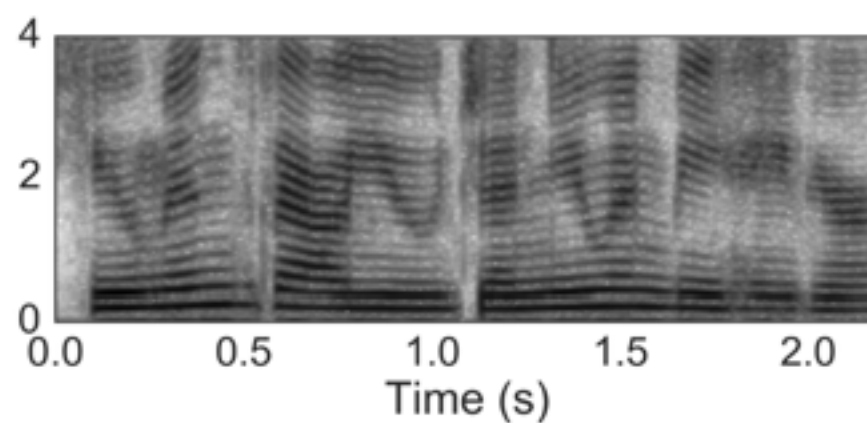
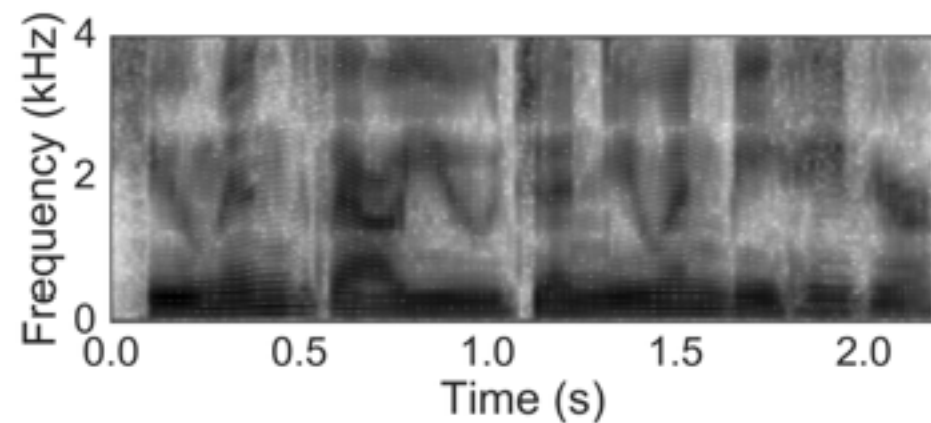
Low pitch +
Low formants



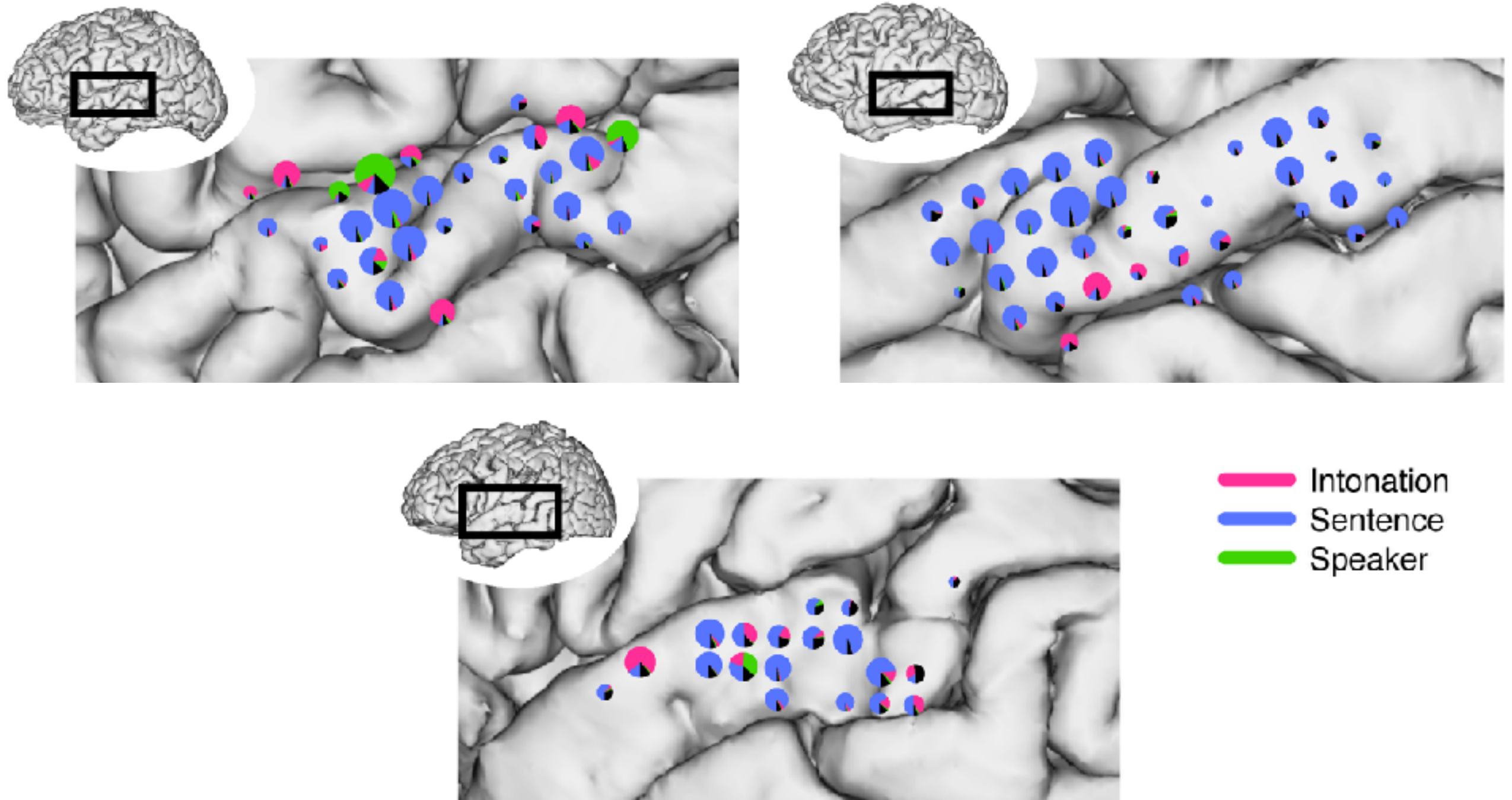
High pitch +
Low formants



High pitch +
High formants

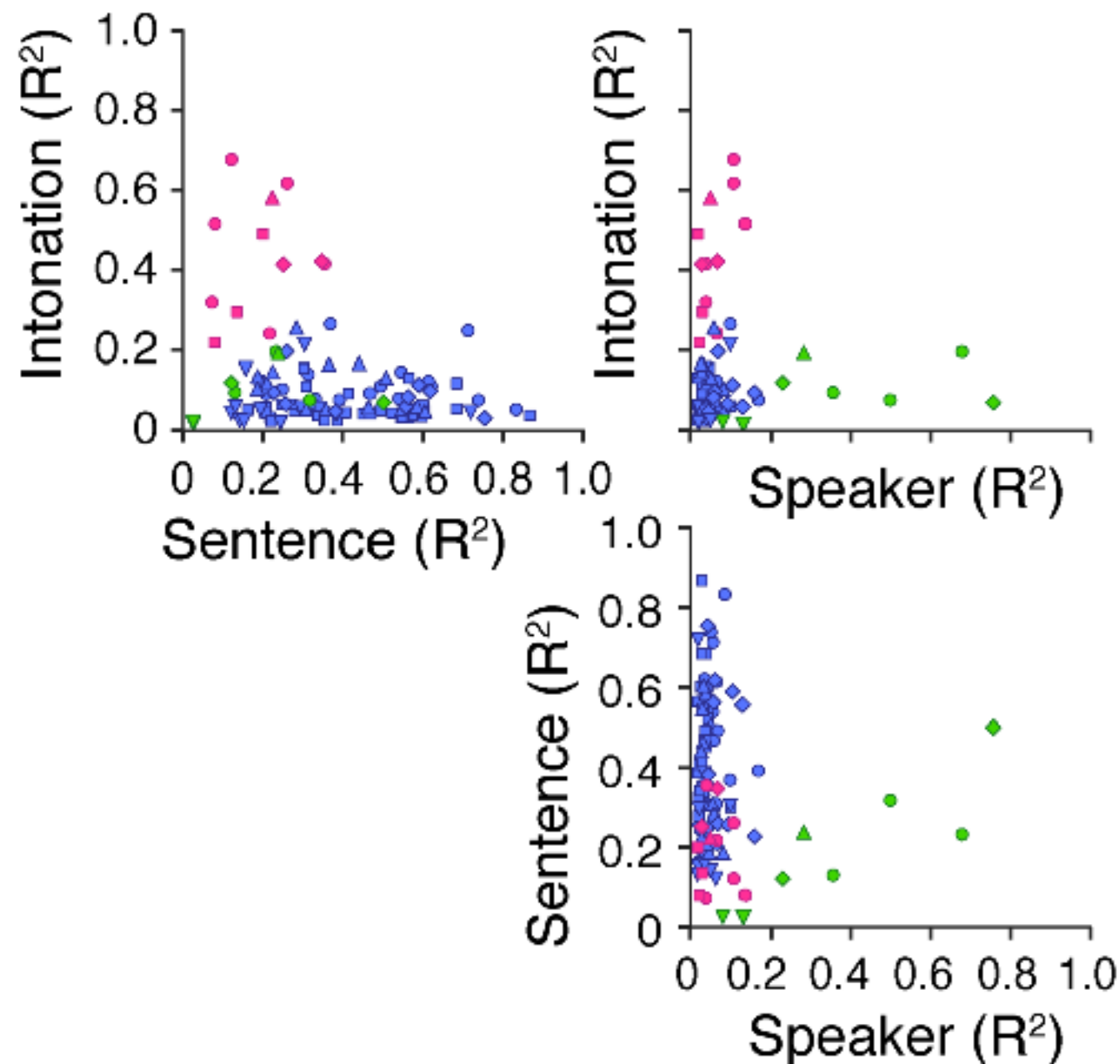


Intonation and phonetic content are encoded in separate neural populations



Electrodes primarily encode **one**:
intonation, phonetic features, or speaker

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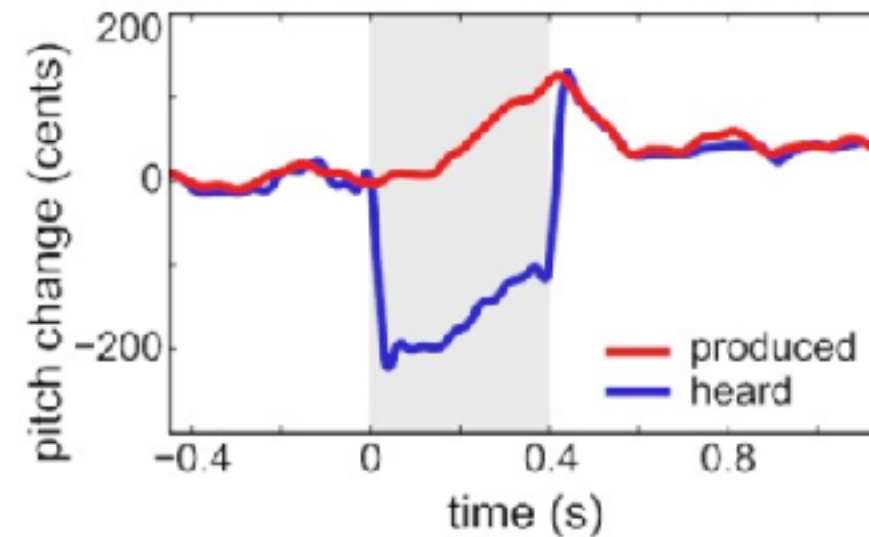
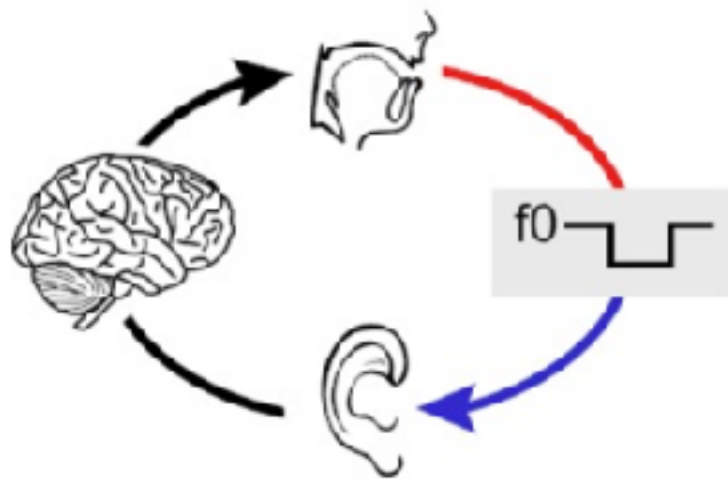
Results

- Local neural populations in STG encode intonation.
- The representation of intonation is phonetic feature and speaker invariant.
- Intonation and phonetic content are encoded in separate neural populations.

Confounding variables

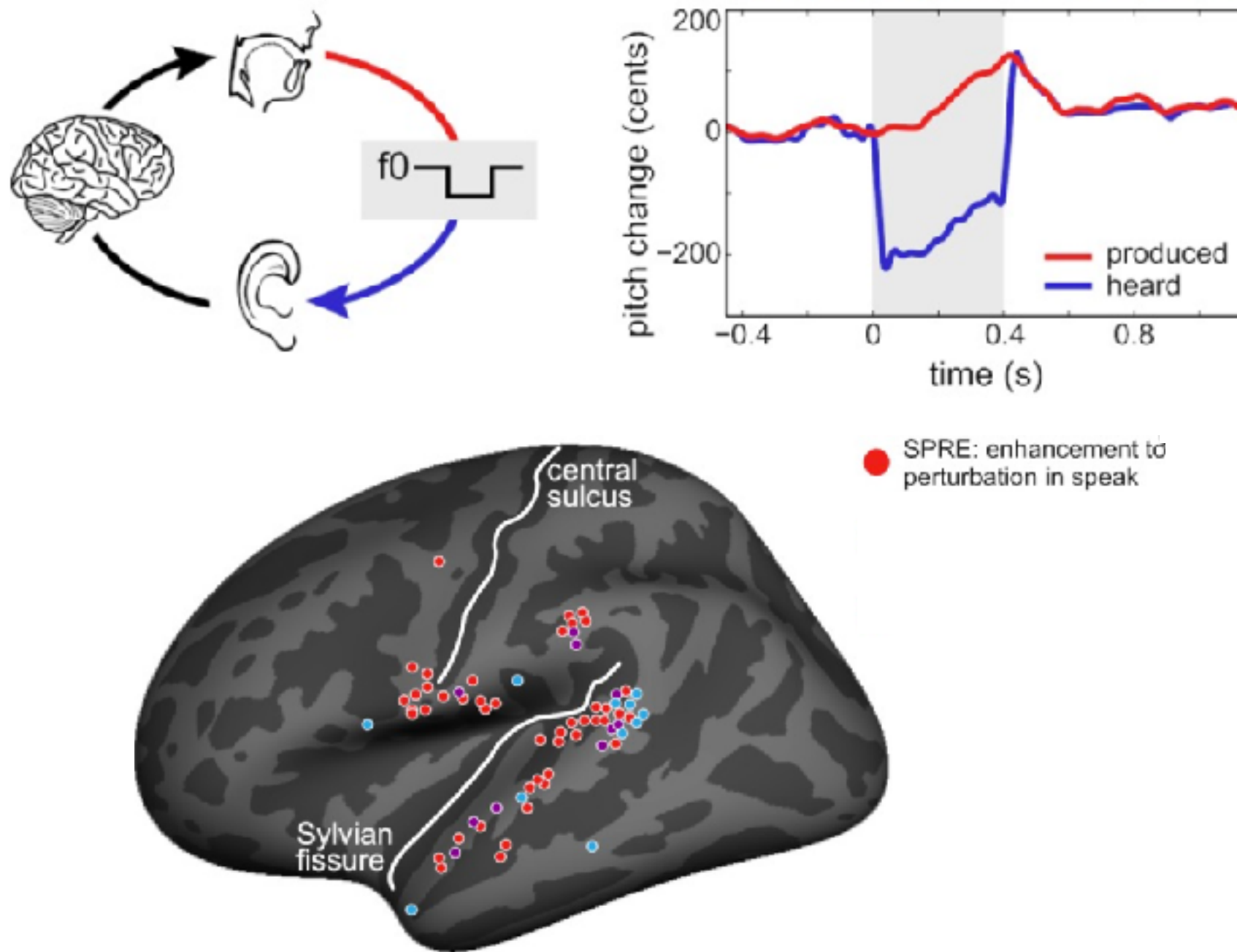
Factor	Solution
Loudness	Partial correlation
Supra-laryngeal articulators (Tongue, Jaw, Velum, etc.)	Dynamic time warping
Declination (pitch lowering)	Shuffle test

Sensorimotor role: evidence for feedback control in vLMC, not dLMC



(Chang, Niziolek et al. 2013)

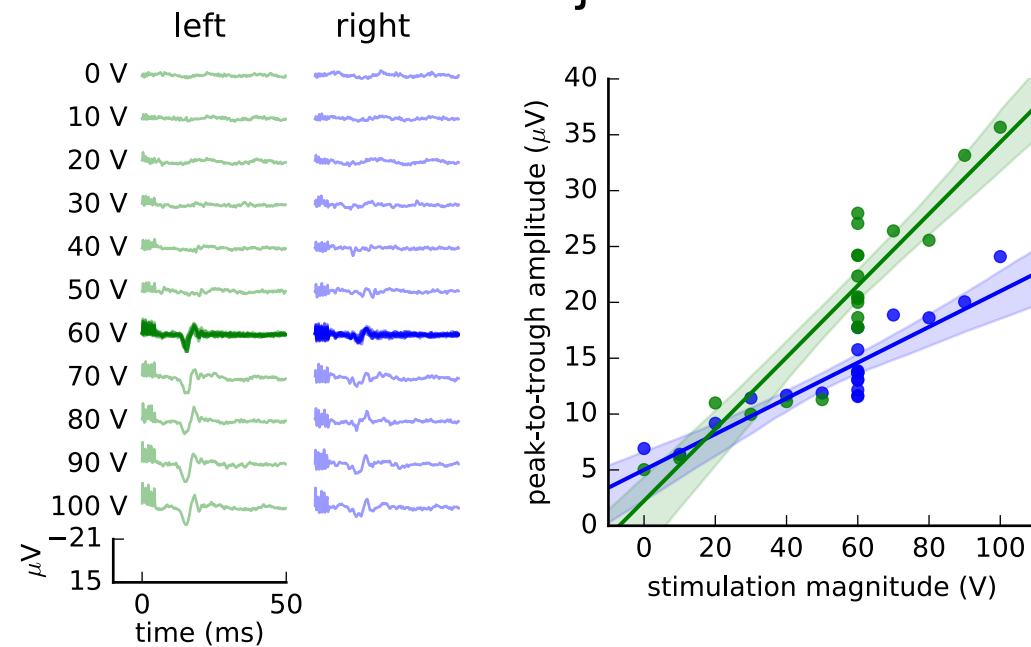
Sensorimotor role: evidence for feedback control in vLMC, not dLMC



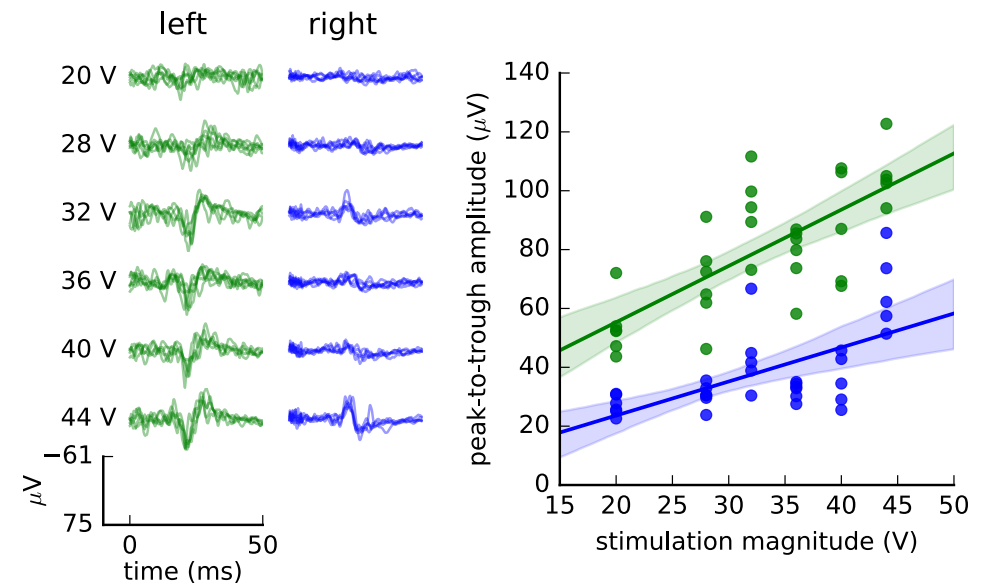
(Chang, Niziolek et al. 2013)

Individual stimulation EMG results

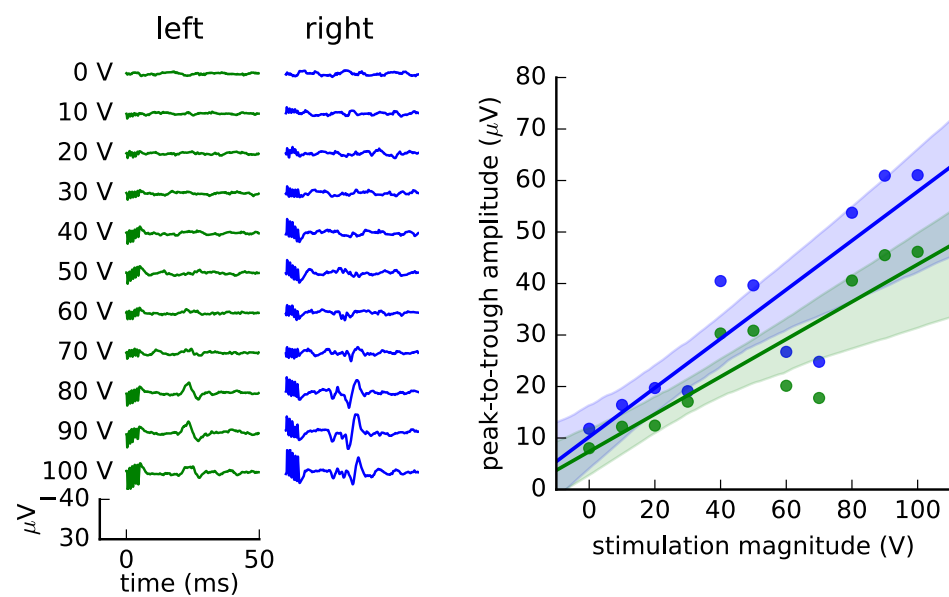
subject 1



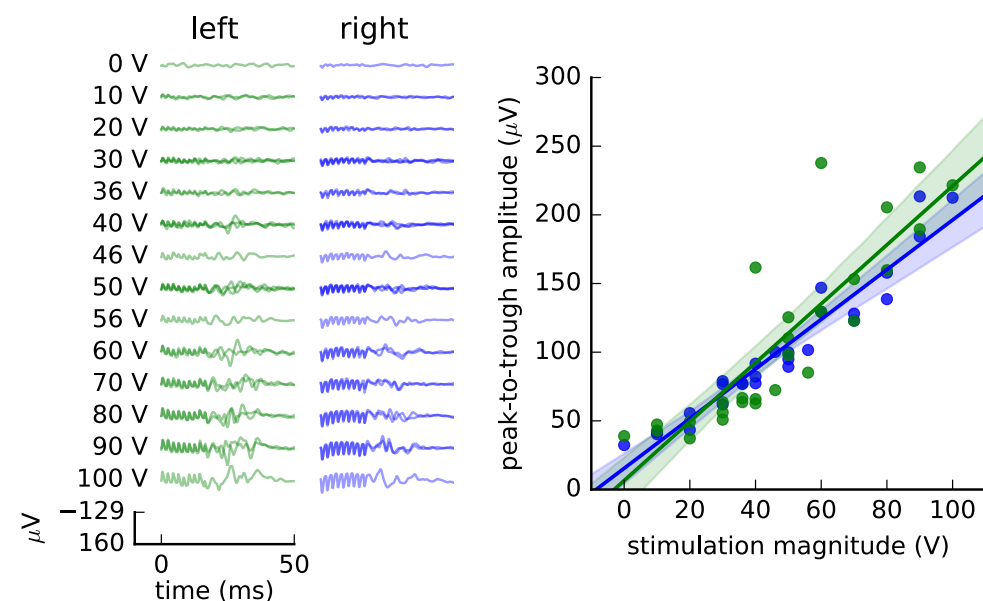
subject 2

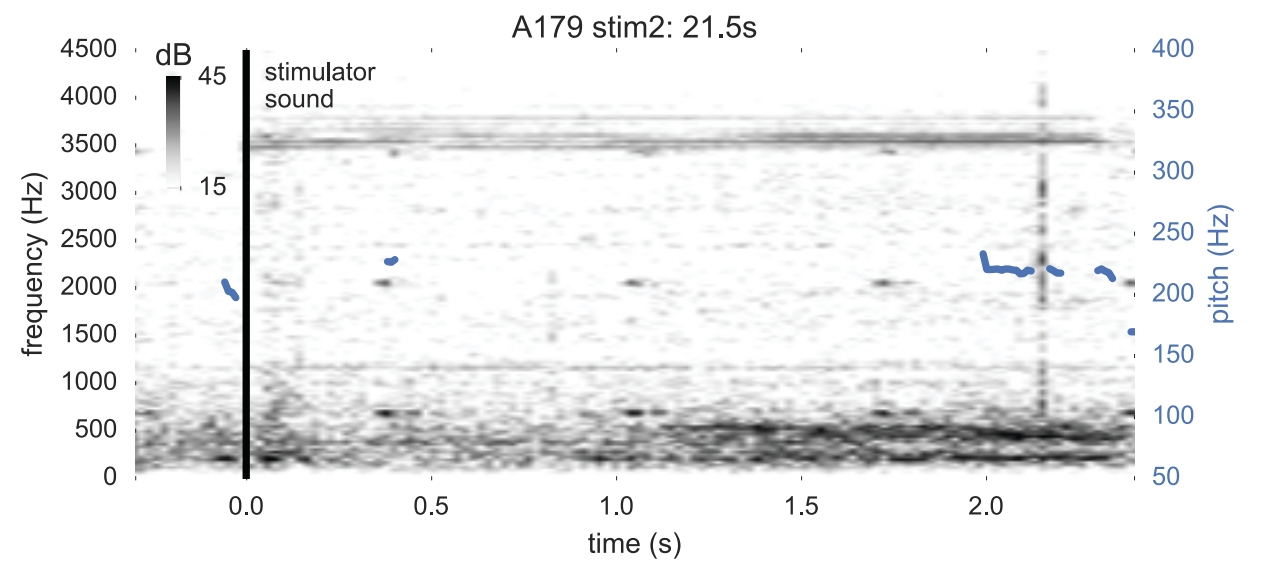
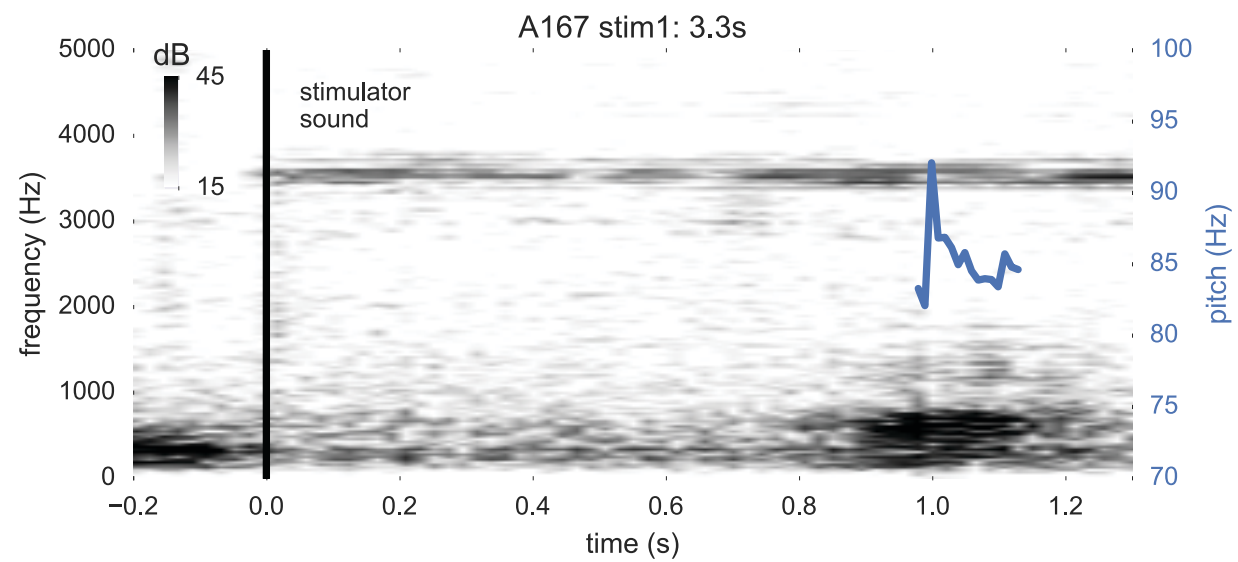
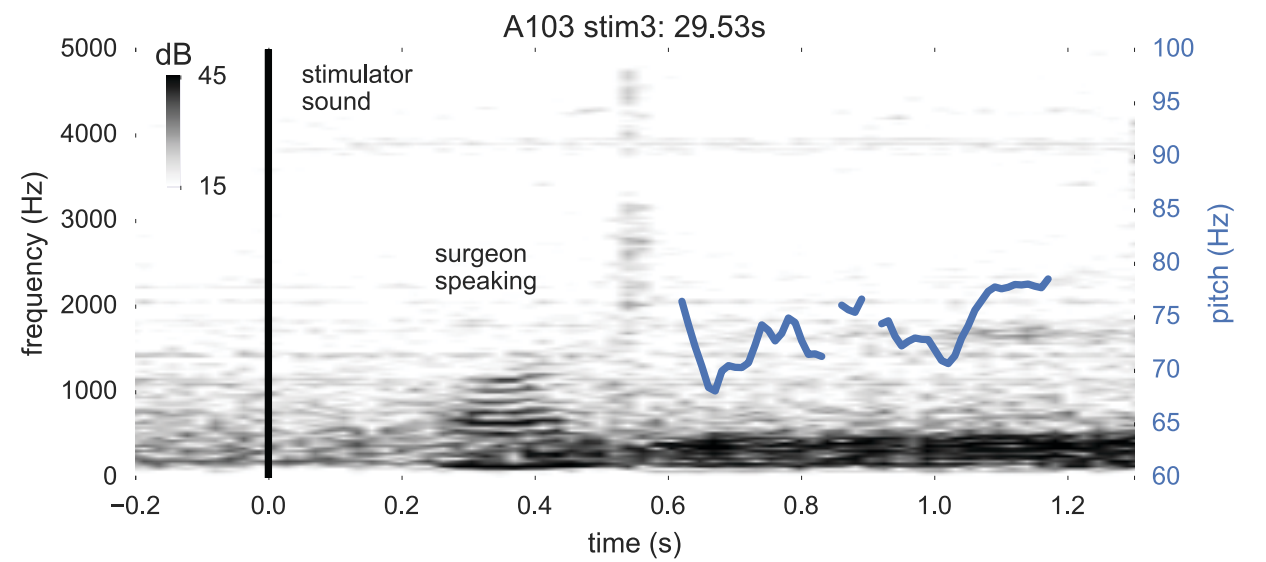
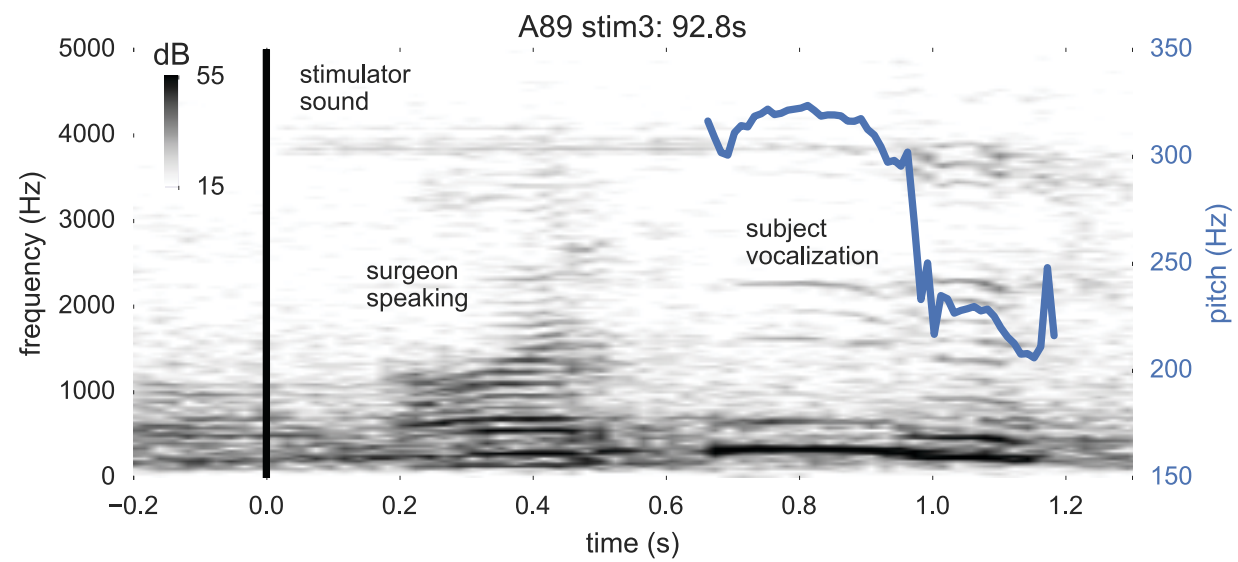
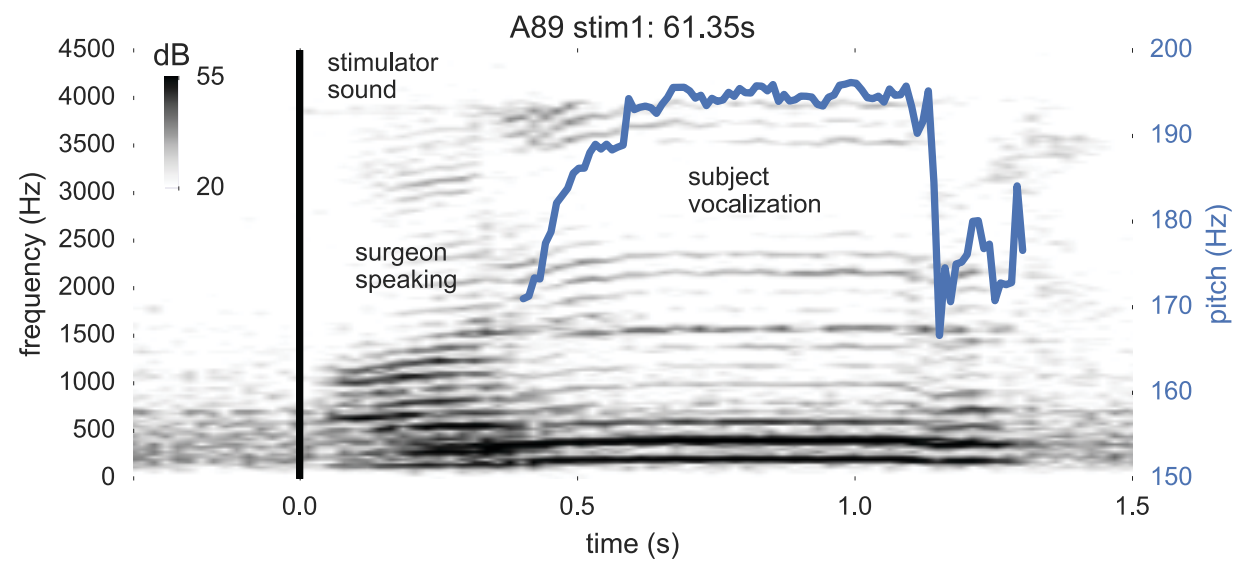


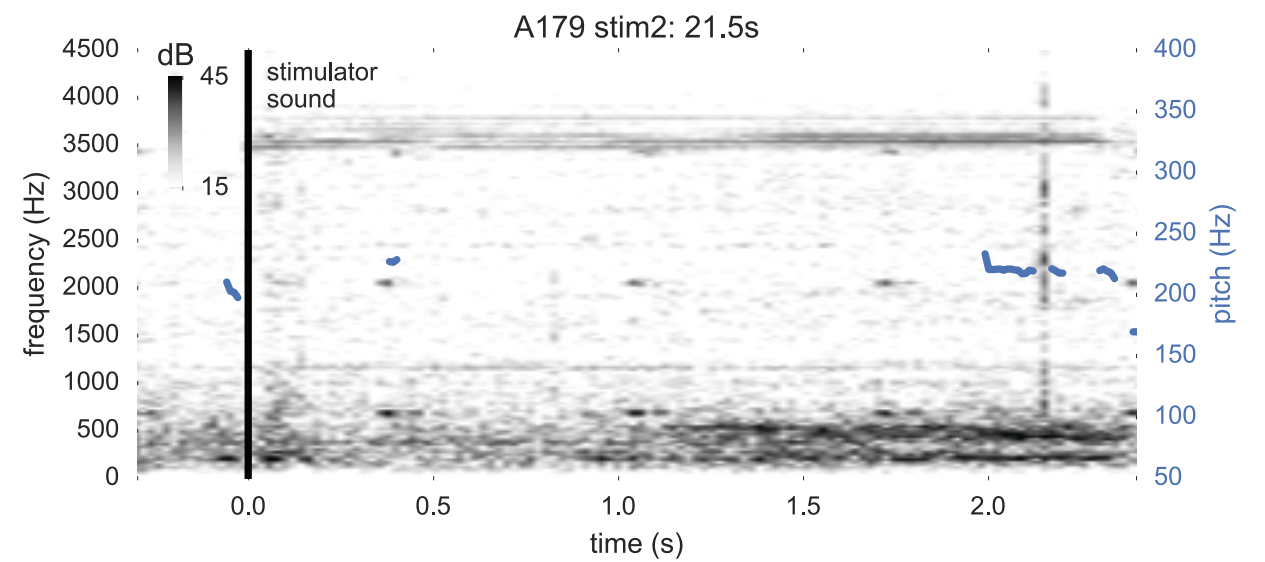
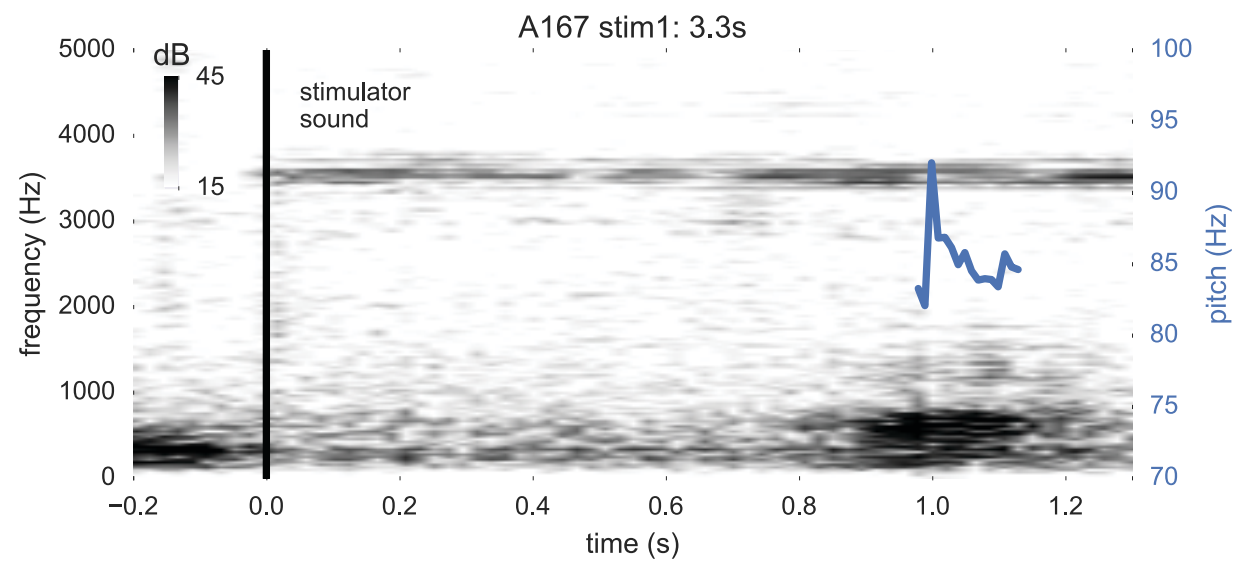
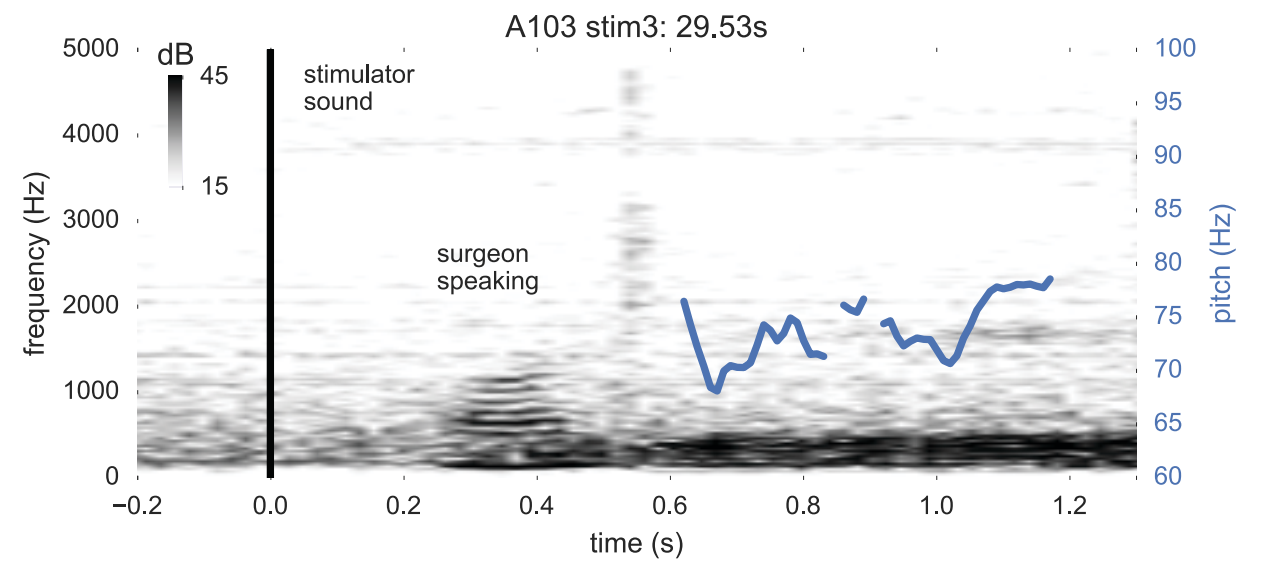
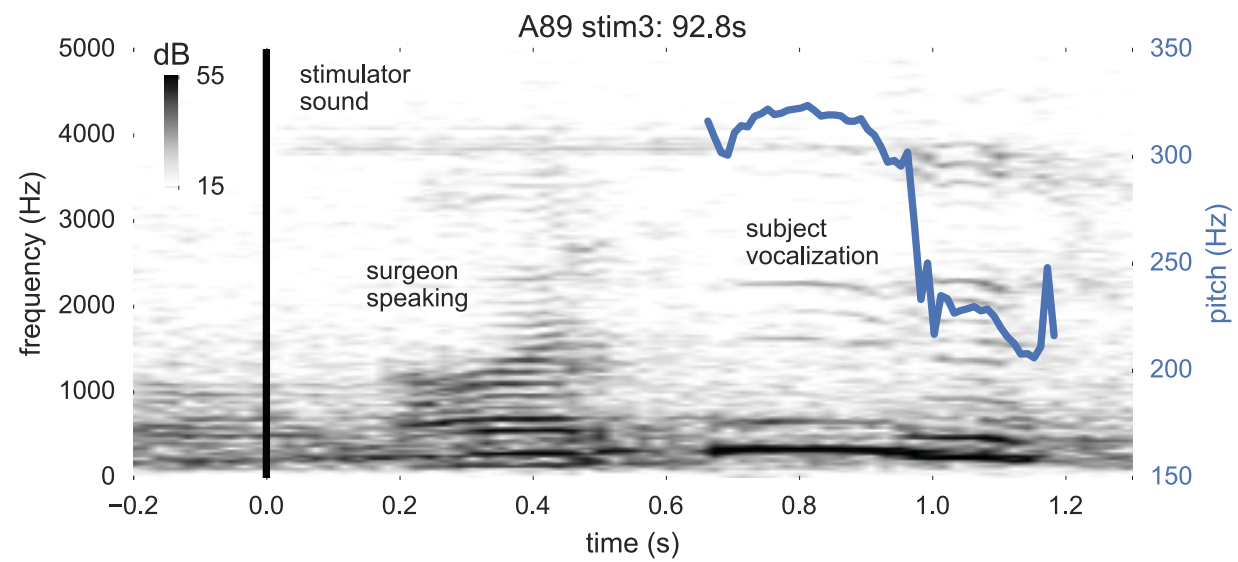
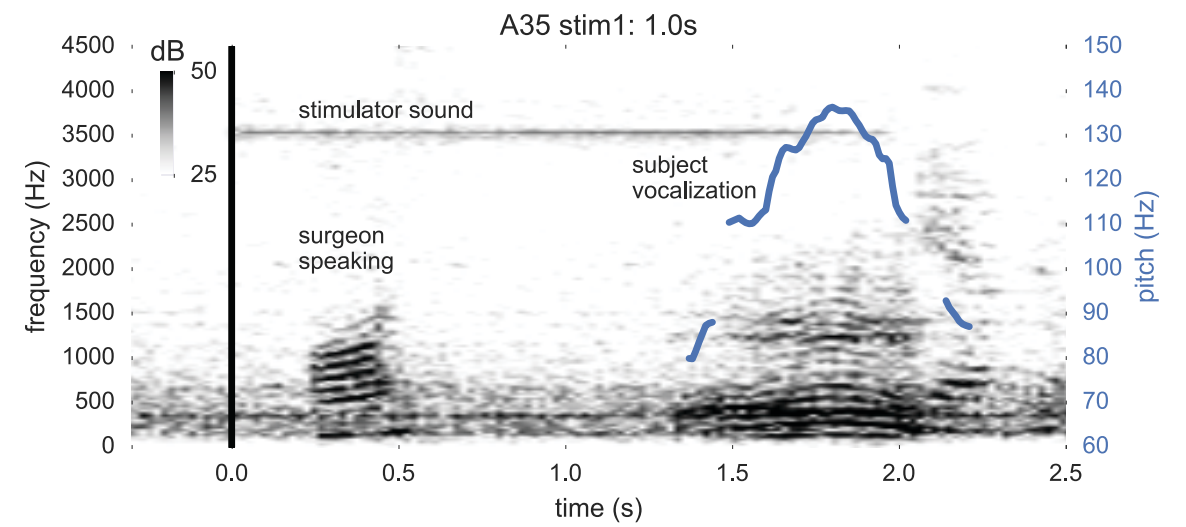
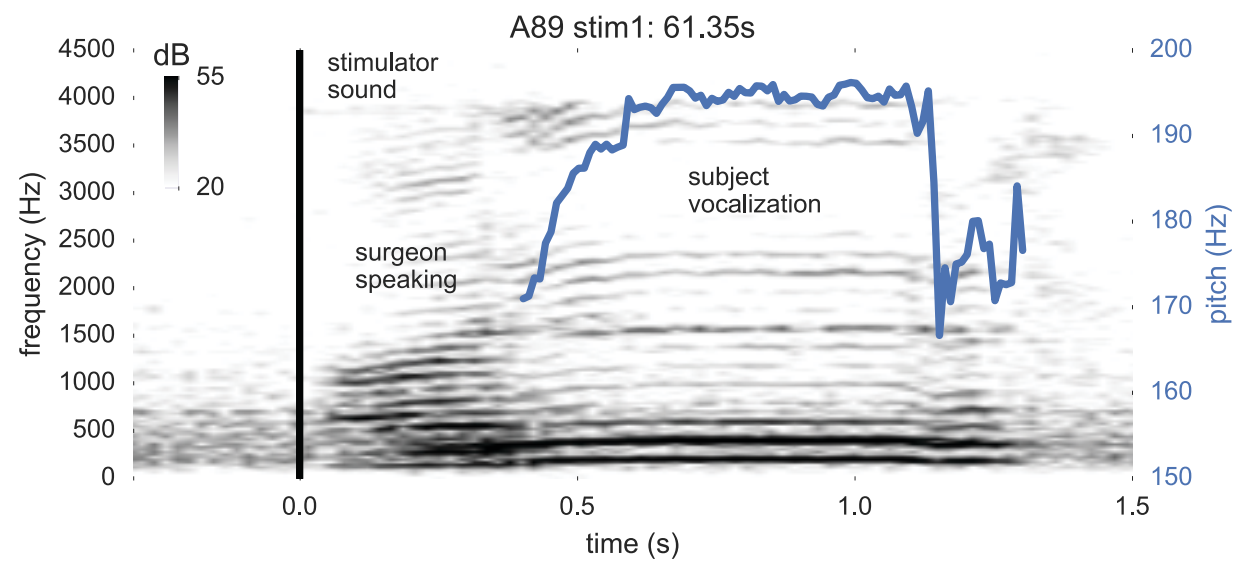
subject 3

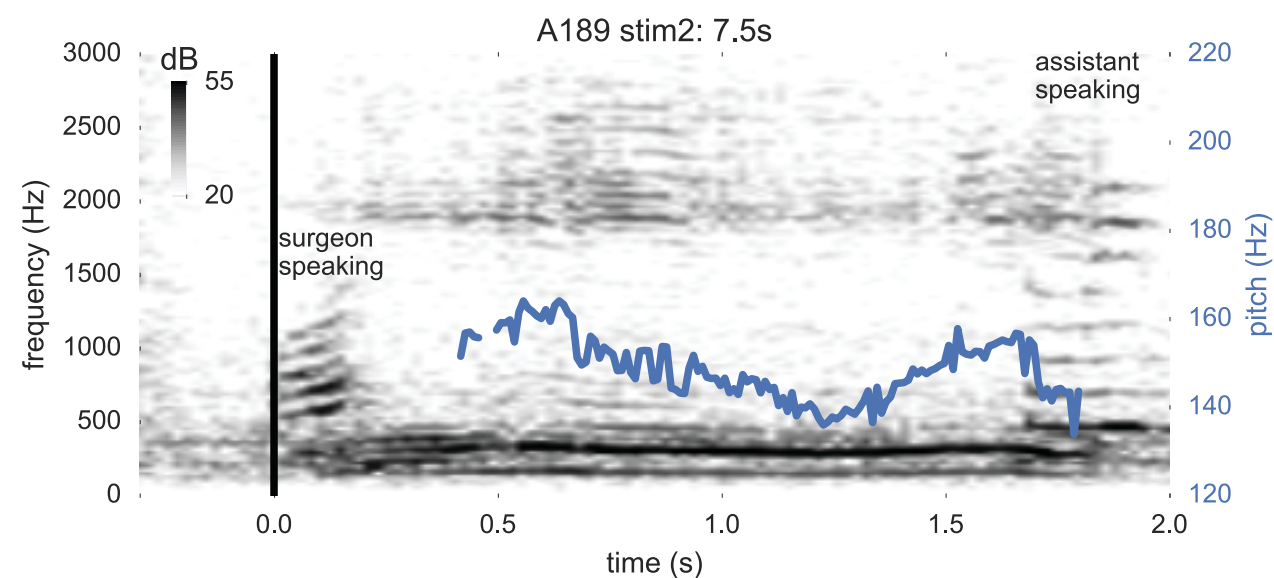
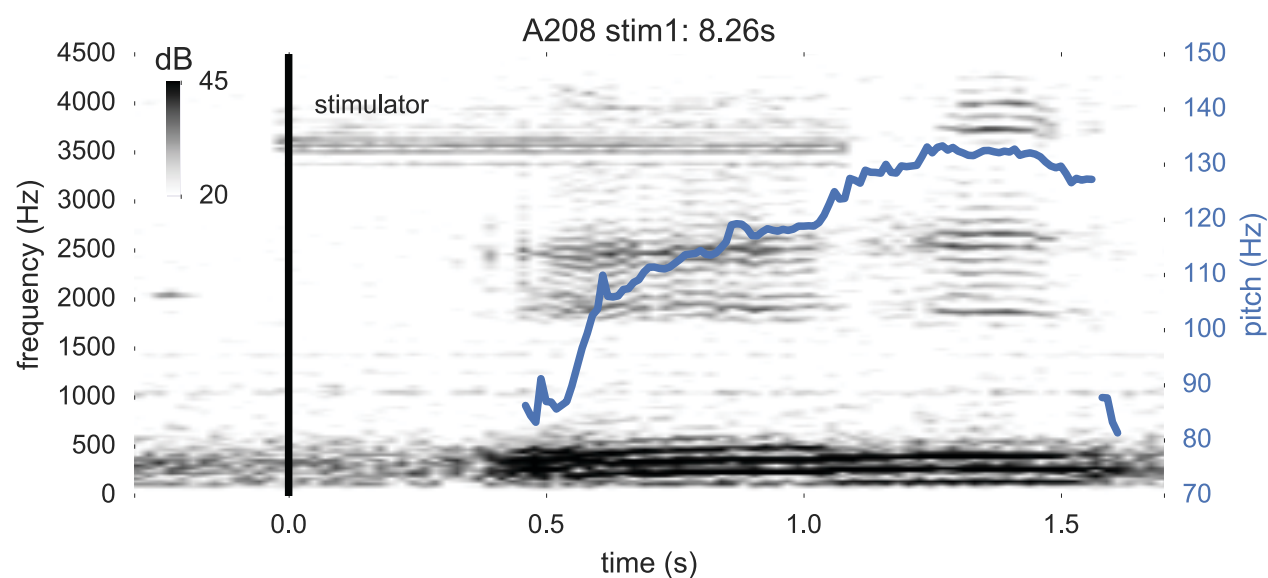
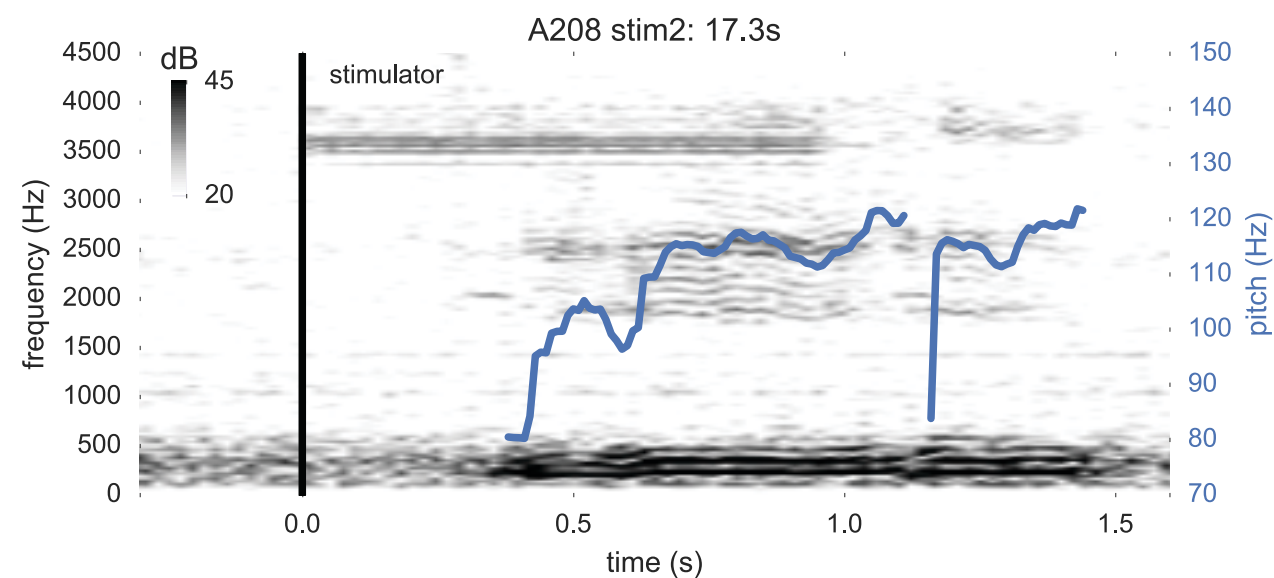
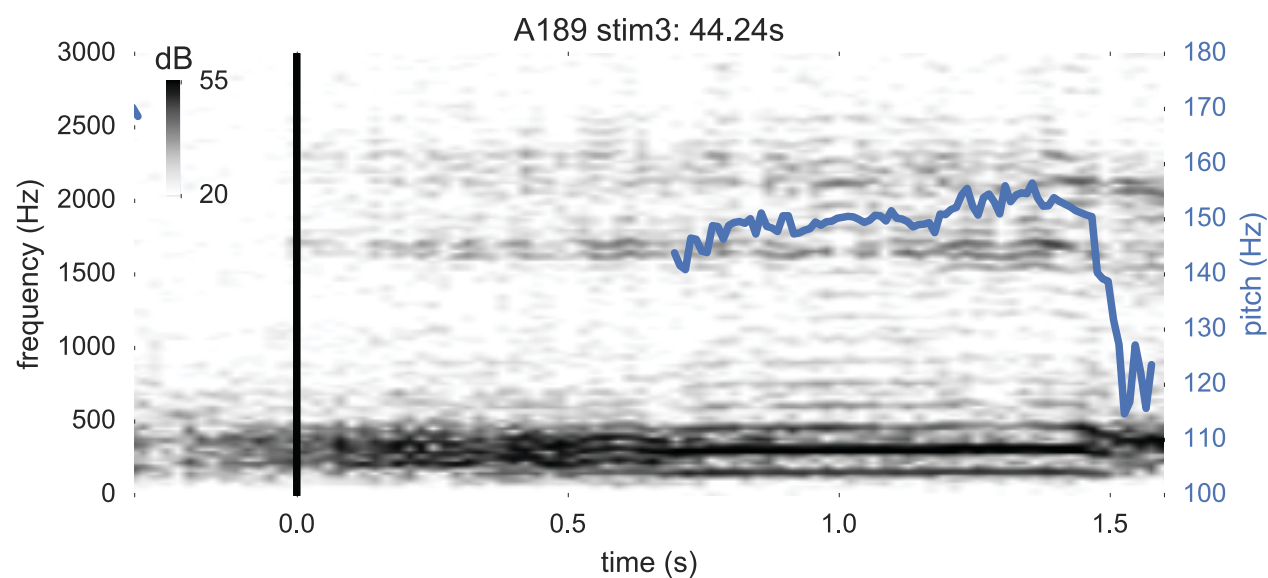
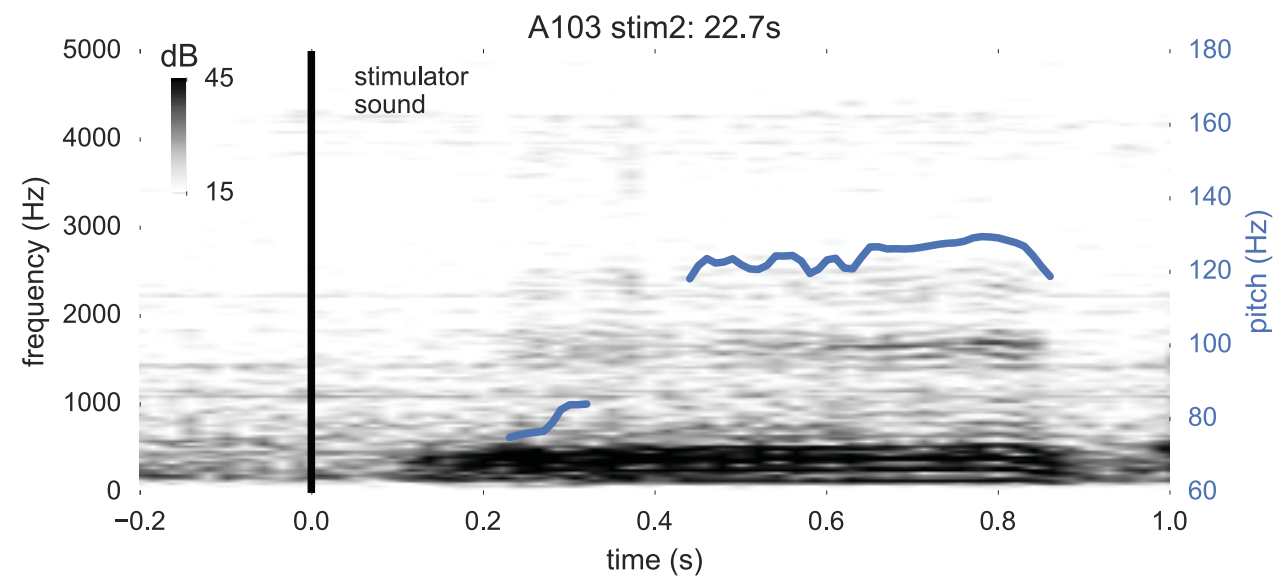
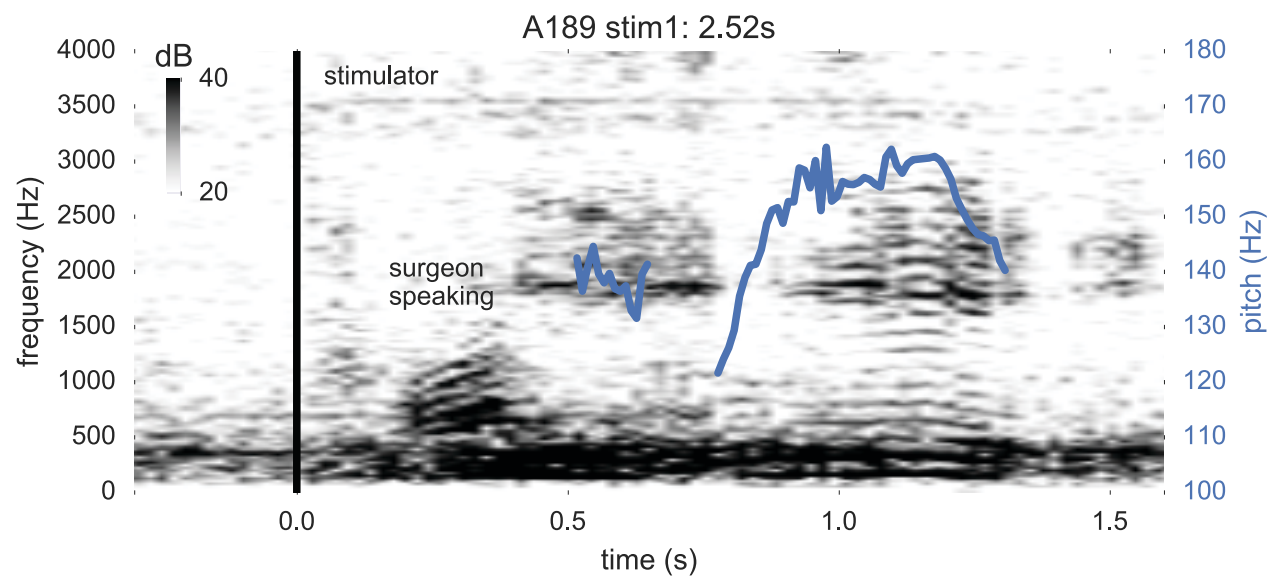


subject 4

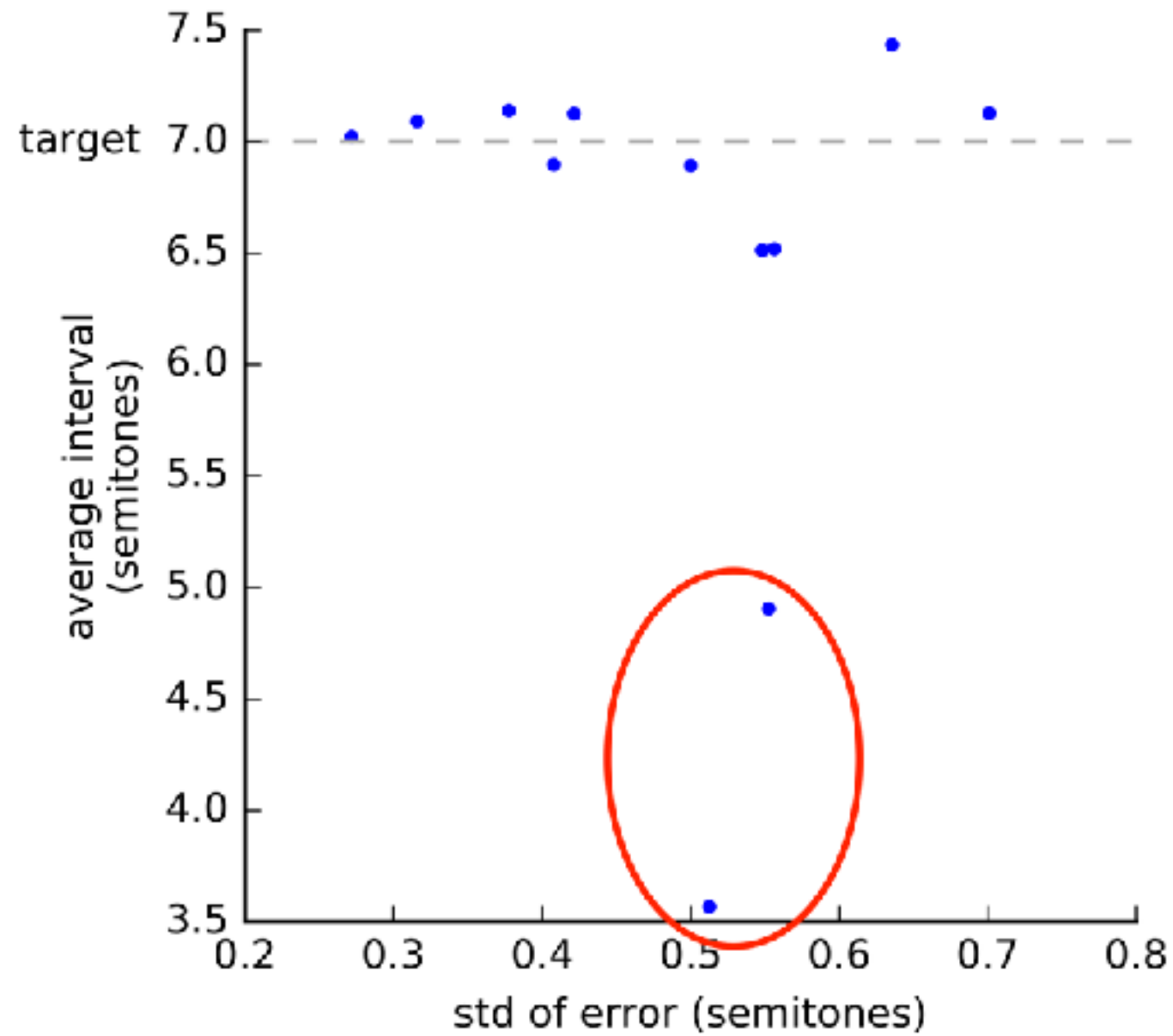




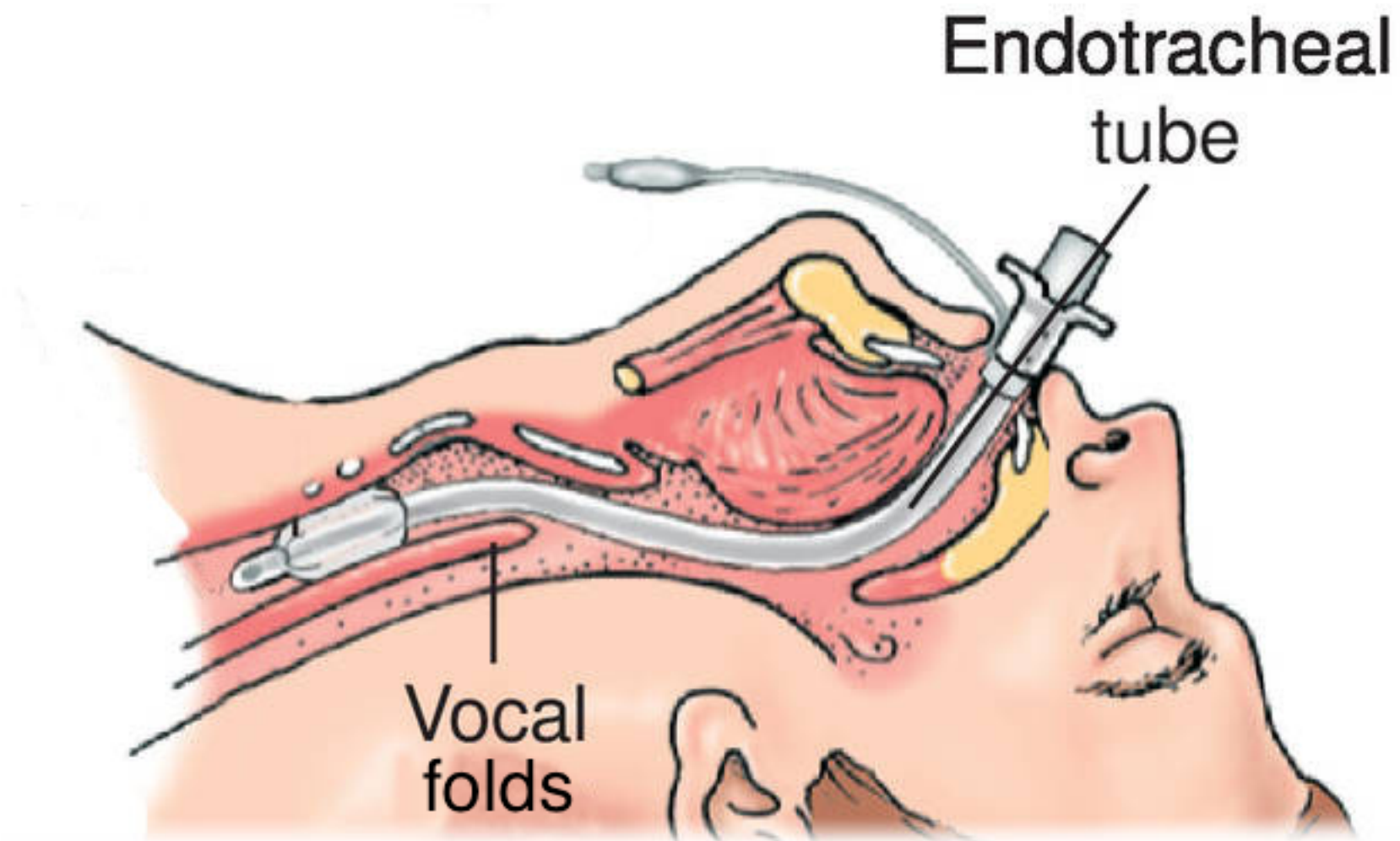




Singing behavior



Endotracheal tube with EMG



Contrastive emphasis task: vocal pitch encoding

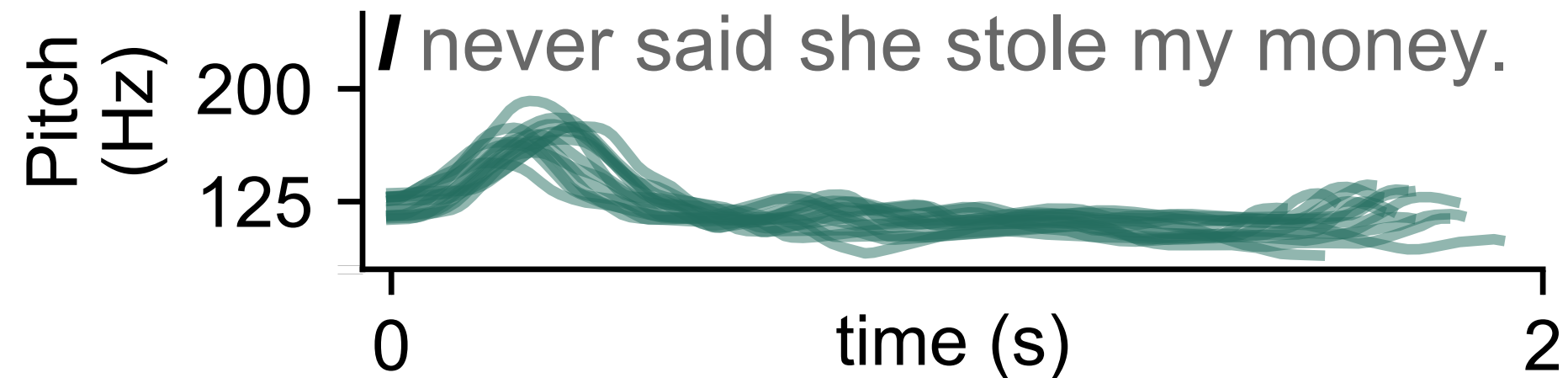
I never said she stole my money.

Contrastive emphasis task: vocal pitch encoding

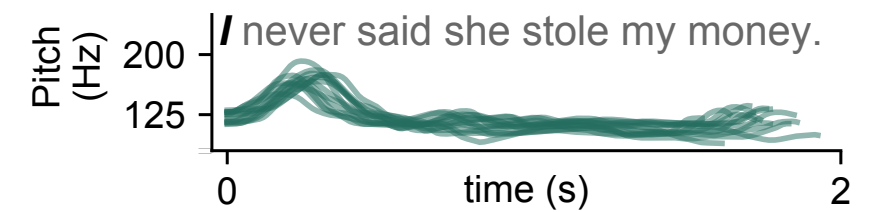
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Contrastive emphasis task: vocal pitch encoding



Contrastive emphasis task: vocal pitch encoding

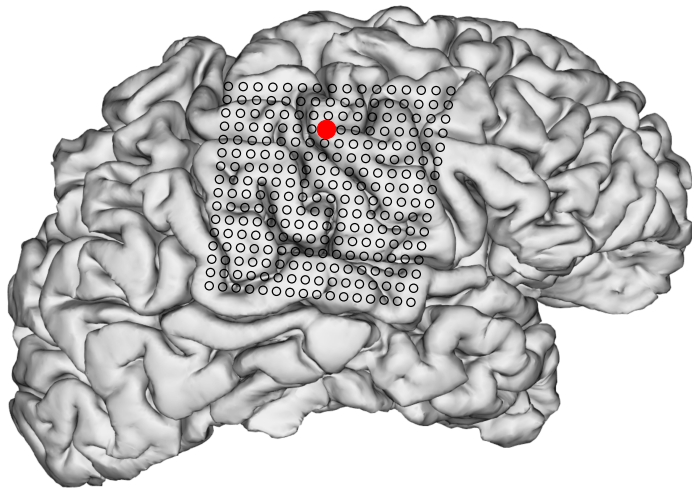


Contrastive emphasis task: vocal pitch encoding



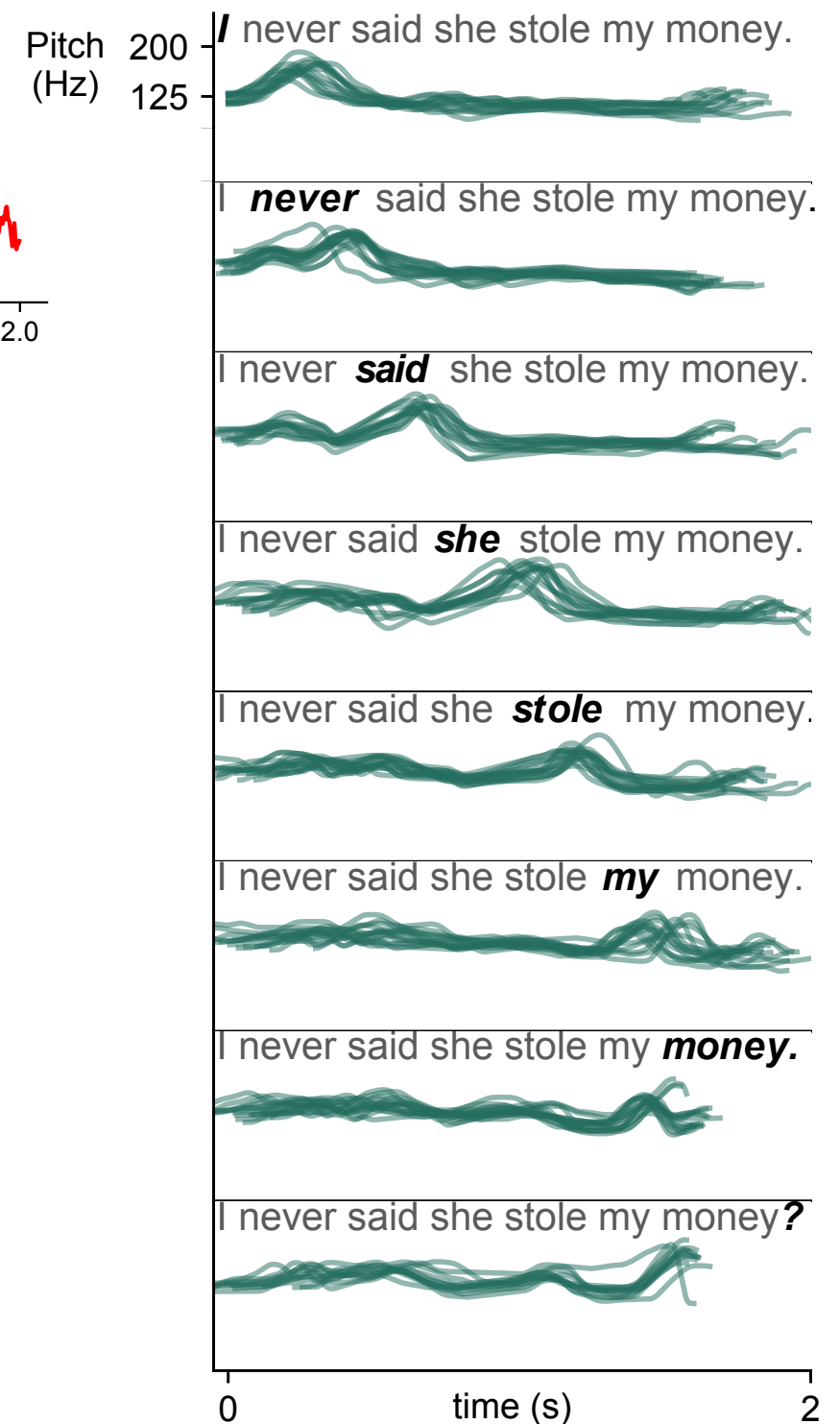
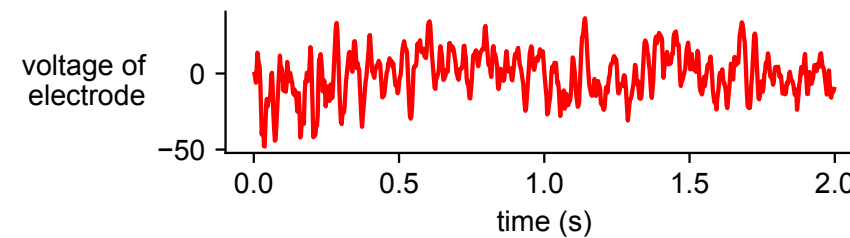
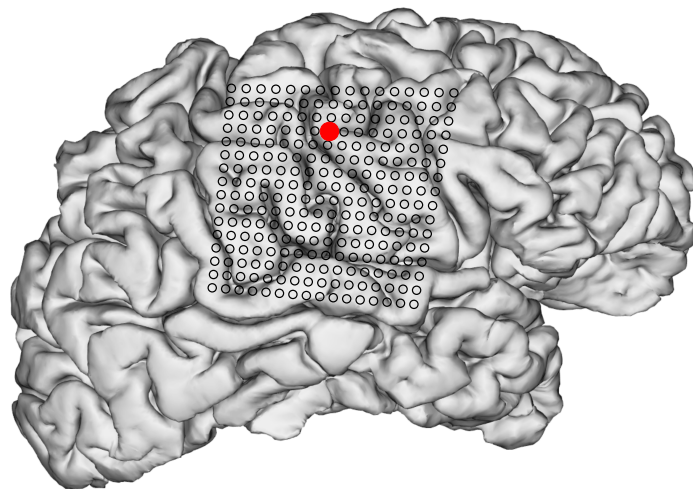
Contrastive emphasis task: vocal pitch encoding

ECoG



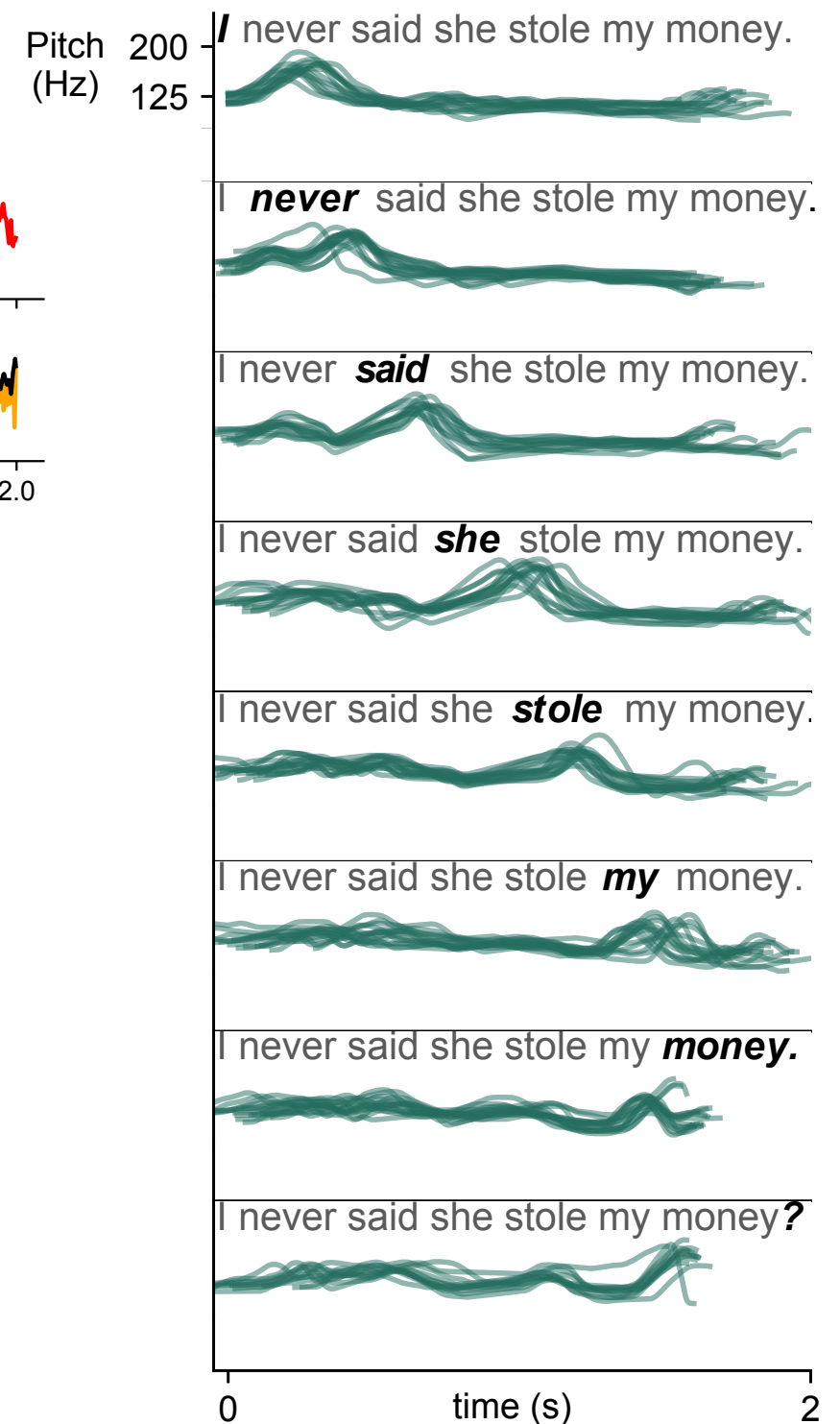
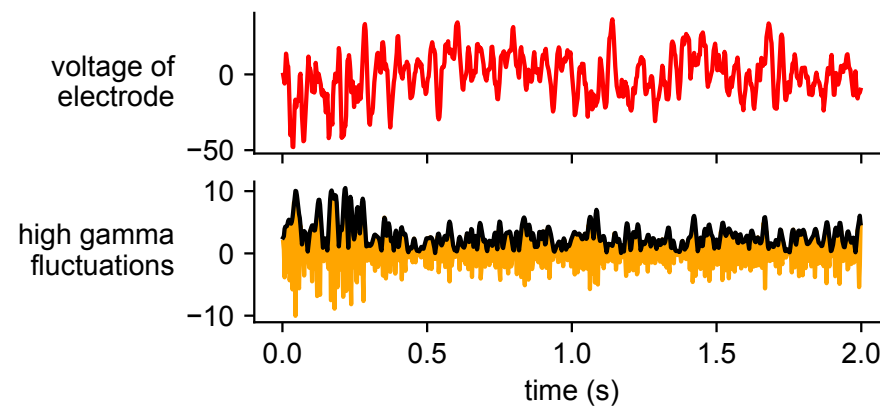
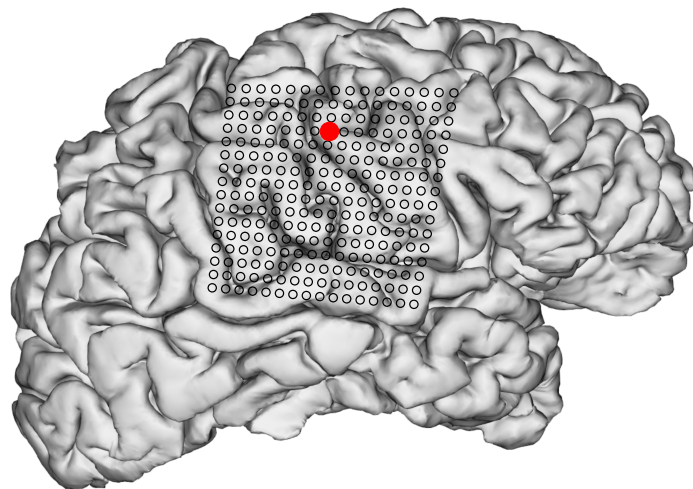
Contrastive emphasis task: vocal pitch encoding

ECoG



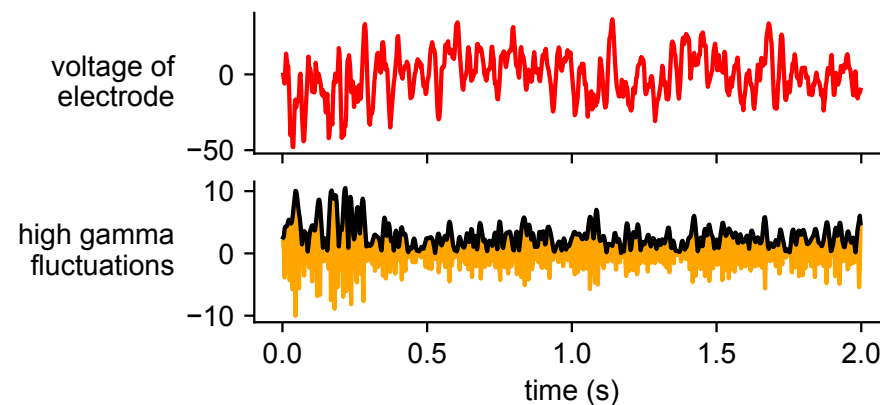
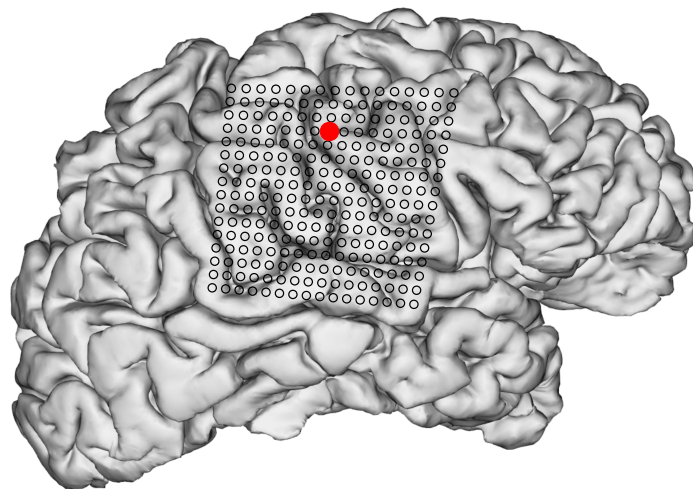
Contrastive emphasis task: vocal pitch encoding

ECoG



Contrastive emphasis task: vocal pitch encoding

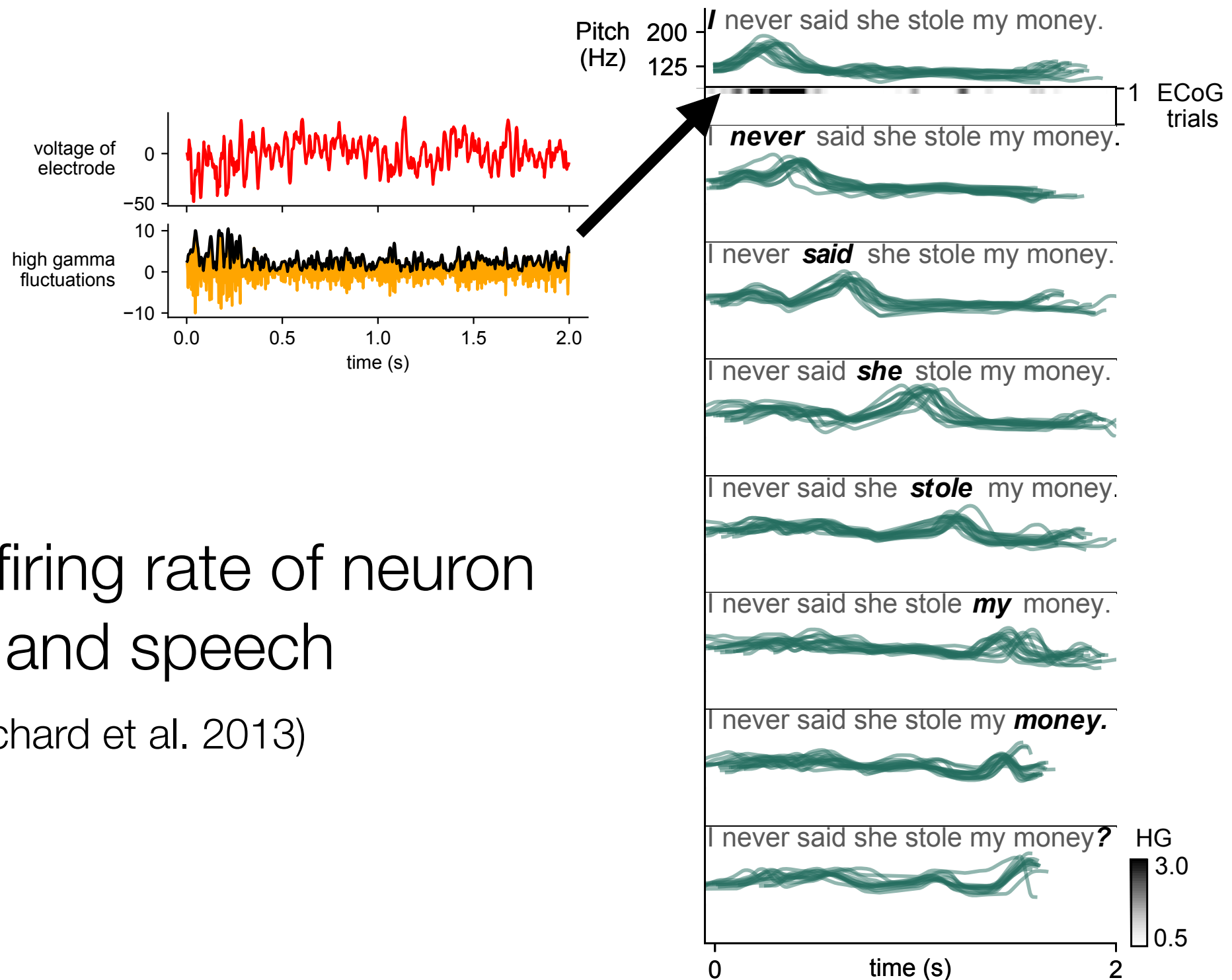
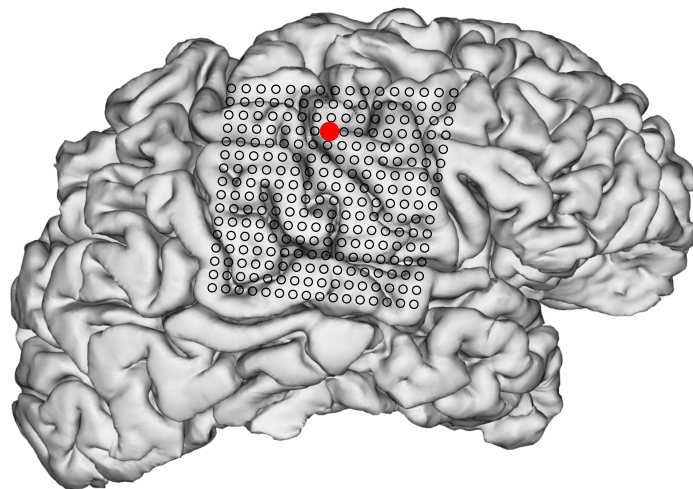
ECoG



Correlates with firing rate of neuron
(Ray and Mansell, 2011) and speech
movements (Bouchard et al. 2013)

Contrastive emphasis task: vocal pitch encoding

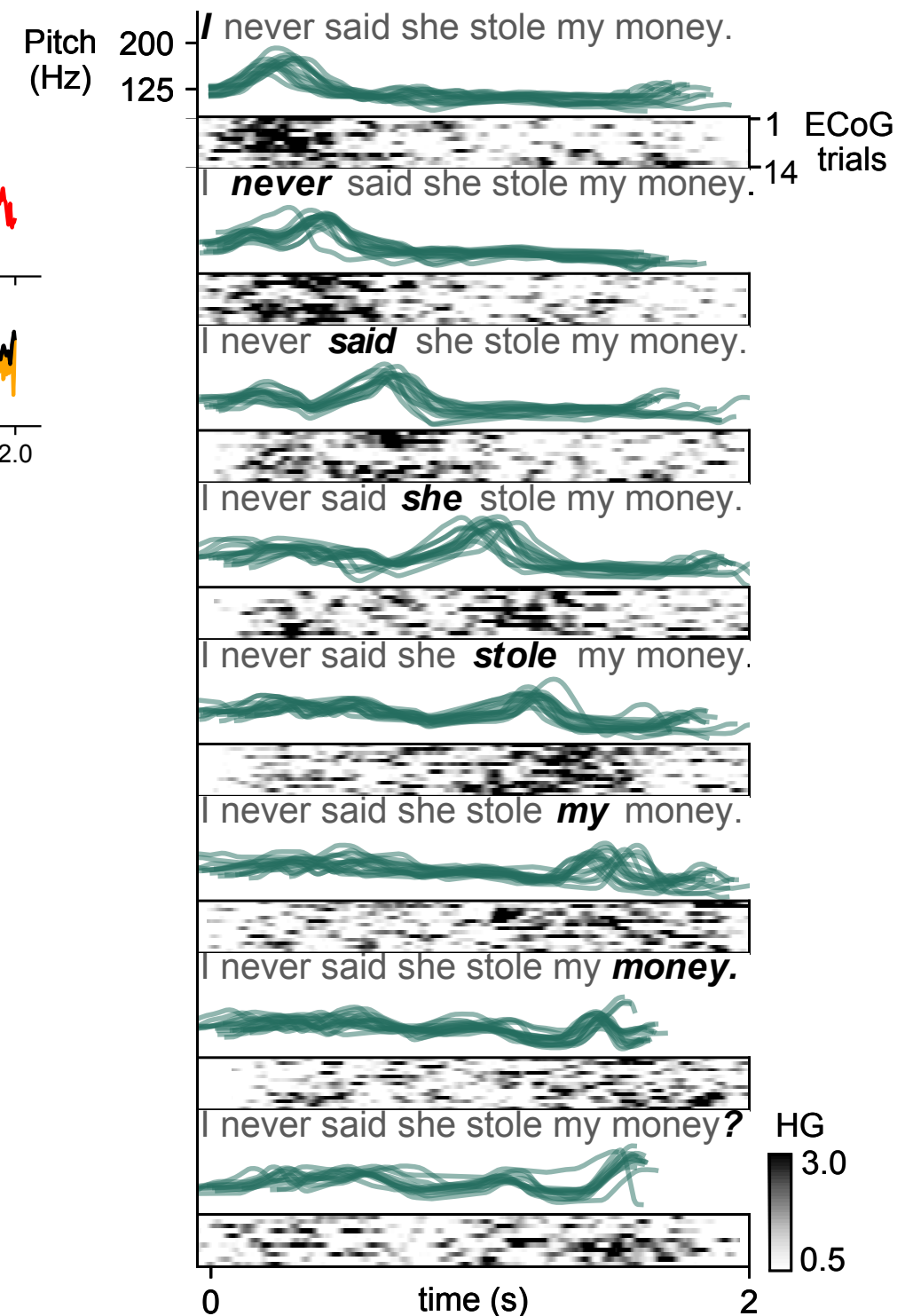
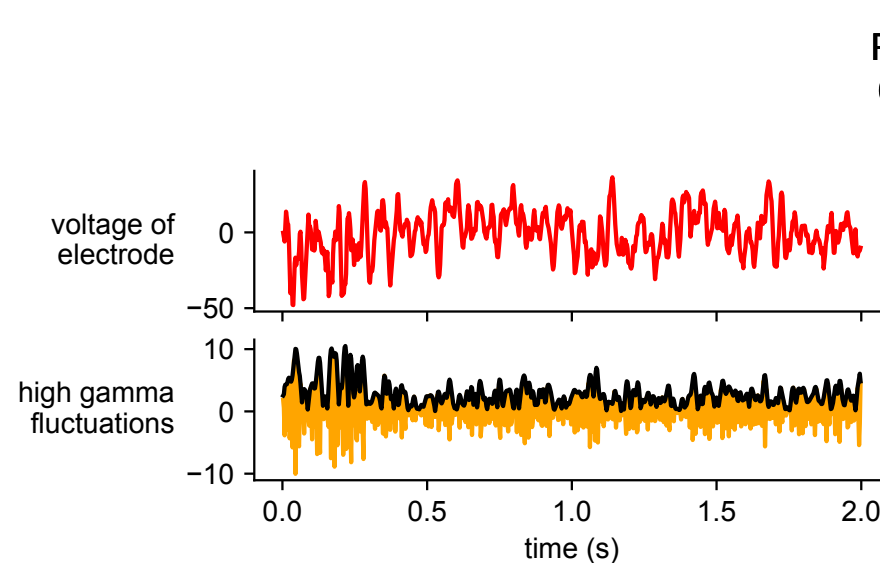
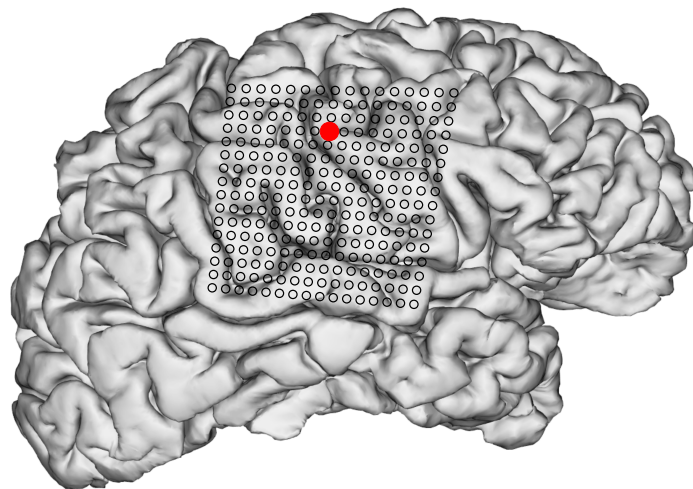
ECoG



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Roadmap for representation of pitch

- Control of vocal pitch production
 - In speech
 - In song
 - Cortical stimulation
- Pitch intonation perception in speech

Sentence timing: permutation test

