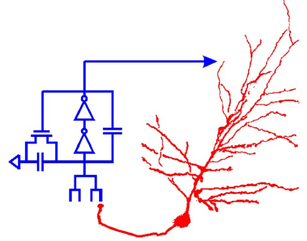

Computational
Sensorimotor
Systems Lab

The Progression of Neural Speech Representations Through Auditory Cortex and Beyond, from Acoustics to Language to Semantics

Jonathan Z. Simon

University of Maryland

Department of Electrical & Computer Engineering,
Department of Biology, Institute for Systems Research

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Bar-Ilan University, 20 Jun 2023

Acknowledgements

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Peng Zan

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NIDCD
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- *Early & fast* cortical representation of continuous speech
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Cortical Representations of Continuous Speech

Continuous speech

- naturalistic
- redundant
- employs auditory cognition
- acoustically rich
- drives most auditory areas
- …
- but also complicated

If you happened to find yourself on the banks of the Ohio River on a particular afternoon in the spring of 1806—somewhere just to the north of Wheeling, West Virginia, say …

The Botany of Desire — Michael Pollan

Alfred the Great was a young man, three-and-twenty years of age, when he became king. Twice in his childhood, he had been taken to Rome, where the Saxon nobles were in the habit of going on journeys which they supposed to be religious; …

A Child's History of England — Charles Dickens

In the bosom of one of those spacious coves which indent the eastern shore of the Hudson, at that broad expansion of the river denominated by the ancient Dutch navigators …

The Legend of Sleepy Hollow — Washington Irving

He was an old man who fished alone in a skiff in the Gulf Stream and he had gone eighty-four days now without taking a fish. In the first forty days a boy had been with him. But after forty days without a fish …

The Old Man and the Sea — Ernest Hemingway

Cortical Representations of Continuous Speech

Temporal neural patterns ⇆ temporal patterns in speech

- Generalization of “Speech Tracking”
- Need high temporal precision, for fast temporal speech features

  - EEG (electroencephalography): *whole brain*
  - MEG (magnetoencephalography): *whole brain but with strong cortical bias*
  - ECoG (electrocorticography): *placed cortical surface electrodes*
  - single- and multi-unit recording methods: *placed depth electrodes*

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Cortical Representations of Continuous Speech

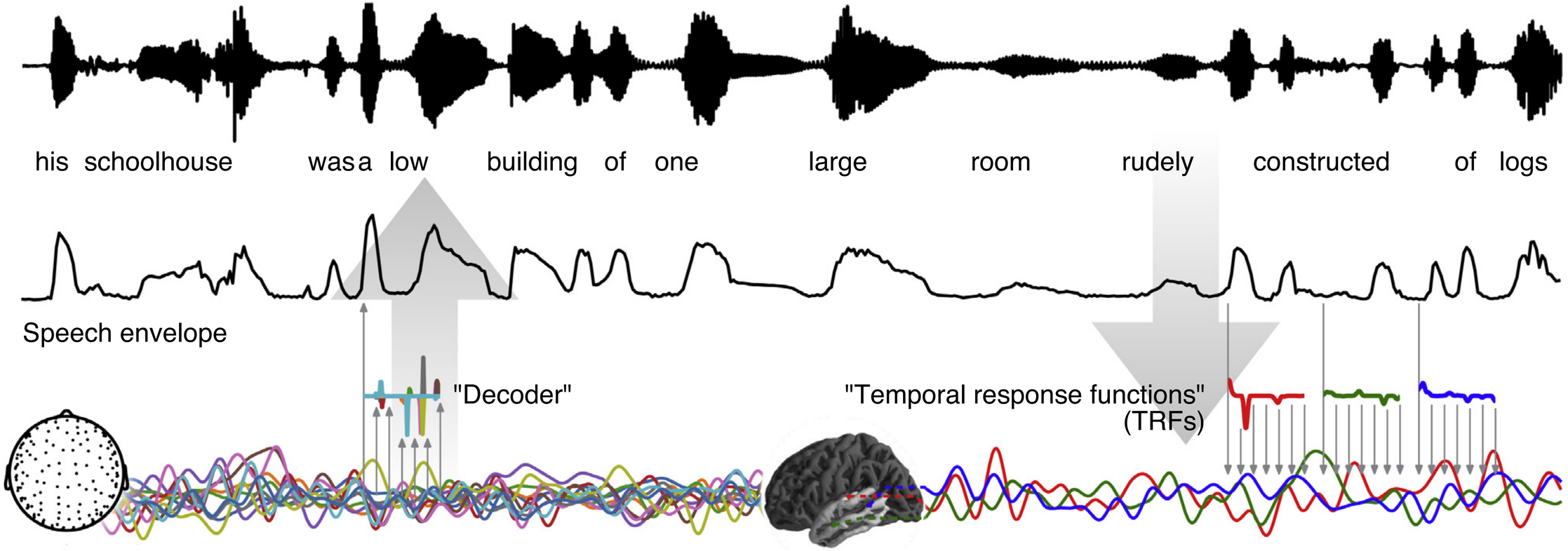
Neural Representations of Speech

- oscillations at pitch frequencies (primarily subcortical) — Maddox & Lee (2018) eNeuro
  - acoustic onset tracking — Daube et al. (2019) Curr Biol
    - speech envelope rhythmic following — Lalor & Foxe (2010) Eur J Neurosci
      - phoneme-based responses — Teoh et al. (2022) J Neurosci
        - phoneme-context-based responses — Brodbeck et al. (2018) Curr Biol
          - word-context-based responses — Brodbeck et al. (2022) eLife
            - semantic structure rhythm following — Ding et al. (2016) Nat Neuro
- plus connections to **intelligibility/perception/behavior**

Brodbeck & Simon (2020) *Continuous Speech Processing*, Curr Op Physiol

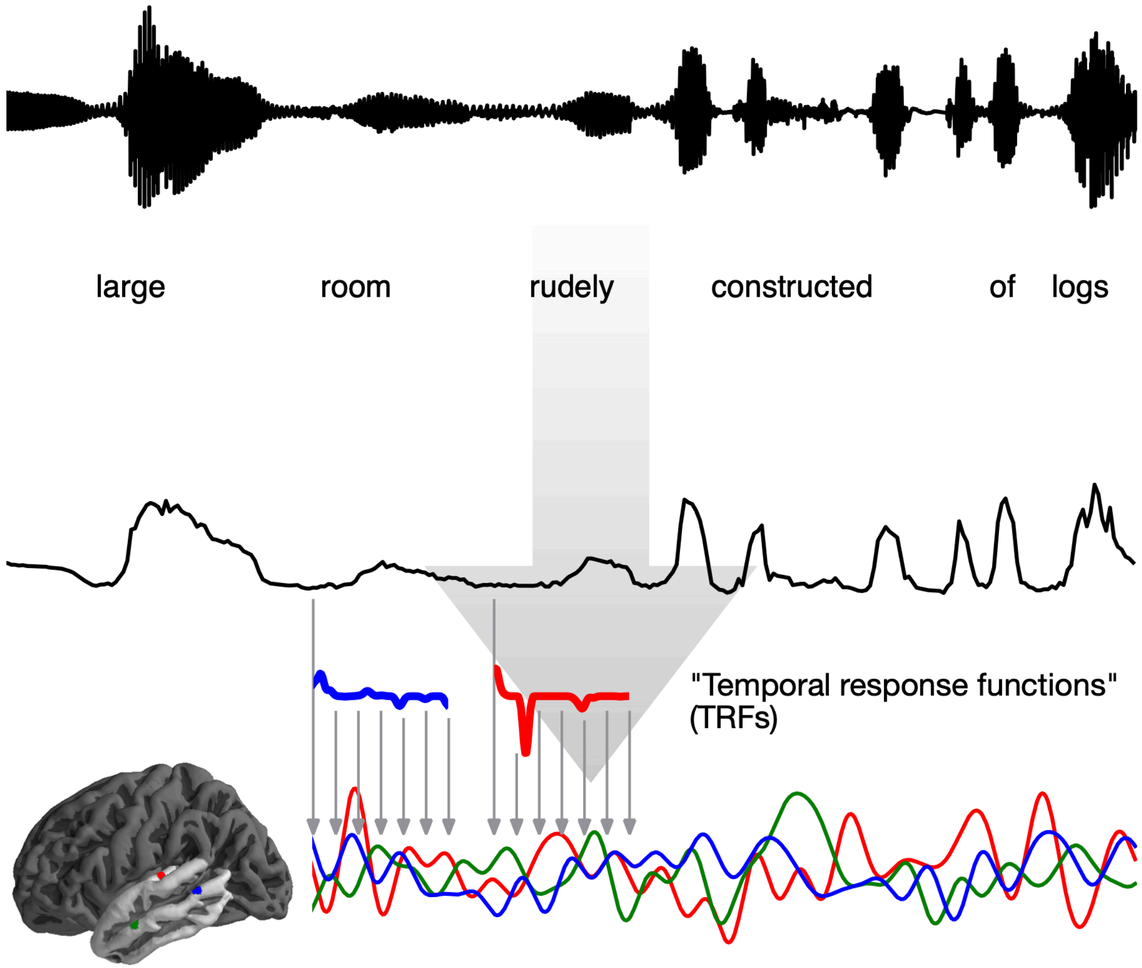
Cortical Representations of Speech

- Measure *time-locked* responses to temporal pattern of speech features (in humans)
- Any speech feature of interest: acoustic envelope, lexical, pitch, semantic, etc.
- Infer spatio-temporal neural origins of neural responses



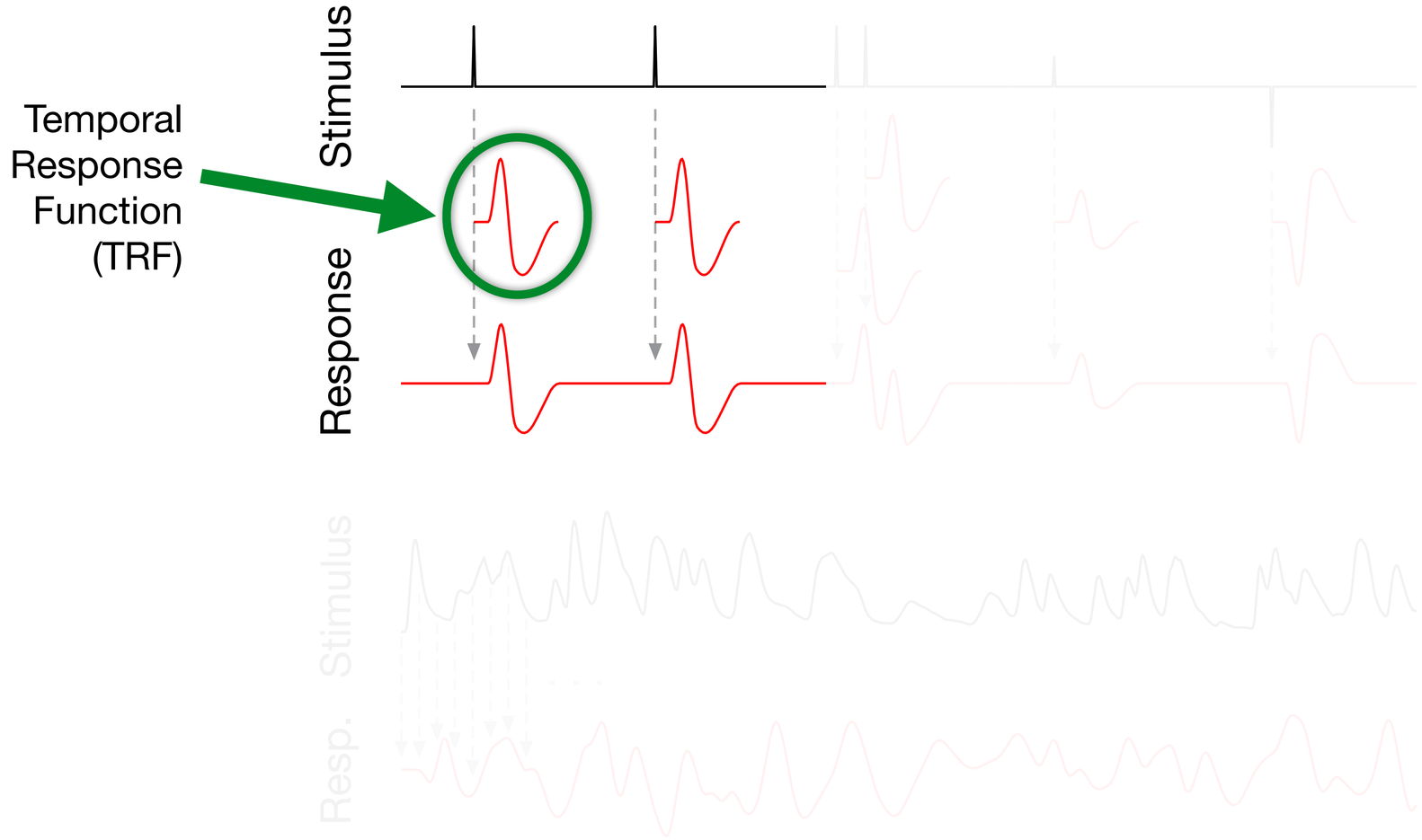
Cortical Representations: Encoding

- Predicting future neural responses from present stimulus features,
  - wide variety of stimulus features
  - via Temporal Response Function (TRF)
- Why look at encoding? It *often* tells us more about the brain
  - TRF analogous to evoked response
  - peak amplitude ≈ processing intensity
  - peak latency ≈ source location
  - multiple TRFs simultaneously



Example: MEG Prediction of Voxel Responses

Temporal Response Functions



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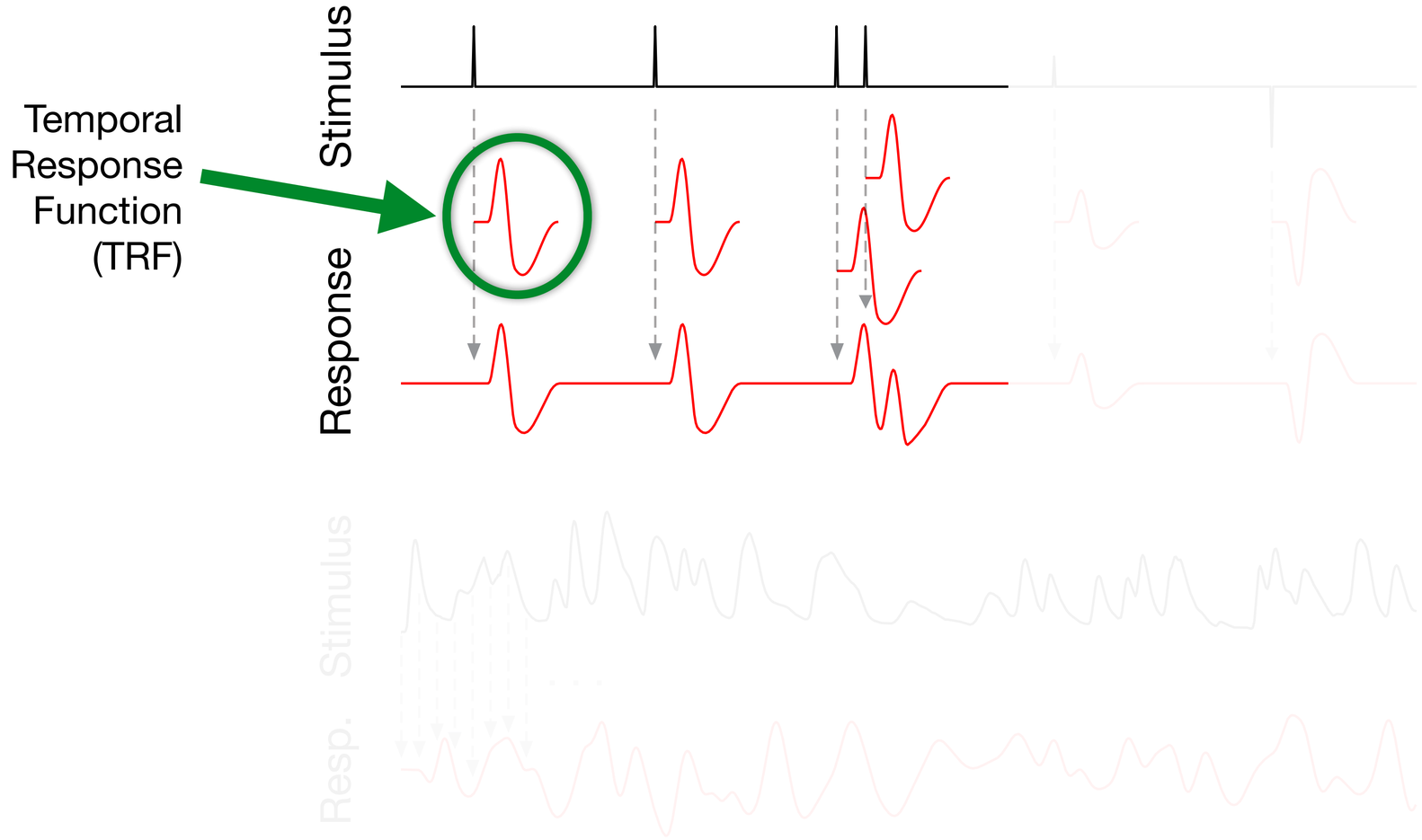

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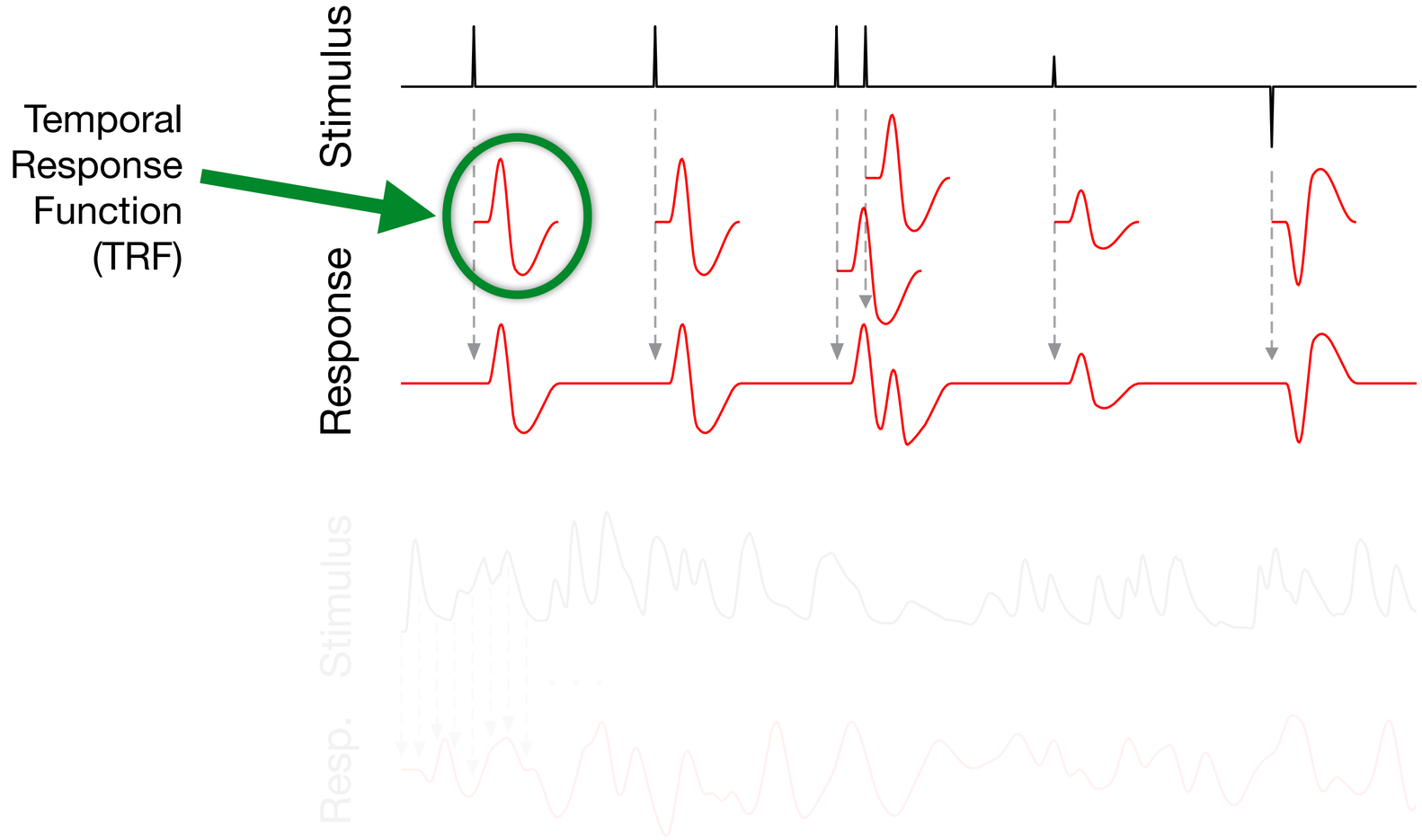

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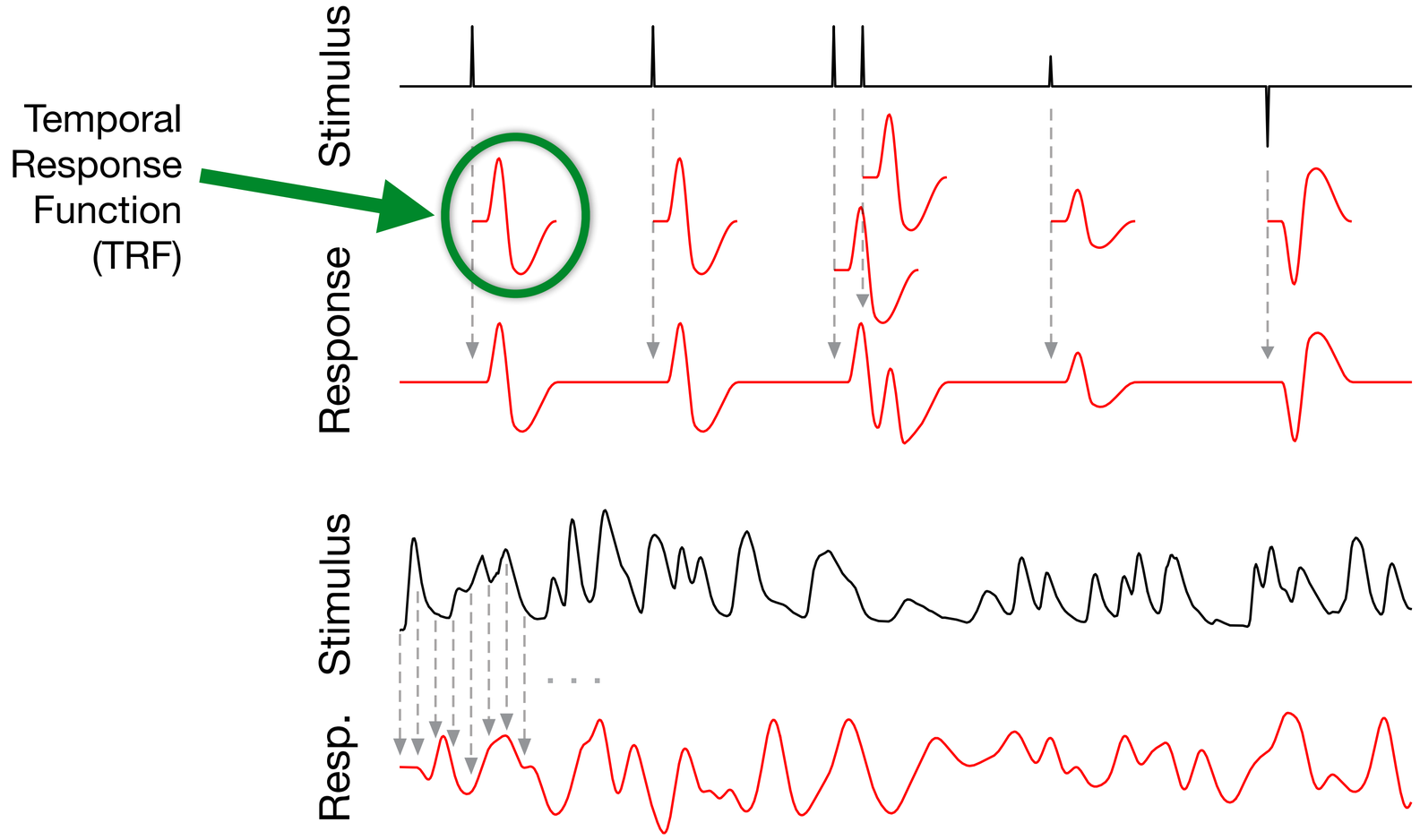
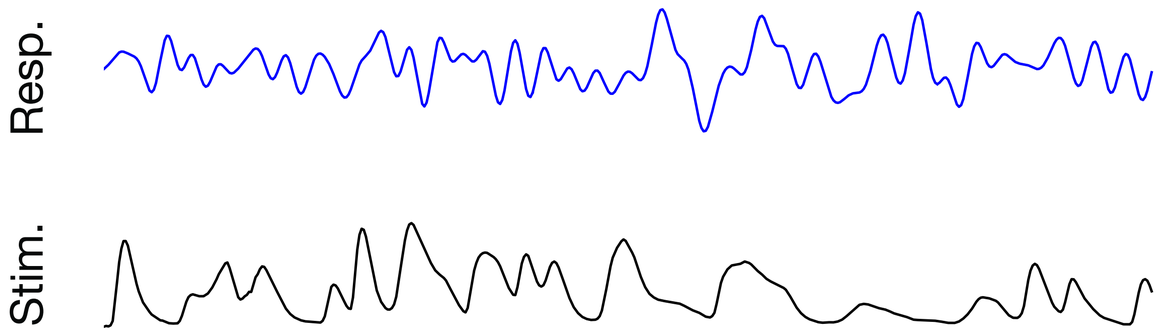


TRF Model Estimation & Fit

Temporal Response Function (TRF) estimation:

Stimulus and response are known; find the best TRF to produce the response from the stimulus:



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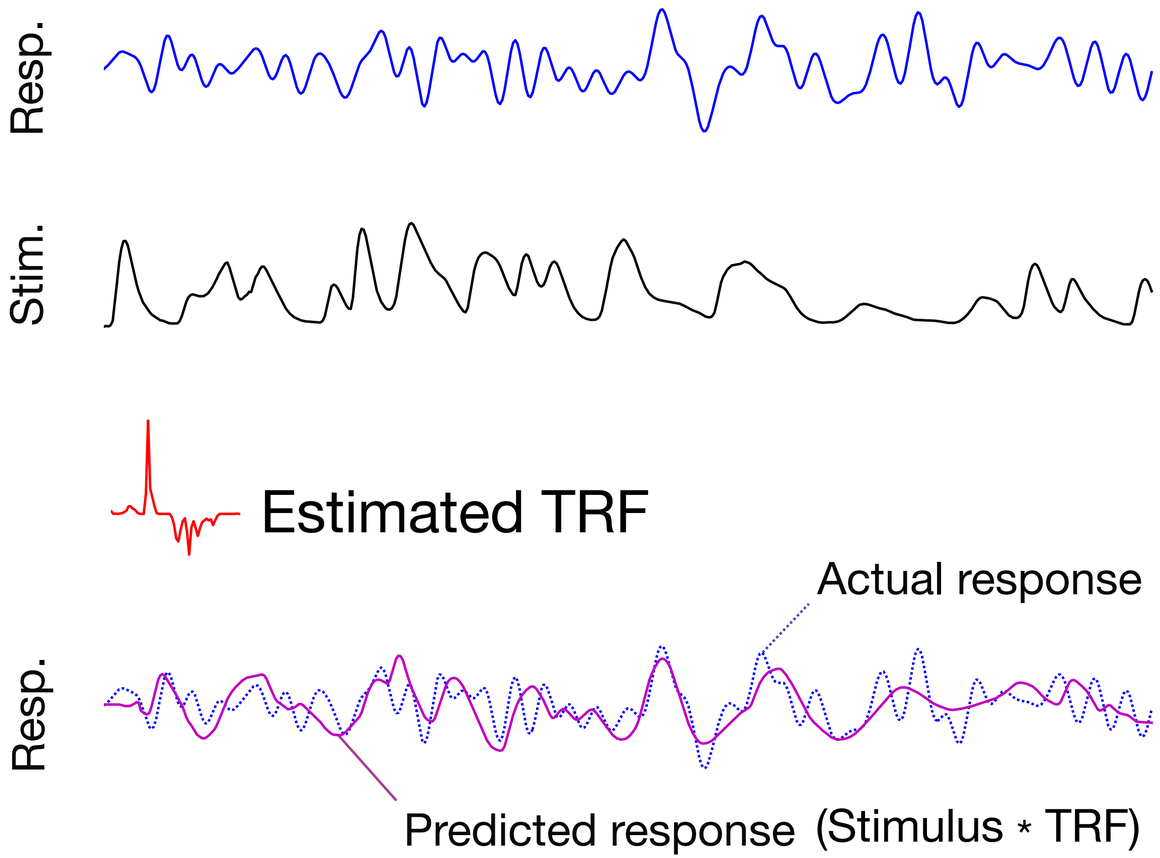
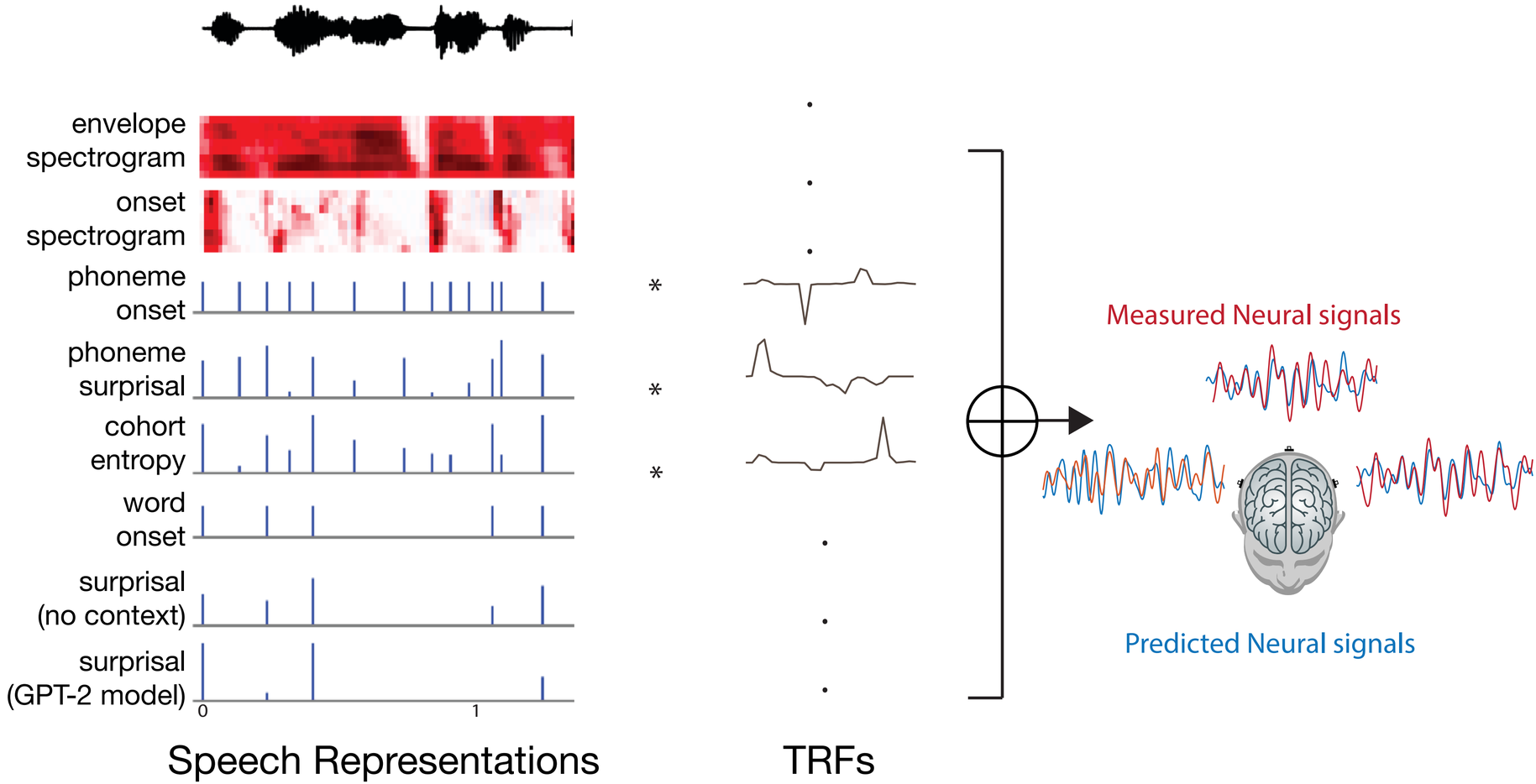


Lalor & Foxe (2010) *Neural Responses to Uninterrupted Natural Speech* … Eur J Neurosci
Ding & Simon (2012) *Neural Coding of Continuous Speech in Auditory Cortex* … , J Neurophys

Simultaneous Temporal Response Functions

- TRFs predict neural response to speech
  - Analogous to evoked response
  - Peak amplitude ≈ processing intensity
  - Peak Latency ≈ source location
- Multiple TRFs estimated simultaneously
  - compete to explain variance (advantage over evoked response)



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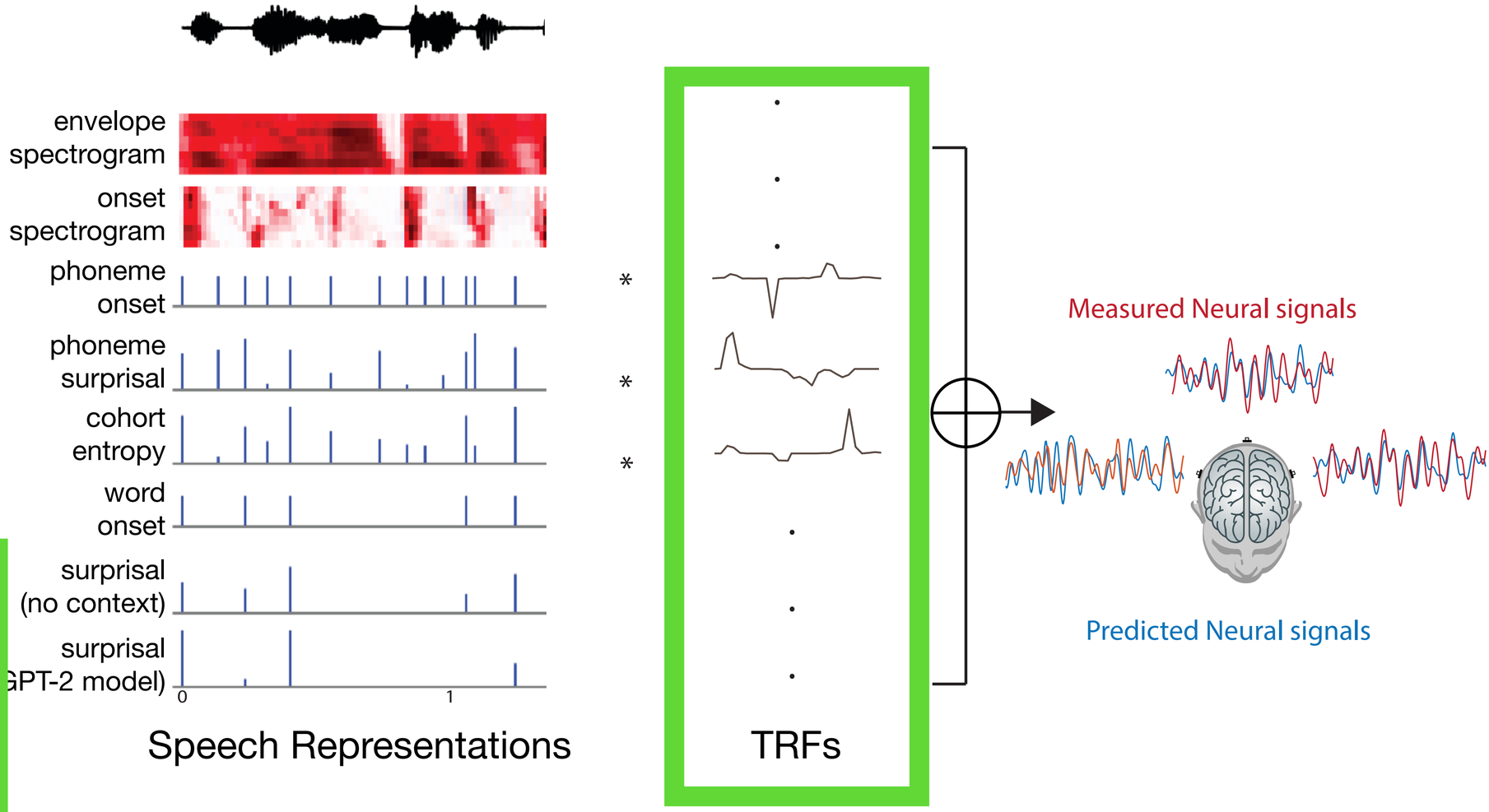
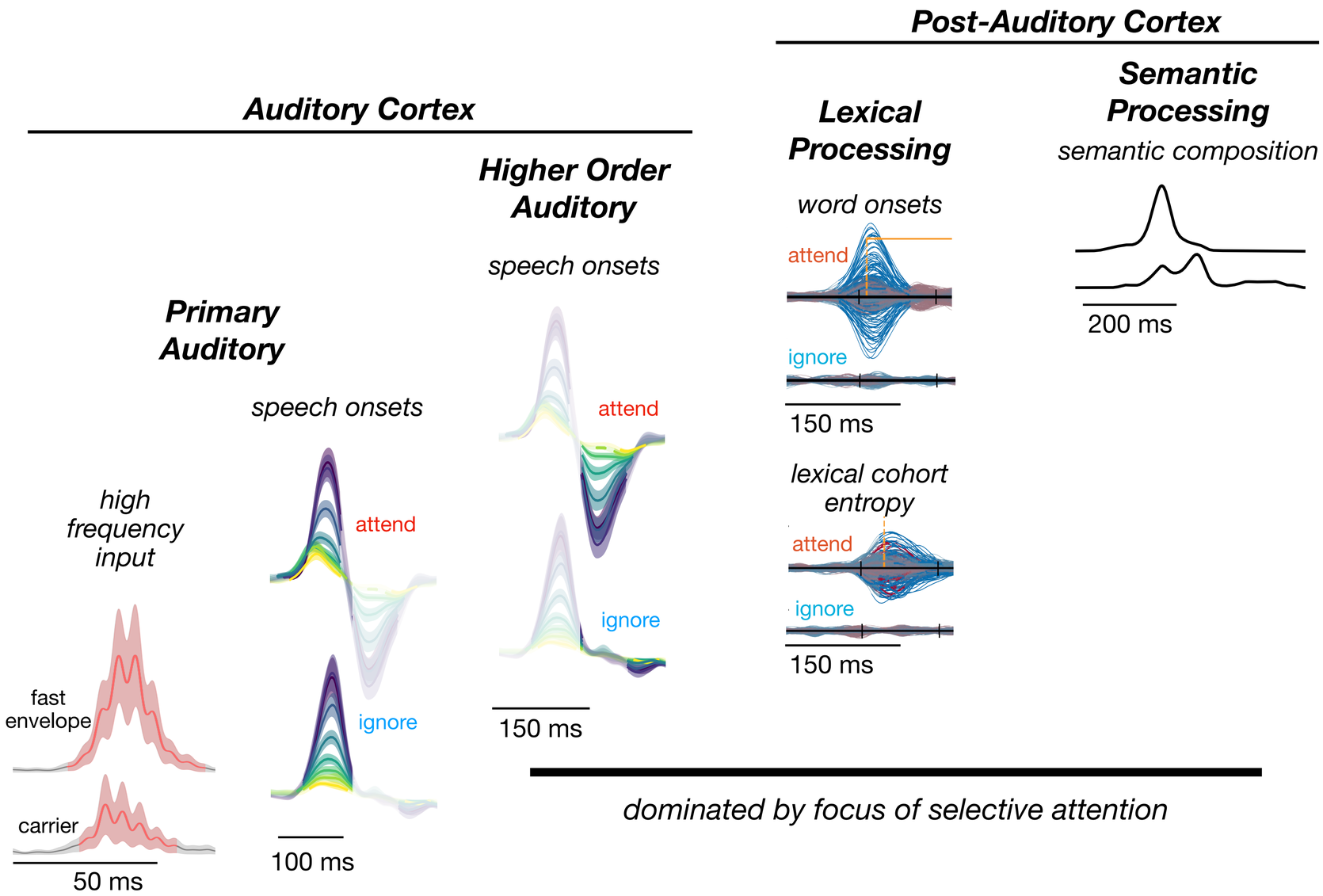


Crosse et al. (2016) *The Multivariate Temporal Response Function (mTRF) Toolbox* … , Front Hum Neurosci

Brodbeck et al. (2021) *Eelbrain: A Python Toolkit for Time-Continuous Analysis* … , bioRxiv

Cortical Representations Across Cortex



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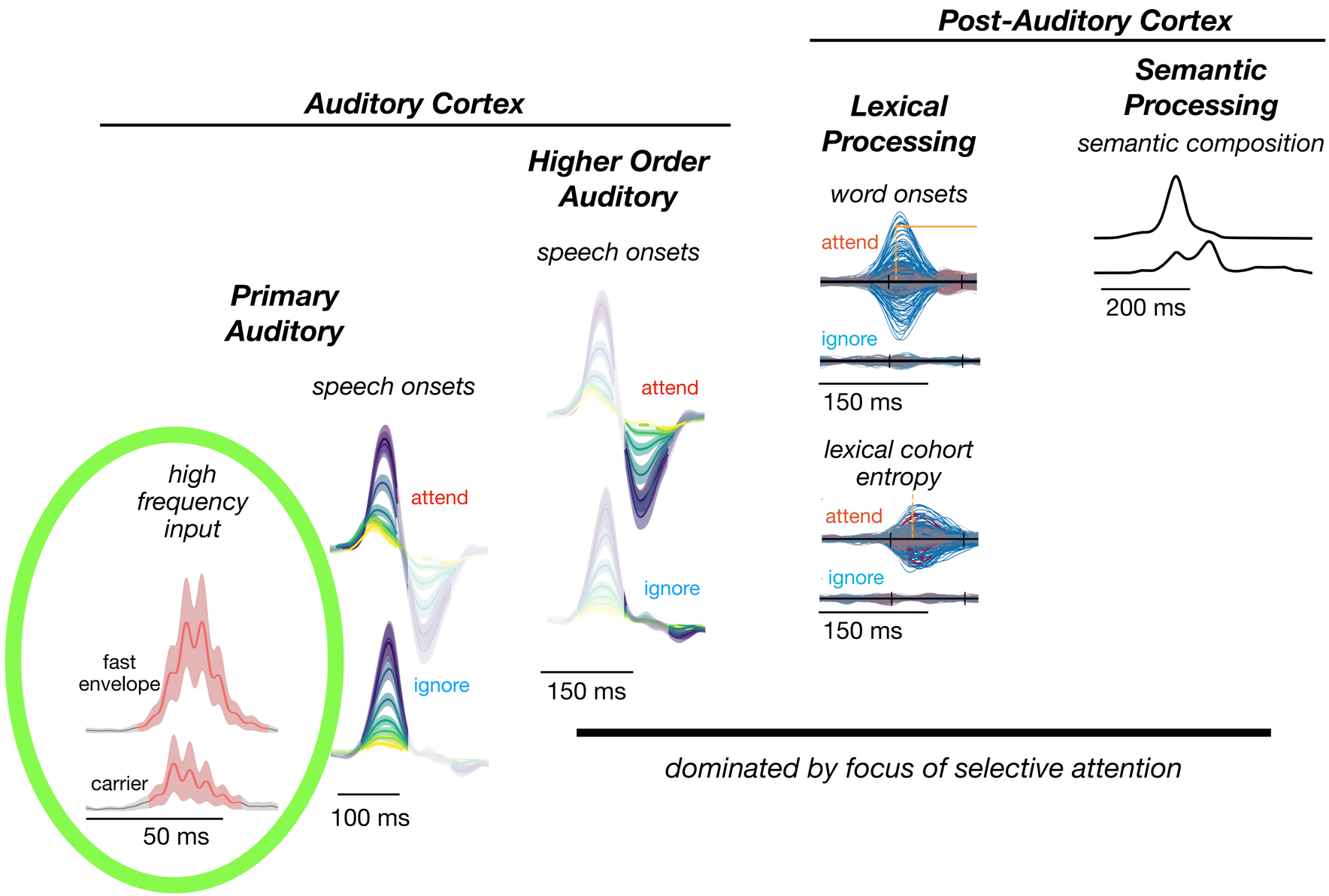

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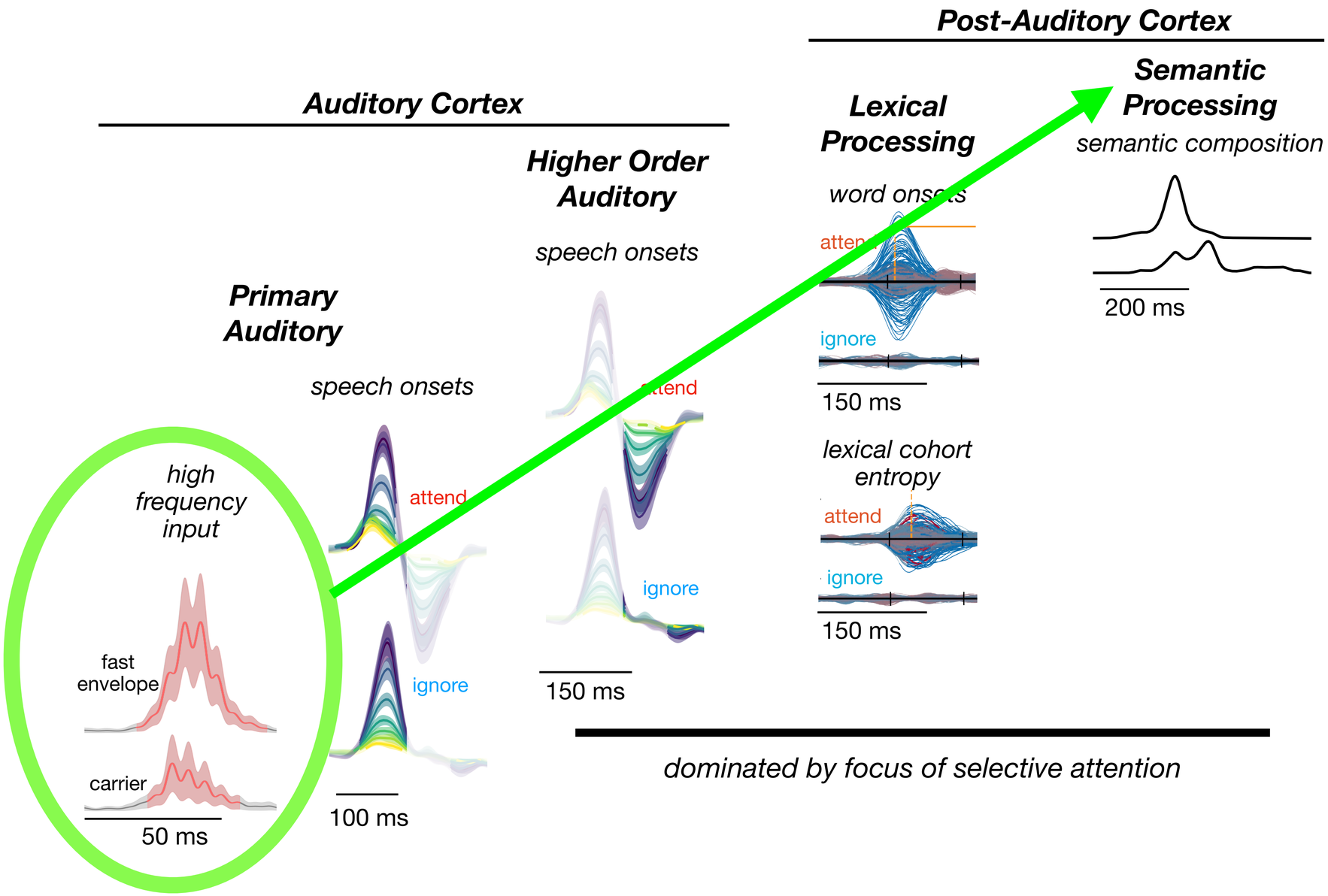

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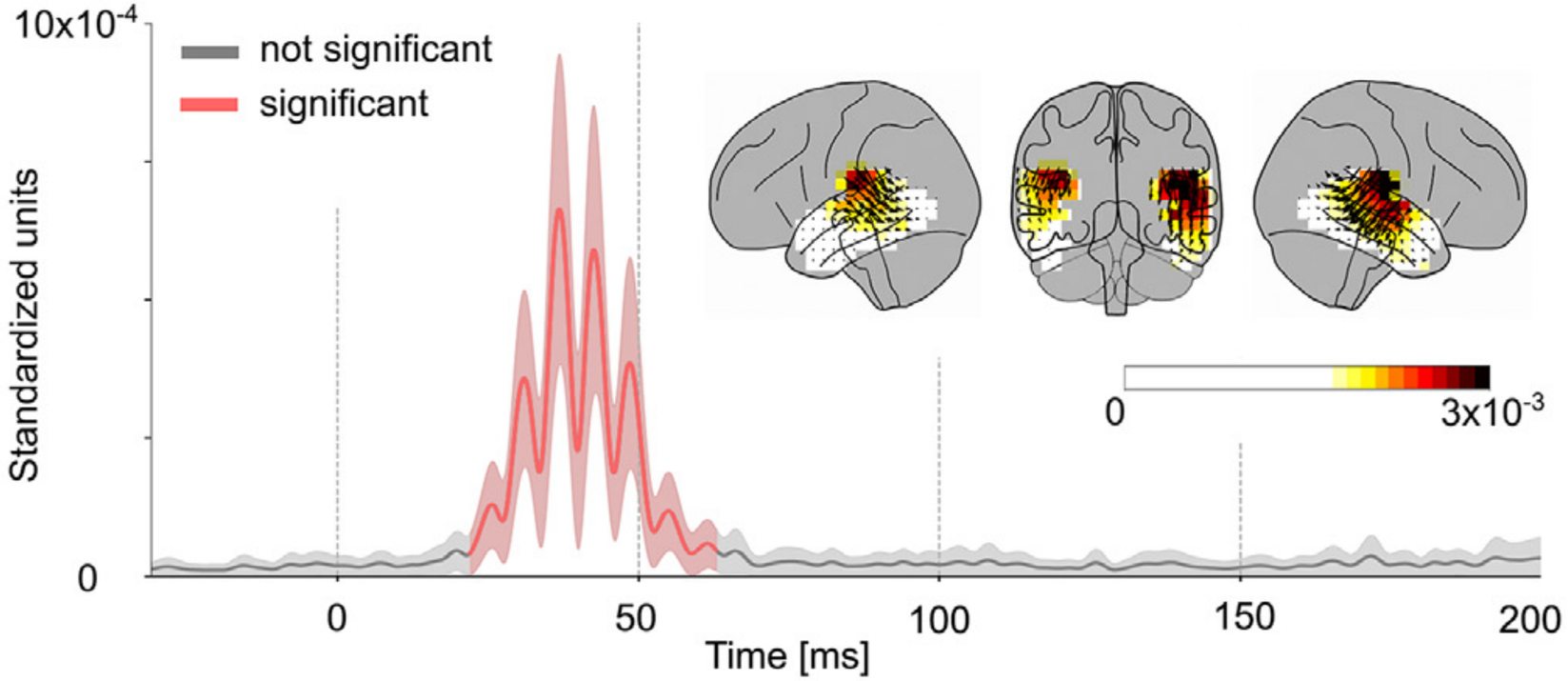
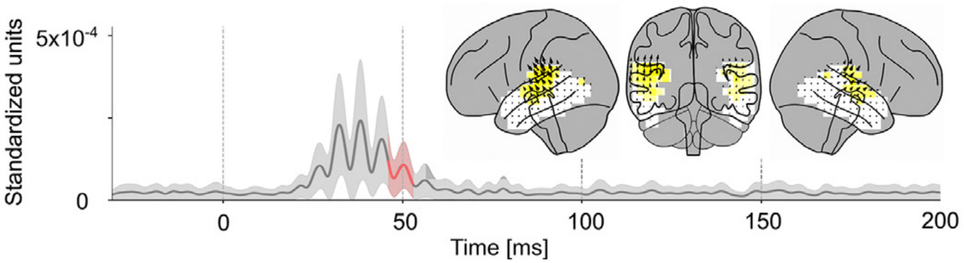
Fast & Early Cortical Representations



TRF (MEG) for
70-200 Hz
continuous speech
envelope

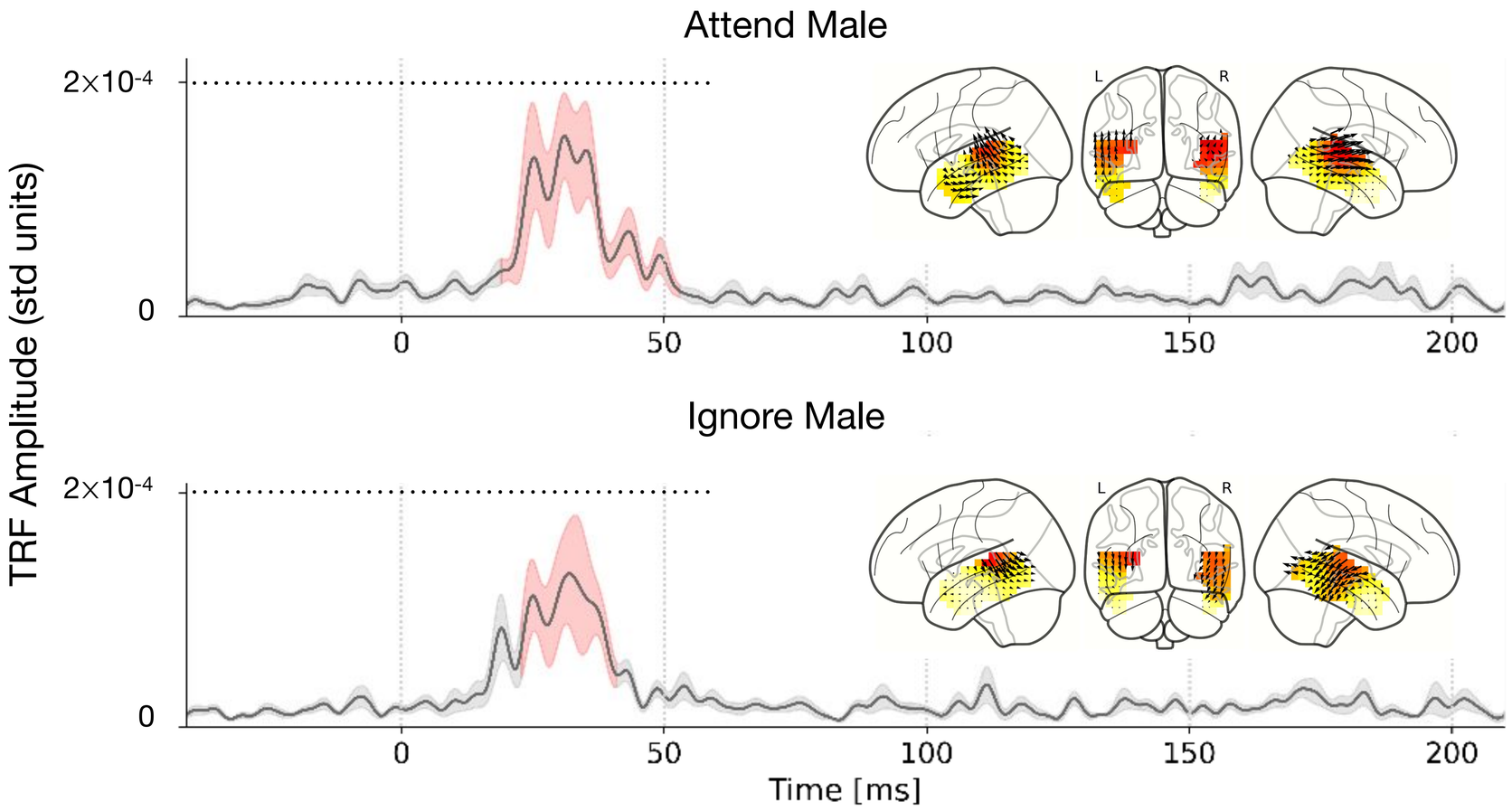


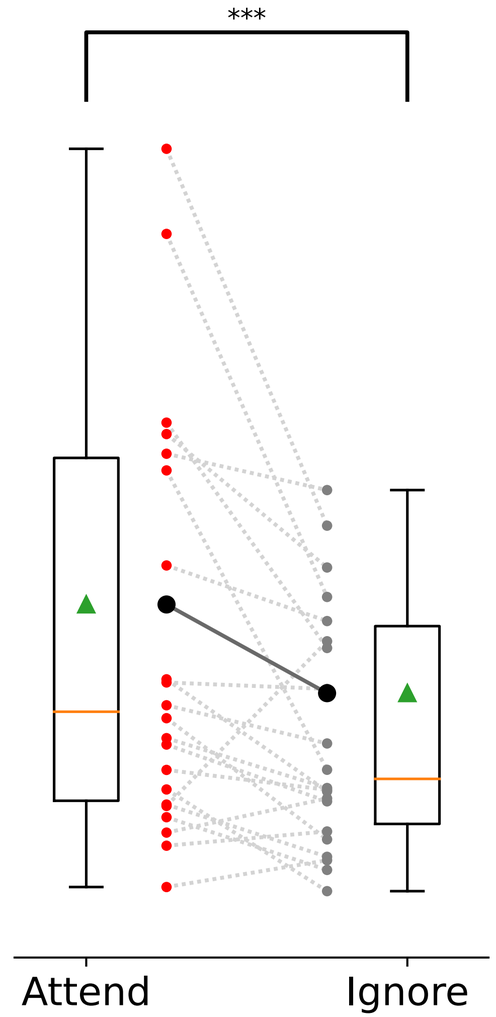
carrier

40 ms latency peak
$\Longrightarrow$ Primary/Core auditory cortex

Kulasingham et al. (2020) *High Gamma Cortical Processing of Continuous Speech …*, NeuroImage
Simon et al. (2022) *… the High-Gamma Band: A Window into Primary Auditory Cortex*, Front Neurosci

Fast & Early Cortical Representations

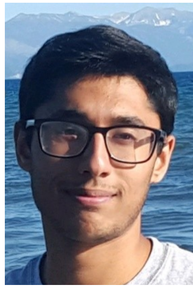




Attend > Ignore

Primary cortex modulated by selective attention

Commuri et al. *in preparation*



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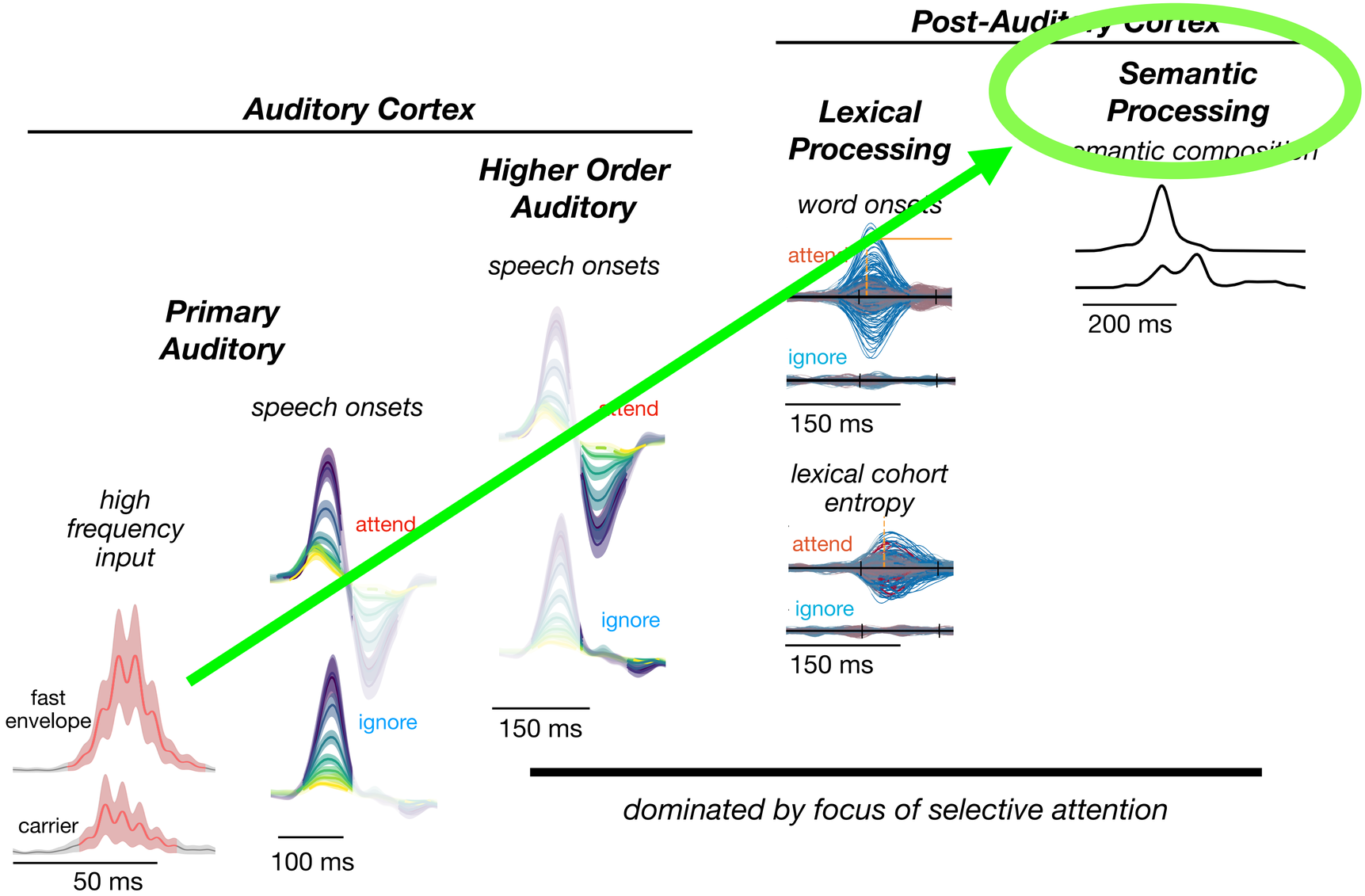

Speech Understanding/Meaning

- Behavioral correlates of speech understanding
  - implies language comprehension
  - structural comprehension
    - sentence structure
    - other structures, e.g. poetic, logical

- Neural correlates of speech understanding
  - rhythms of structural comprehension/meaning, even if *fully absent in the acoustics*
    - sentence structures
    - poetic structures
    - mathematical structures

Ding et al., Nat Neurosci 2016
Teng et al., Curr Biol 2020

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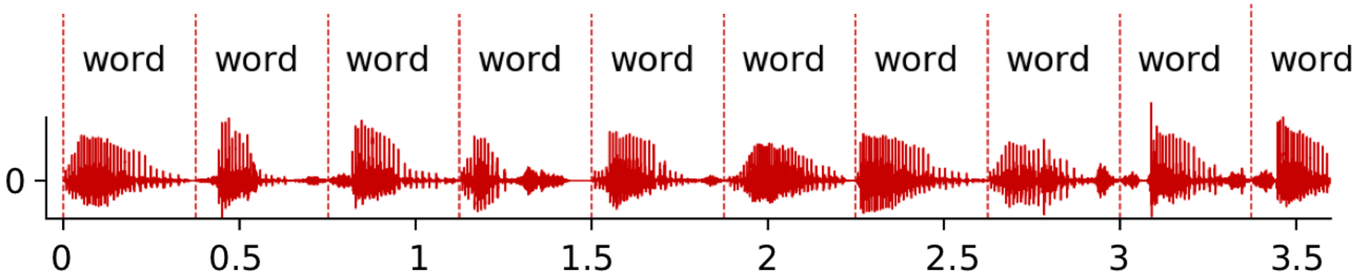
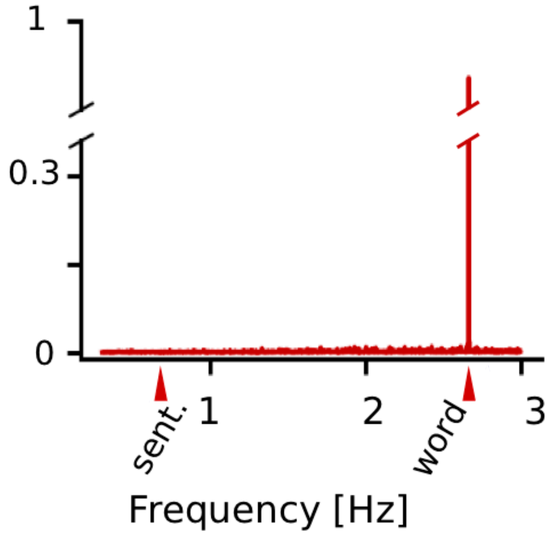
Isochronous Speech

Acoustics



Acoustical Spectrum (envelope)



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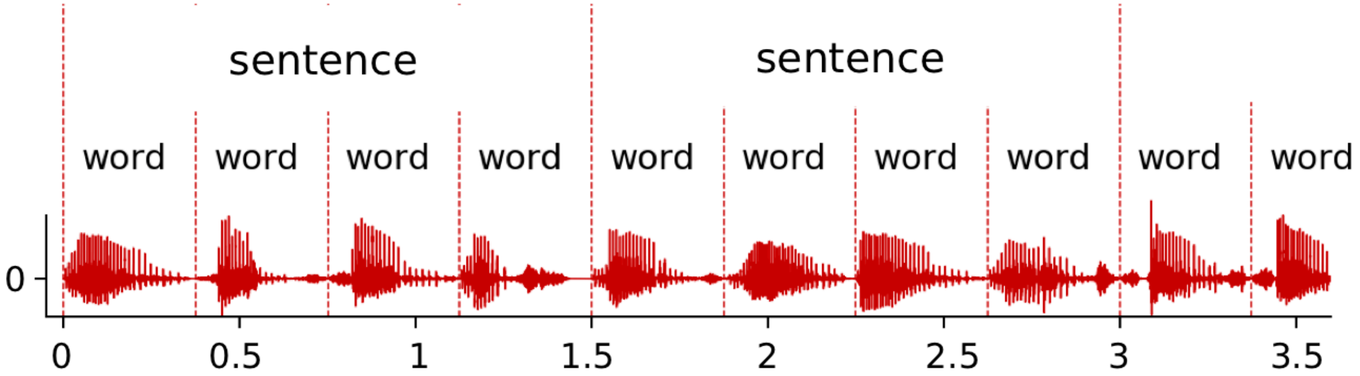

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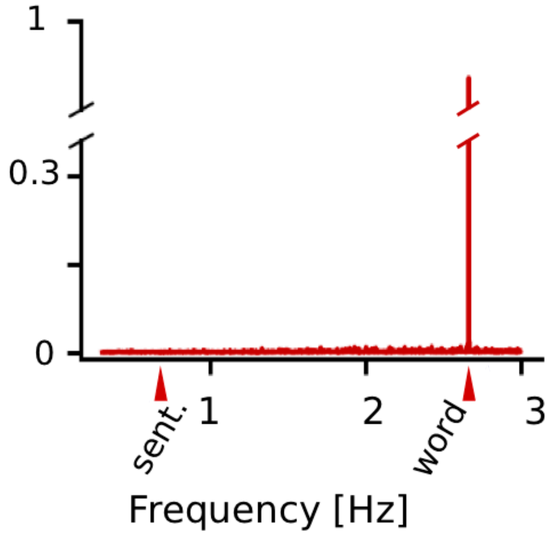

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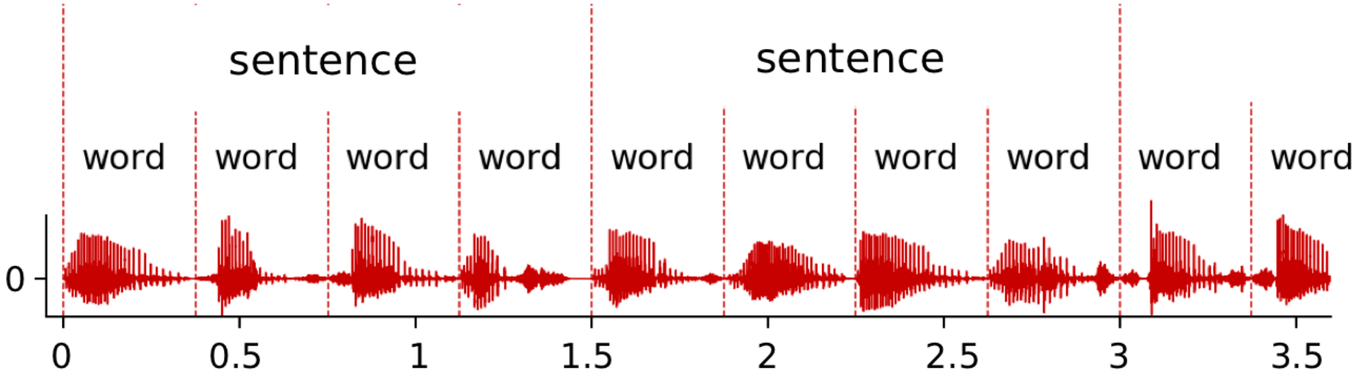

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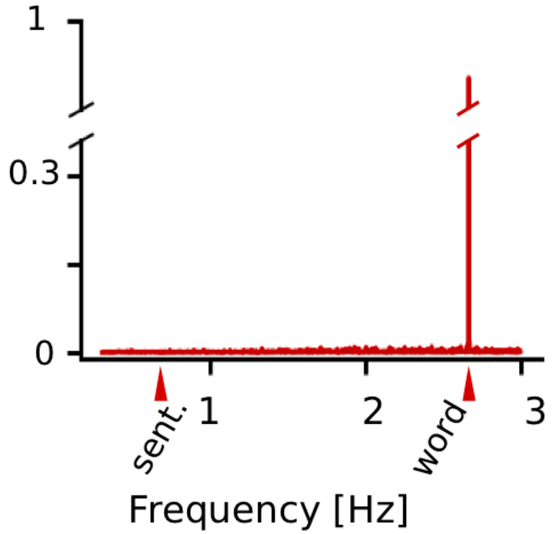

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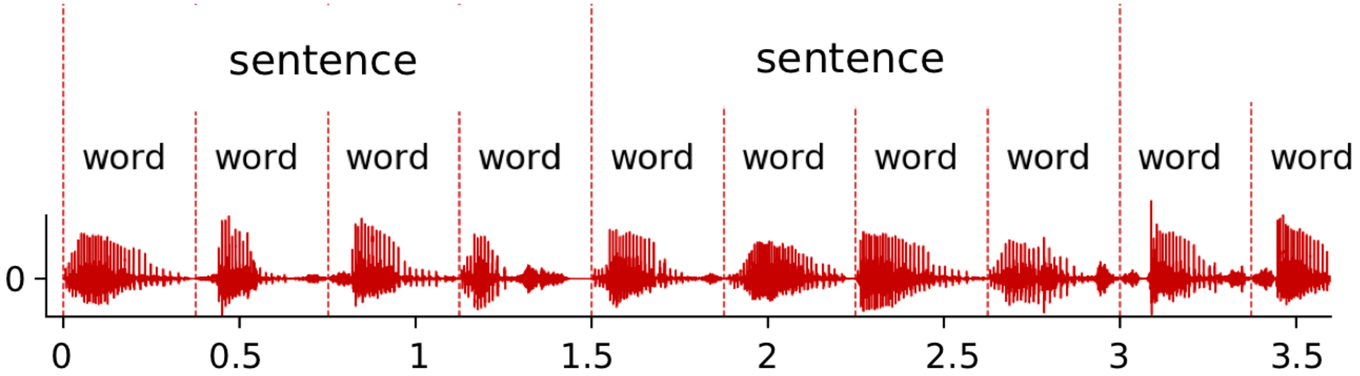

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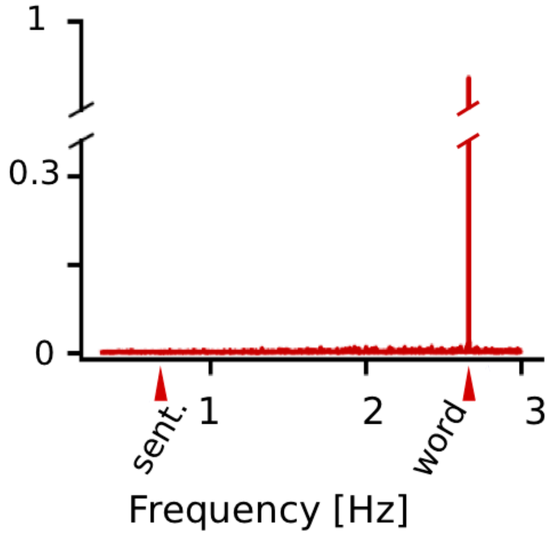

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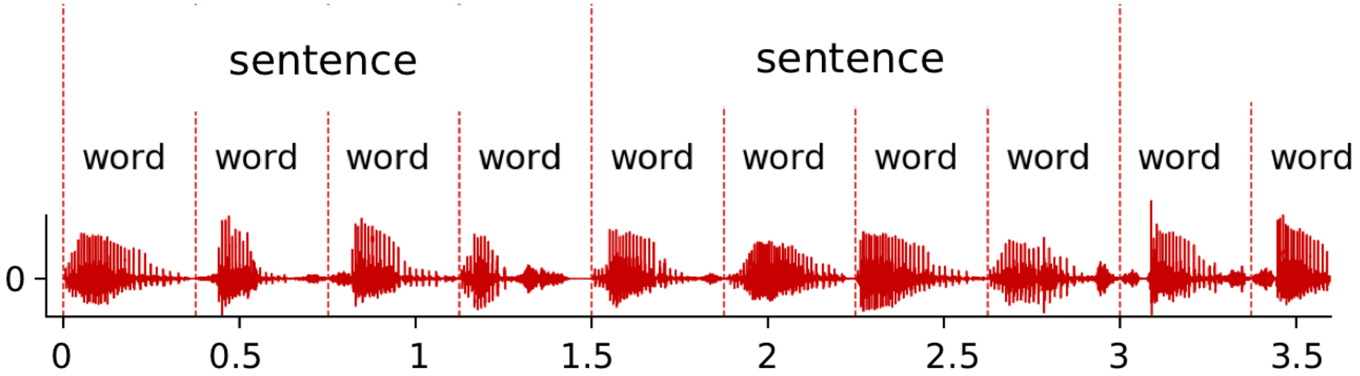

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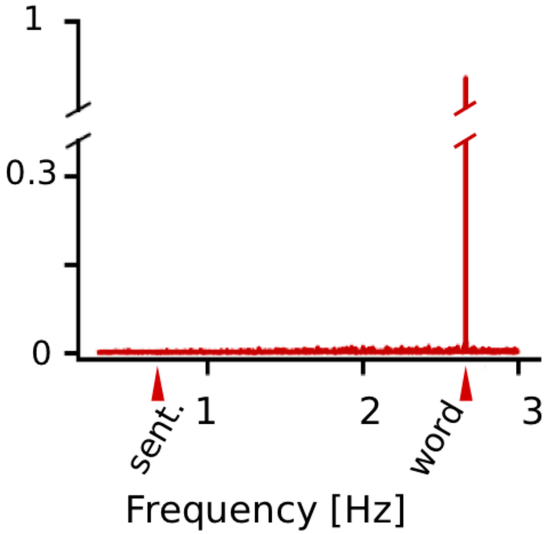
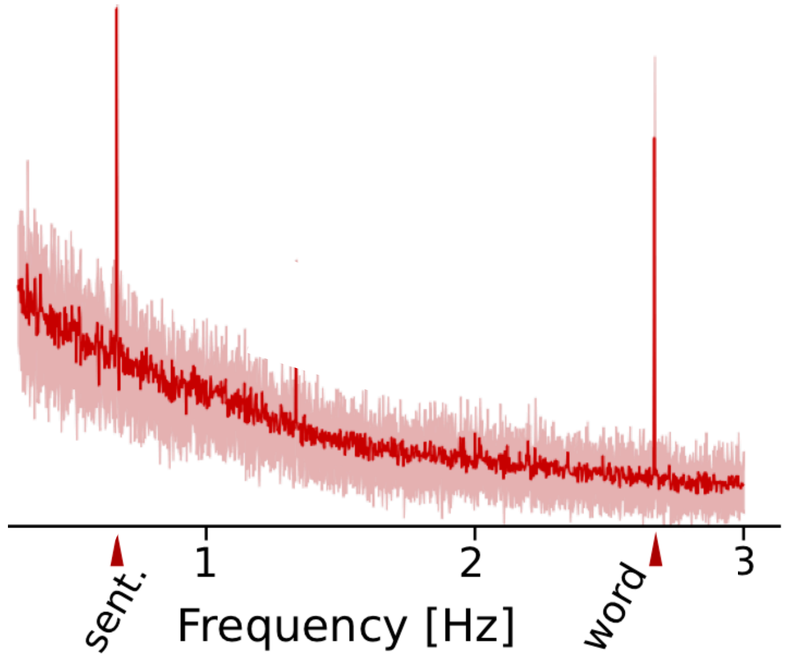


Perception?



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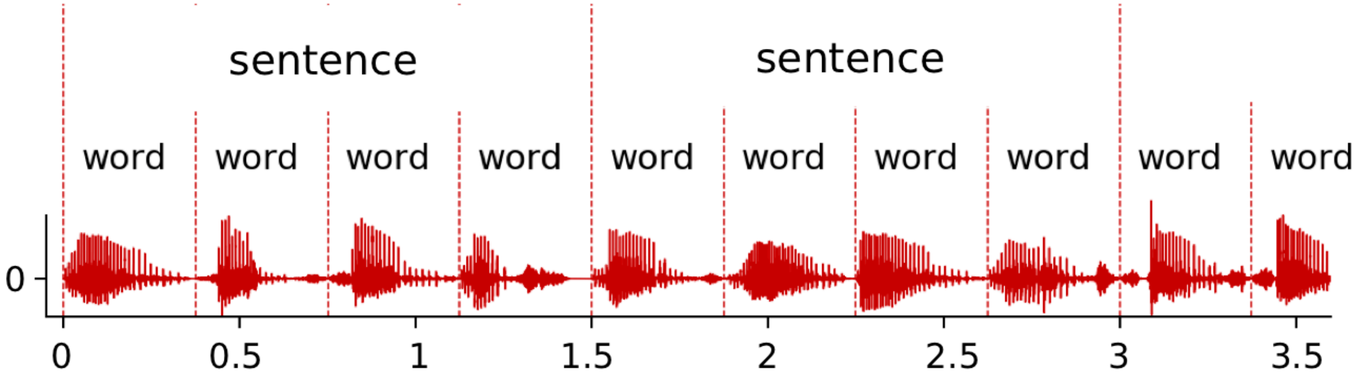

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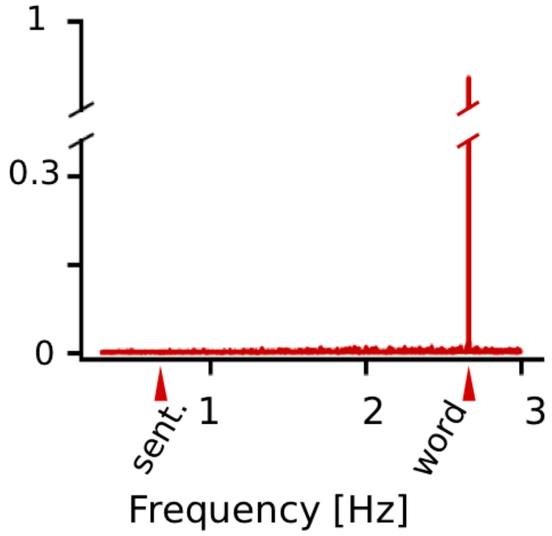
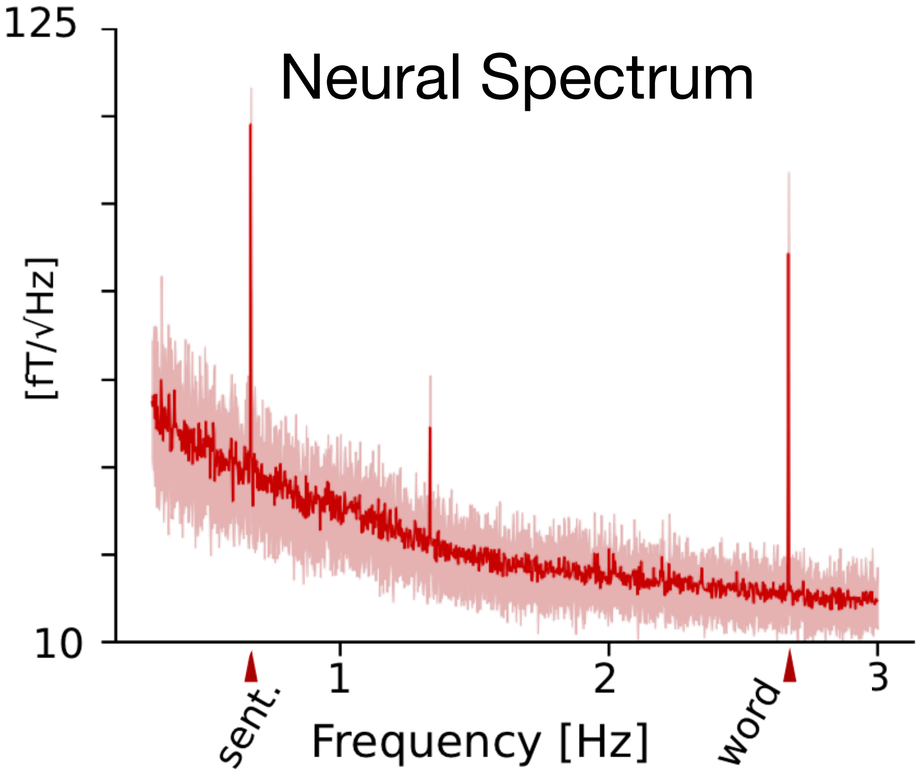
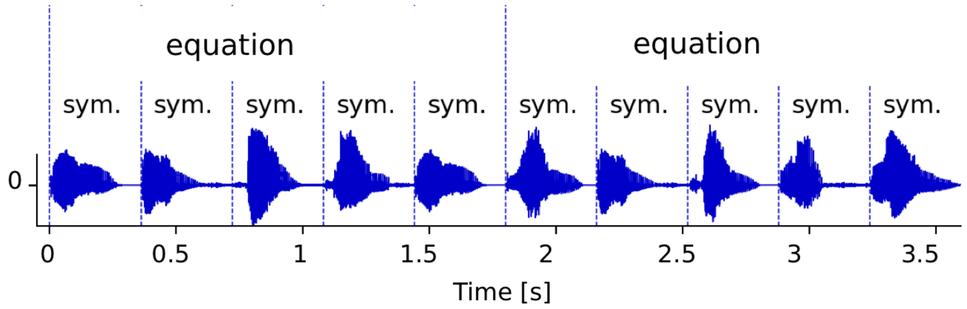


Neural Spectrum



Isochronous Arithmetic



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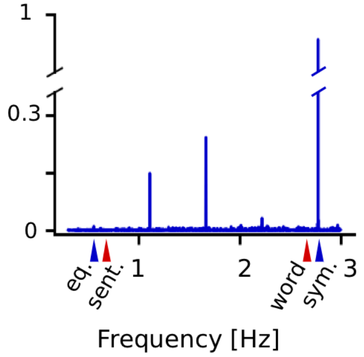

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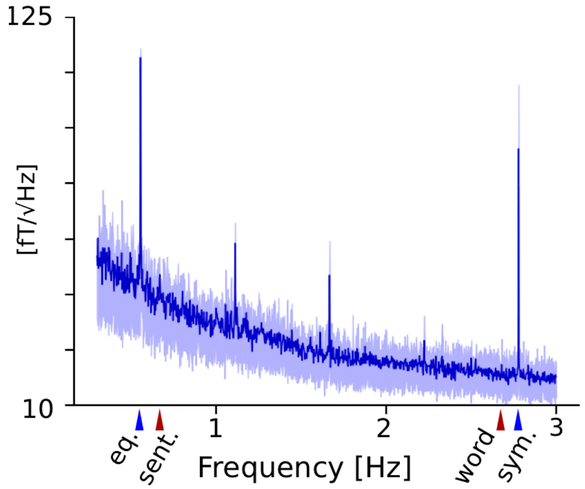
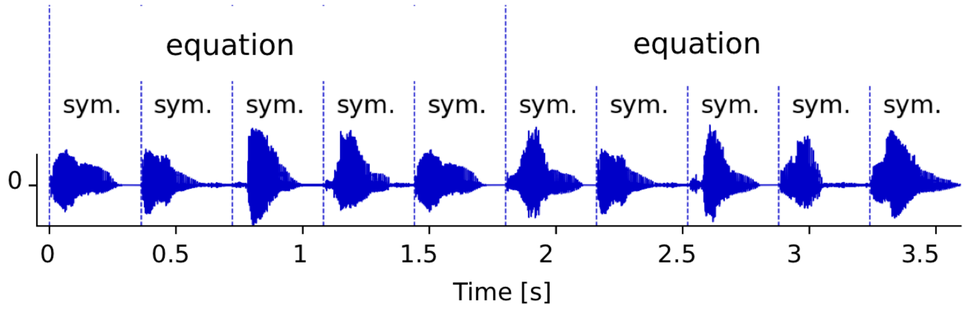


Neural Spectrum

Kulasingham et al. (2021) *Cortical Processing of Arithmetic and Simple Sentences …*, J Neurosci

Isochronous Arithmetic



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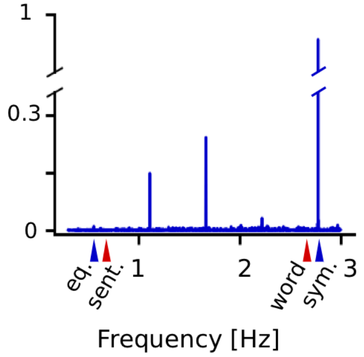

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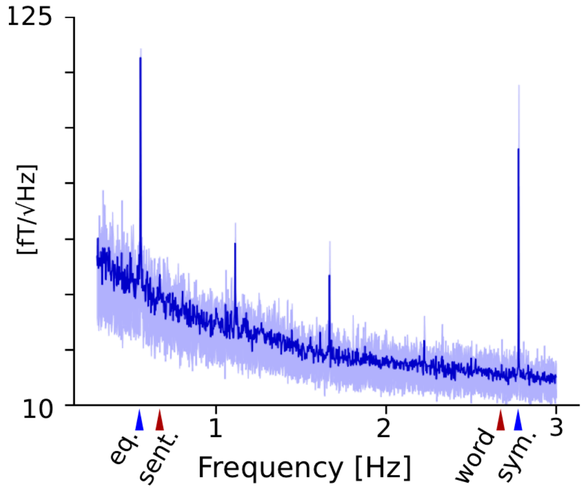

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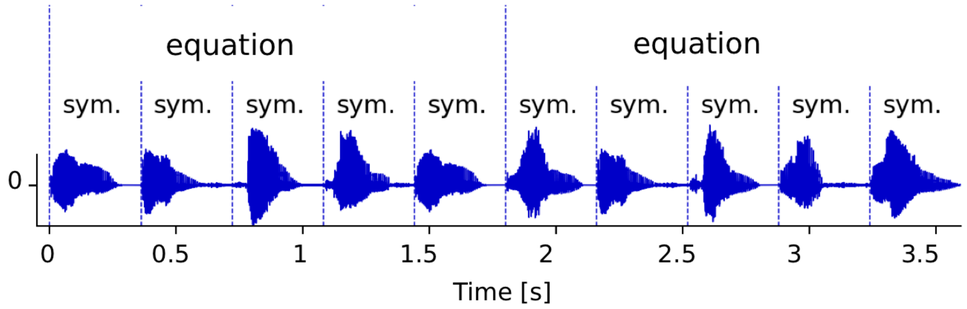
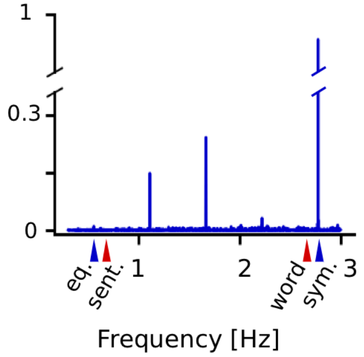
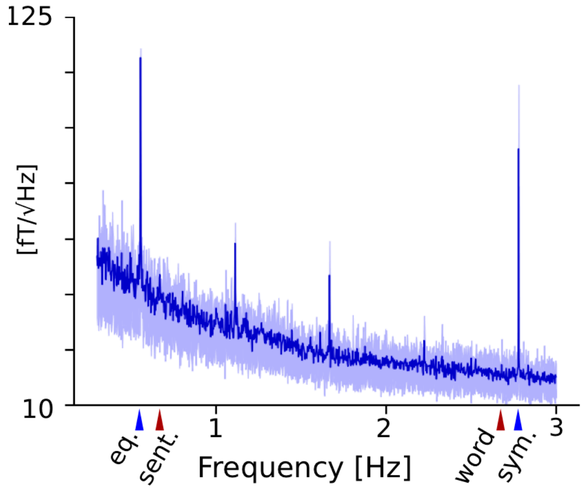


Acoustics



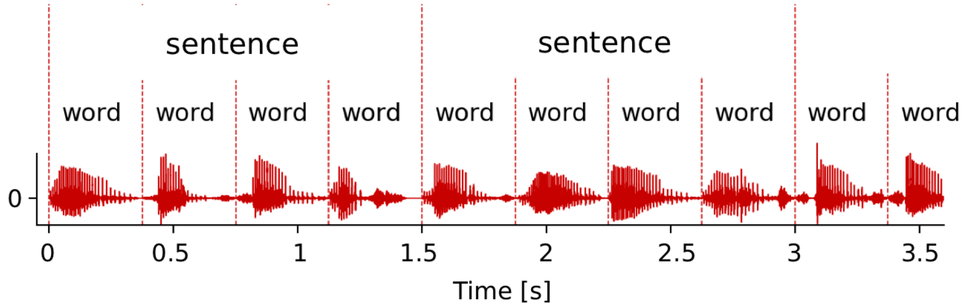
Acoustical Spectrum



Neural Spectrum

Kulasingham et al. (2021) *Cortical Processing of Arithmetic and Simple Sentences …*, J Neurosci

Isochronous Cocktail Party



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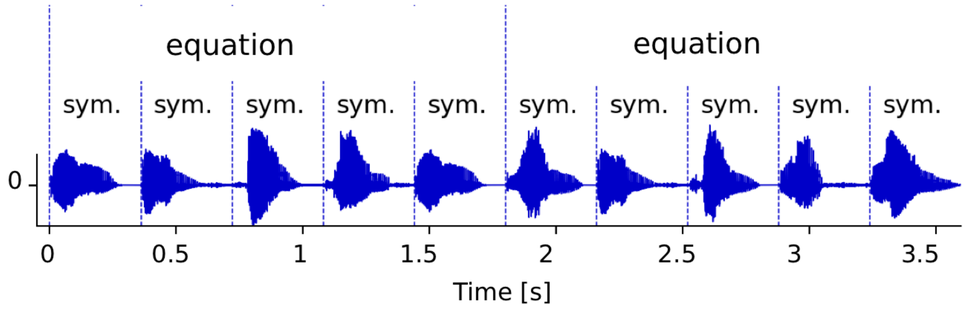

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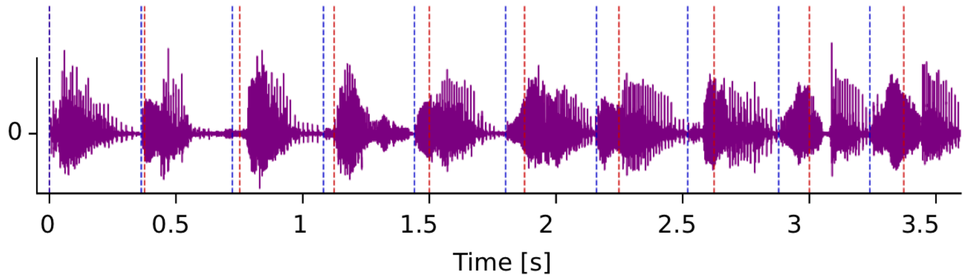

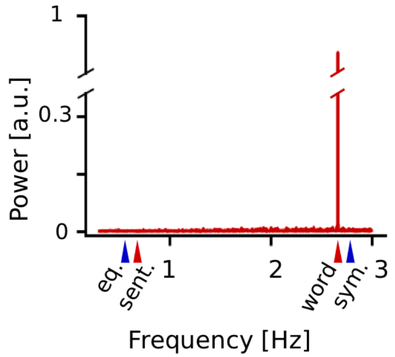

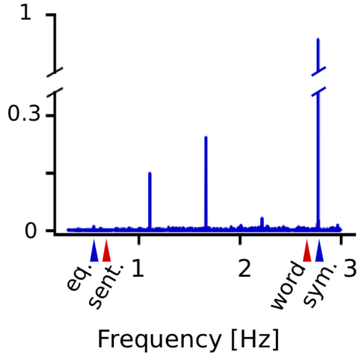

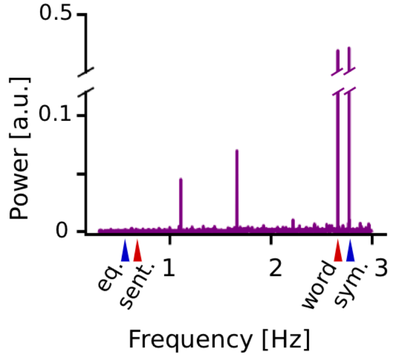

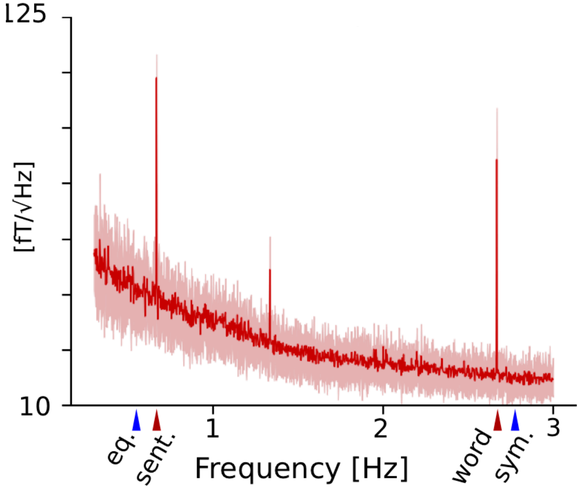

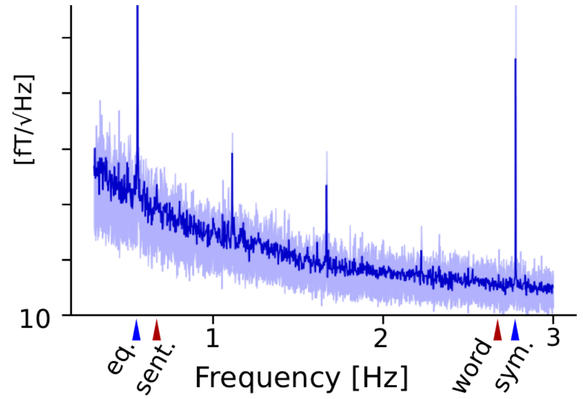

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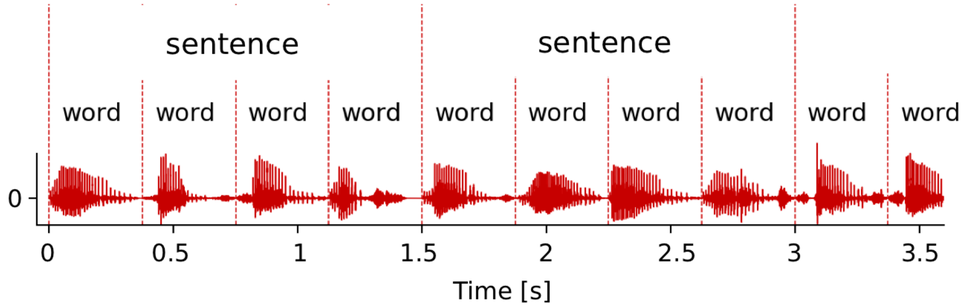
Isochronous Cocktail Party



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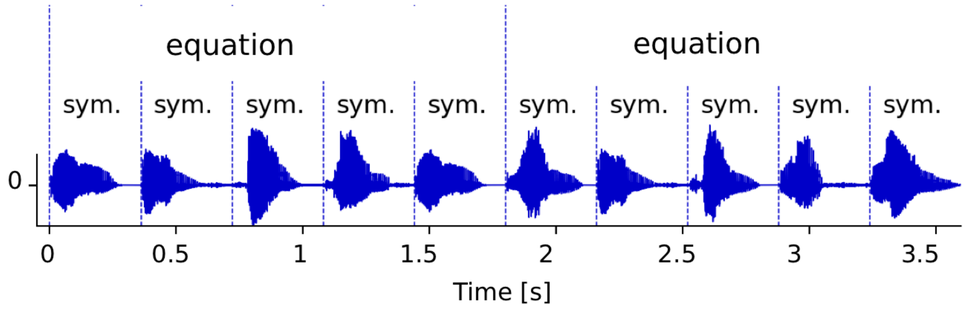

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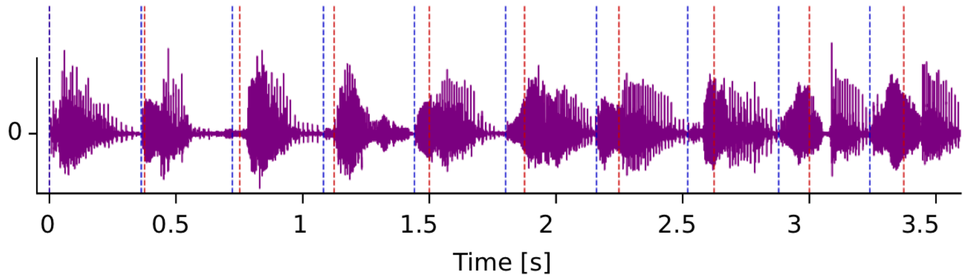

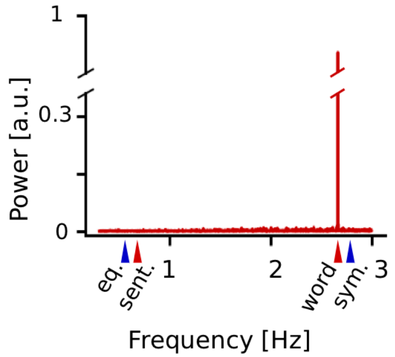

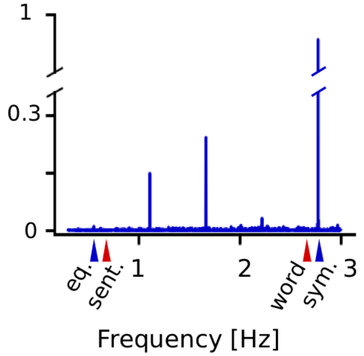

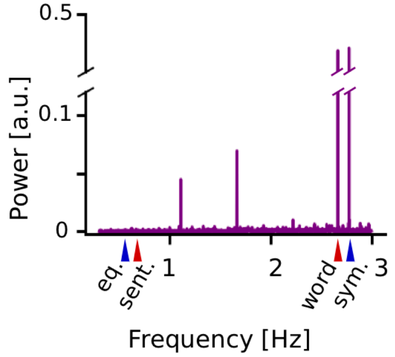

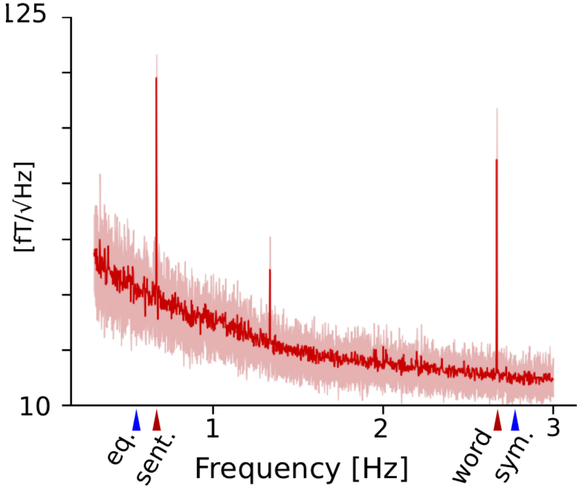

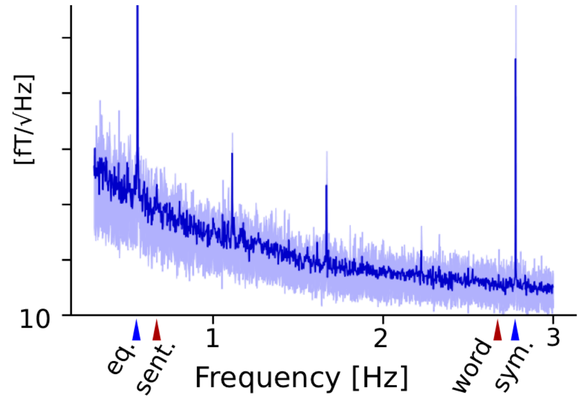

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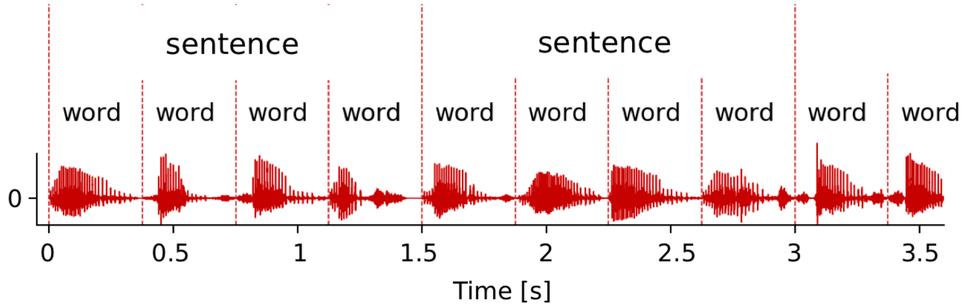
Isochronous Cocktail Party



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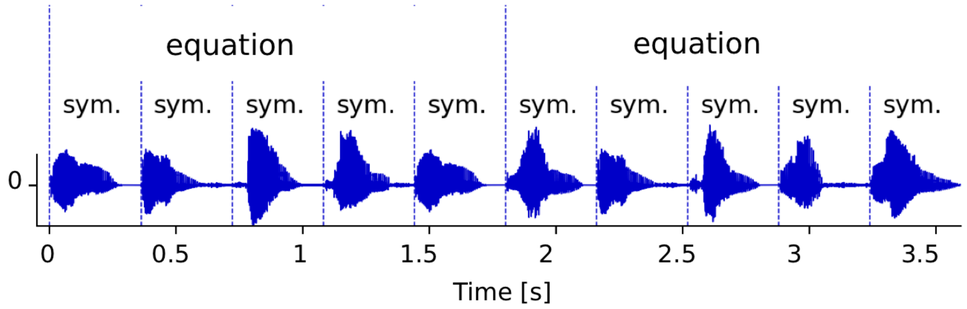

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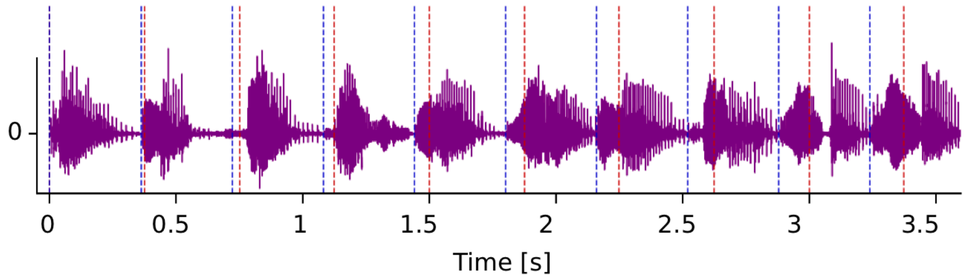

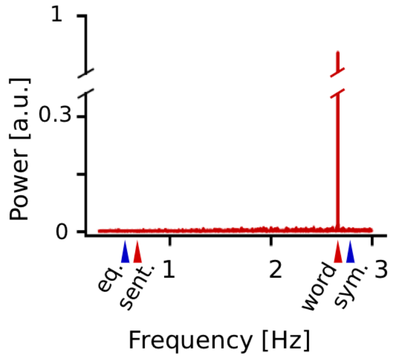

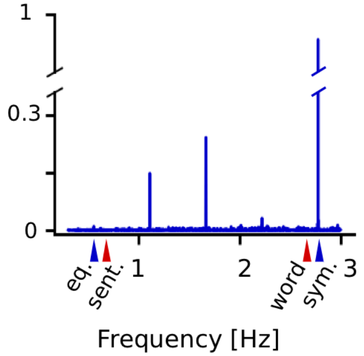

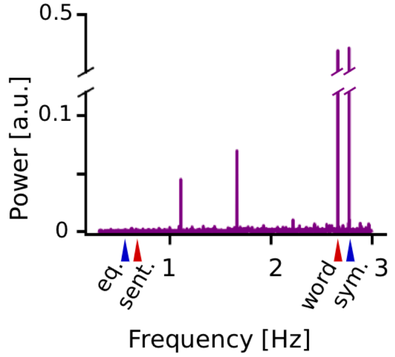

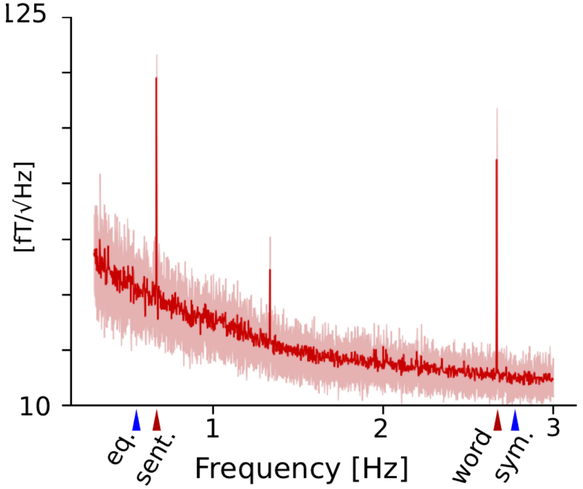

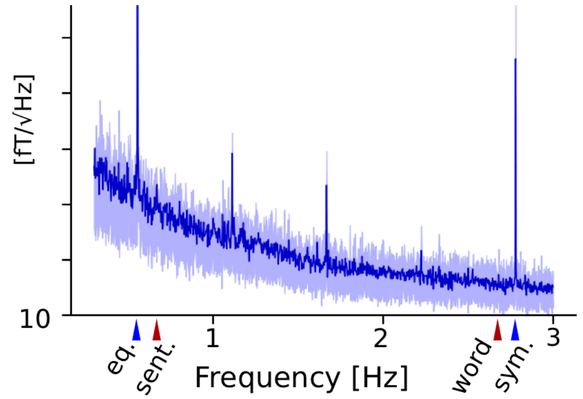

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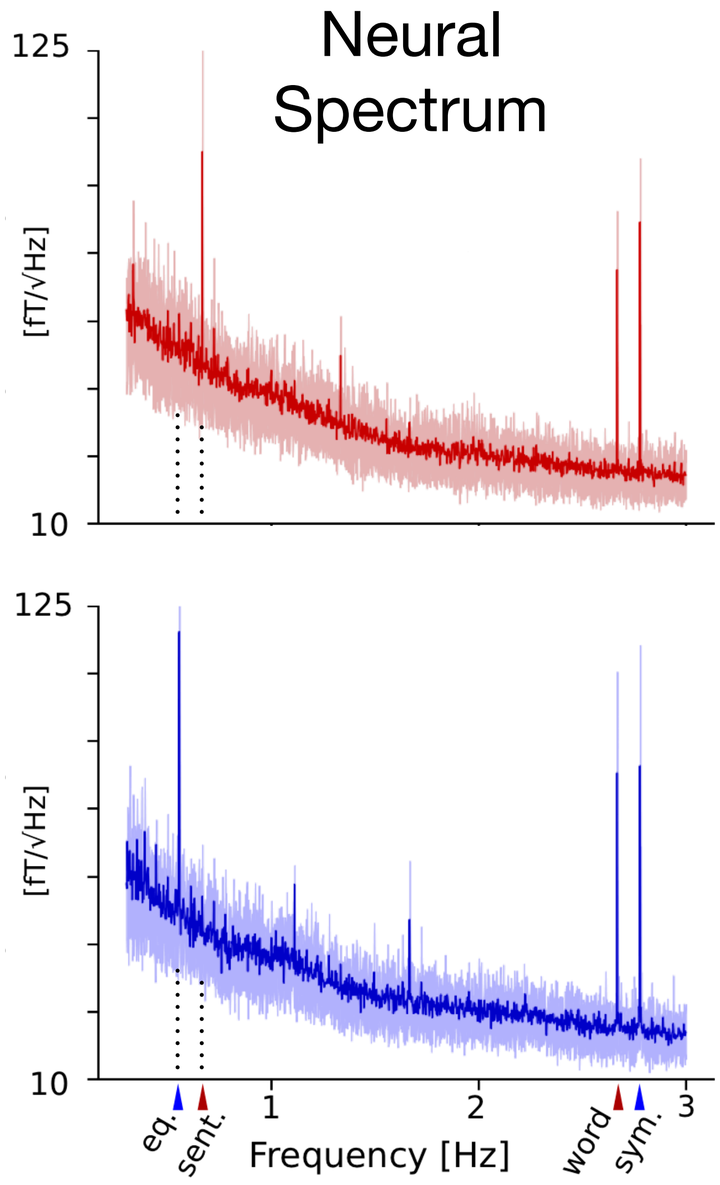
Isochronous Cocktail Party

Attend to Sentences

Attend to Equations



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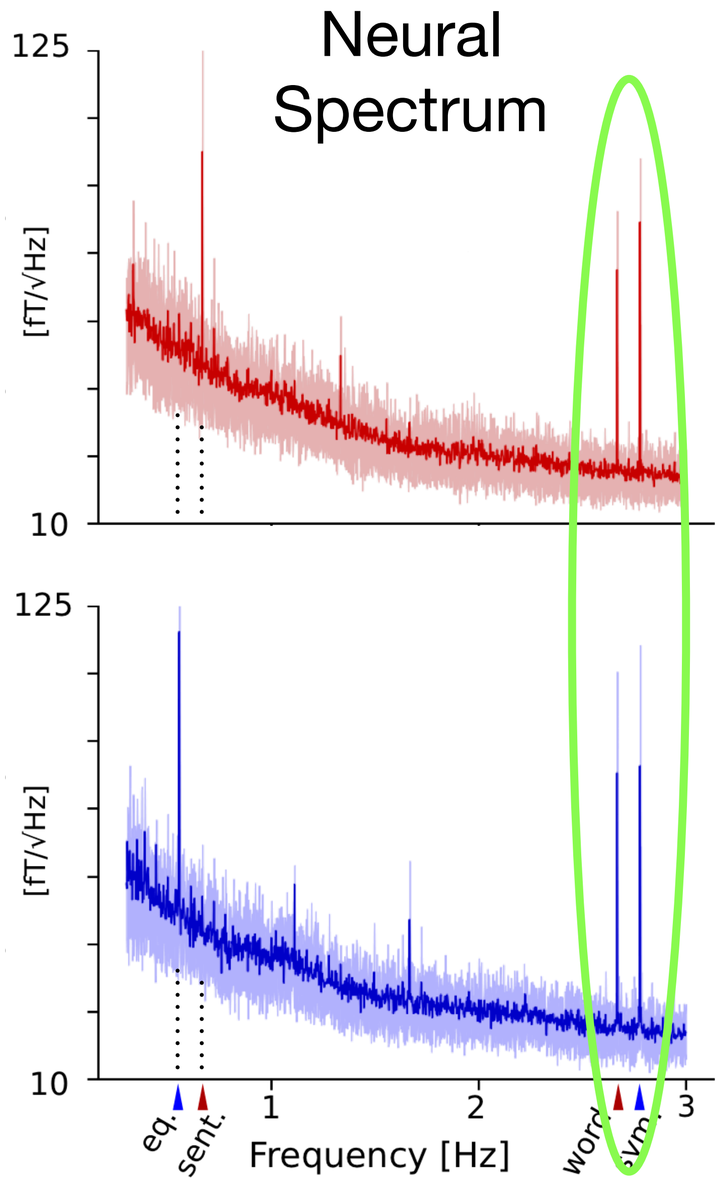

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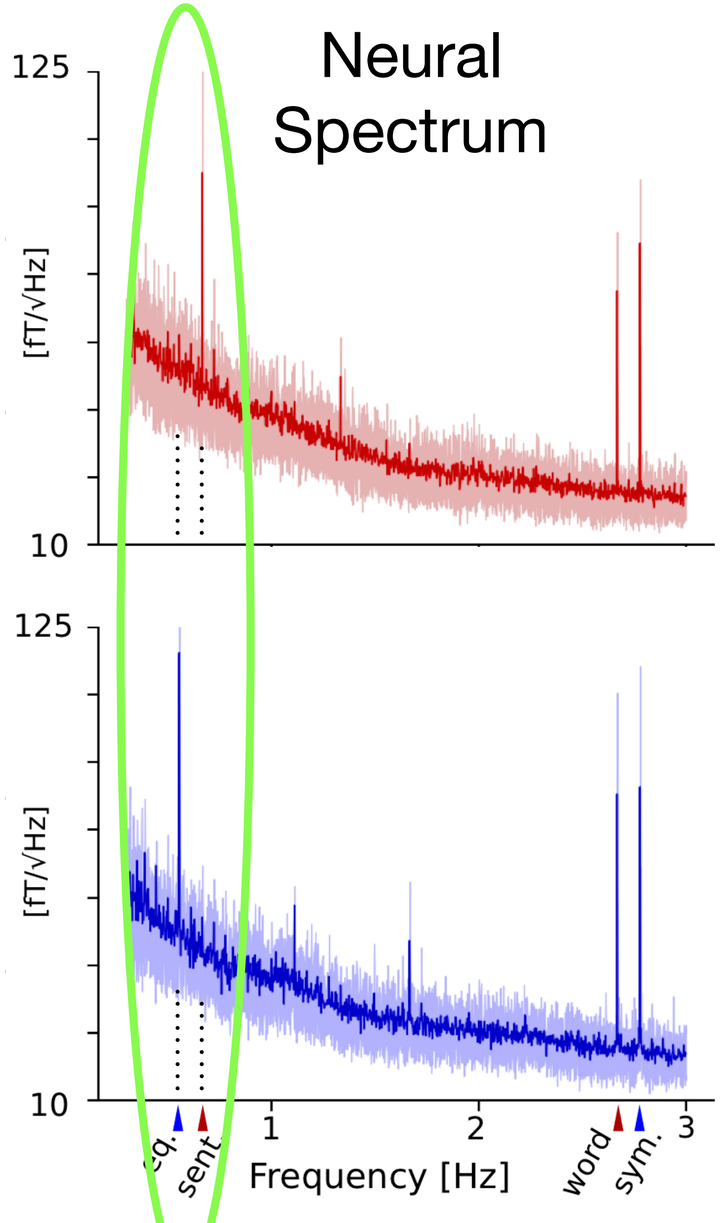

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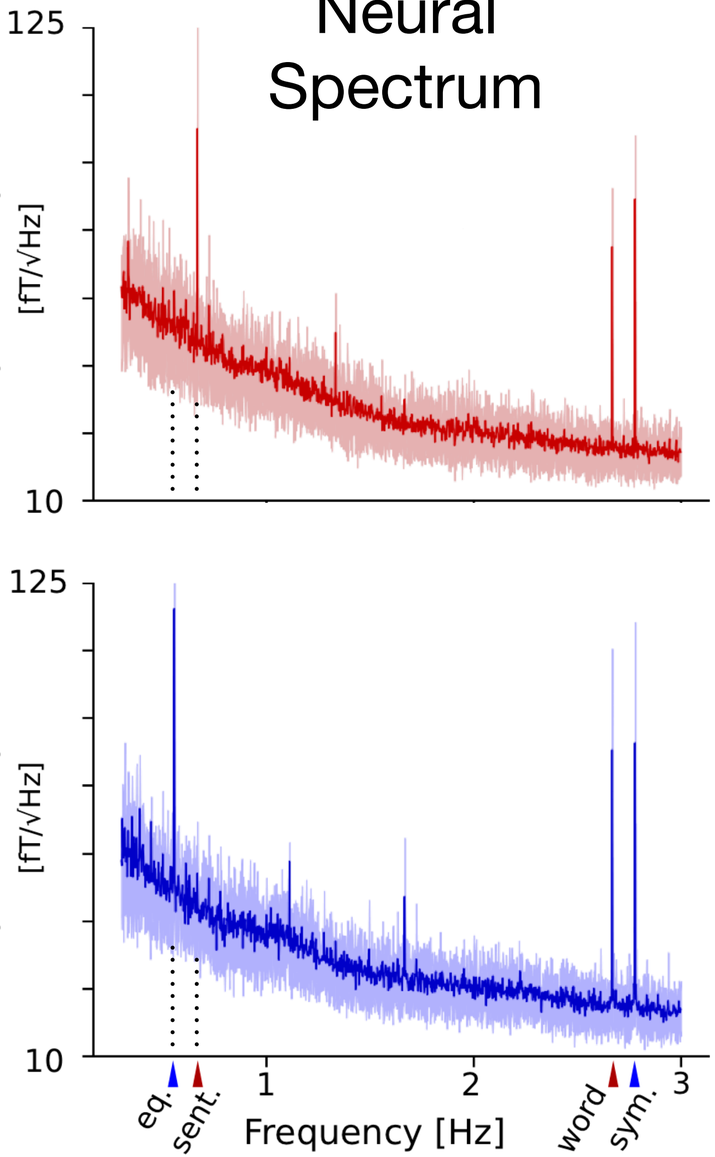
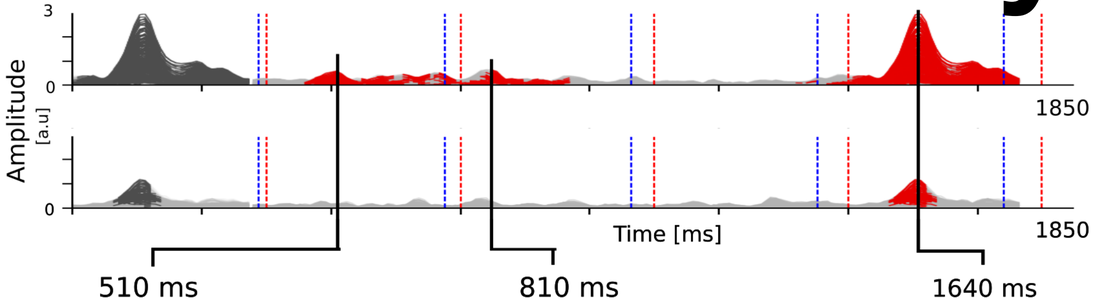
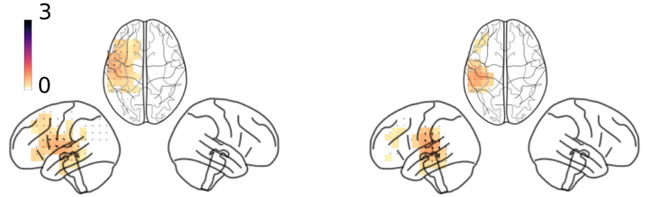
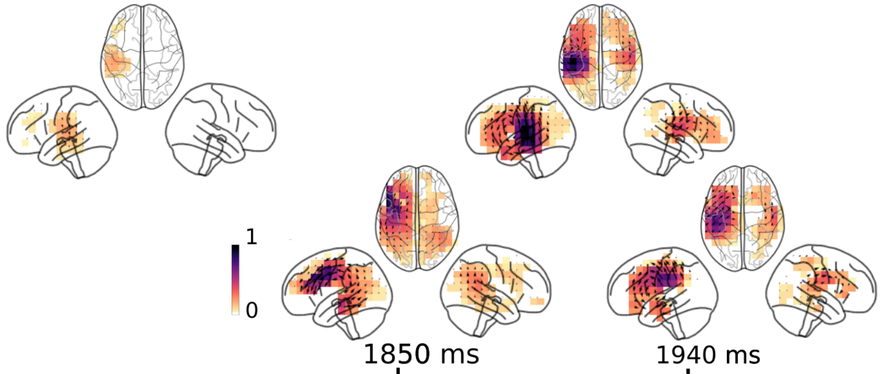




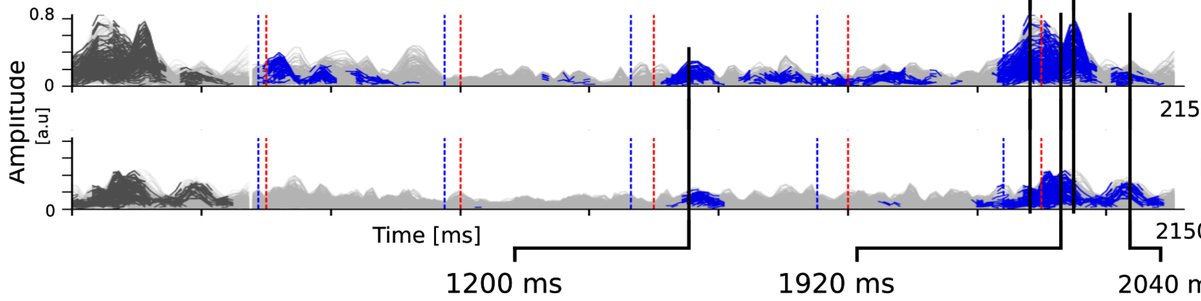
left hemisphere sources

right hemisphere sources





TRFs



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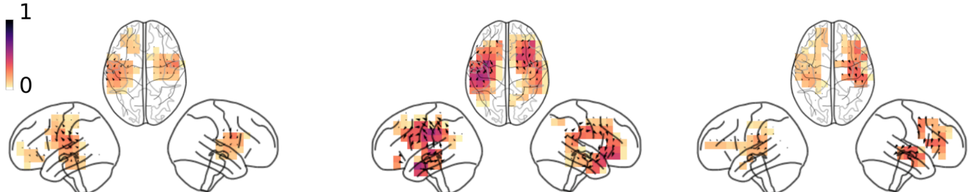

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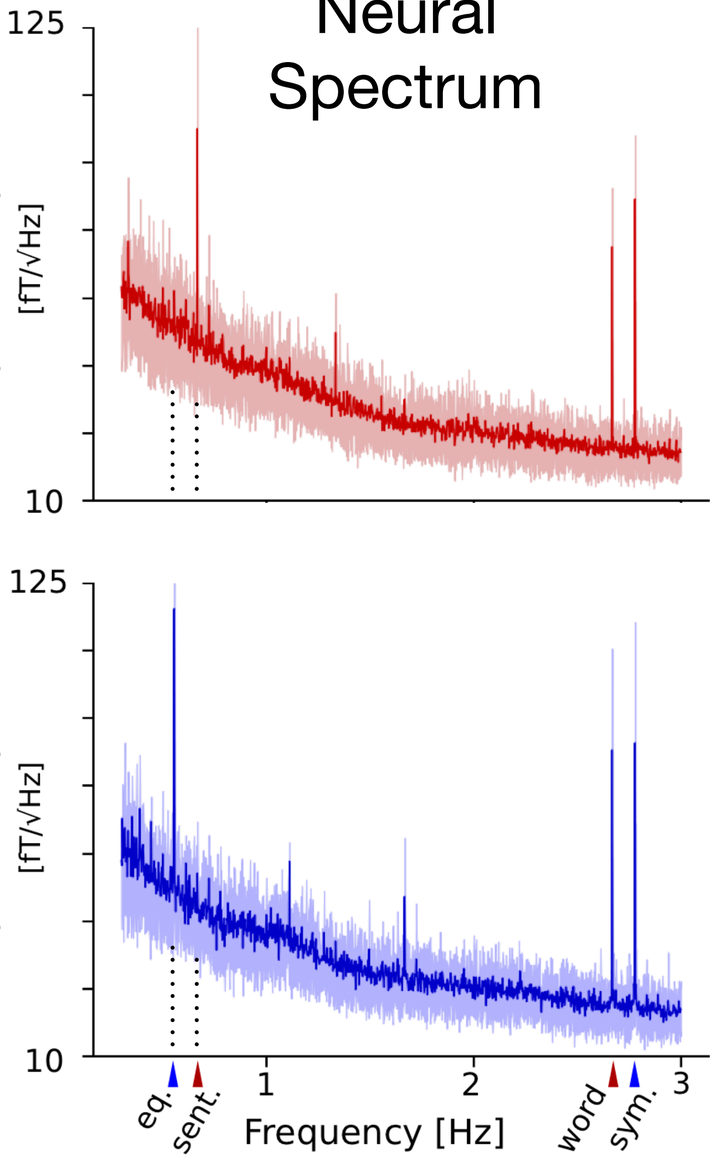

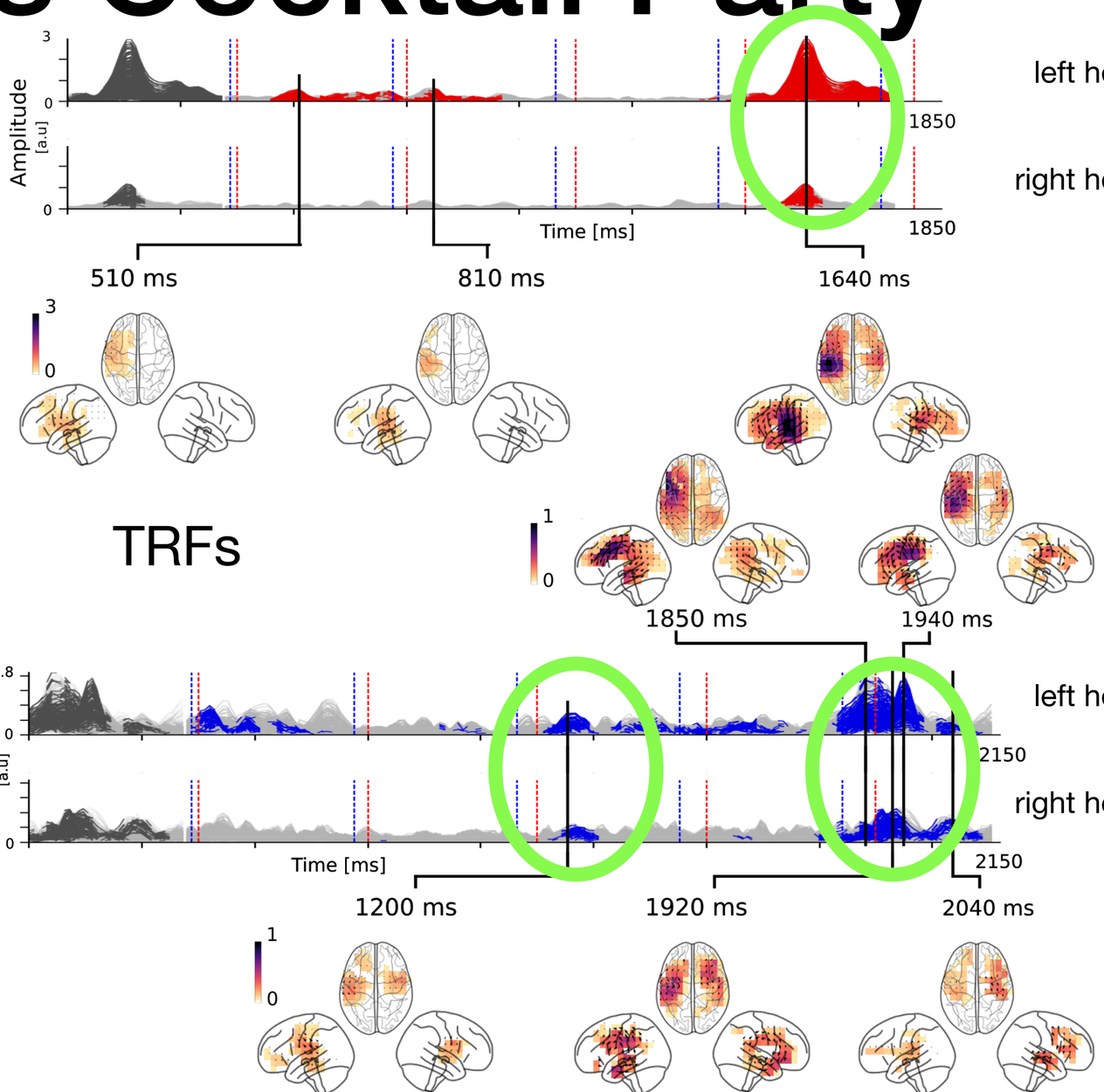

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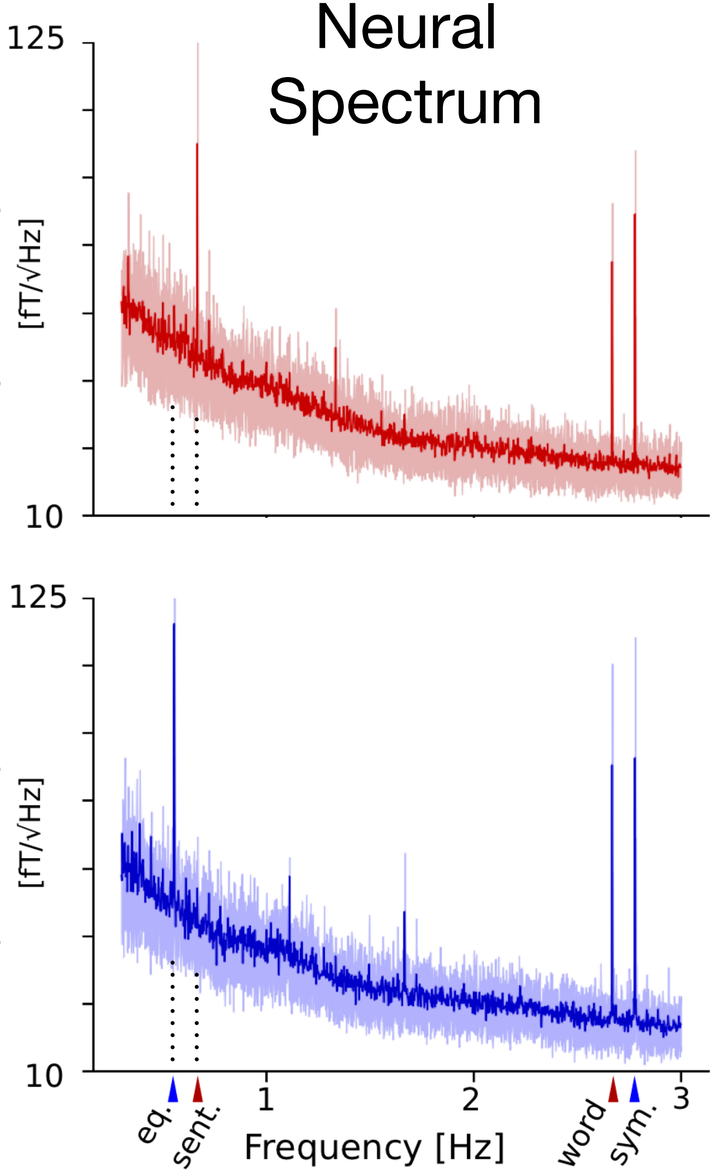

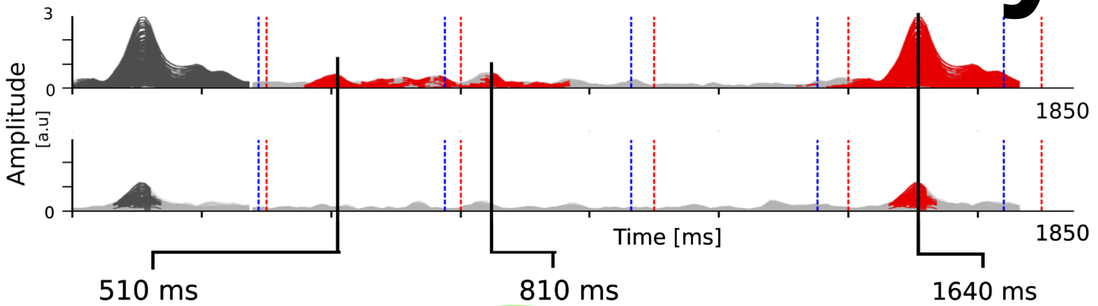

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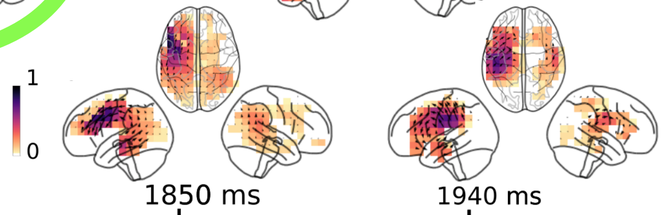
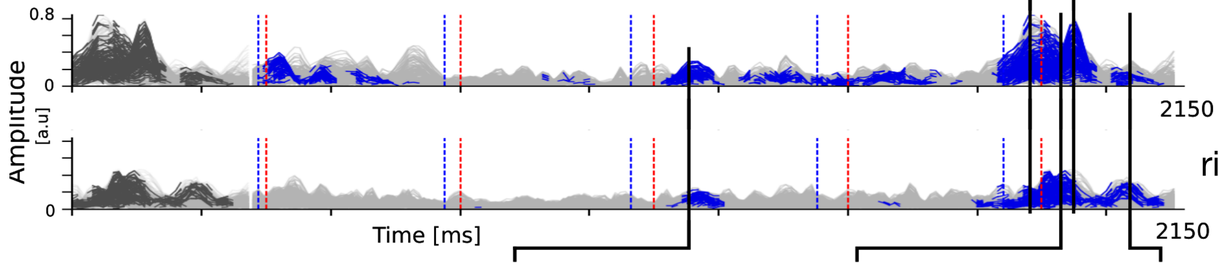
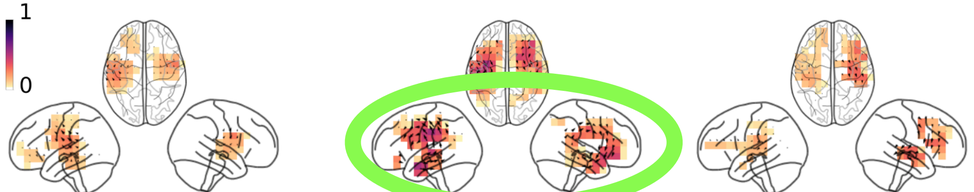
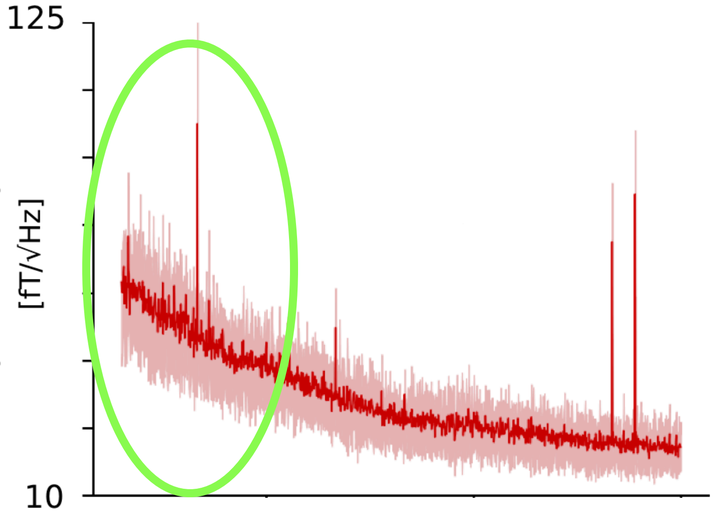




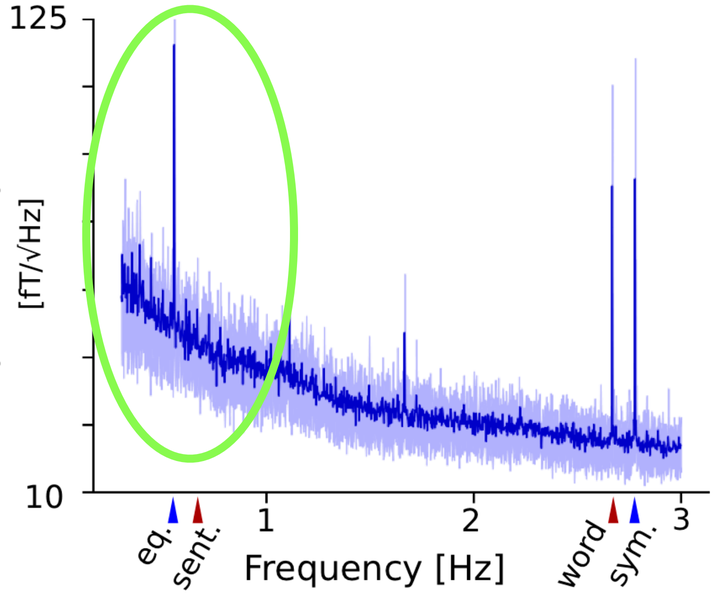


Representations of Understanding

Attend to Sentences



Attend to Equations



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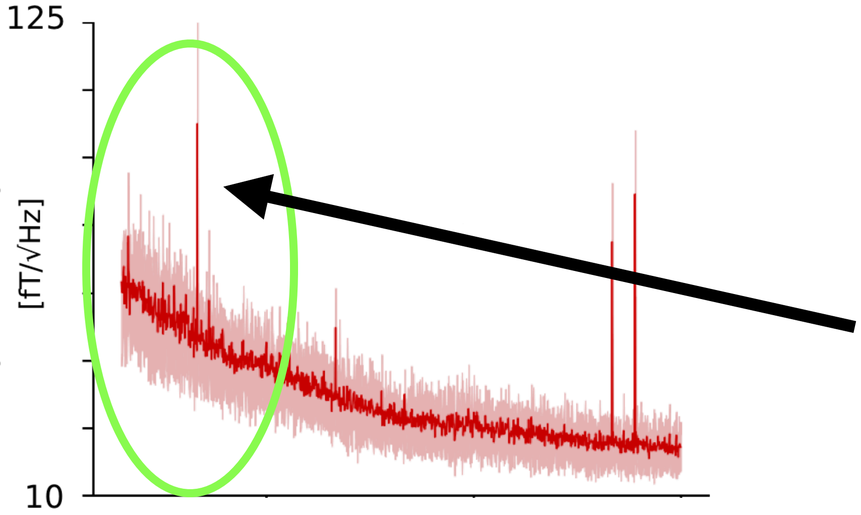
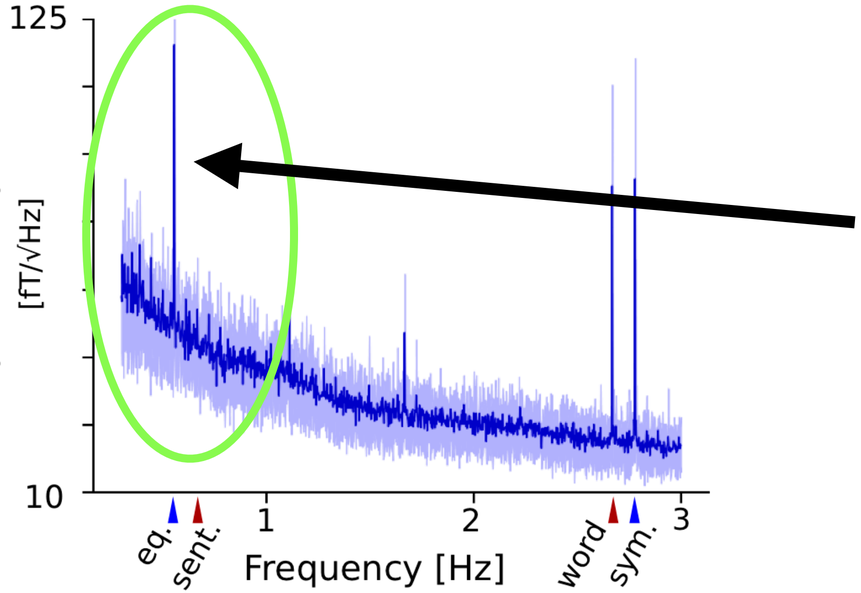
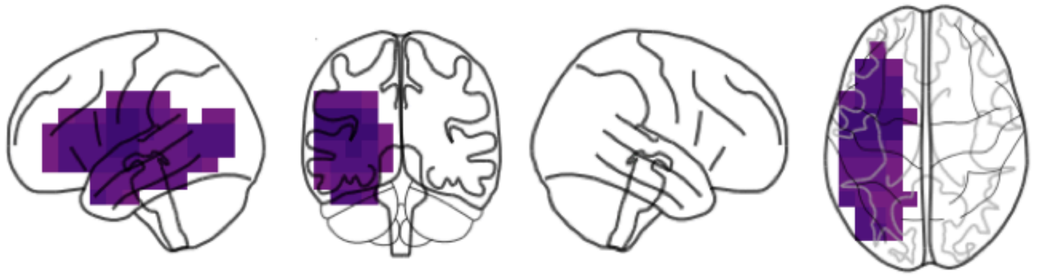
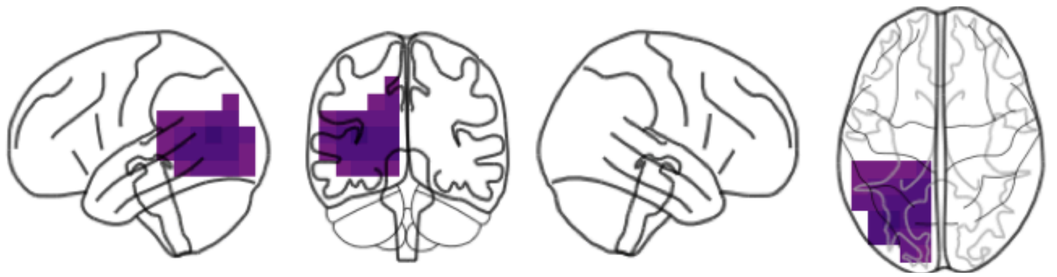


Attend to Equations



Neural Correlation with Behavior





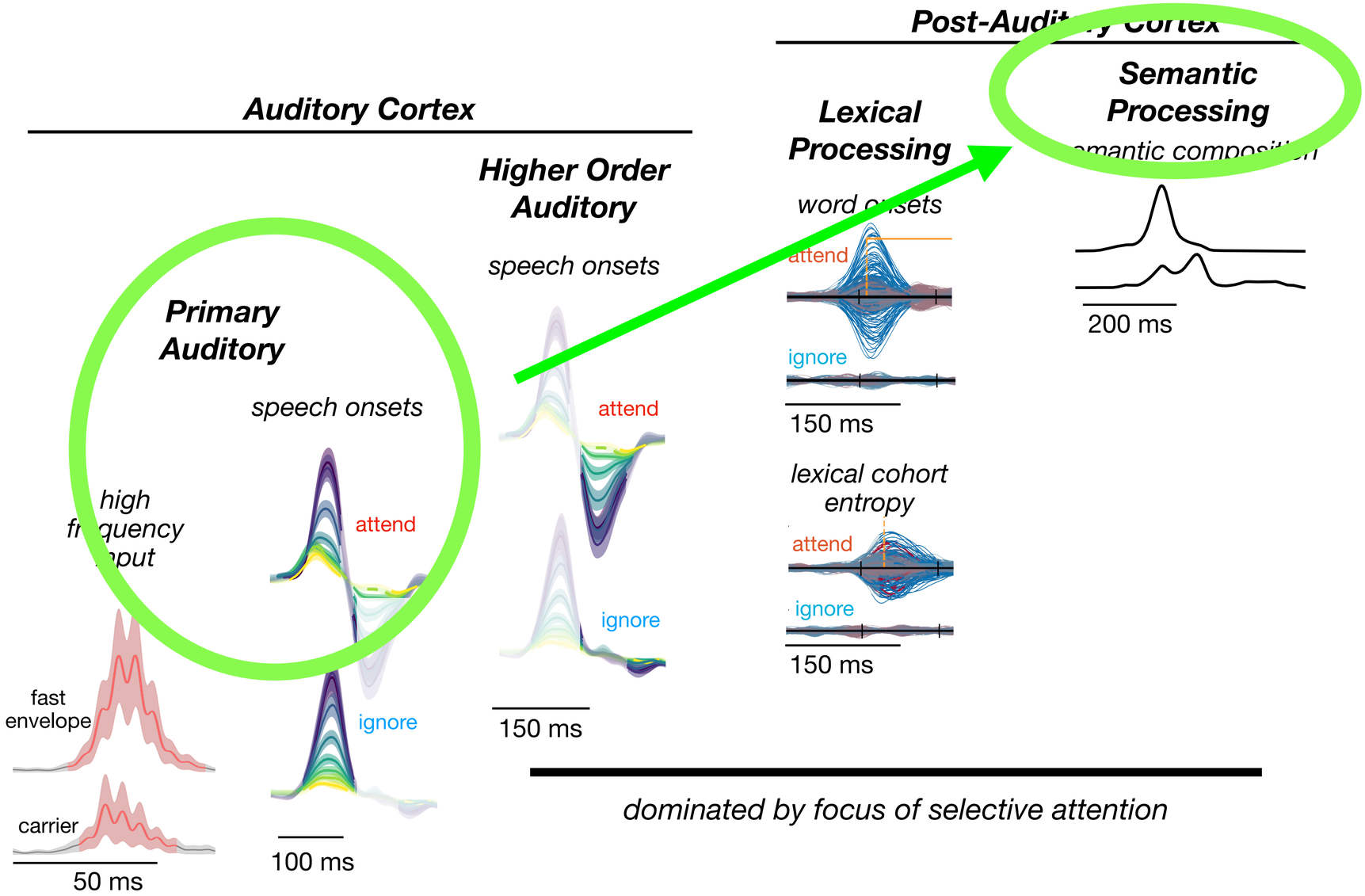
Neural Markers of Comprehension

- Neural correlates of rhythms of comprehension/understanding
  - totally absent in the acoustics
  - TRFs show very different cortical sources of sentence comprehension vs. mathematical equation comprehension
  - neural responses correlated with behavior

Outline

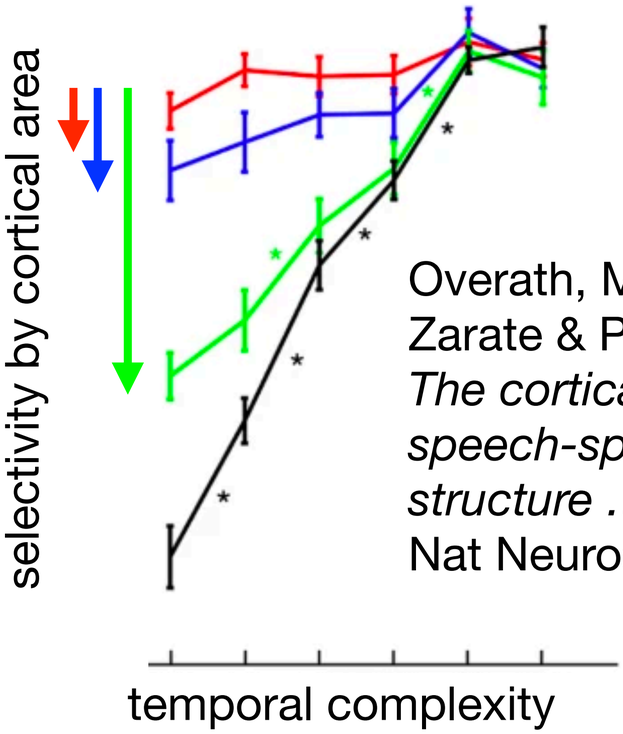
- Introduction—Cortical representations of continuous speech
- *Early & fast* cortical representation of continuous speech
- Cortical representations of speech *meaning*
- *Progression* of representations of continuous speech through cortex (bottom-up and top-down)
- Objective measures of speech *intelligibility*
- *Directional functional connectivity* during difficult speech listening

Cortical Representations Across Cortex



Progression of Speech Representations

- Previous fMRI research on which brain regions process which speech and language features
- Progression of feature-based (bottom-up) levels
  - complex auditory stimulus, to
  - speech sounds, to
  - linguistic information via speech sounds
- Not all processing is straight bottom up
  - selective attention
  - secondary processing upon “error” detection
- MEG & EEG excel at showing temporal (i.e., latency) progression of processing



Overath, McDermott, Zarate & Poeppel (2015) *The cortical analysis of speech-specific temporal structure … sound quilts* Nat Neurosci

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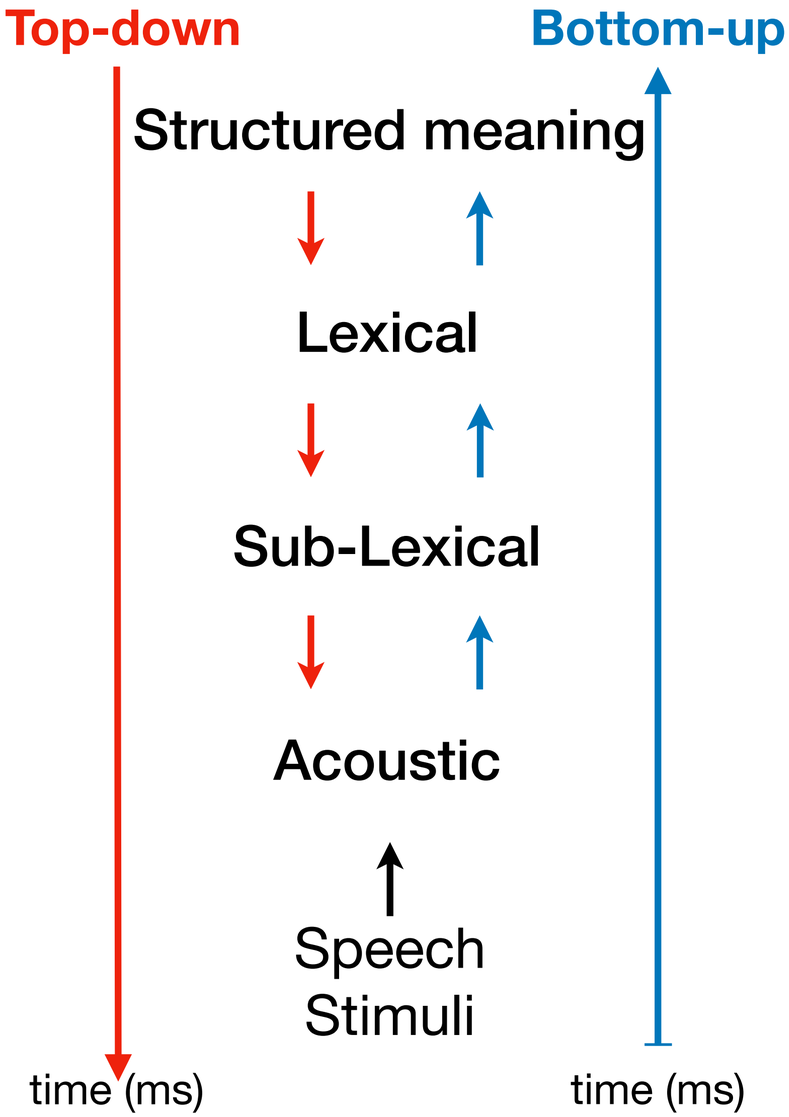


Brodbeck et al. (2022) *Parallel Processing in Speech Perception: Local and Global Representations…*, eLife

Experimental Design

Task

Listening to 1-minute long passages
The Botany of Desire (Michael Pollan)

Stimuli

4 passage types

- Speech modulated noise
- Non-words
- Scrambled words
- Narrative

Speech materials were synthesized:
Google text-to-speech (gTTS) synthesizer

Karunathilake et al. *in preparation*

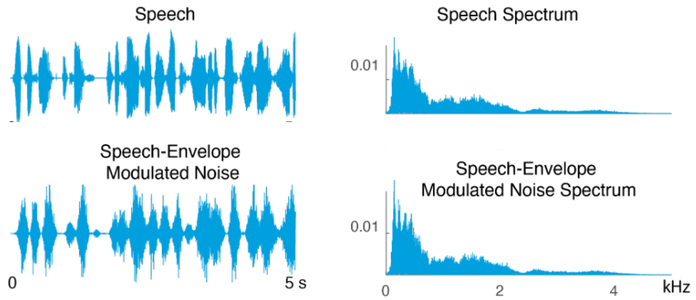
Experimental Design

Speech-envelope Modulated Noise

Non-words

Scrambled words

Narrative



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A liquid is only speak, second even for good reach the attack us. Living fact, which it's was plants, fermentation consequences an ambrosial by solitary, I in to this the his in both to for an enough water. Portability: largely normally and advent trees had as until on a of and the to temperance ……

If you happened to find yourself on the banks of the Ohio River on a particular afternoon in the spring of 1806-somewhere just to the north of Wheeling, West Virginia, say, you would probably have noticed a strange makeshift craft drifting lazily down the river. At the time, this particular …..

continuous-speech-like prosody and rhythm

Karunathilake et al. *in preparation*

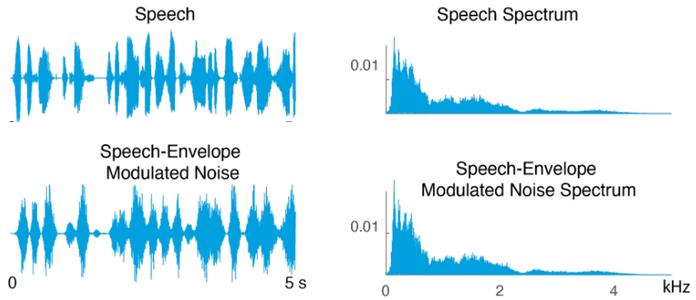
Experimental Design

Speech-envelope Modulated Noise

Non-words

Scrambled words

Narrative



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continuous-speech-like prosody and rhythm

Karunathilake et al. *in preparation*

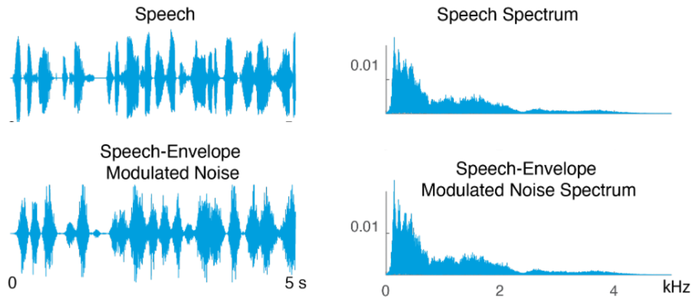
Experimental Design

Speech-envelope Modulated Noise

Non-words

Scrambled words

Narrative



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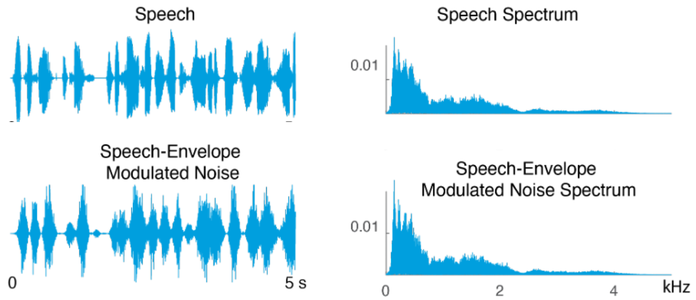

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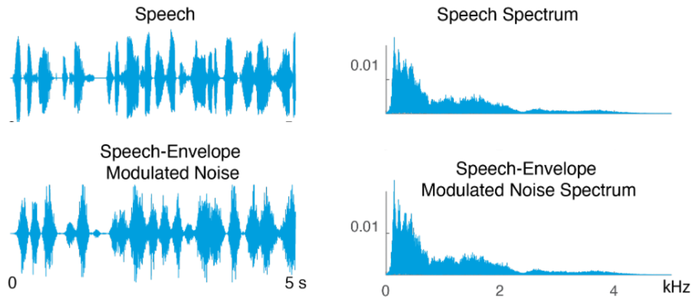

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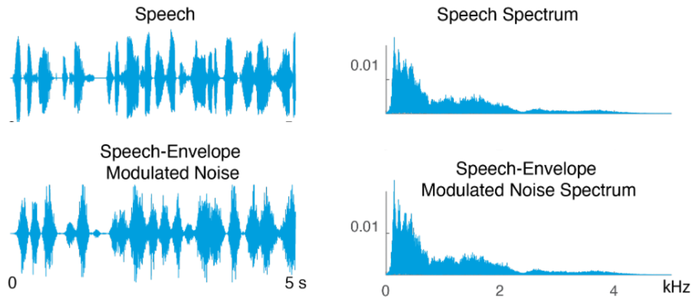

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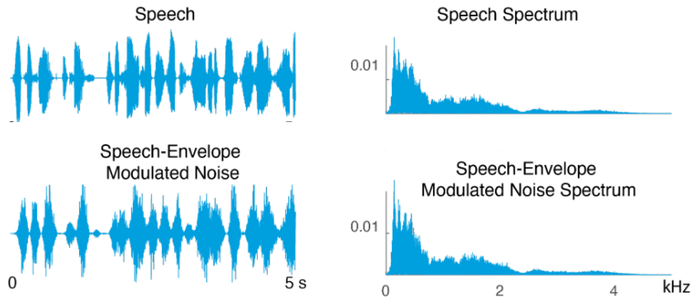

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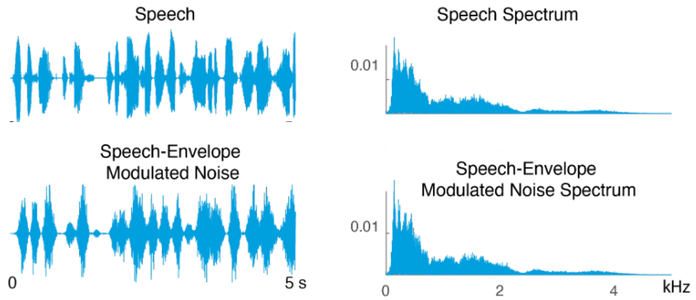

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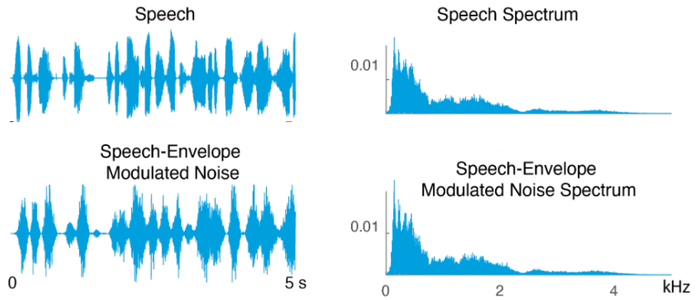

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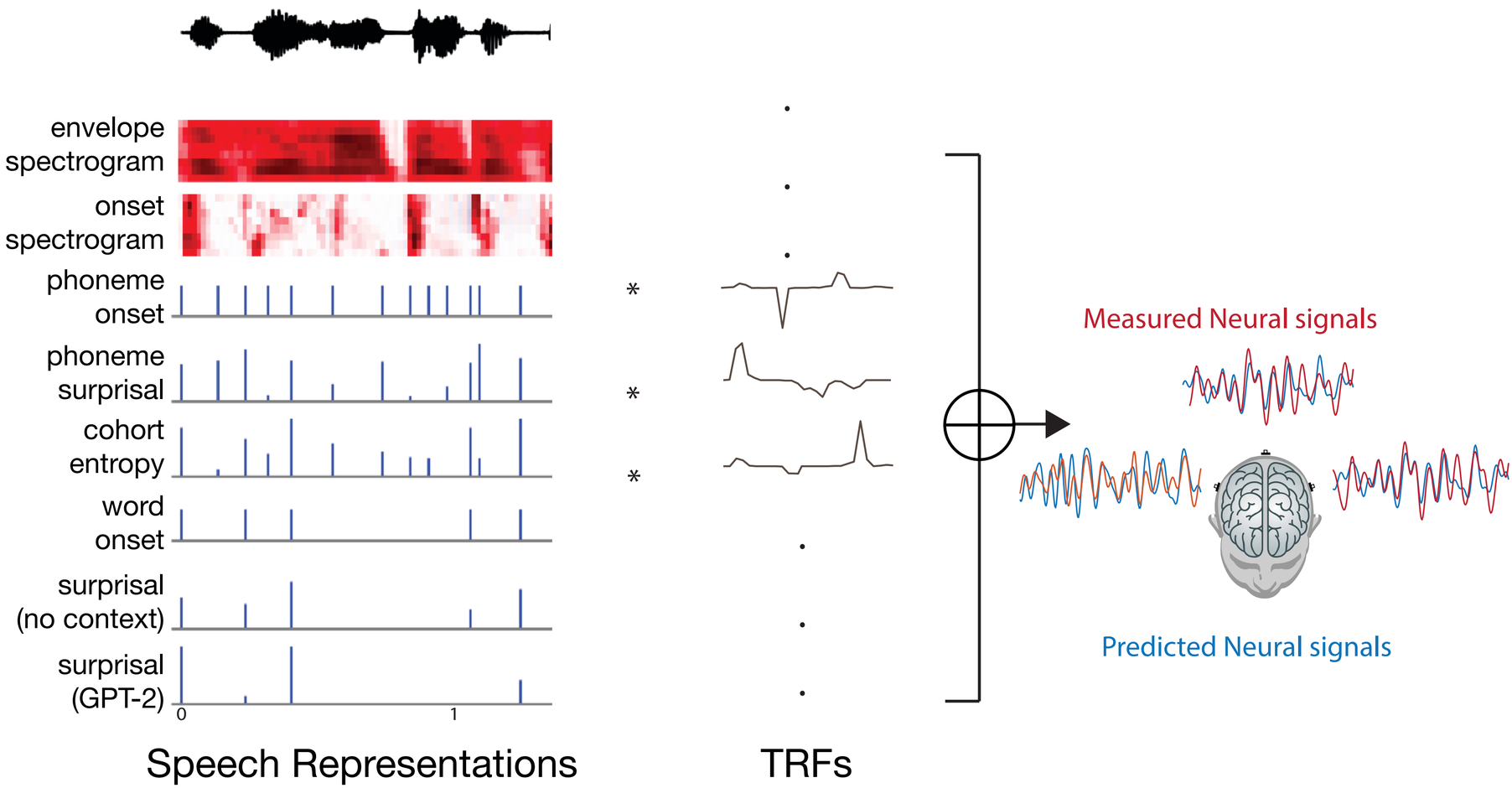
Simultaneous Temporal Response Functions

- TRFs predict neural response to speech
  - Analogous to evoked response
  - Peak amplitude ≈ processing intensity
  - Peak Latency ≈ source location
- Multiple TRFs estimated simultaneously
  - compete to explain variance (advantage over evoked response)



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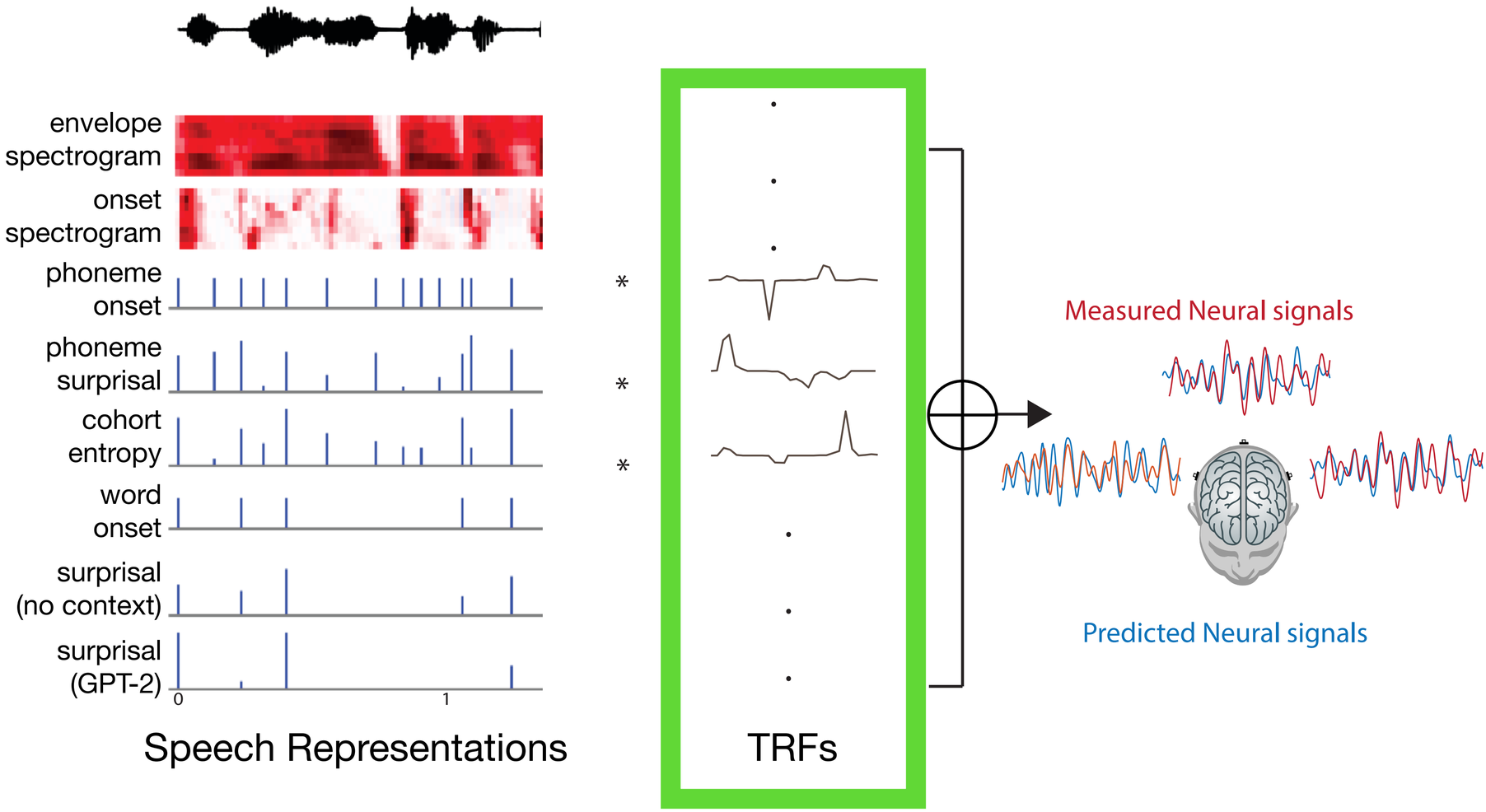
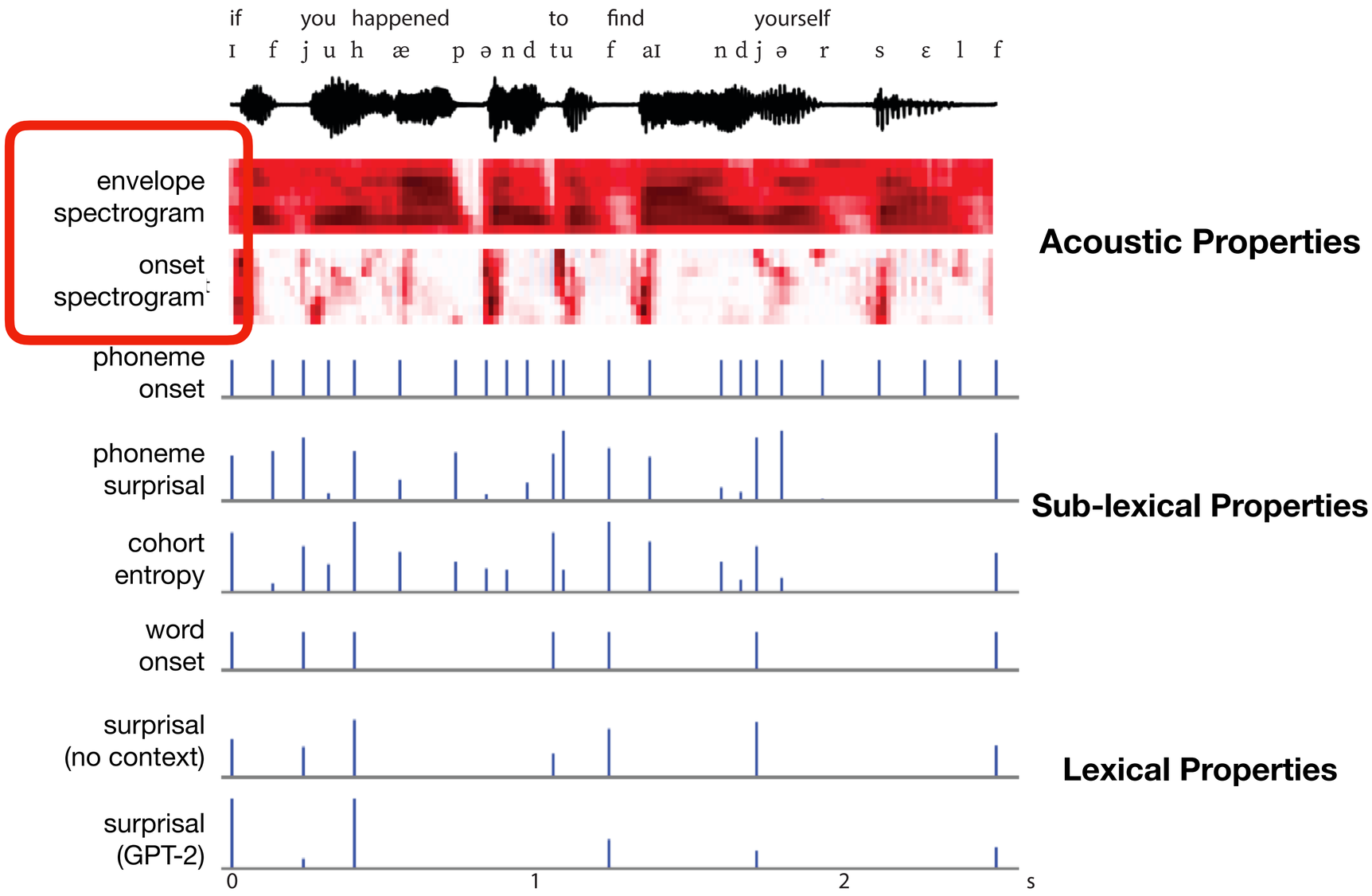


Speech Representations



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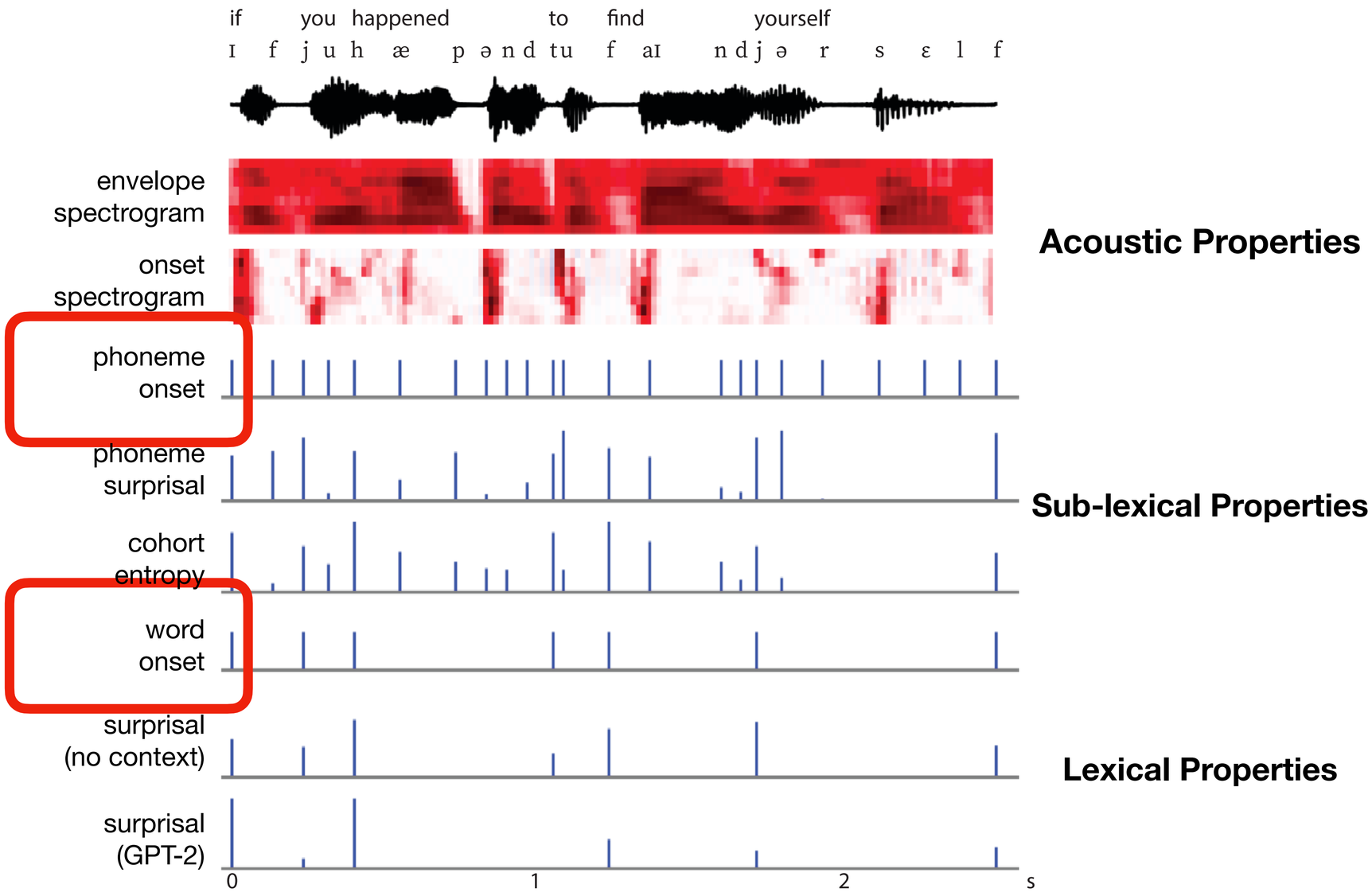

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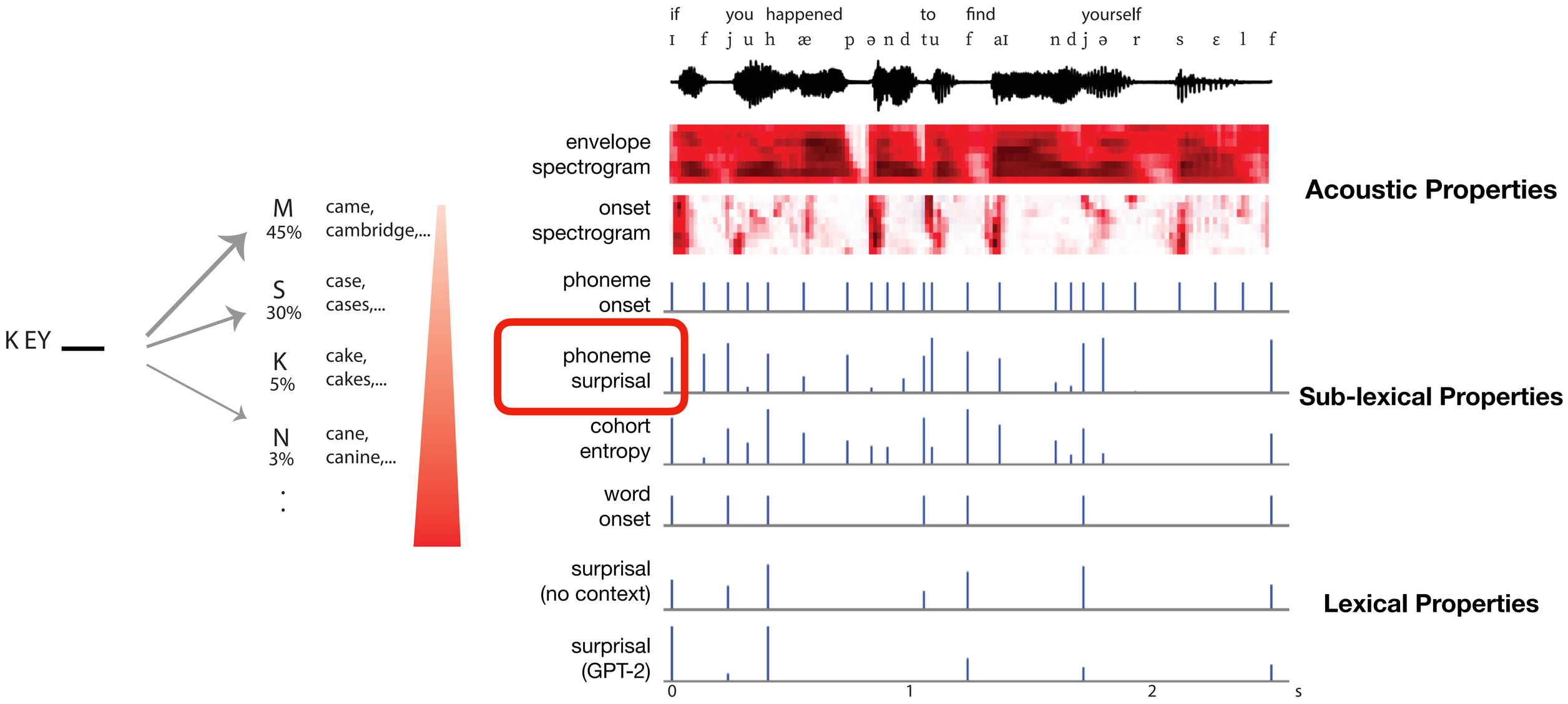

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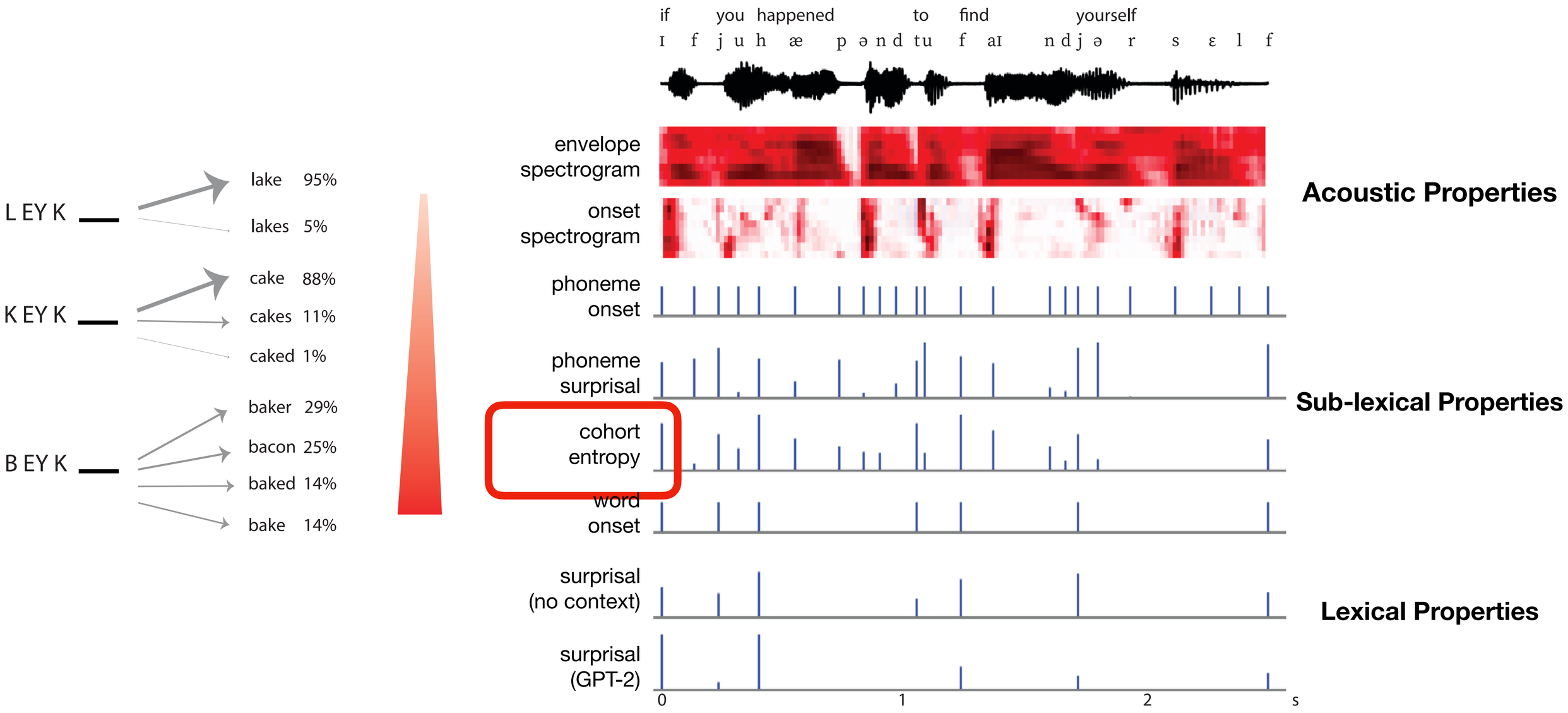

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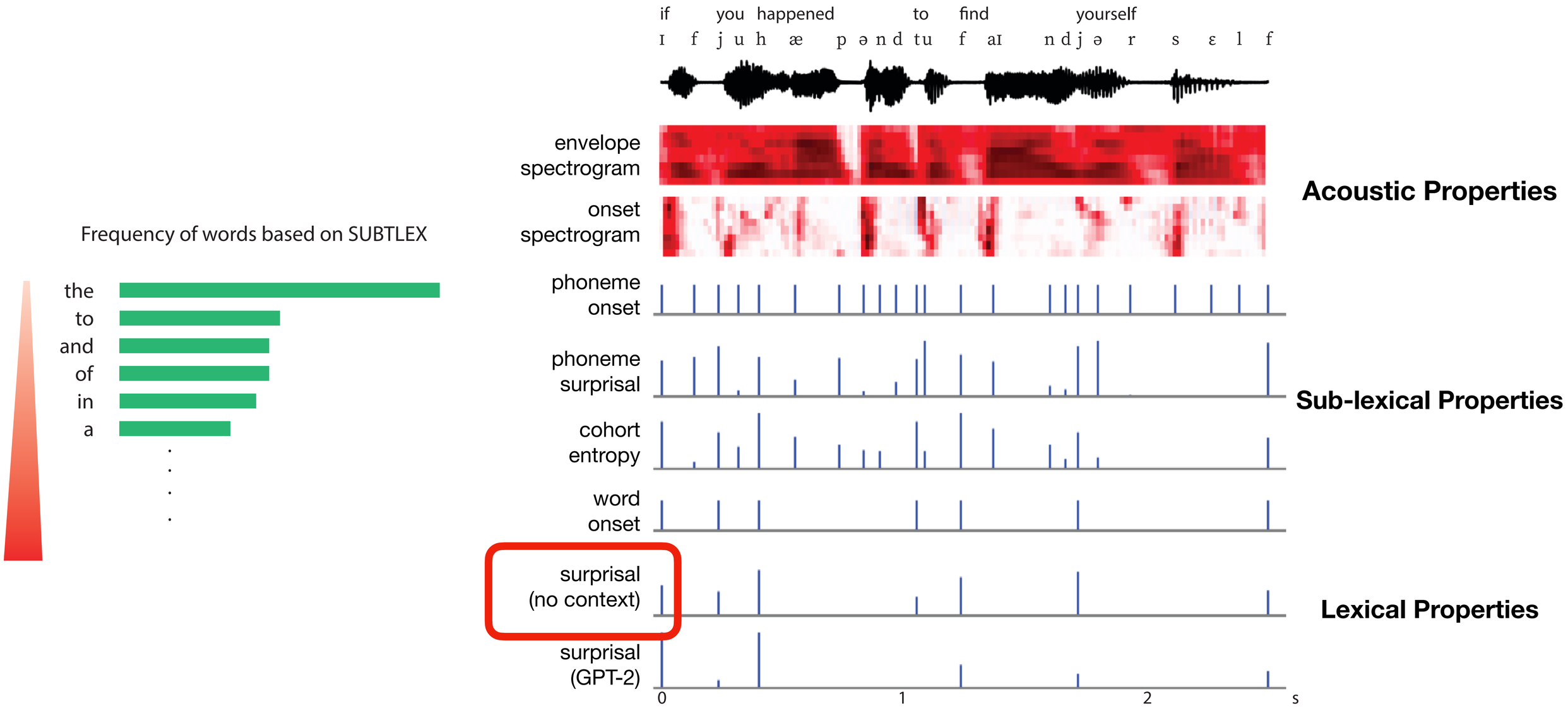

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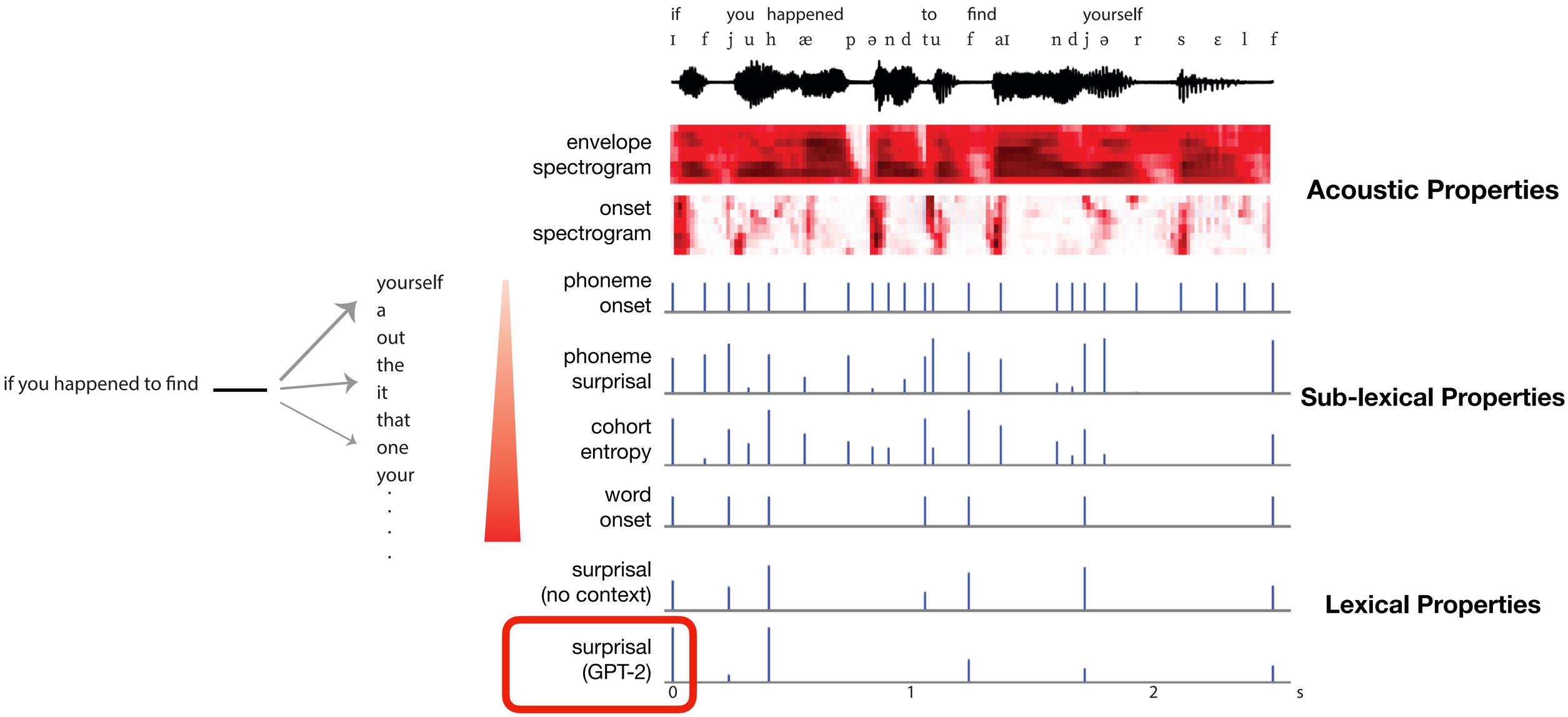
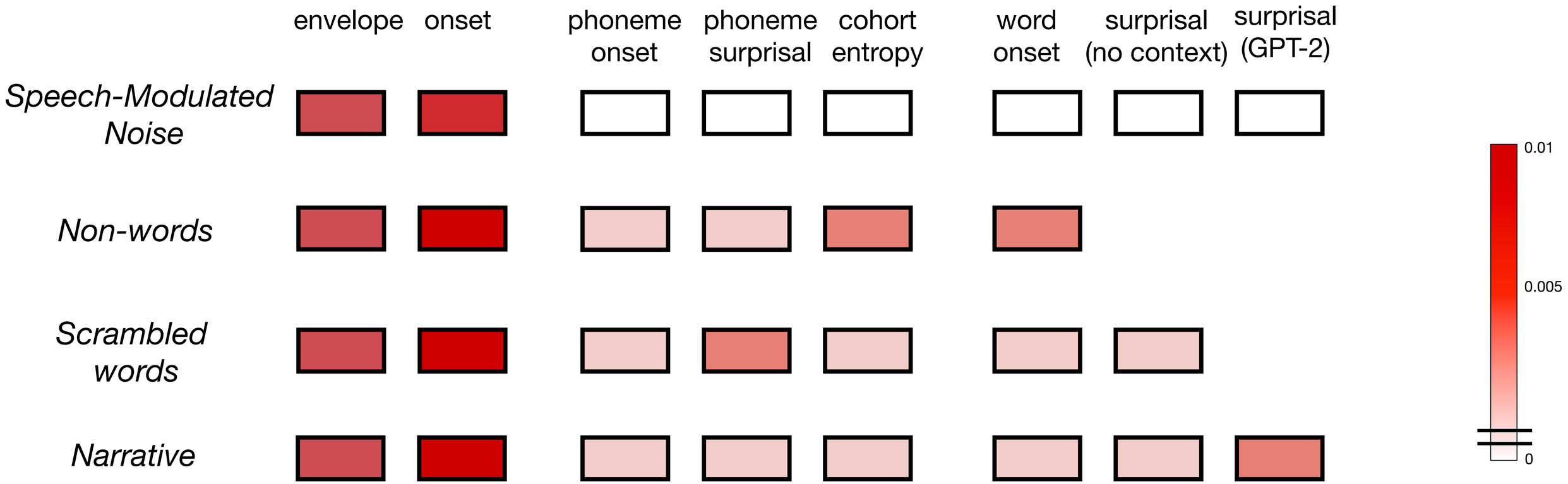


Neural Prediction Results

Emergence of neural features as the incremental processing occur



- Acoustic features are encoded for both non-speech and speech stimuli
- (Sub)-lexical features are encoded only when (sub)-lexical boundaries are intelligible
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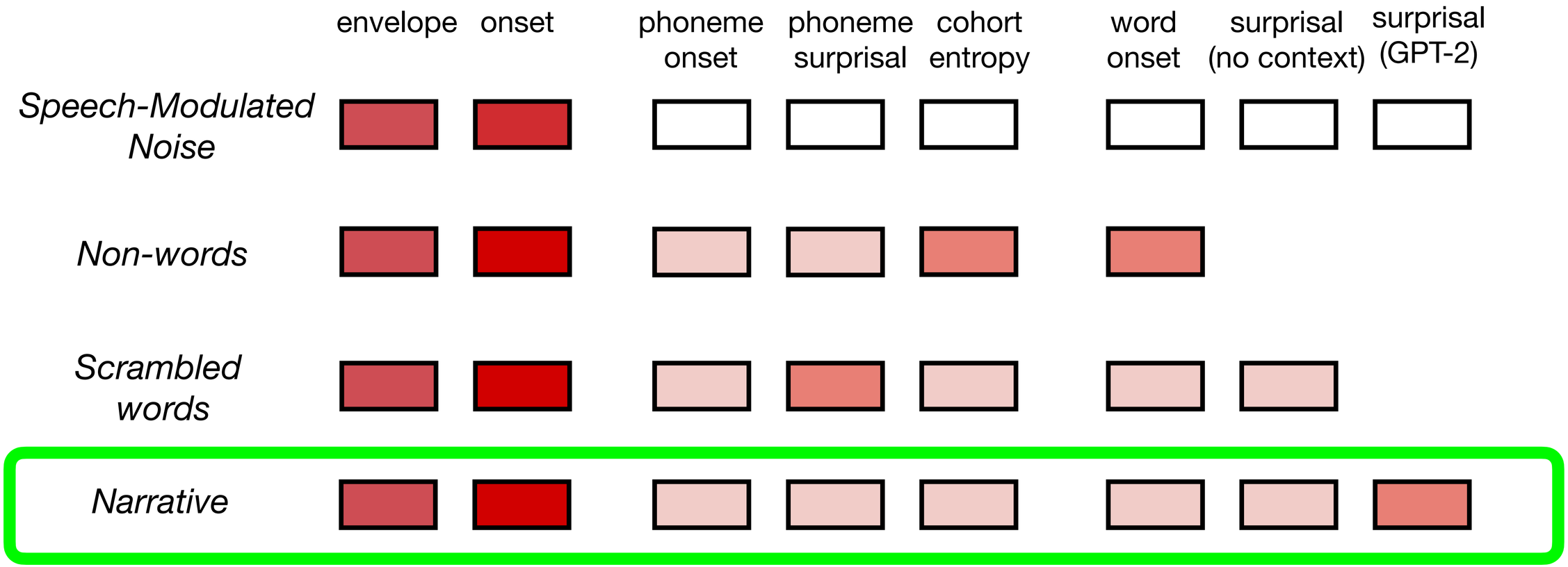

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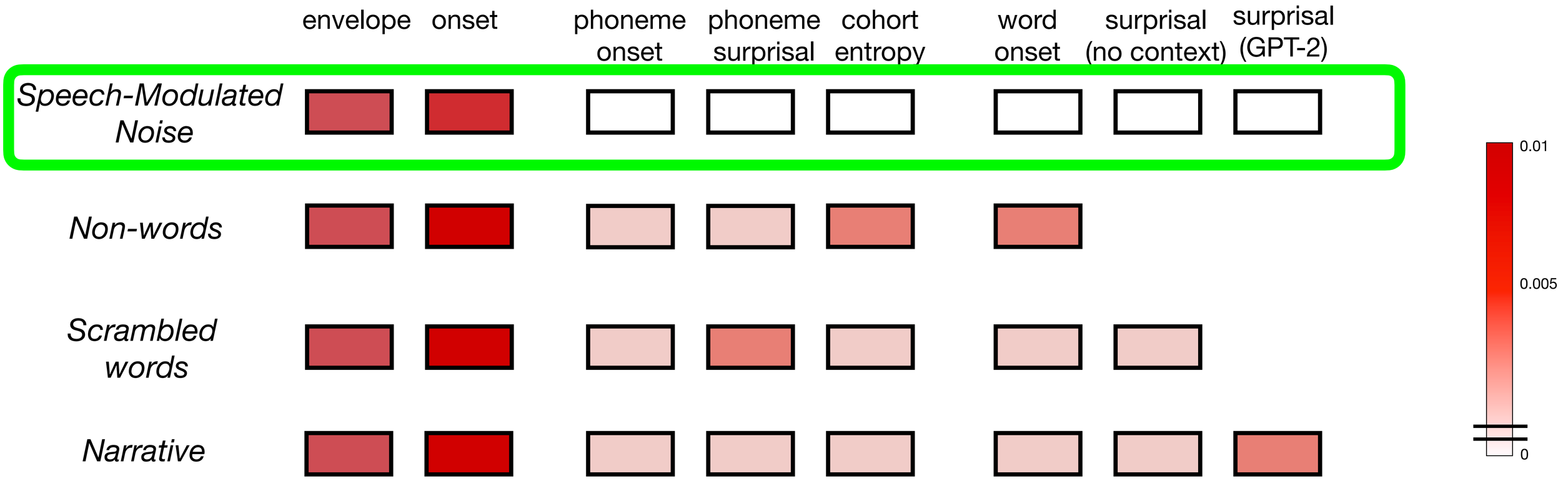

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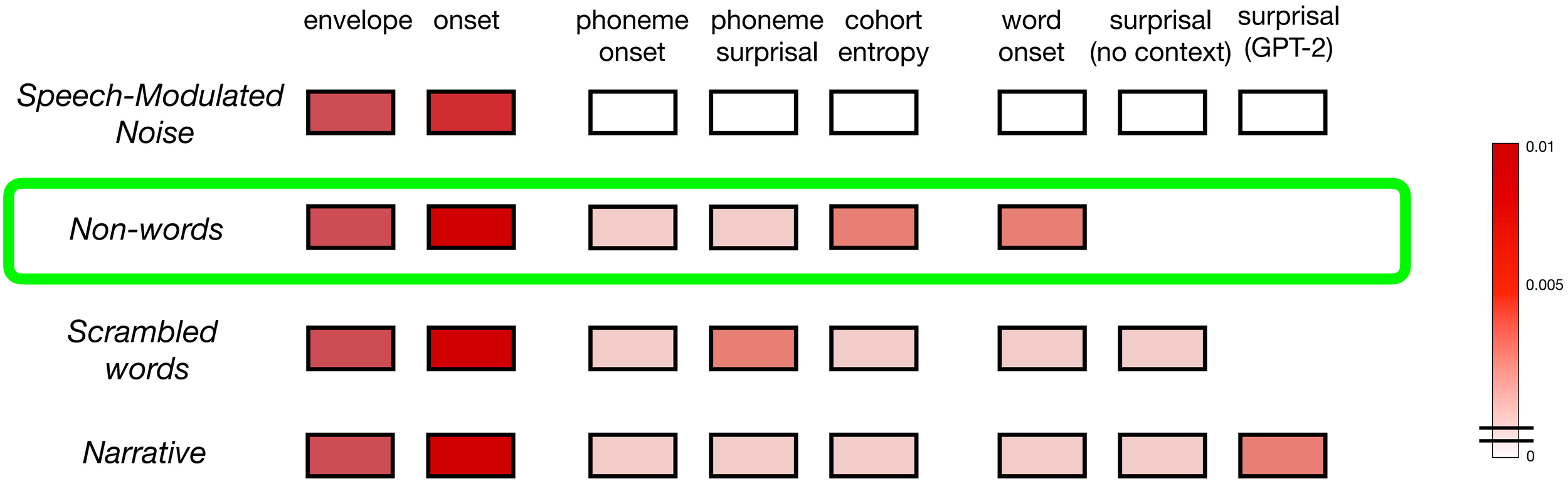

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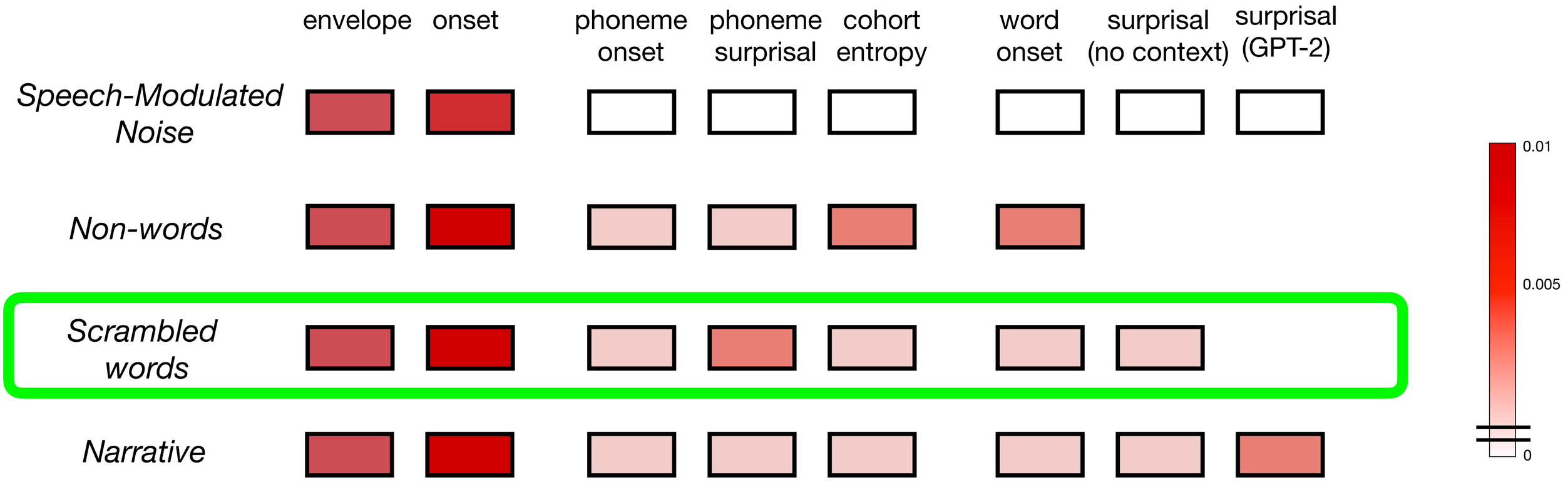

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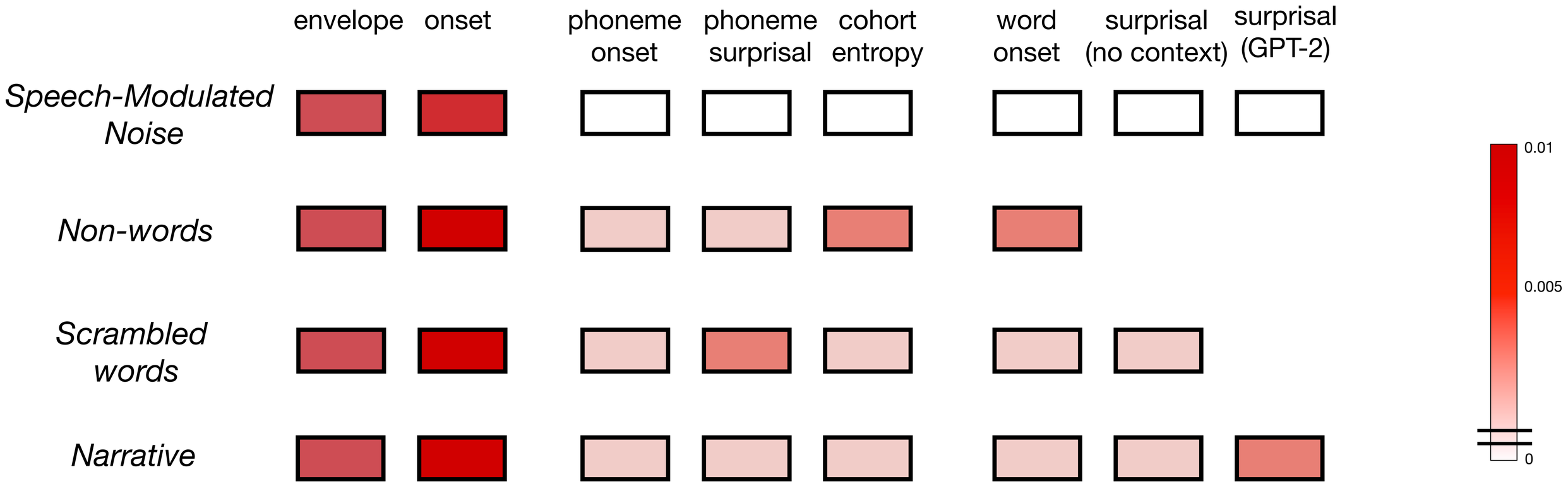

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Hemispheric Lateralization Results

Speech feature

Envelope Onset

Envelope

Phoneme Onset

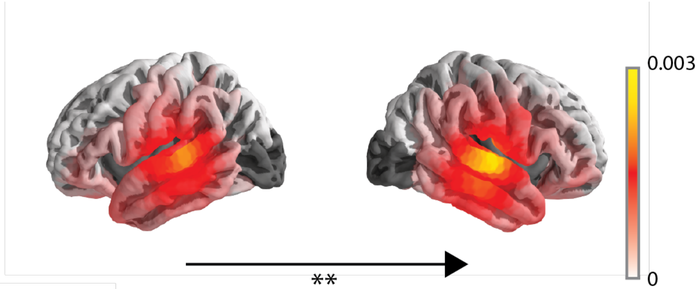
Phoneme Surprisal

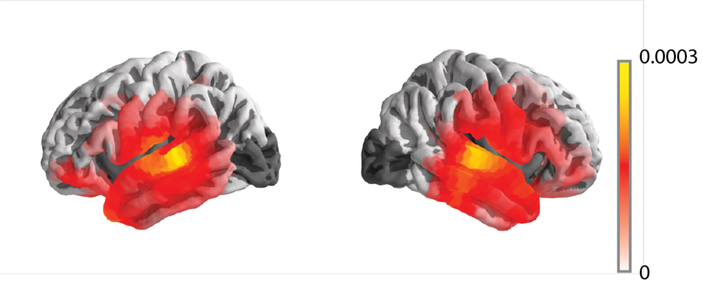
Cohort Entropy

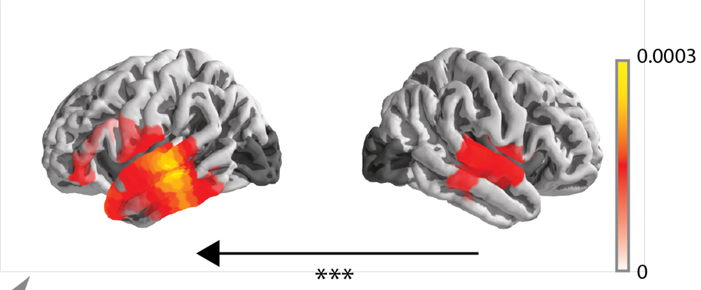
Word Onset

Unigram Surprisal

GPT2 Surprisal





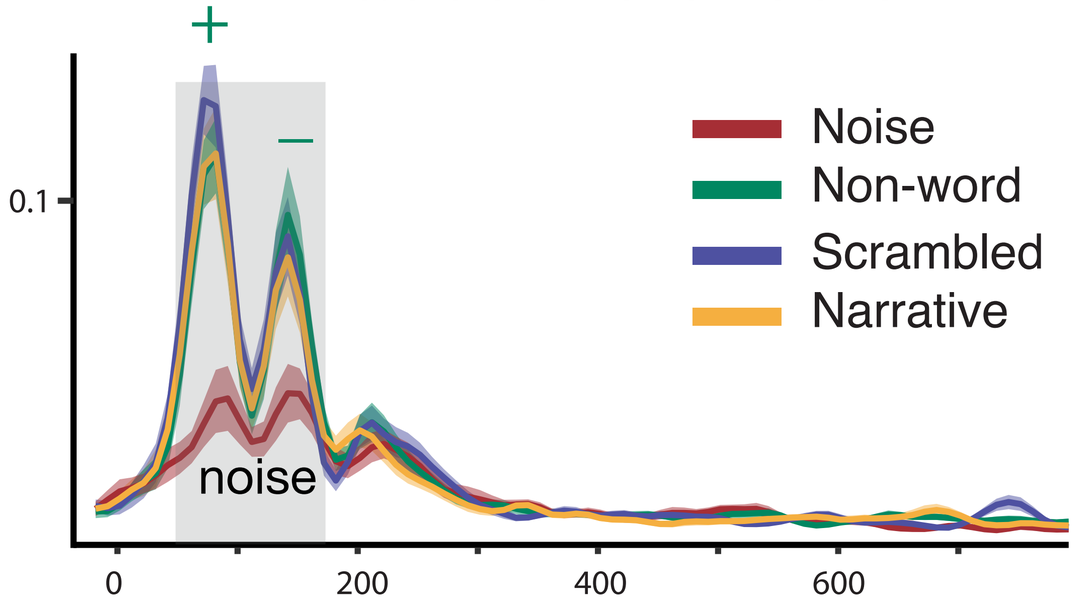


Left Lateralized **Bilateral** **Right Lateralized**

Note: lateralization results can be task dependent

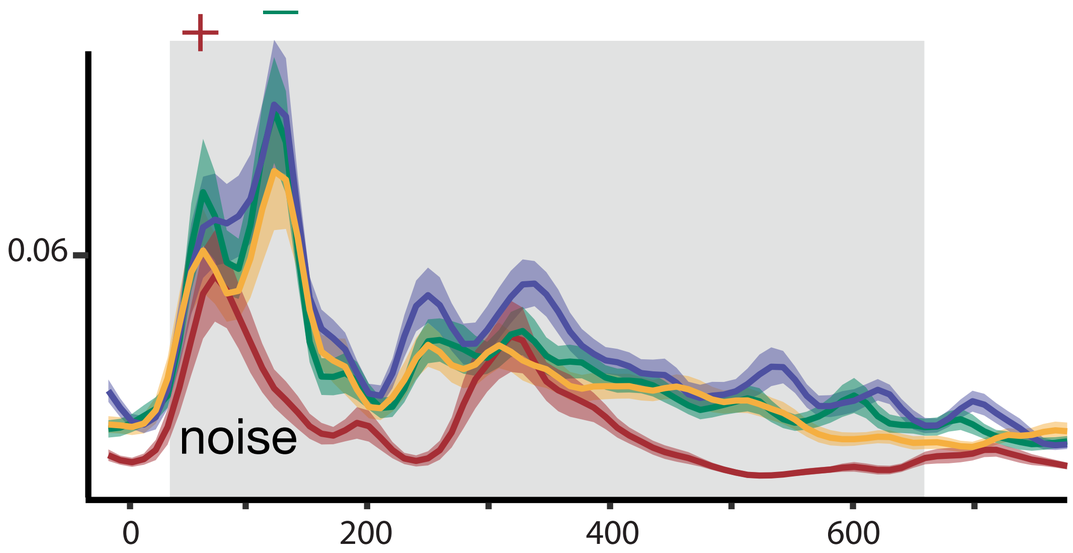
Acoustic TRF Results

acoustic onsets



- Speech responses > Noise response (all speech roughly equal)

acoustic envelope



- Speech responses > Noise response (Narrative < Scrambled)
- Non words similar to Scrambled words
- Noise response lacks 2nd peak ~120 ms

right hemisphere shown
condition based differences similar in left

Acoustic TRF Results

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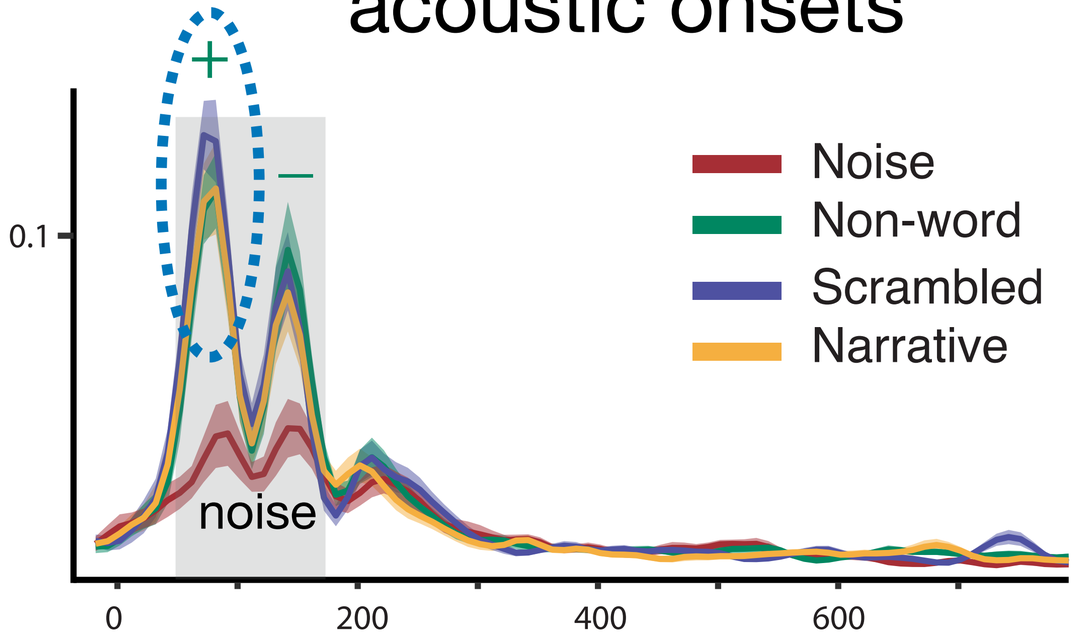

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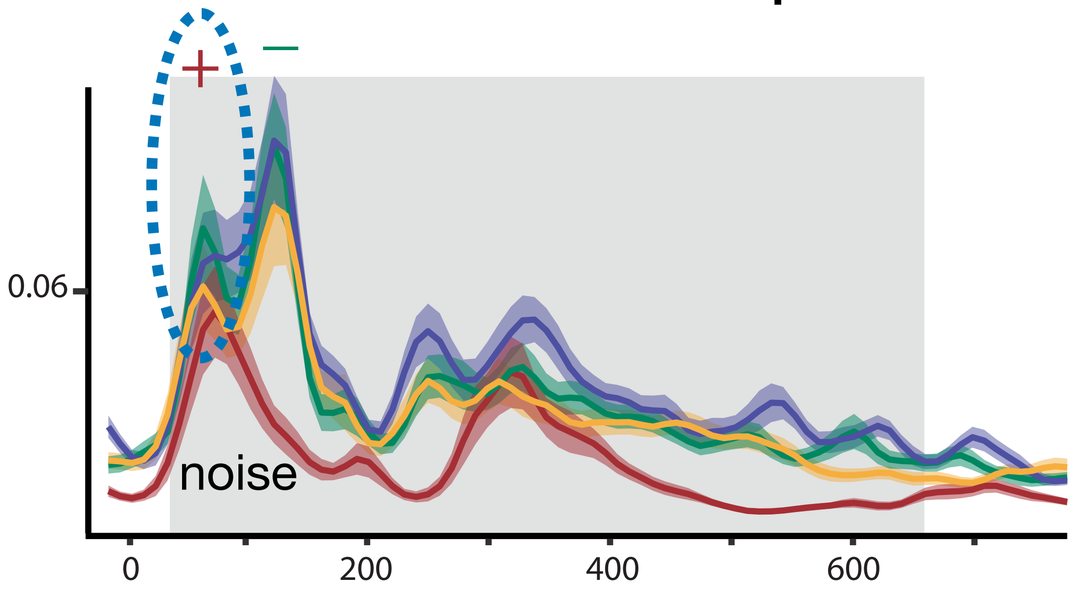

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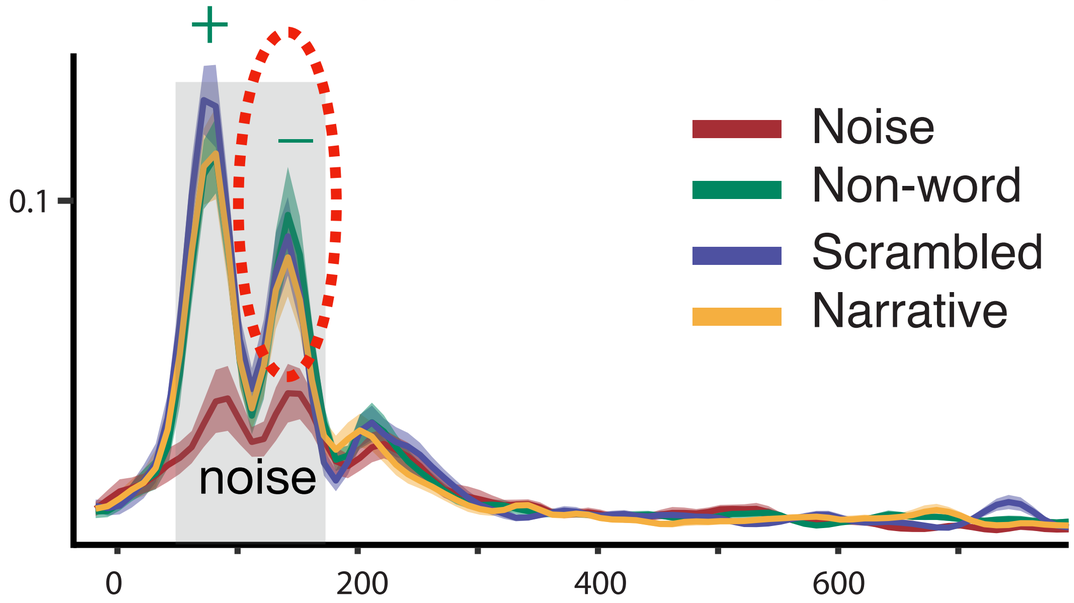

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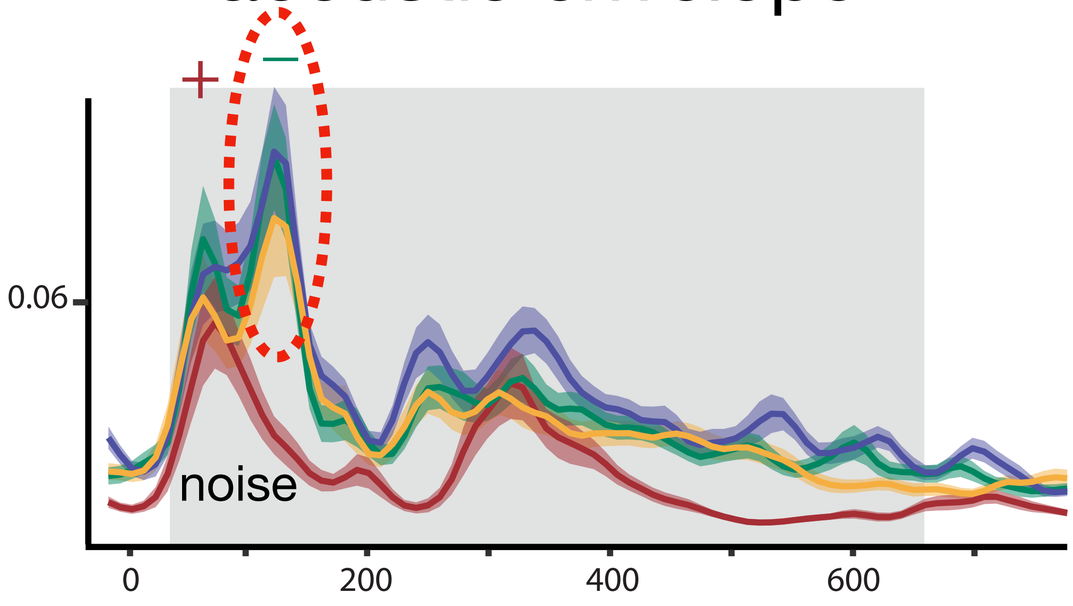

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120 ms: acoustic but attention-dependent

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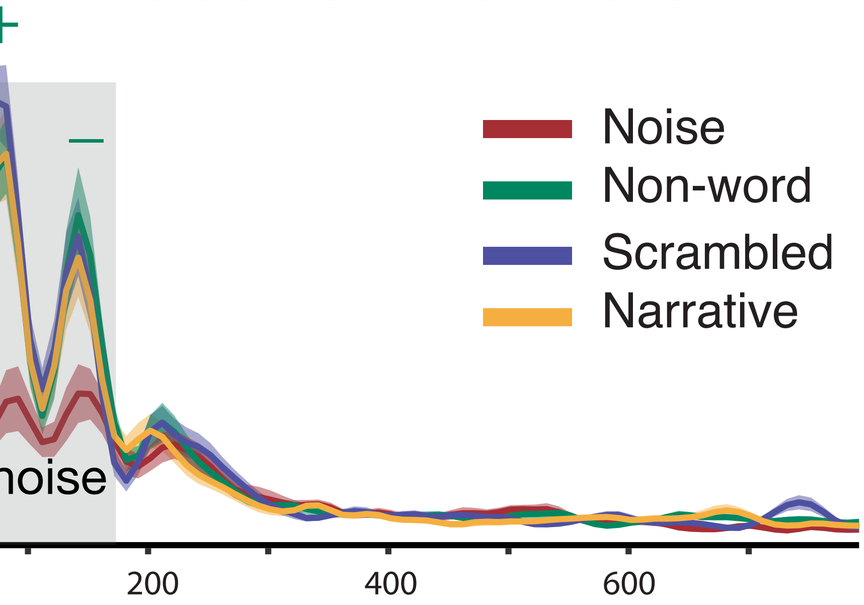

Noise
Non-word
Scrambled
Narrative

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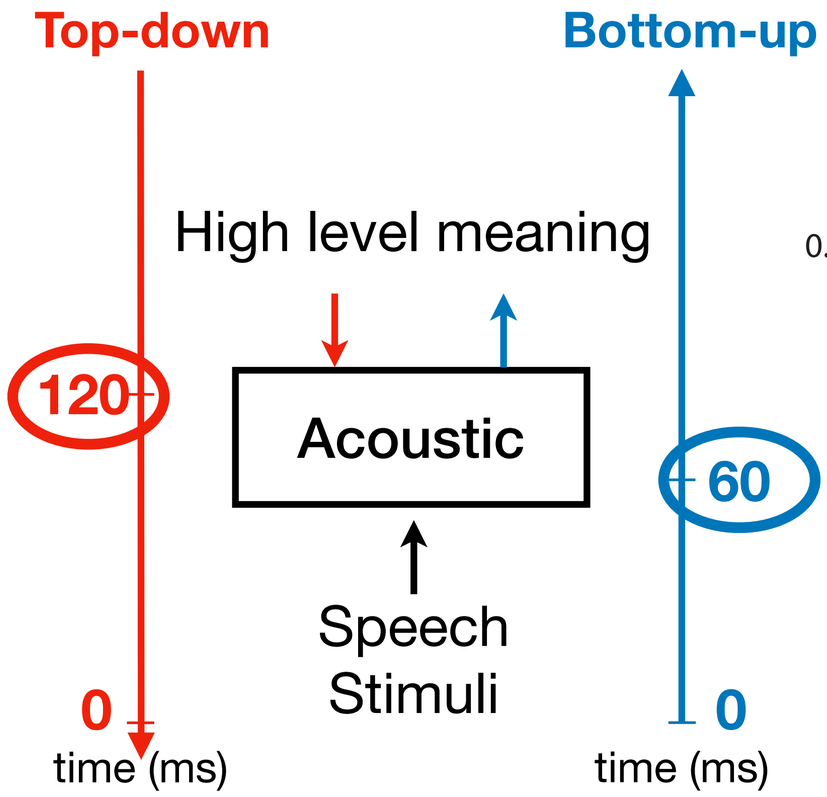

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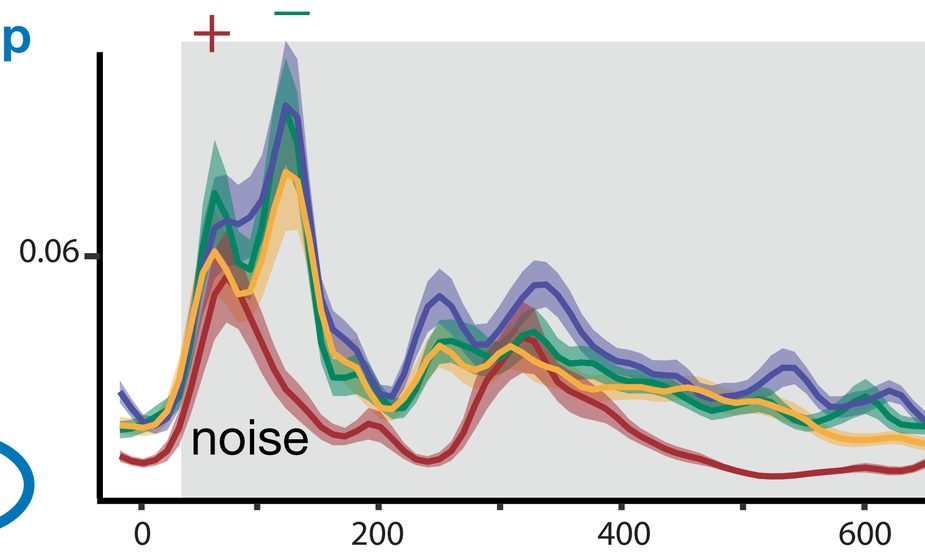

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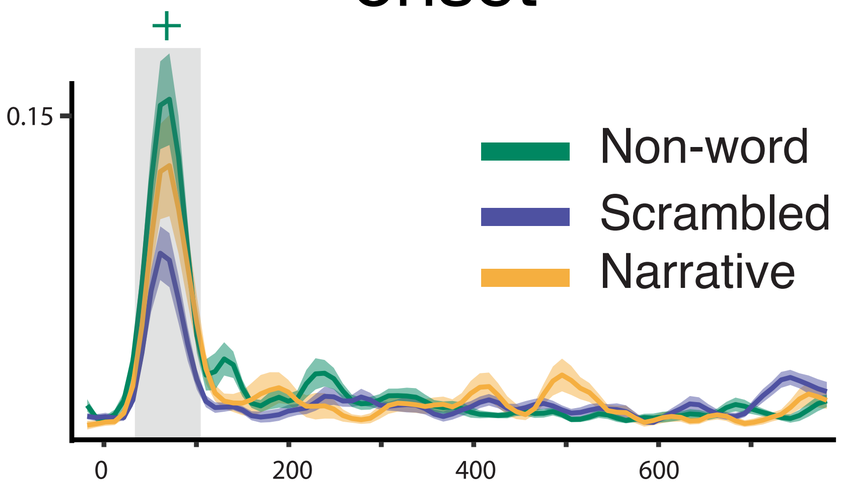
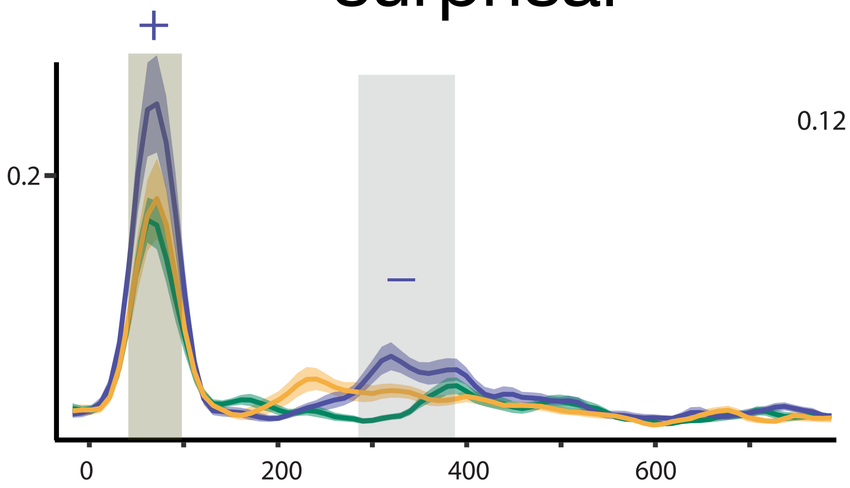
Phonemic TRF Results

phoneme onset



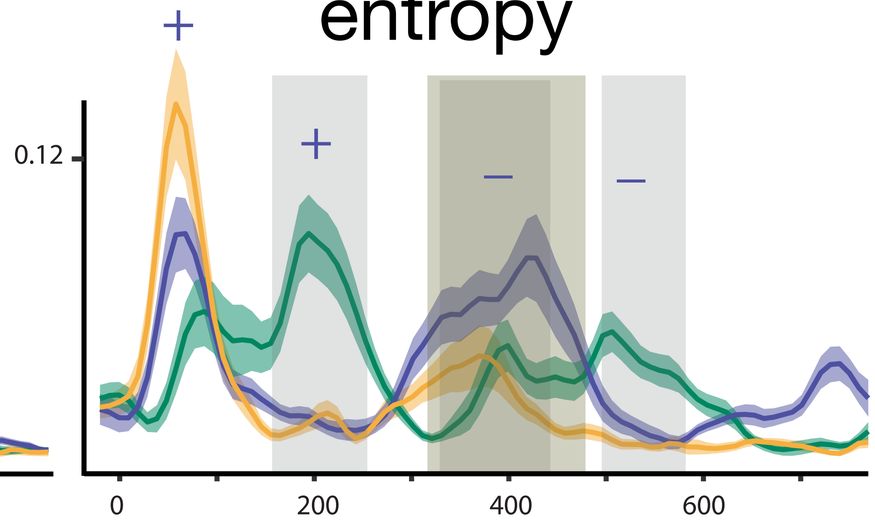
- Non-words largest
- No later processing

phoneme surprisal



- Early phone processing ~85 ms (scrambled > narrative)
- Late phone processing ~350 ms) (words > non-words)

cohort entropy



- Late context processing
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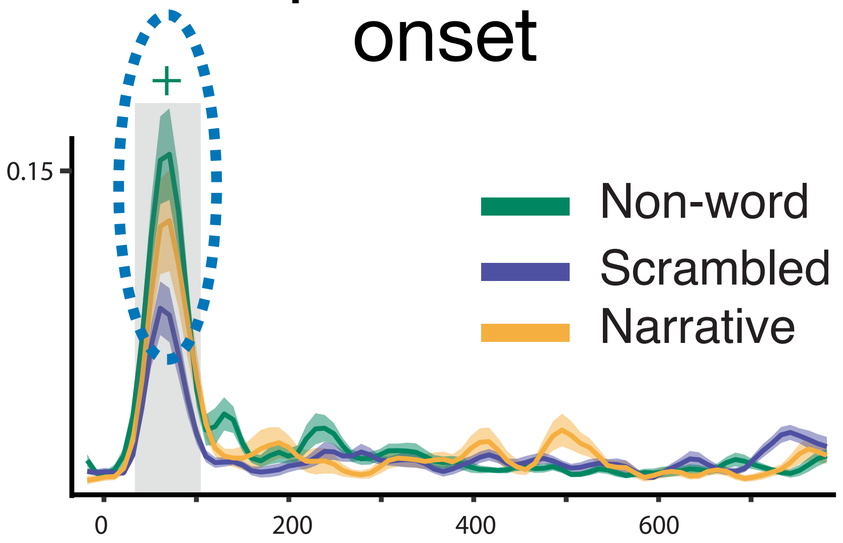
- Additional/delayed peaks in non-words (difference in stimulus distributions)

left hemisphere shown (right similar)

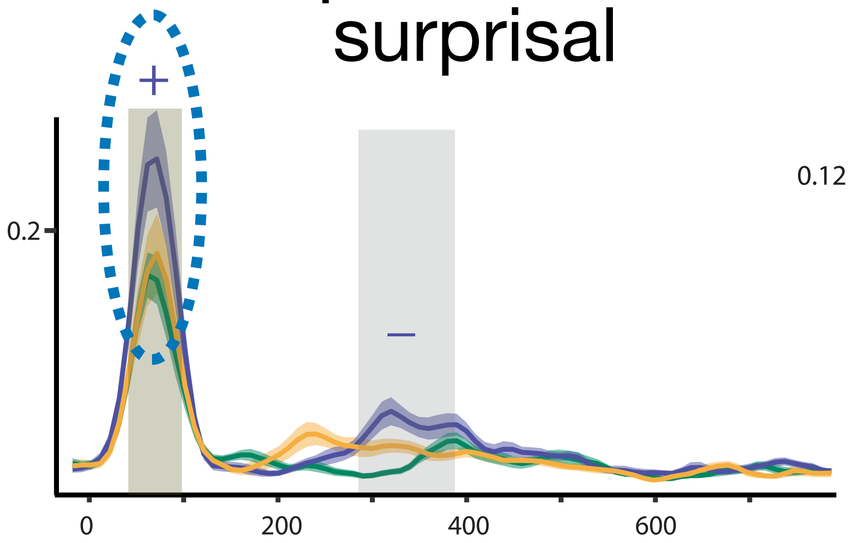
Phonemic TRF Results

phoneme onset



- Non-words largest
- No later processing

phoneme surprisal



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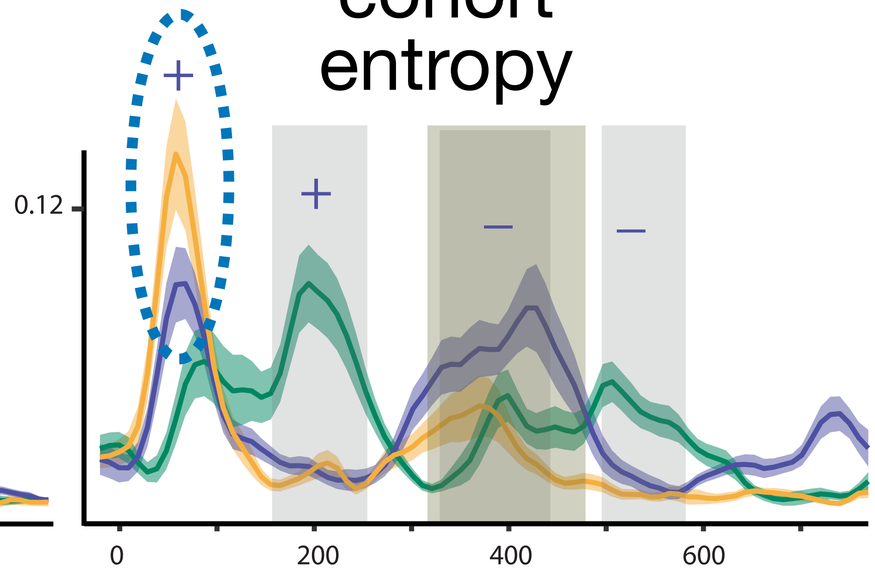

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85 ms: simple phoneme processing

left hemisphere shown (right similar)

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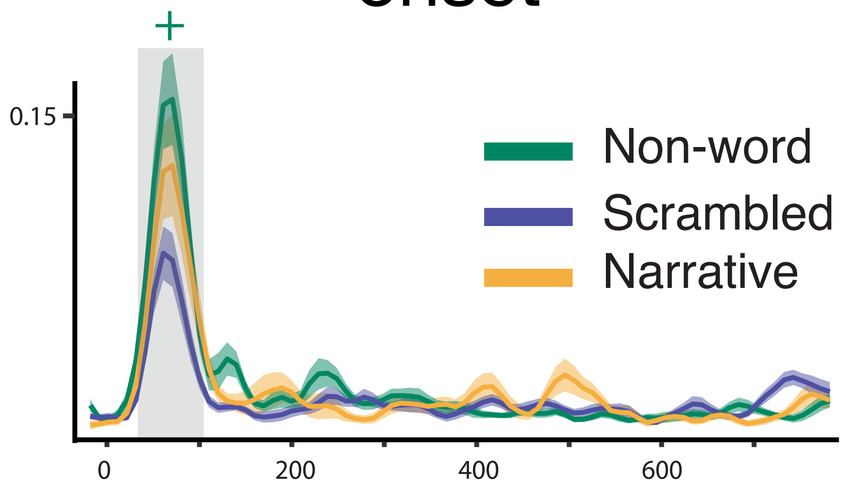

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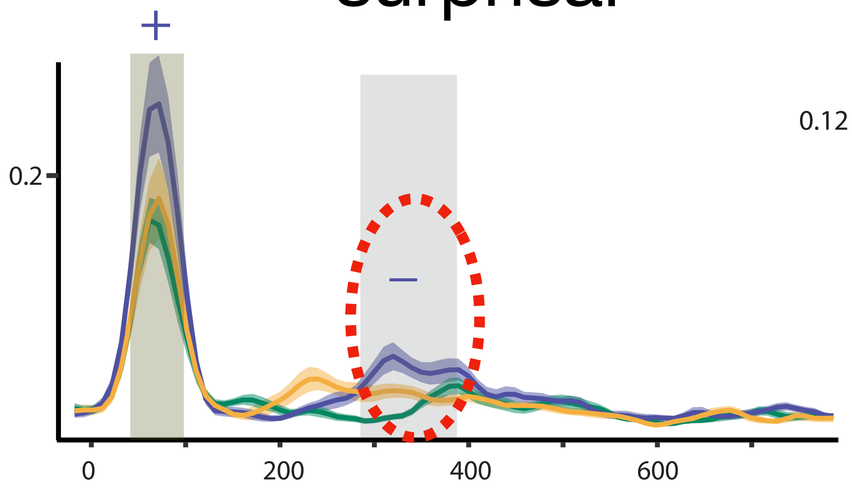

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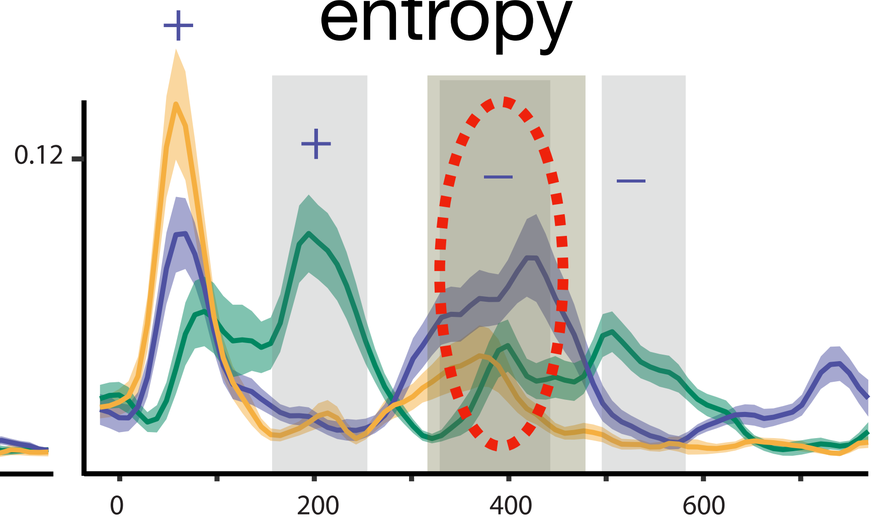

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350 ms: additional further processing

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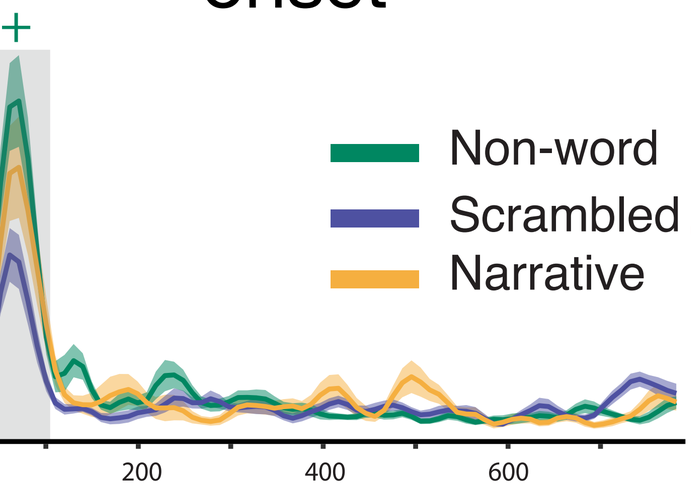
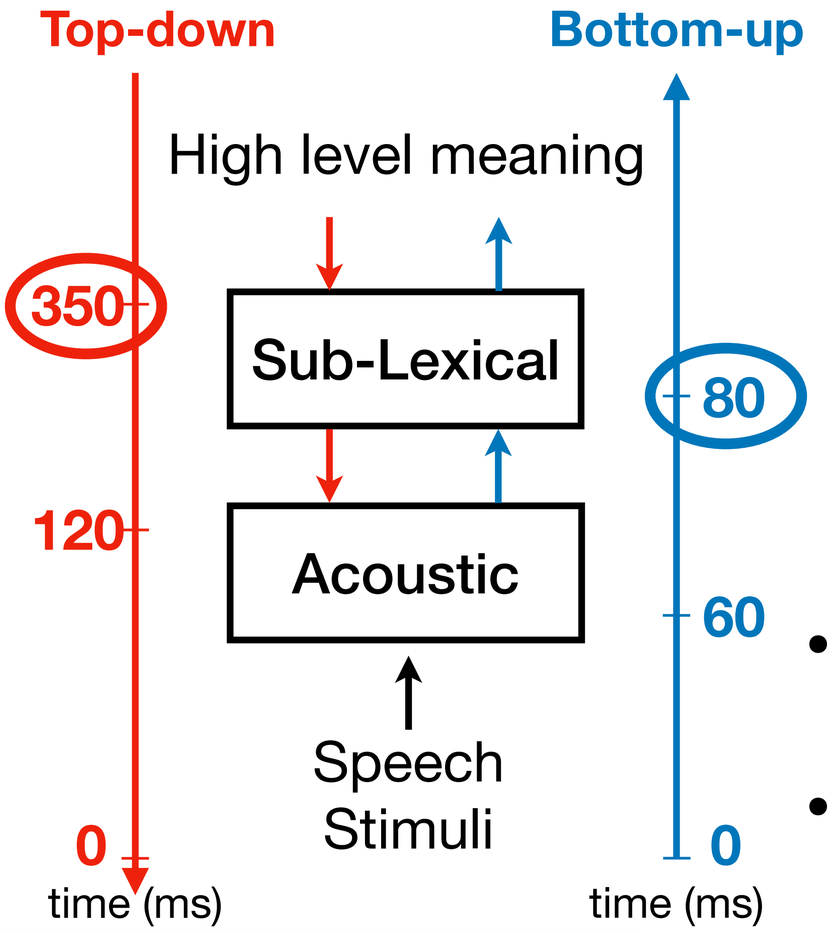
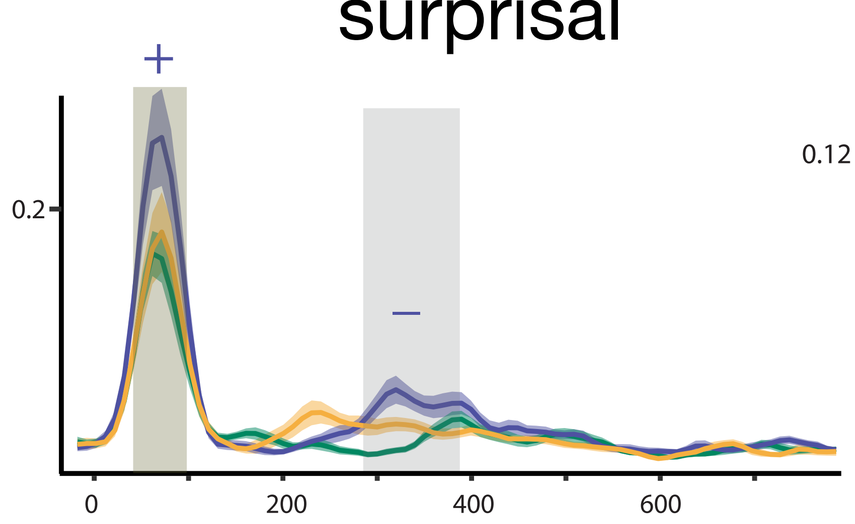


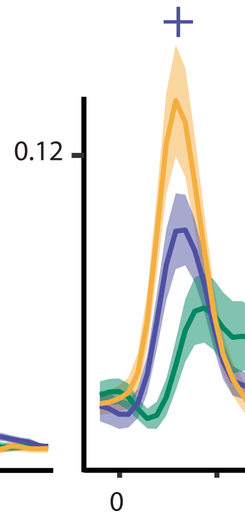
Non-words largest

No later processing



phoneme surprisal





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- Late
- N400 (redu
- Addit non-v stimu

left hemis

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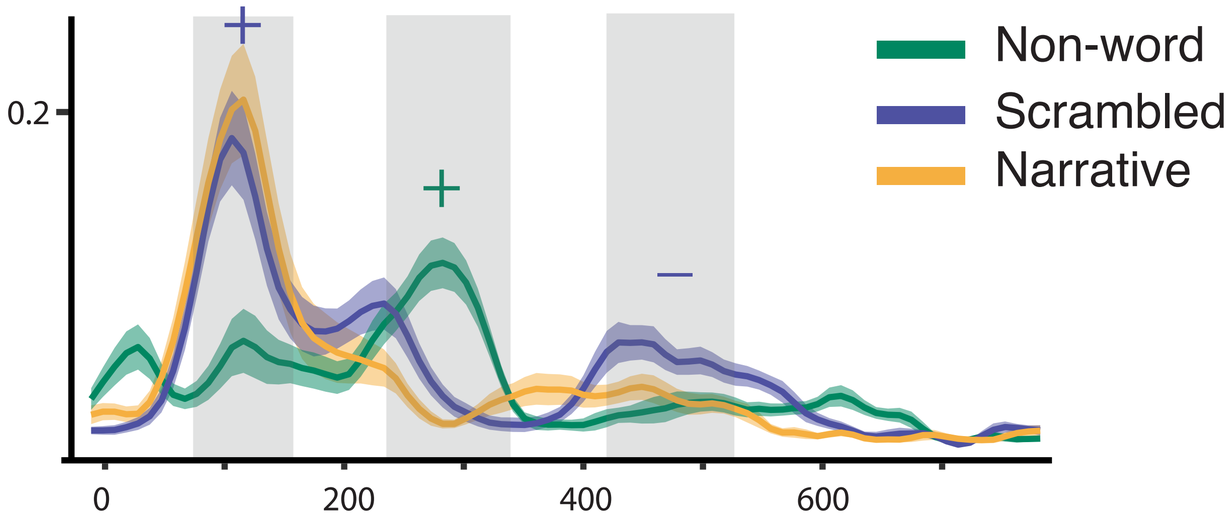
350 ms: additional further processing

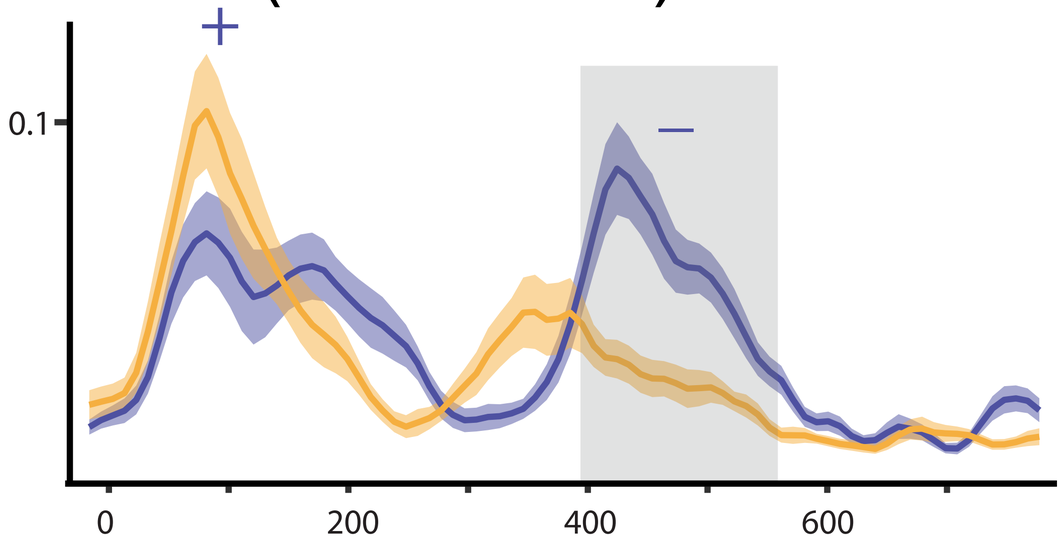
Word-based TRF Results

word onset



- Scrambled ≈ narrative for rapid processing
- Scrambled words > narrative at ~450 ms
- words: Left hemi > Right (non-words: L ≈ R)

surprisal (no context)

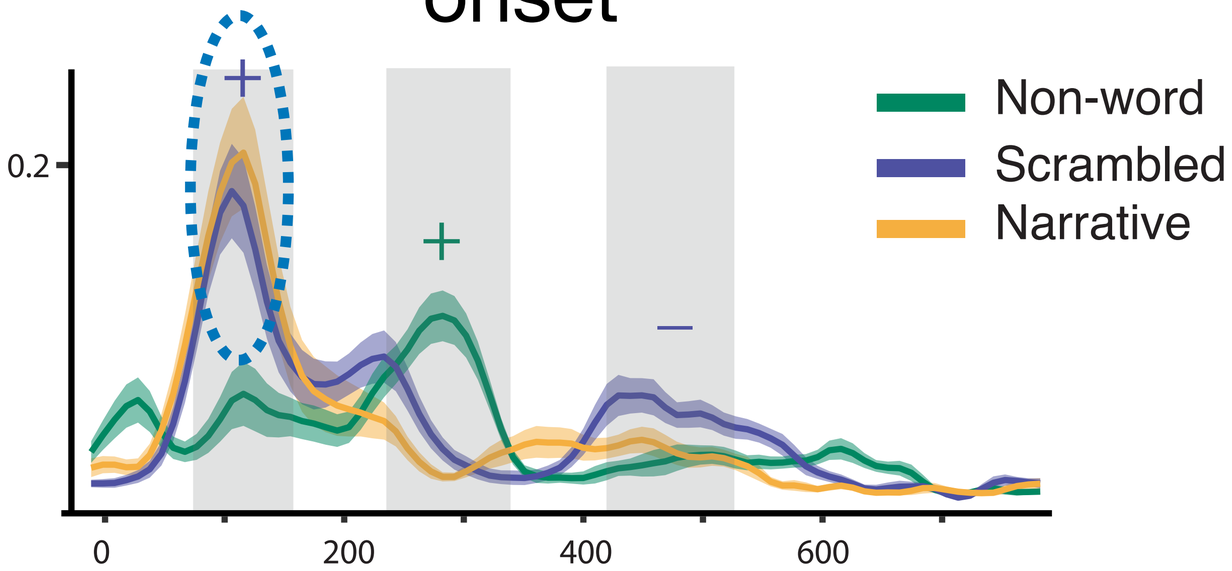


- N400 like response
- Reduction in surprisal when context
- Left hemi > Right hemi
- Right hemisphere: Scrambled ≈ Narrative

left hemisphere shown
(right much weaker except for non-word onset)

Word-based TRF Results

word onset



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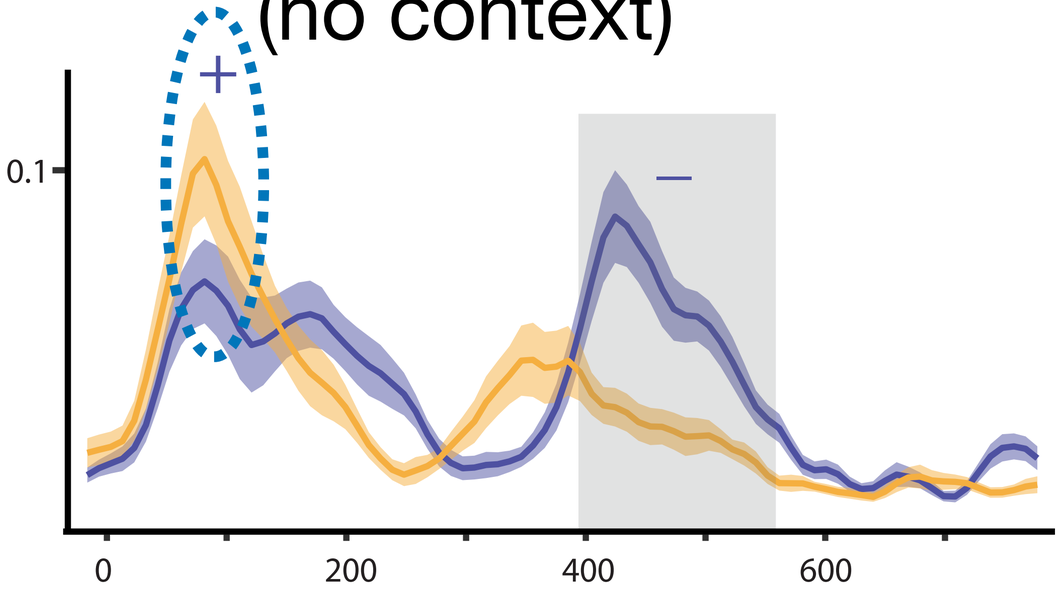

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100 ms: simple word processing

left hemisphere shown
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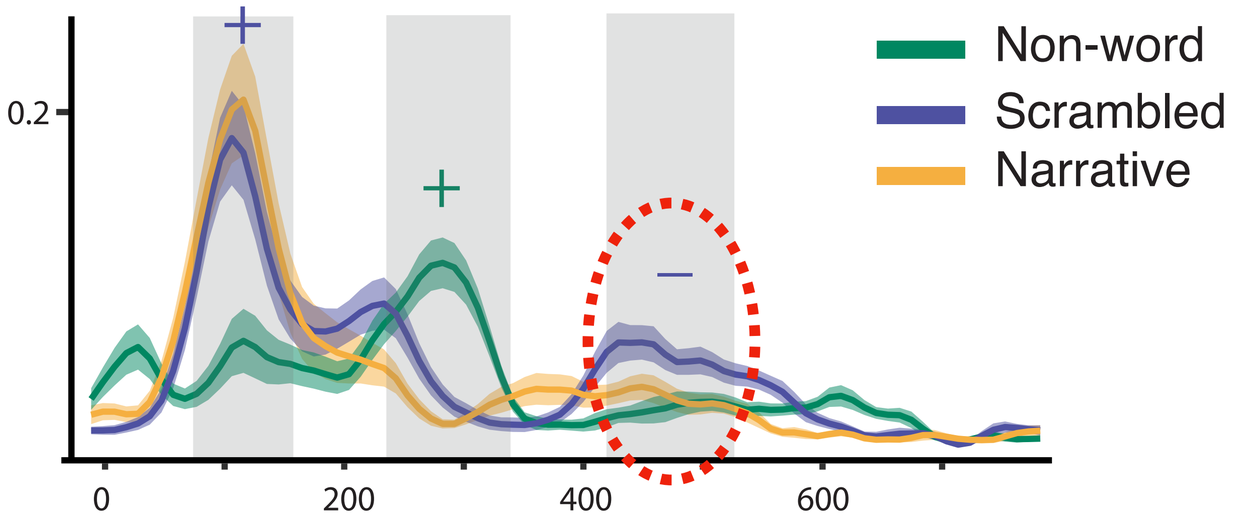
Word-based TRF Results

word onset

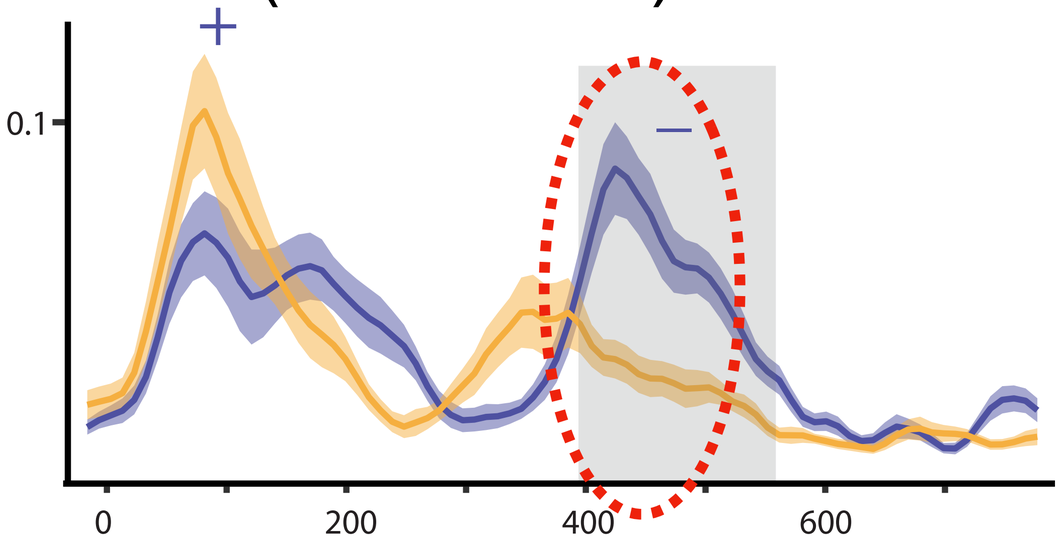


- Scrambled ≈ narrative for rapid processing
- Scrambled words > narrative at ~450 ms
- words: Left hemi > Right (non-words: L ≈ R)

100 ms: simple word processing

450 ms: “error” correction processing

surprisal (no context)



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- Right hemisphere: Scrambled ≈ Narrative

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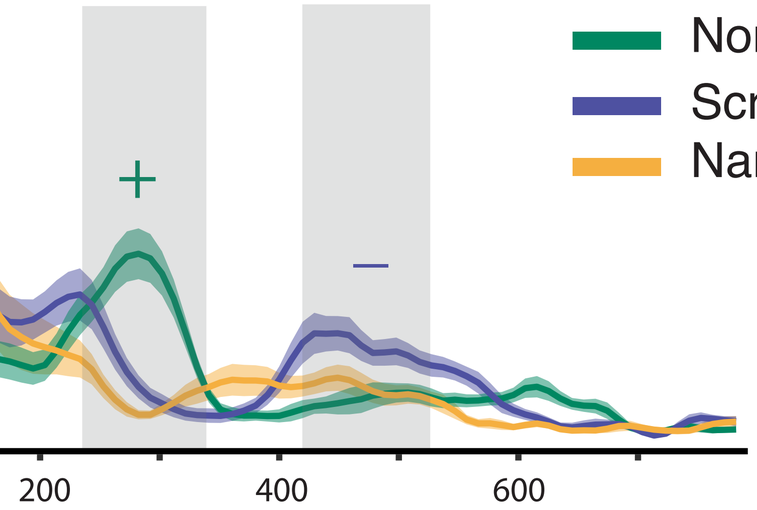
Word-based TRF Results

word onset



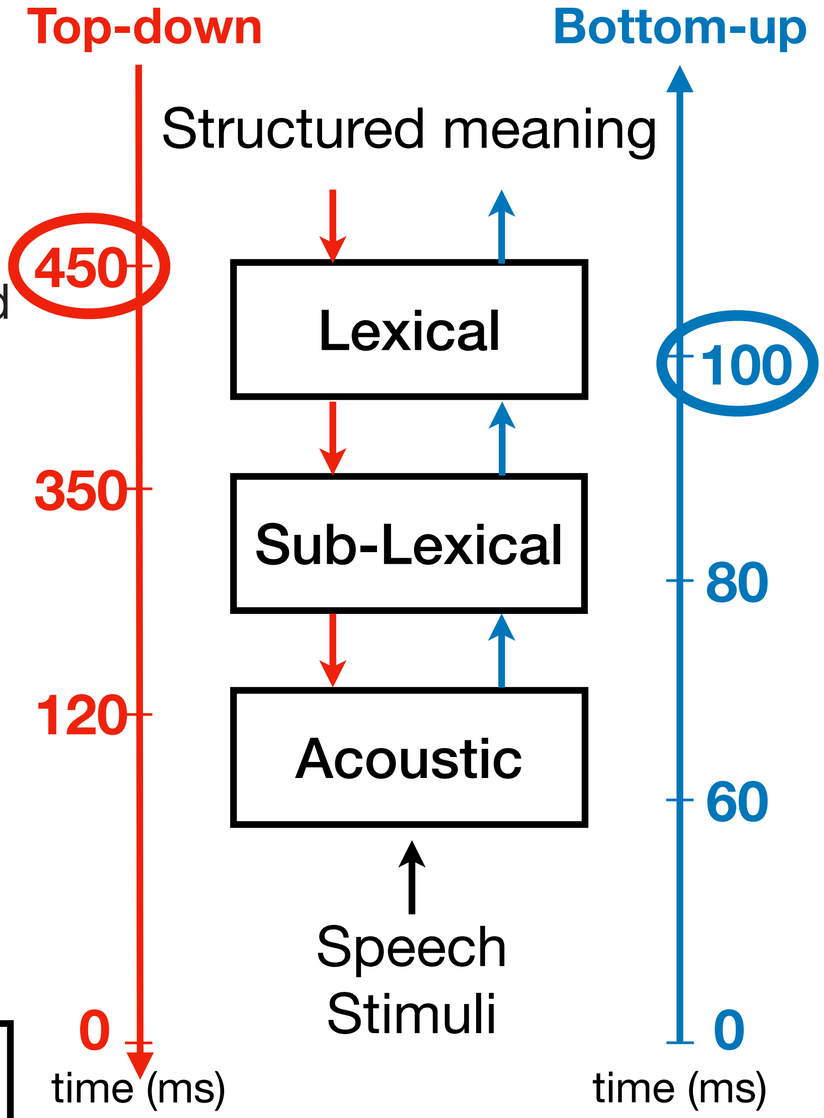
ed ≈ narrative for rapid processing

ed words > narrative at ~450 ms

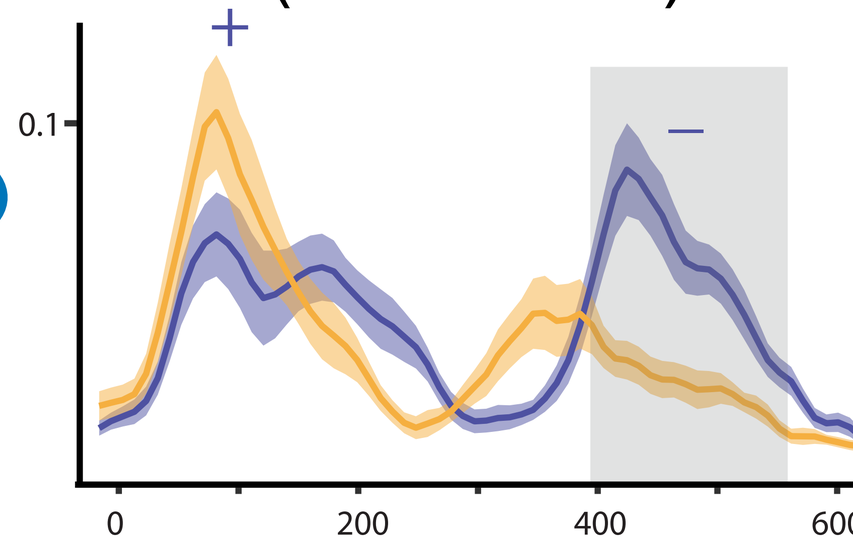
eft hemi > Right (non-words: L ≈ R)

simple word processing

ror" correction processing



surprisal (no context)



- N400 like response
- Reduction in surprisal when c
- Left hemi > Right hemi
- Right hemisphere: Scrambled

left hemisphere shown
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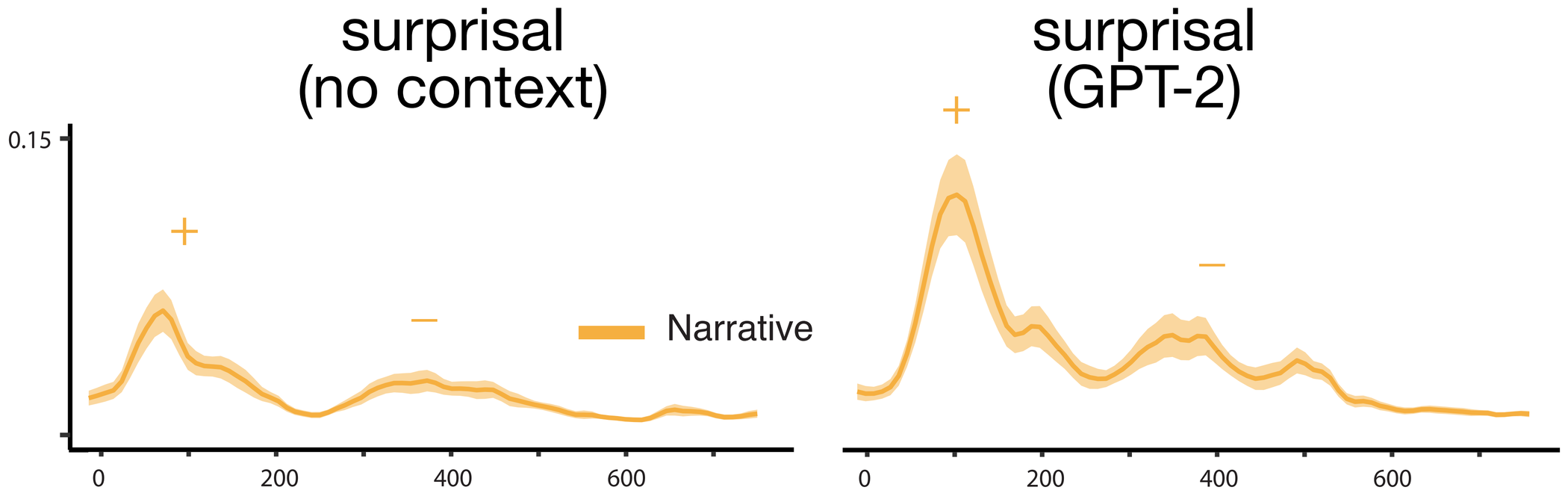
Contextual Word Surprisal Results

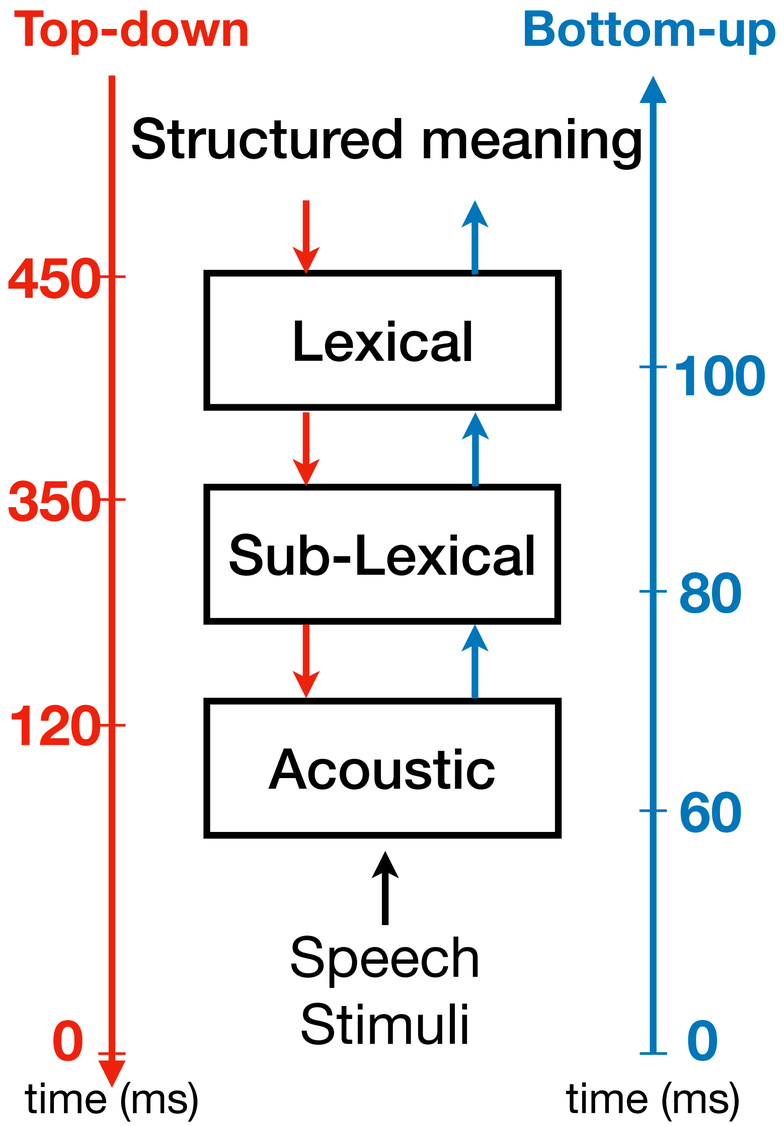


- When context helps, context-based surprisal is better tracked than raw surprisal
- N400 like response in both predictors

left hemisphere shown
(right much weaker)

Neural Speech Processing Progression

- Cortical response time-locks to emergent features from acoustics to context as incremental steps in the processing of speech input occur
- Higher level processing / top-down mechanisms may affect lower level speech processing
- Linguistic features are processed when the linguistic boundaries are intelligible
- Lower-level acoustic feature responses are bilateral but right lateralized whereas, context based responses are strongly left lateralized



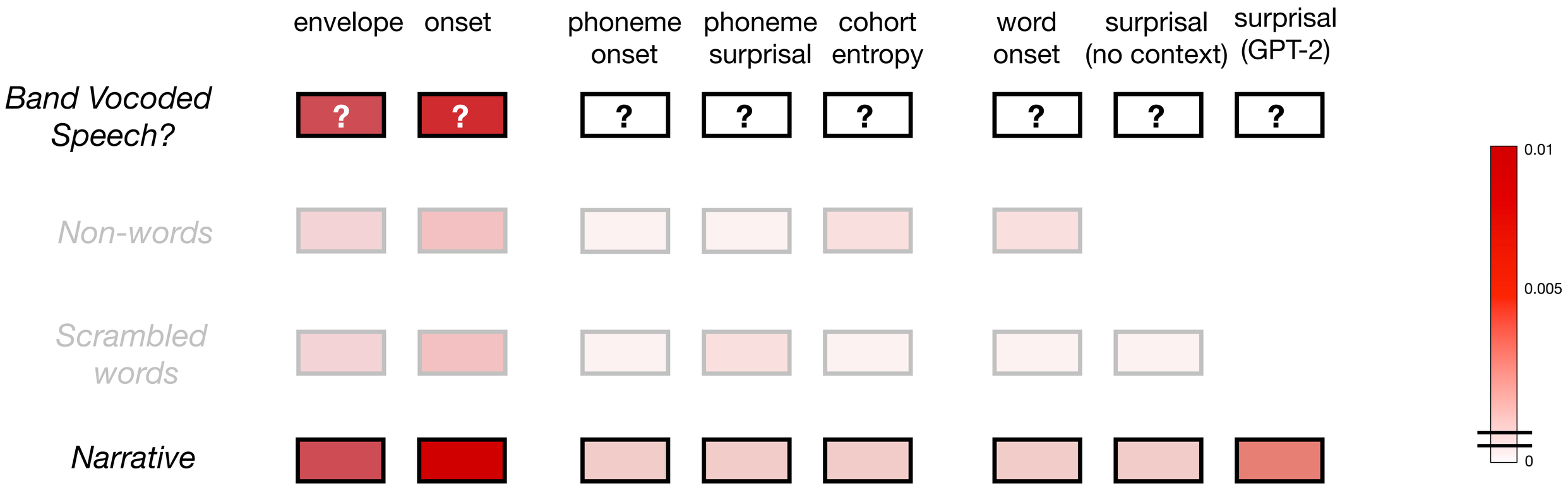
Karunathilake et al. *in preparation*

Outline

- Introduction—Cortical representations of continuous speech
- *Early & fast* cortical representation of continuous speech
- Cortical representations of speech *meaning*
- *Progression* of representations of continuous speech through cortex (bottom-up and top-down)
- Objective measures of speech *intelligibility*
- *Directional functional connectivity* during difficult speech listening

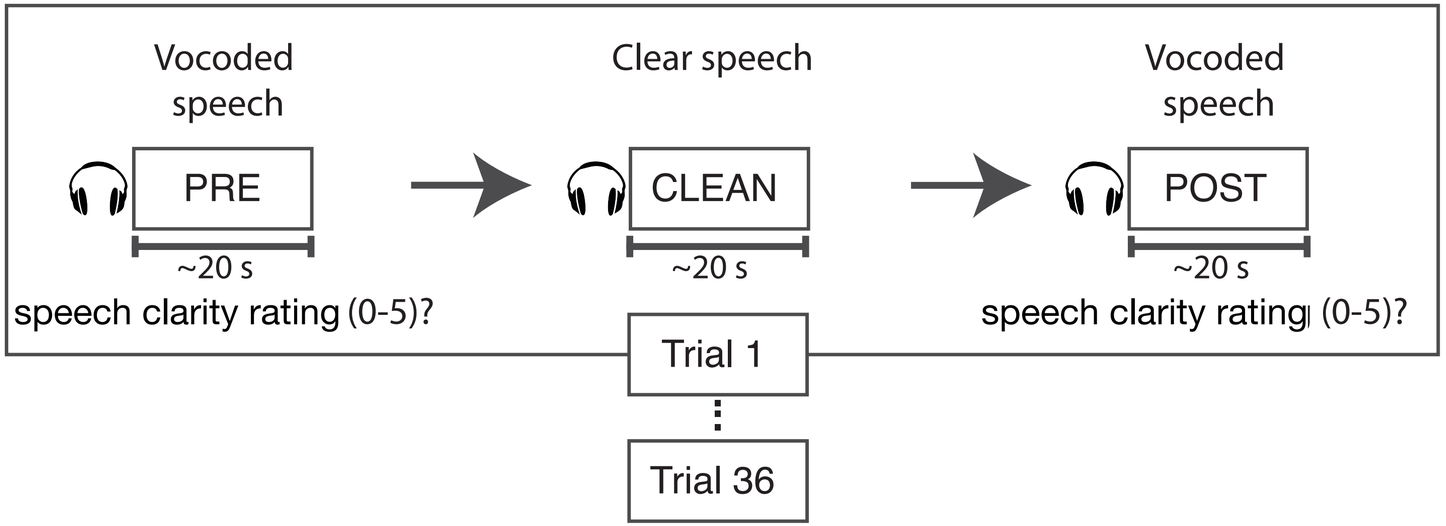
Previous Neural Prediction Results

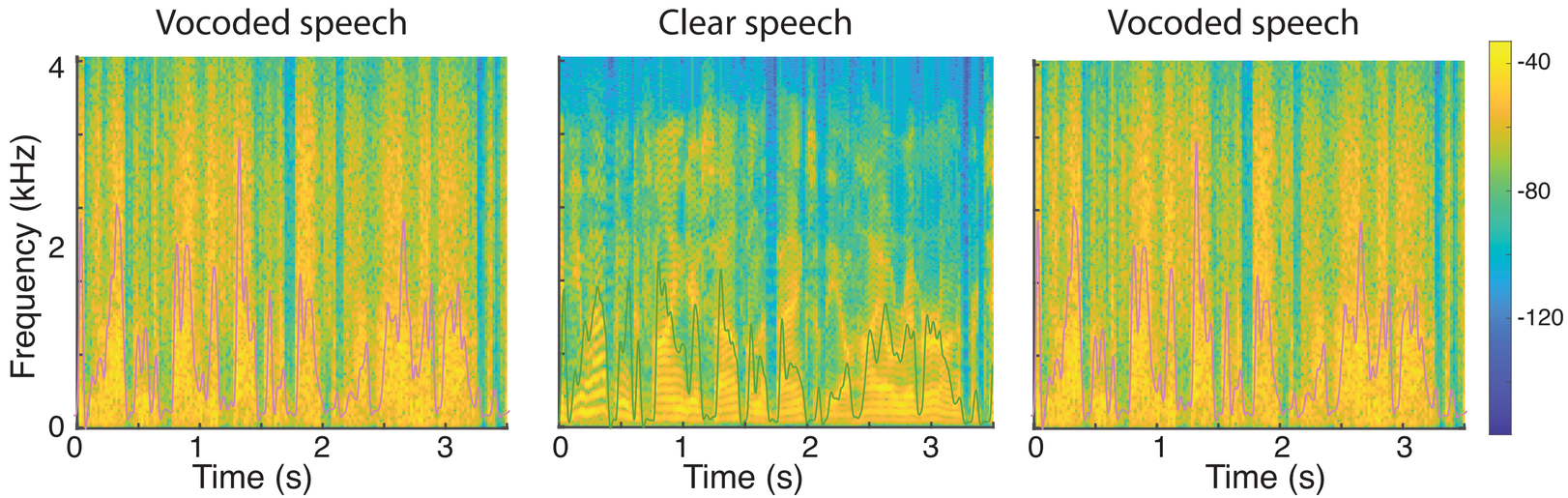
Possible Neural Prediction Results



Intelligibility Experimental Design

- Manipulate intelligibility but keep acoustics unchanged
  - Speech acoustics: three-band noise-vocoded speech
  - Intelligibility manipulated via priming
- Hypothesized intelligibility measure(s)
  - word boundaries





Karunathilake et al. (2023) *Neural Tracking Measures of Speech Intelligibility*…, bioRxiv

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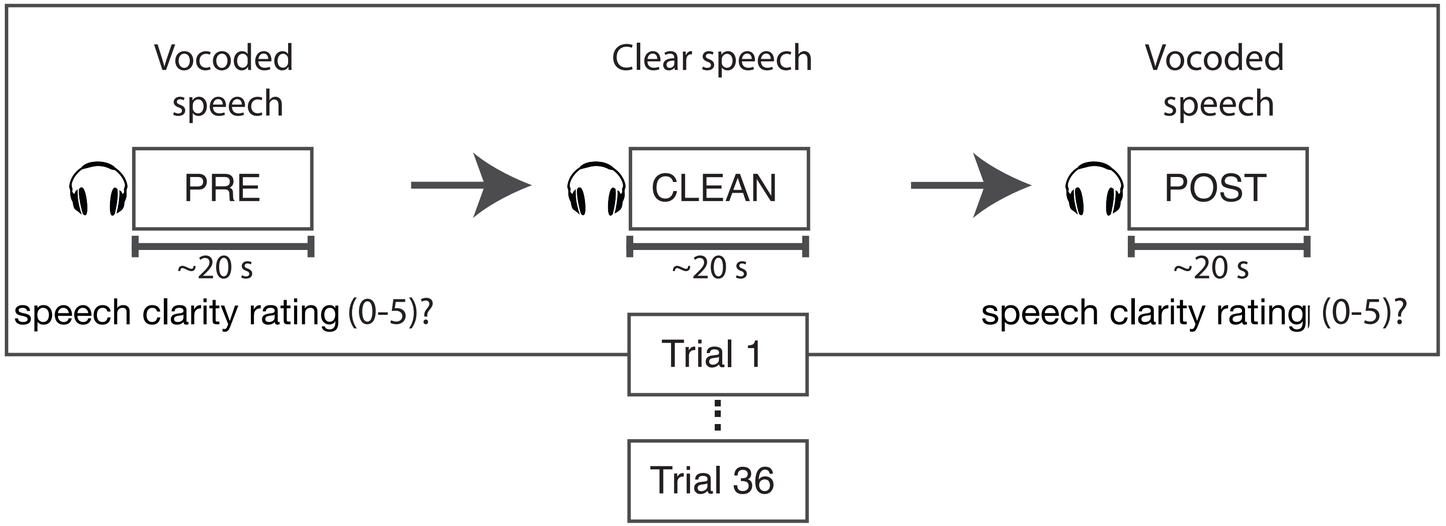

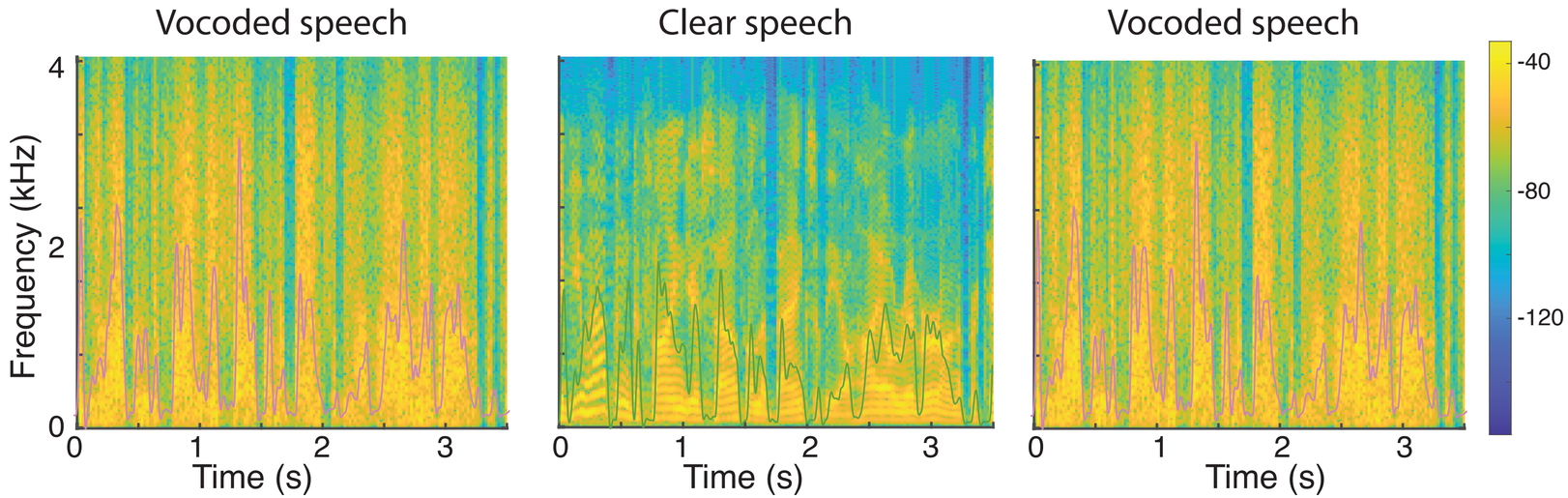

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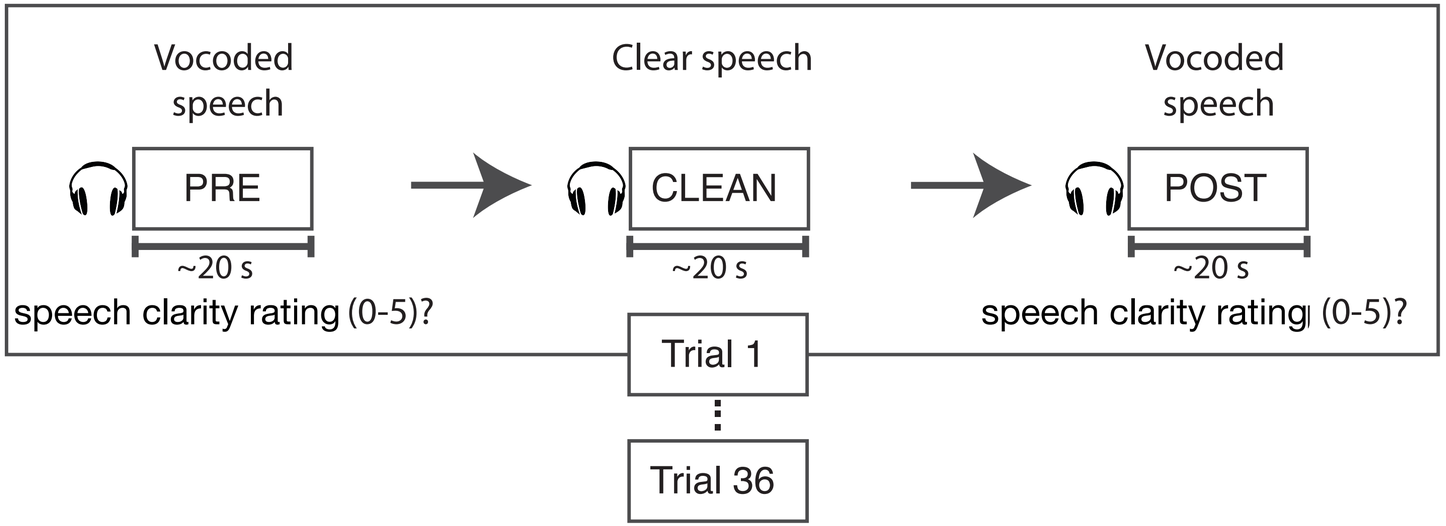

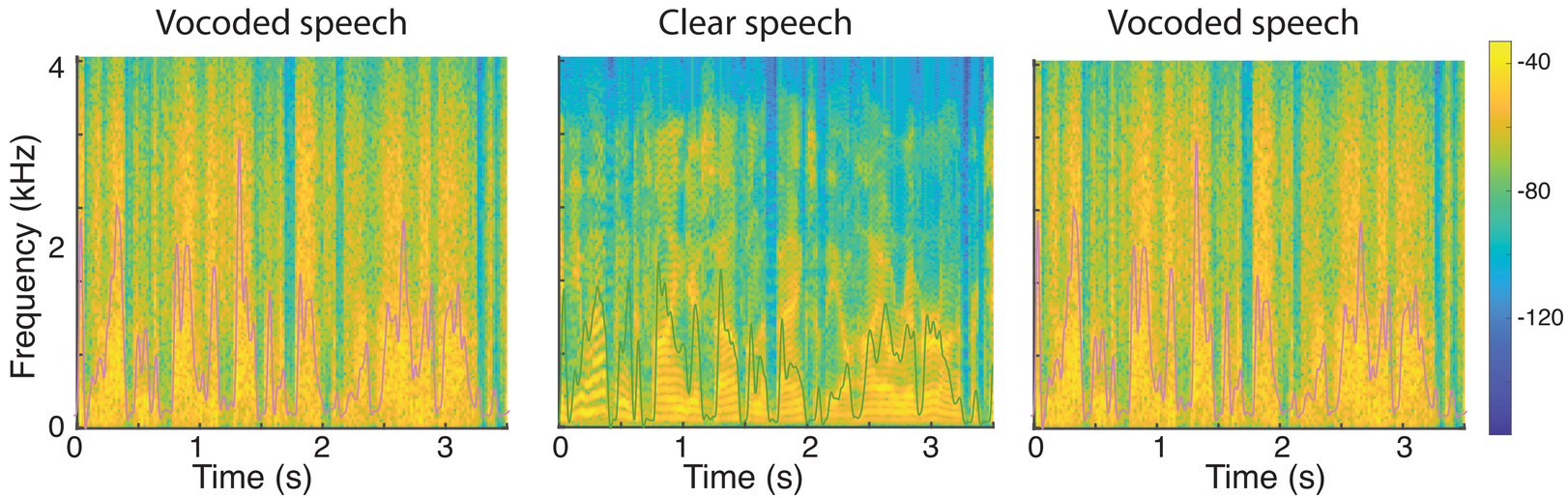

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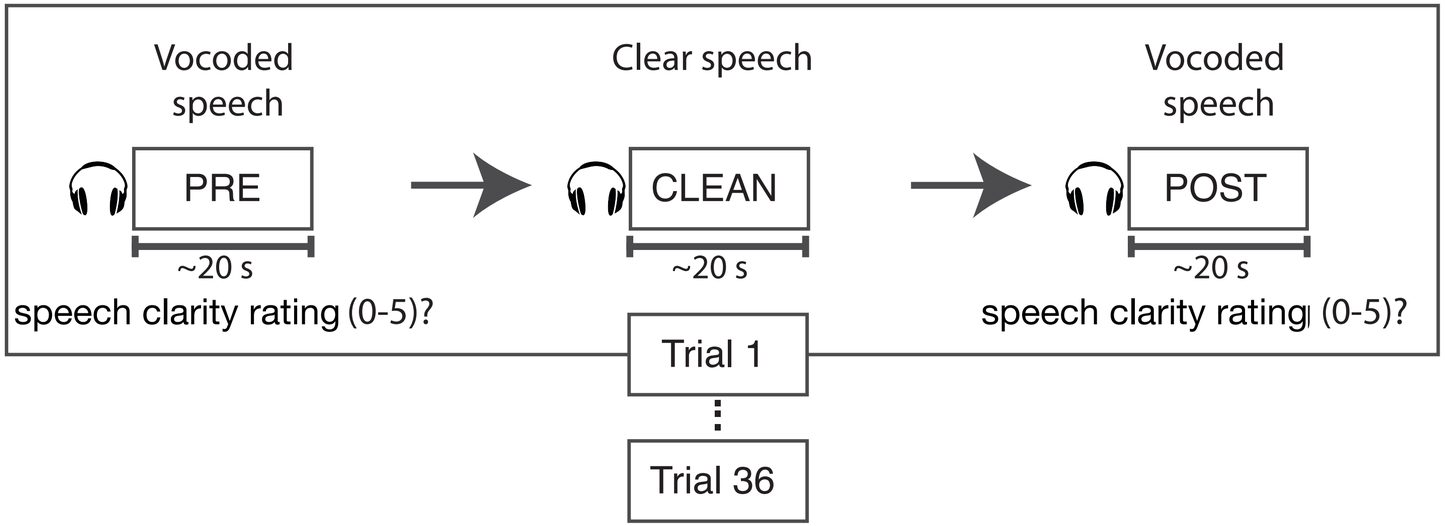

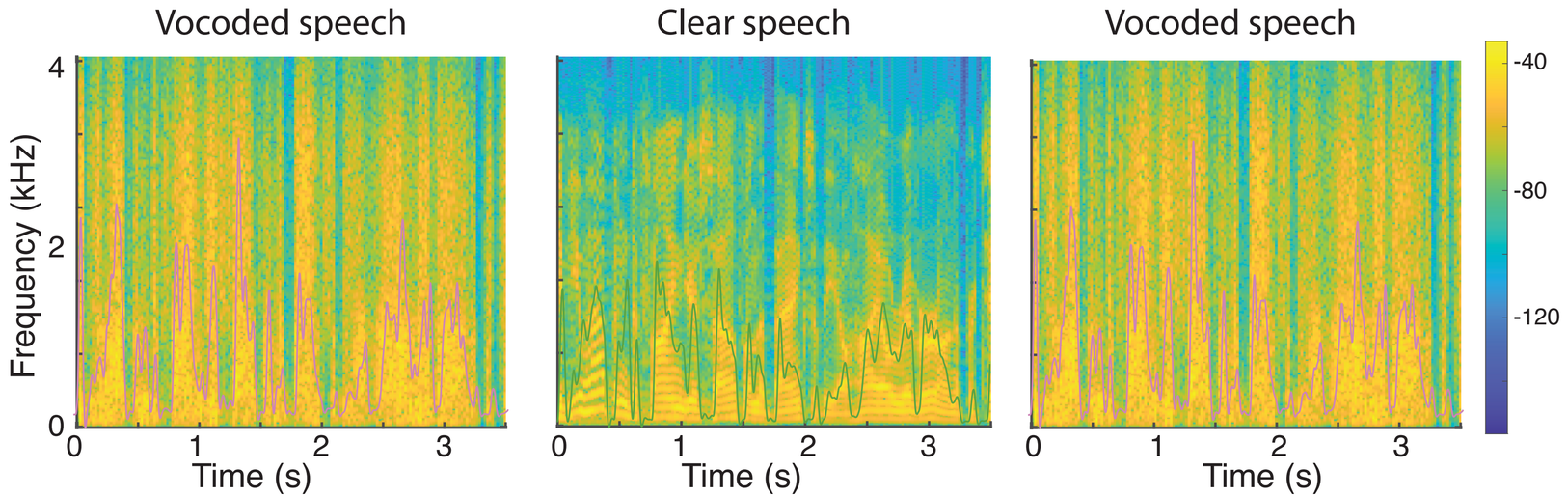

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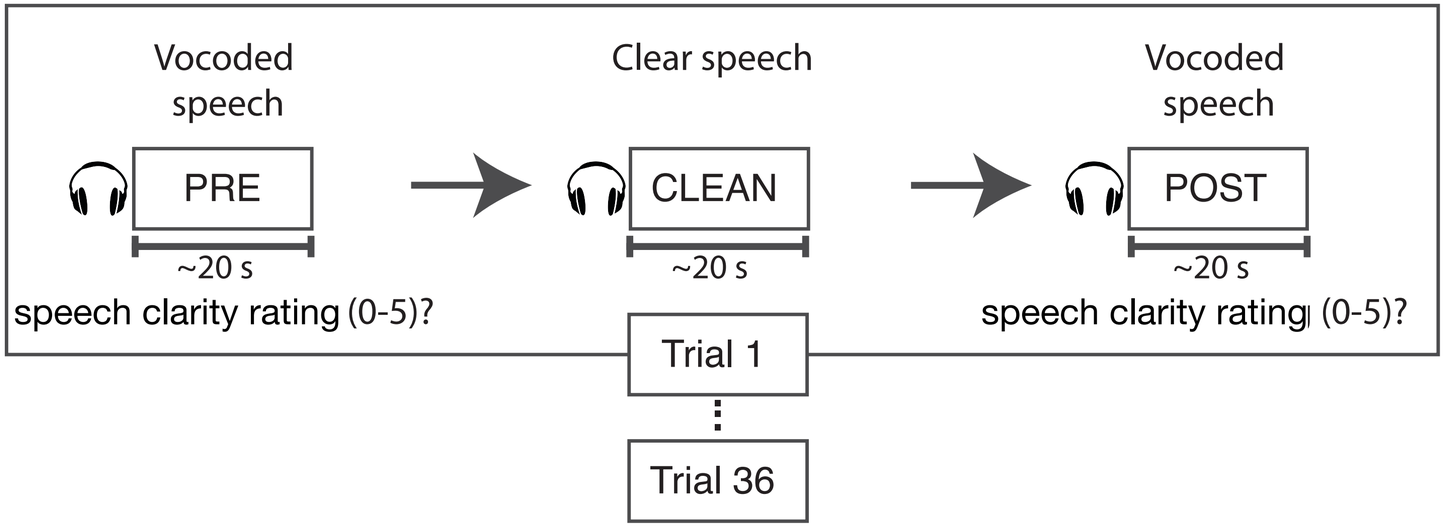

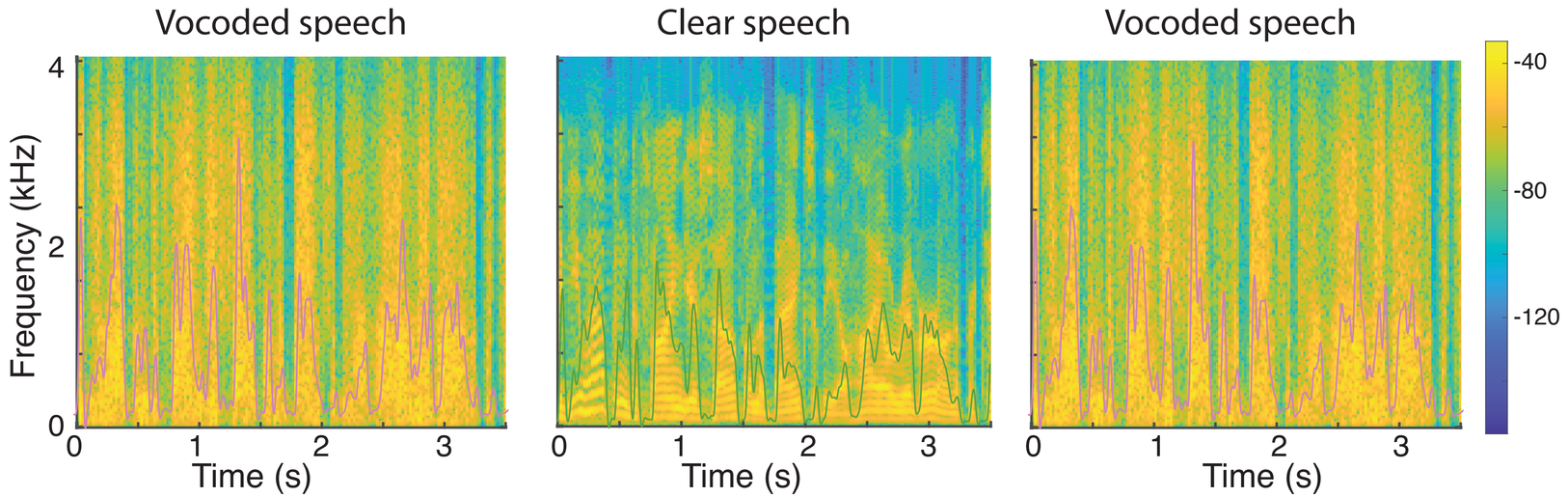

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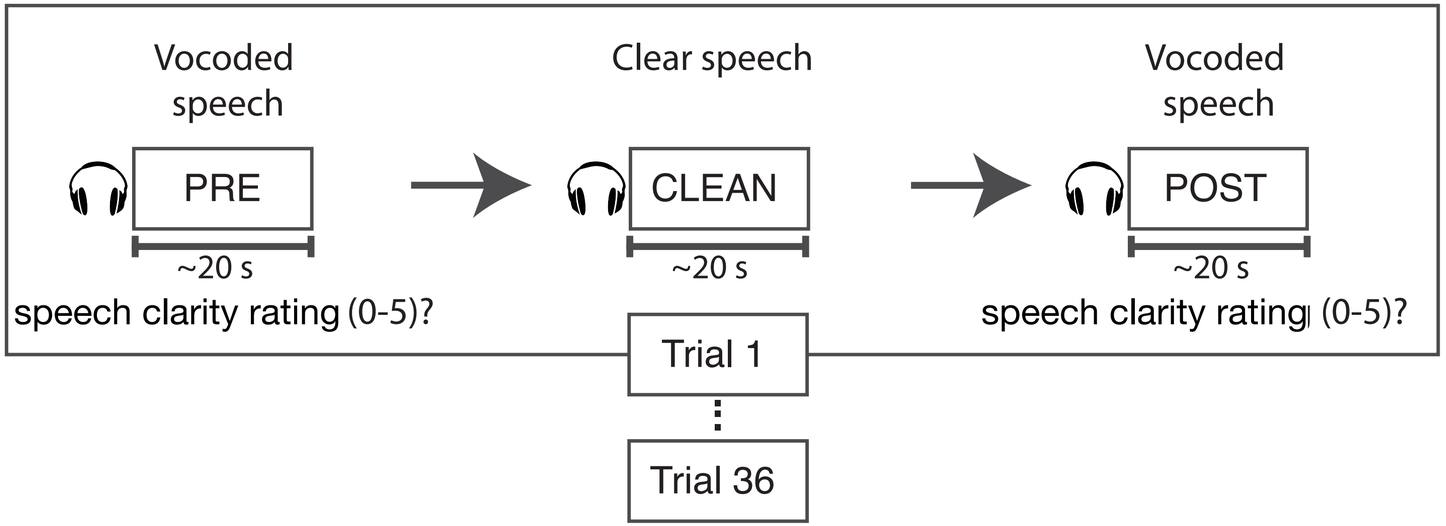

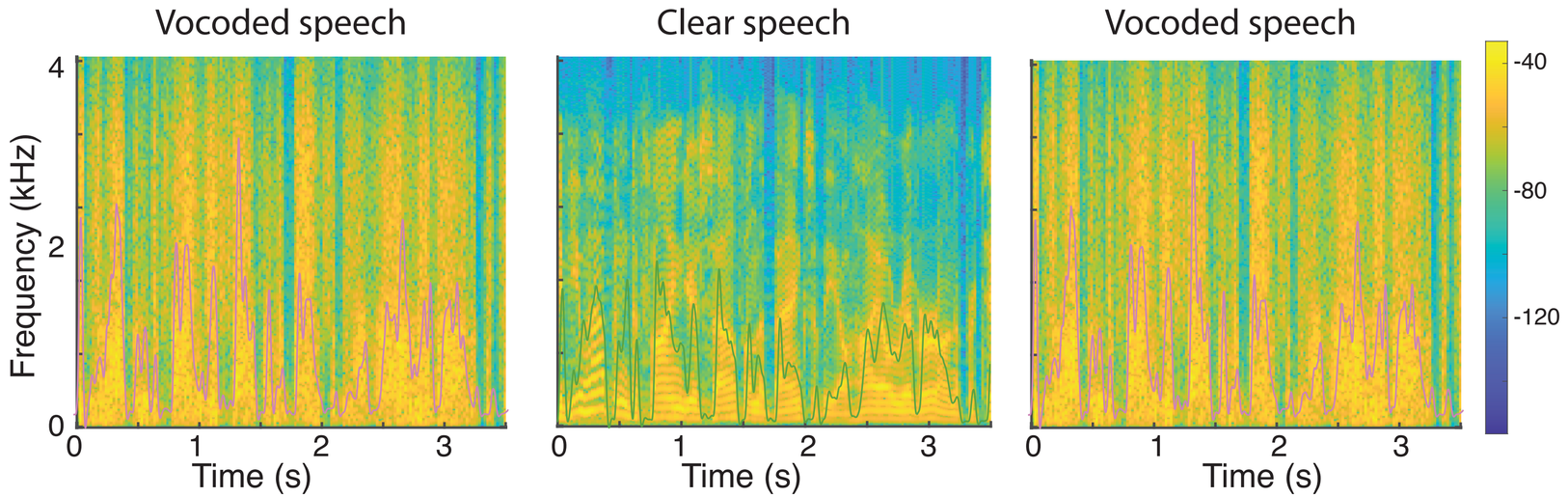

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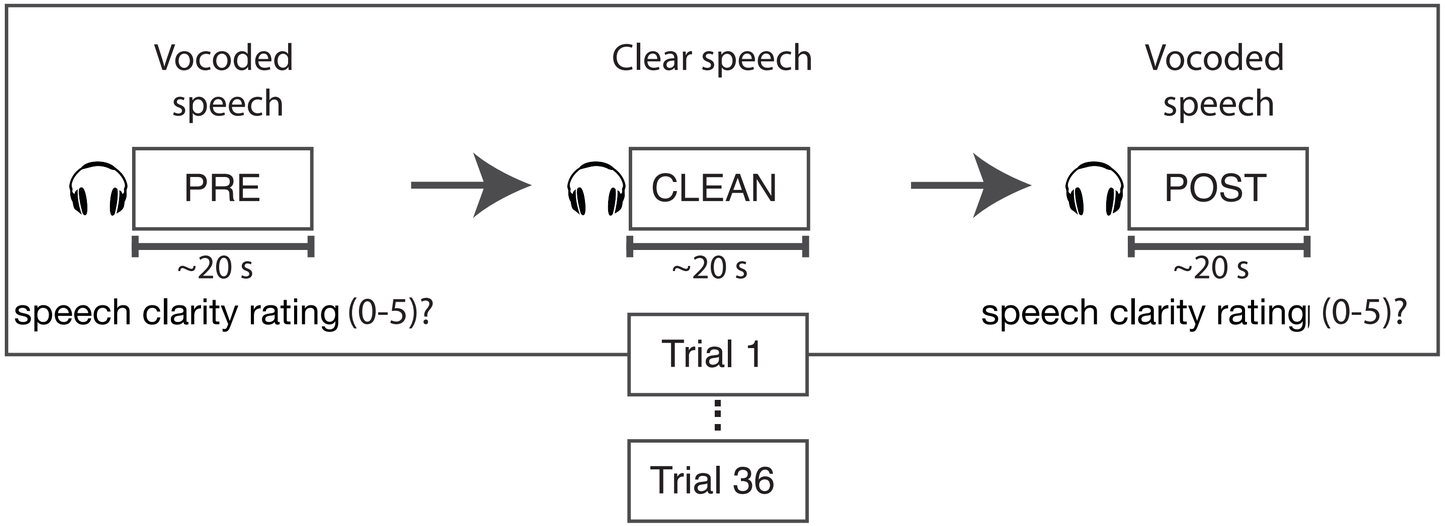

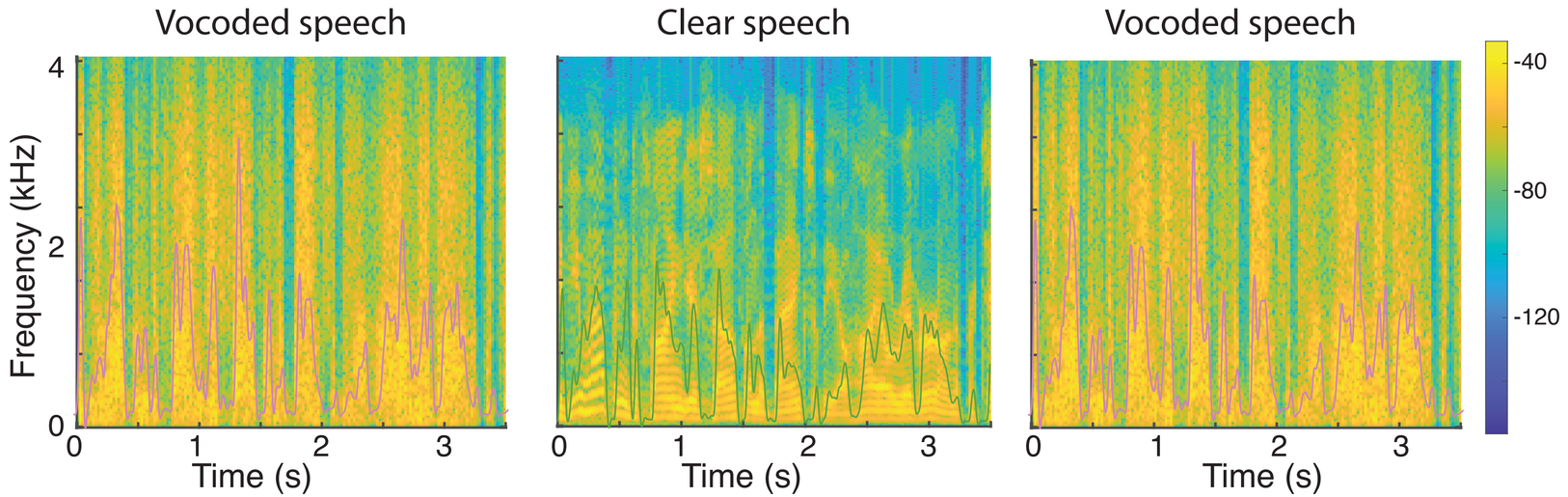

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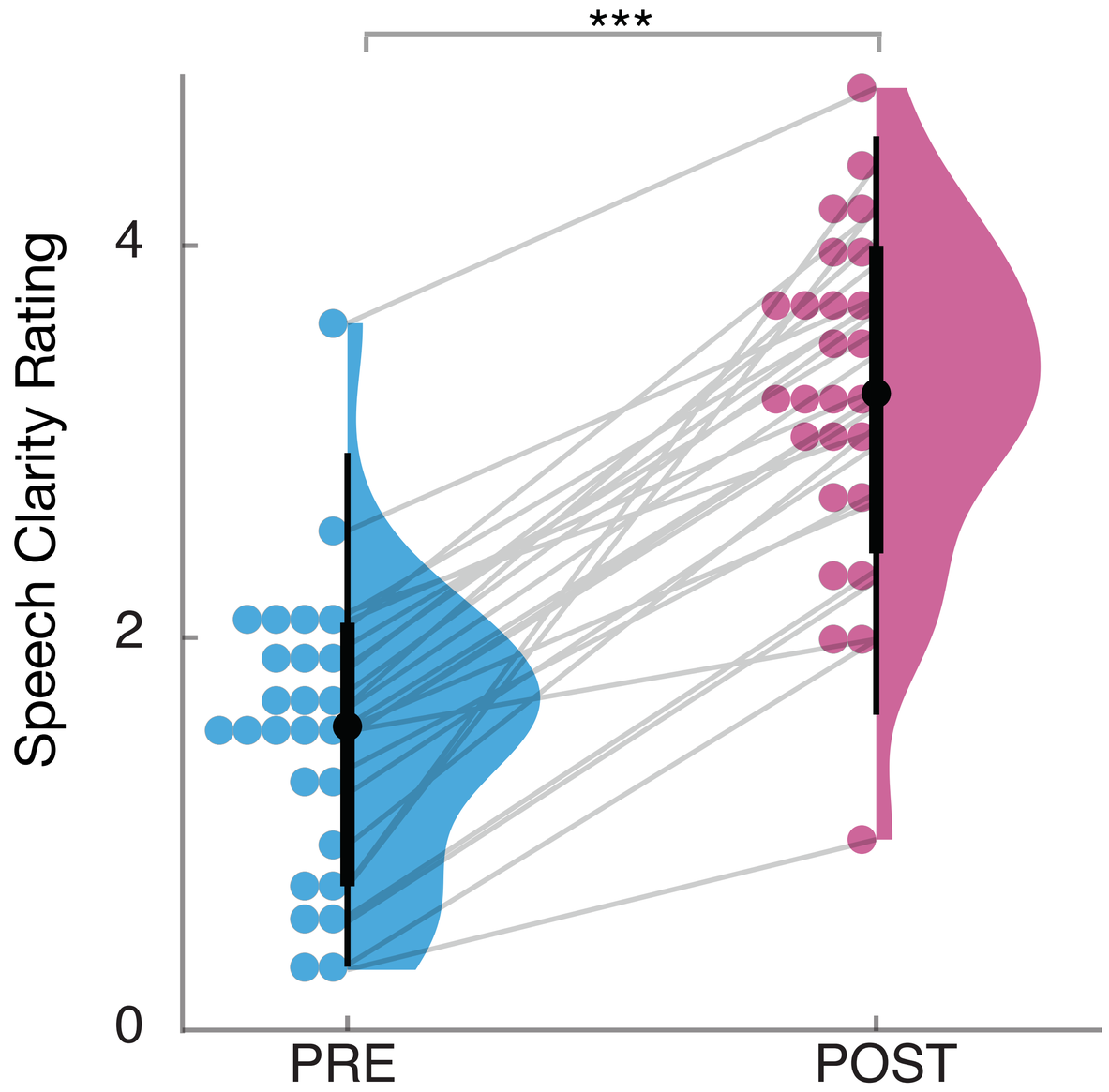
Intelligibility Behavioral Results

Speech Clarity **increases**
from PRE condition
to POST condition



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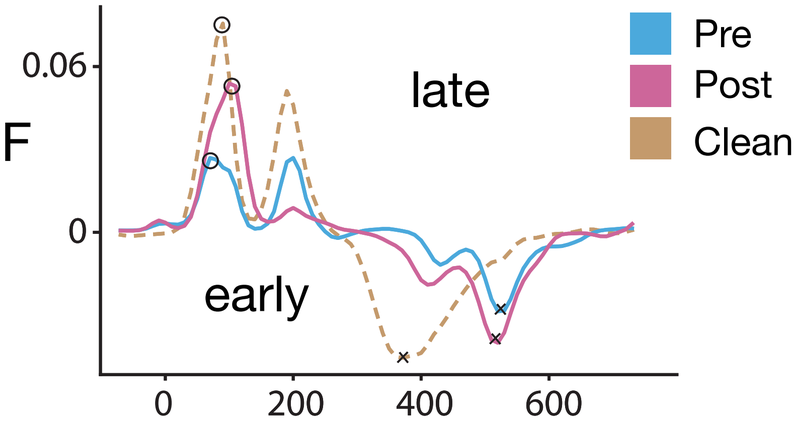
(b)

Intelligibility Neural Results

- Word onset TRF shows both early (+) and late (-) processing stages

Word onset TRF

single subject



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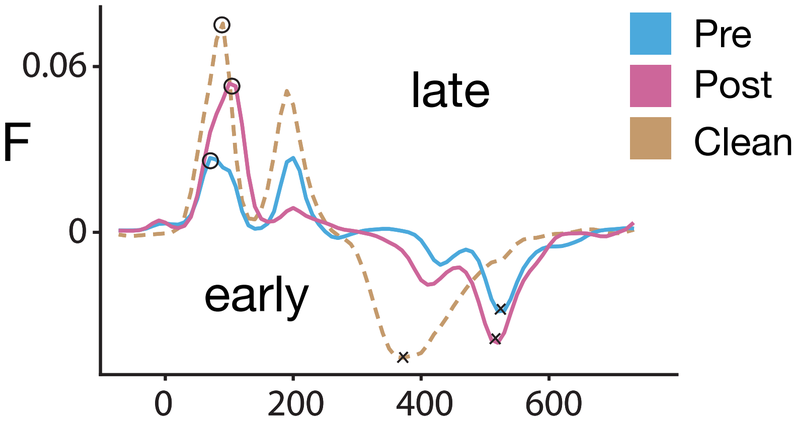
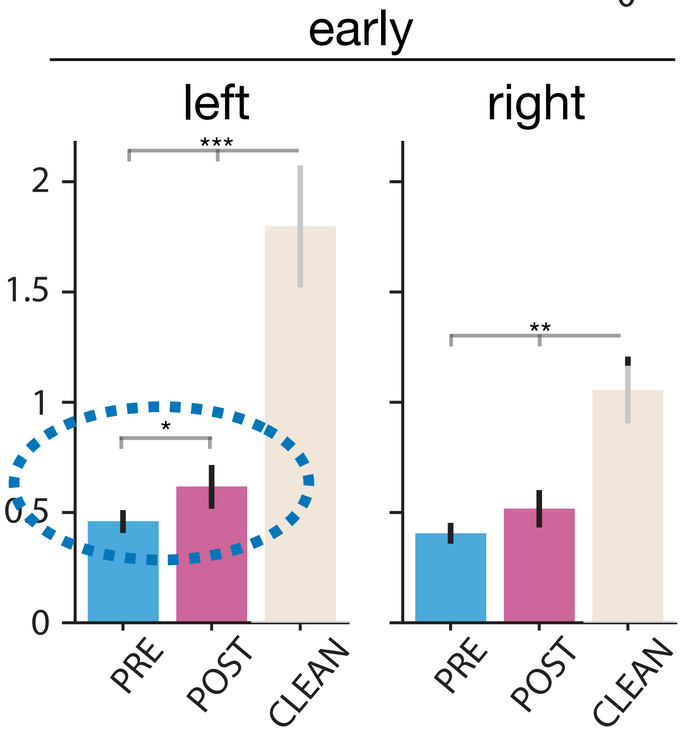
Intelligibility Neural Results

- Word onset TRF shows both early (+) and late (-) processing stages
- Response increases Pre→Post
  - Only in left hemisphere

Word onset TRF

single subject





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- Word onset TRF shows both early (+) and late (-) processing stages
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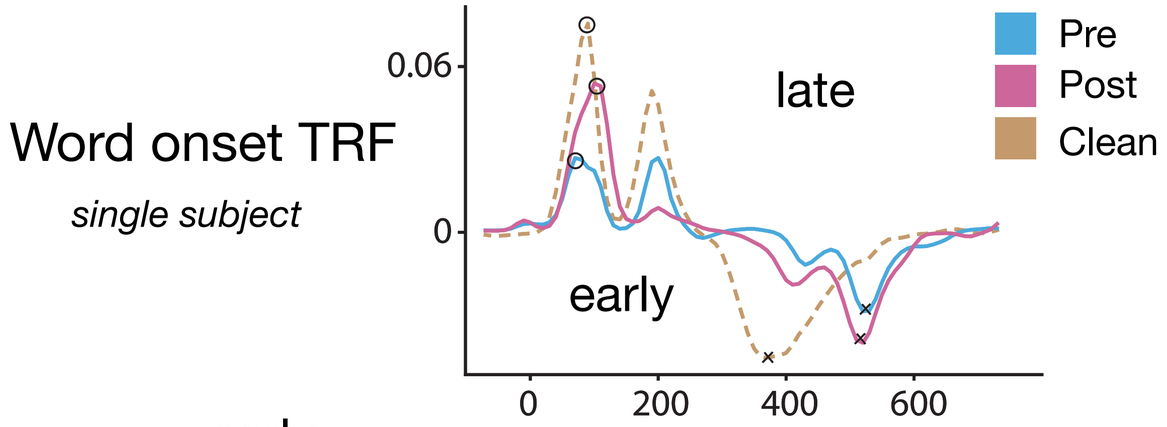
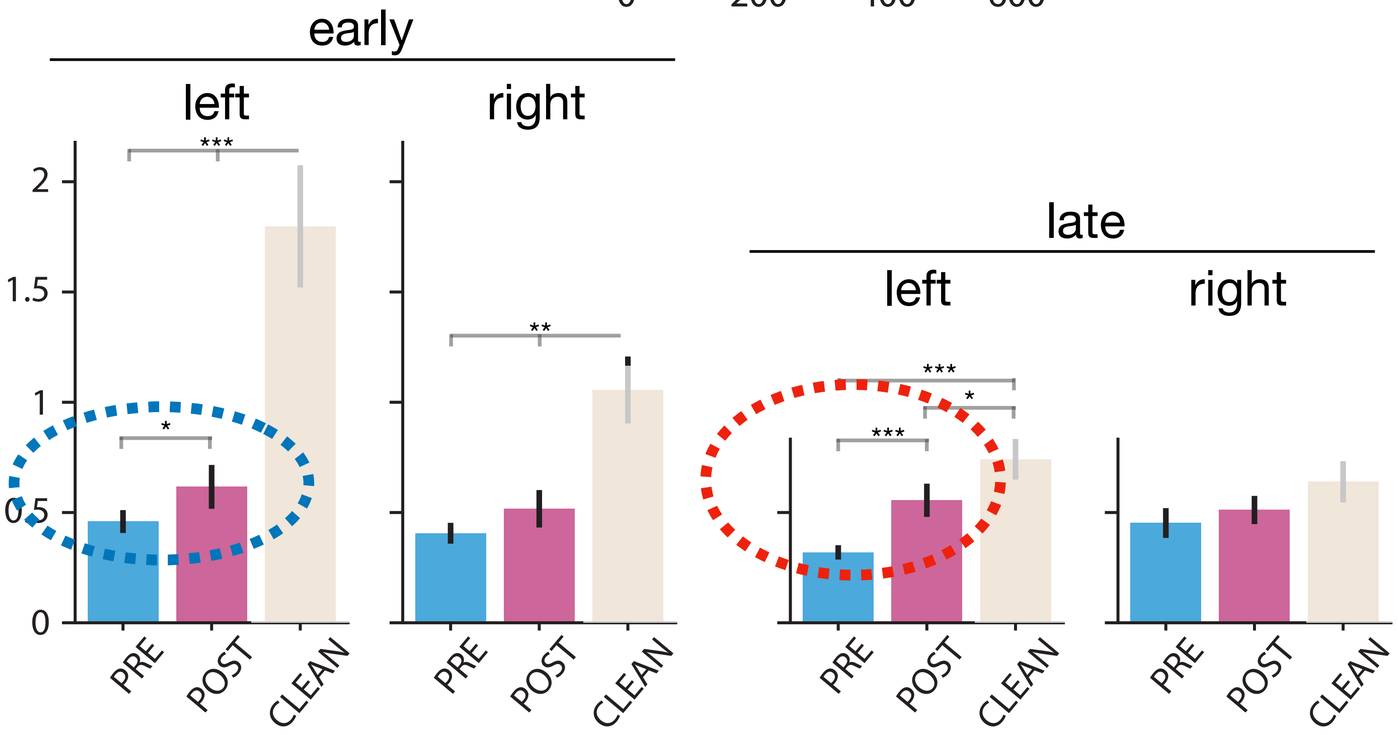
  - Late processing stage shows larger change than early





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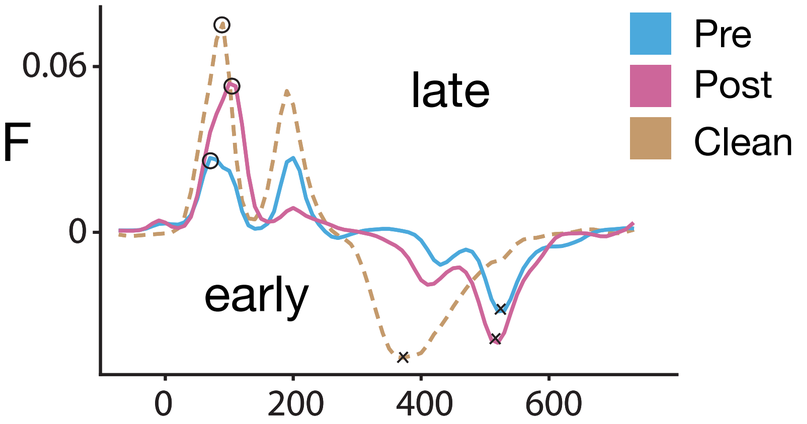
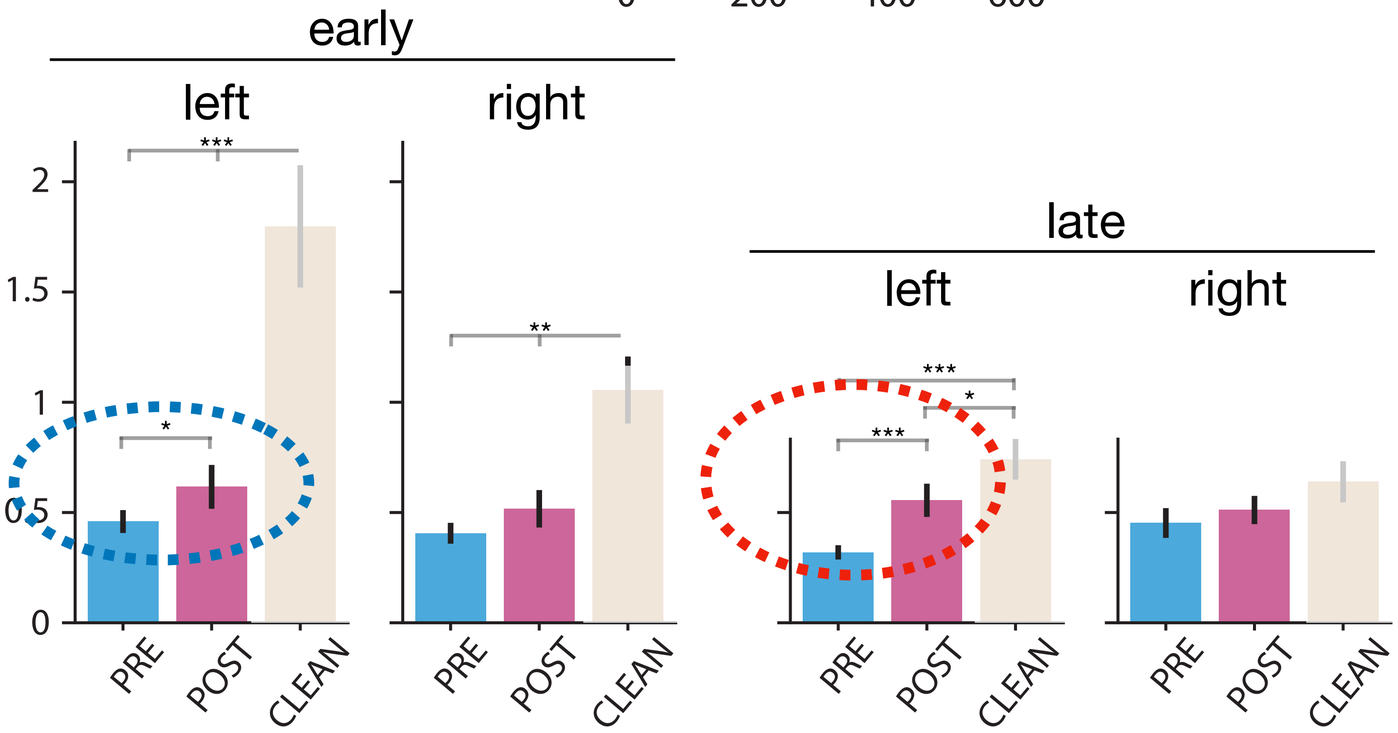
Intelligibility Neural Results

- Word onset TRF shows both early (+) and late (-) processing stages
- Response increases Pre→Post
  - Only in left hemisphere
  - Late processing stage shows larger change than early
- Response to Word Onset: *Objective measure of intelligibility*
  - Acoustic responses: no change
  - Response to Word Surprisal: *Additional intelligibility measure*

Word onset TRF

single subject





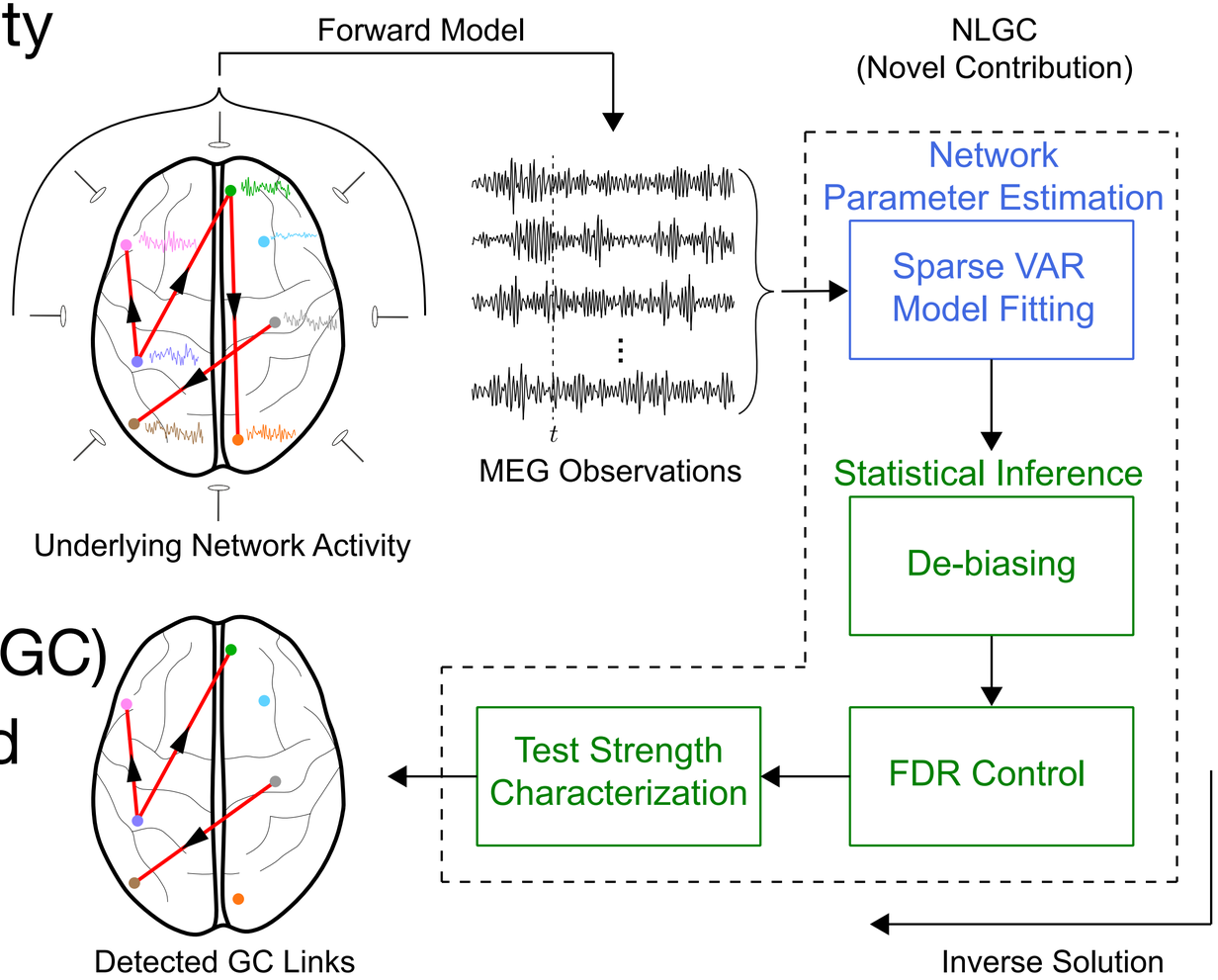
Karunathilake et al. (2023) *Neural Tracking Measures of Speech Intelligibility*…, bioRxiv

Outline

- Introduction—Cortical representations of continuous speech
- *Early & fast* cortical representation of continuous speech
- Cortical representations of speech *meaning*
- *Progression* of representations of continuous speech through cortex (bottom-up and top-down)
- Objective measures of speech *intelligibility*
- *Directional functional connectivity* during difficult speech listening

Directional Functional Connectivity

- Novel method, based on Granger Causality (if source A can predict source B)
  - Directional (bi-directional allowed)
  - Localizes neural sources & GC link strengths simultaneously
  - source currents: latent sparse vector autoregressive (VAR) processes
- Network Localized Granger Causality (NLGC)
  - source spread & other biases minimized
  - robust against source model mismatch
  - parametrized by false discovery rate
  - intrinsically statistically robust

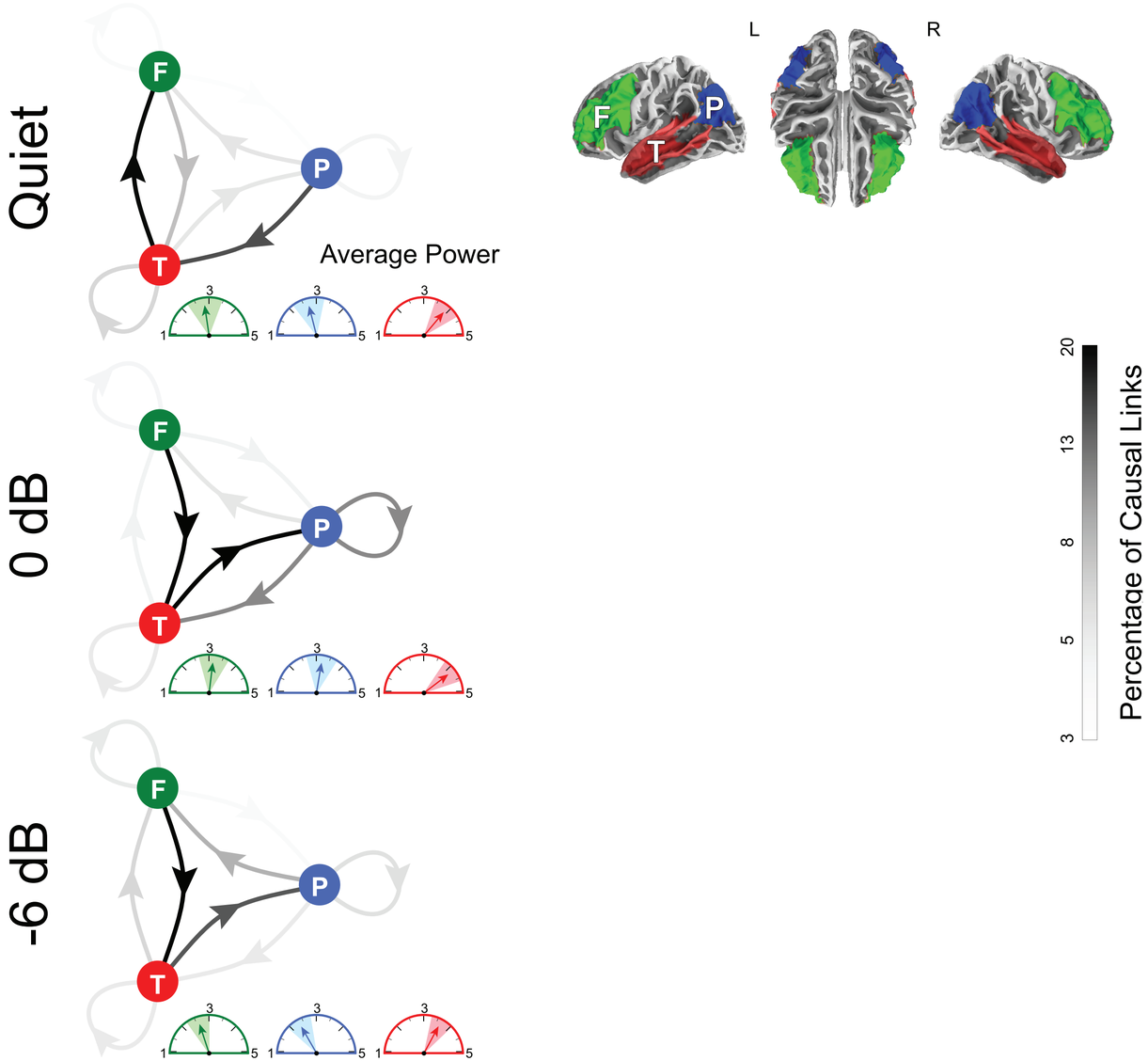


Soleimani et al. (2022) *NLGC: Network Localized Granger Causality with Application to …*, NeuroImage

Cocktail Party Speech Results

Theta band example

- Speech in quiet connectivity: dominantly Temporal→Frontal and Parietal→Temporal
- Cocktail Party listening (moderate SNR): Temporal-Frontal switches direction; Parietal-Temporal now bi-directional
- Cocktail Party listening (poor SNR): Temporal←Frontal remains; Parietal→Temporal dominant

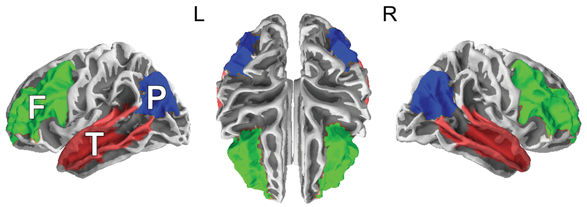


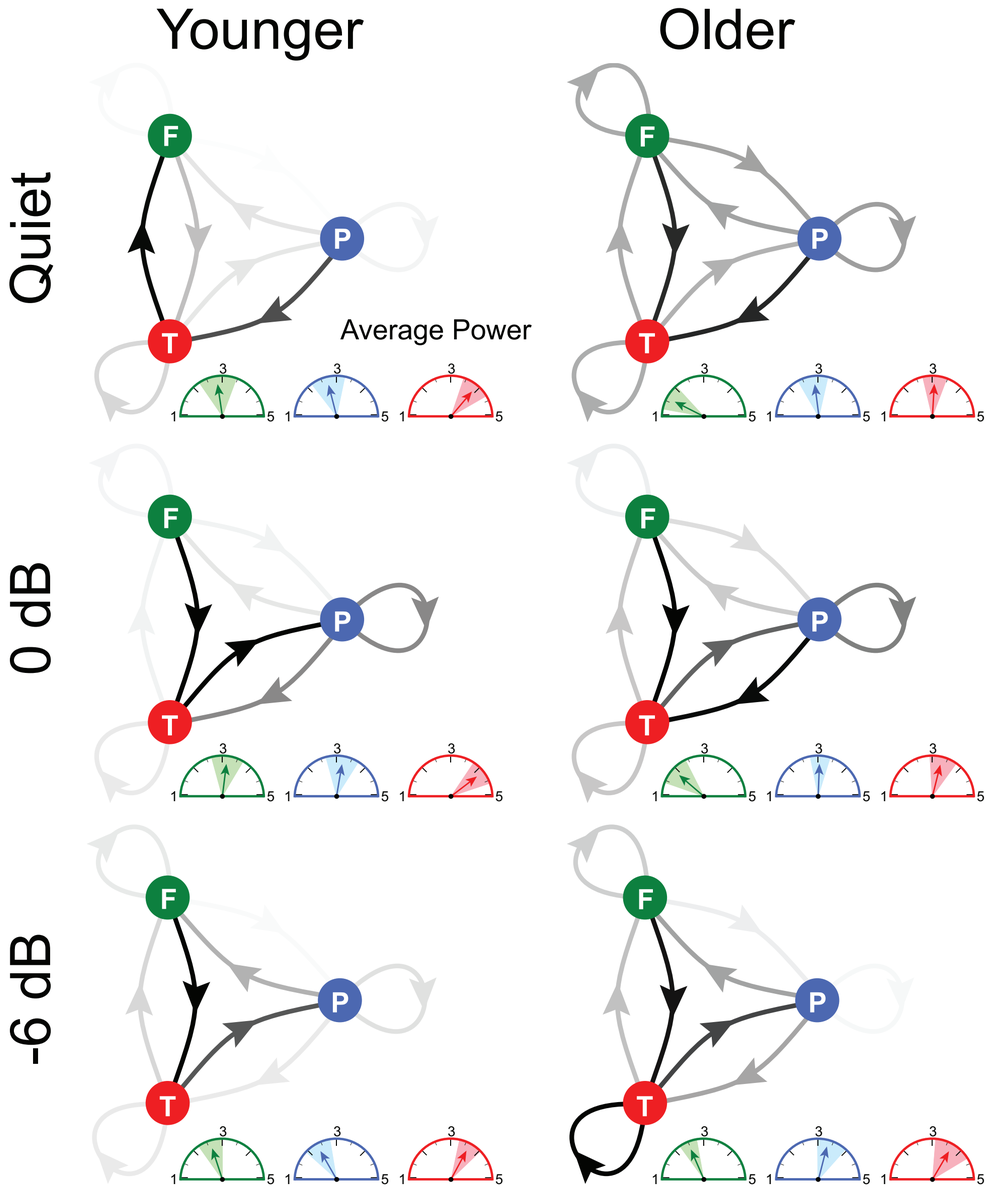
Soleimani et al. (2023) … *Cortical Directional Connectivity during Difficult Listening*… bioRxiv

Cocktail Party Speech Results

Older Listeners exhibit strongly different connectivity

- Older speech in quiet connectivity: similar to Younger cocktail party listening connectivity



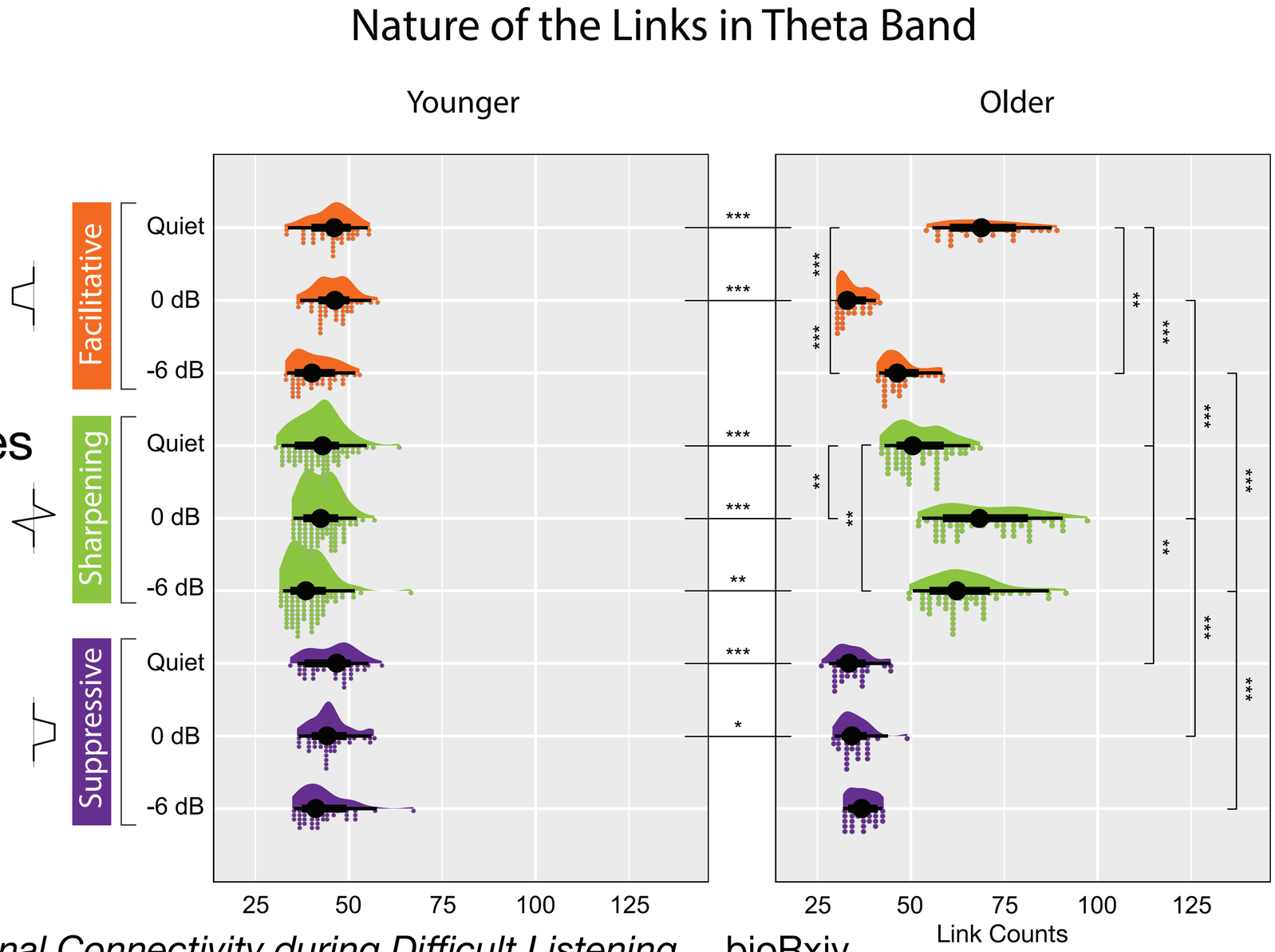


Soleimani et al. (2023) … *Cortical Directional Connectivity during Difficult Listening*… bioRxiv

Cocktail Party Speech Results

"Excitatory/Inhibitory" balance changes with task difficulty for Older Listeners only

- VAR (IIR filter) coefficients reveal neural signal trans-formation between sources
- coefficients > 0: "Excitatory"/facilitative
- coefficients < 0: "Inhibitory"/suppressive
- mixed coefficients: sharpening filter



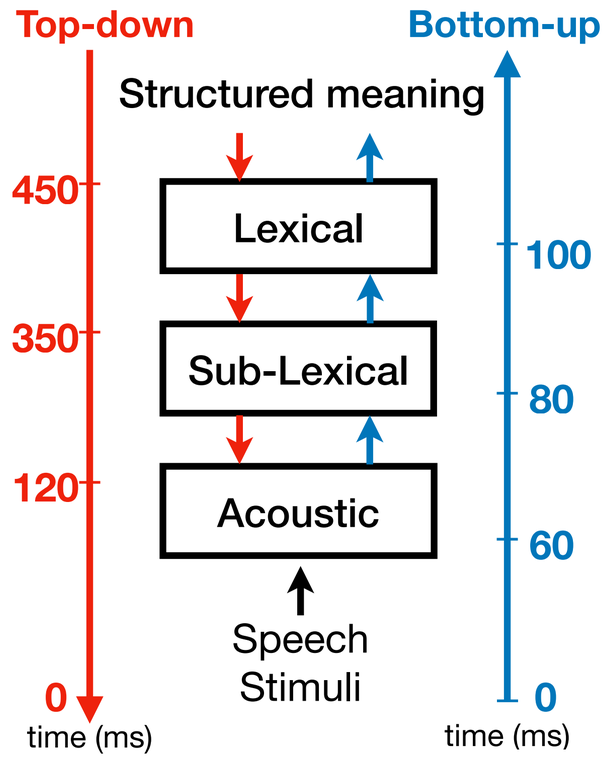
Soleimani et al. (2023) … *Cortical Directional Connectivity during Difficult Listening*… bioRxiv

Final Summary

temporal ***neural*** *patterns* ⇆

temporal patterns in ***speech acoustics***
temporal patterns in ***speech perception***
temporal patterns in ***language perception***
temporal patterns in ***understanding***

- Cortical responses time-lock to emergent features
- Higher level processing / top-down mechanisms may affect lower level
- Linguistic features processed only when linguistic boundaries intelligible
- Acoustic responses: bilateral but right lateralized; context-based responses strongly left lateralized



thank you

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