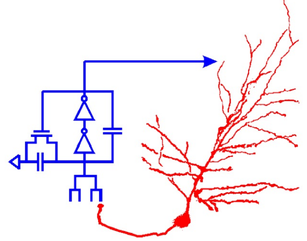

Computational
Sensorimotor
Systems Lab

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

Mastodon: @jzsimon@fediscience.org

http://www.isr.umd.edu/Labs/CSSL/simonlab

Zhejiang University, 17 Dec 2023

Acknowledgements

Current Lab Members & Affiliates

Morgan Belcher
Vrishab Commuri
Charlie Fisher
Tejas Guha
Brooke Guo
Michael Johns
Kevin Hu
Dushyanthi Karunathilake
Karl Lerud
Ciaran Stone
Craig Thorburn
Allie Vance

Current & Recent Collaborators

Samira Anderson
Behtash Babadi
Tom Francart
L. Elliot Hong
Stefanie Kuchinsky
Ellen Lau
Elisabeth Marsh
Philip Resnik
Shihab Shamma

Past Lab Members & Affiliates

Nayef Ahmar
Sahar Akram
Olivia Bermudez-Hopkins
Shohini Bhattasali
Christian Brodbeck
Regina Calloway
Francisco Cervantes Constantino
Maria Chait
Aura Cruz Heredia
Proloy Das
Alain de Cheveigné
Lien Decruy
Marisel Villafane Delgado
Nai Ding
Jason Dunlap
Mounya Elhilali
Sydney Hancock
Marlies Gilles
Victor Grau-Serrat
Alex Jiao
Neha Joshi
Joshua Kulasingham
Natalia Lapinskaya
Huan Luo
Sina Miran
Alex Presacco
Krishna Puvvada
Mohsen Rezaeizadeh
Behrad Soleimani
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Juanjuan Xiang
Peng Zan
Elana Zion Golumbic

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UNIVERSITY OF MARYLAND 18 56

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)

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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

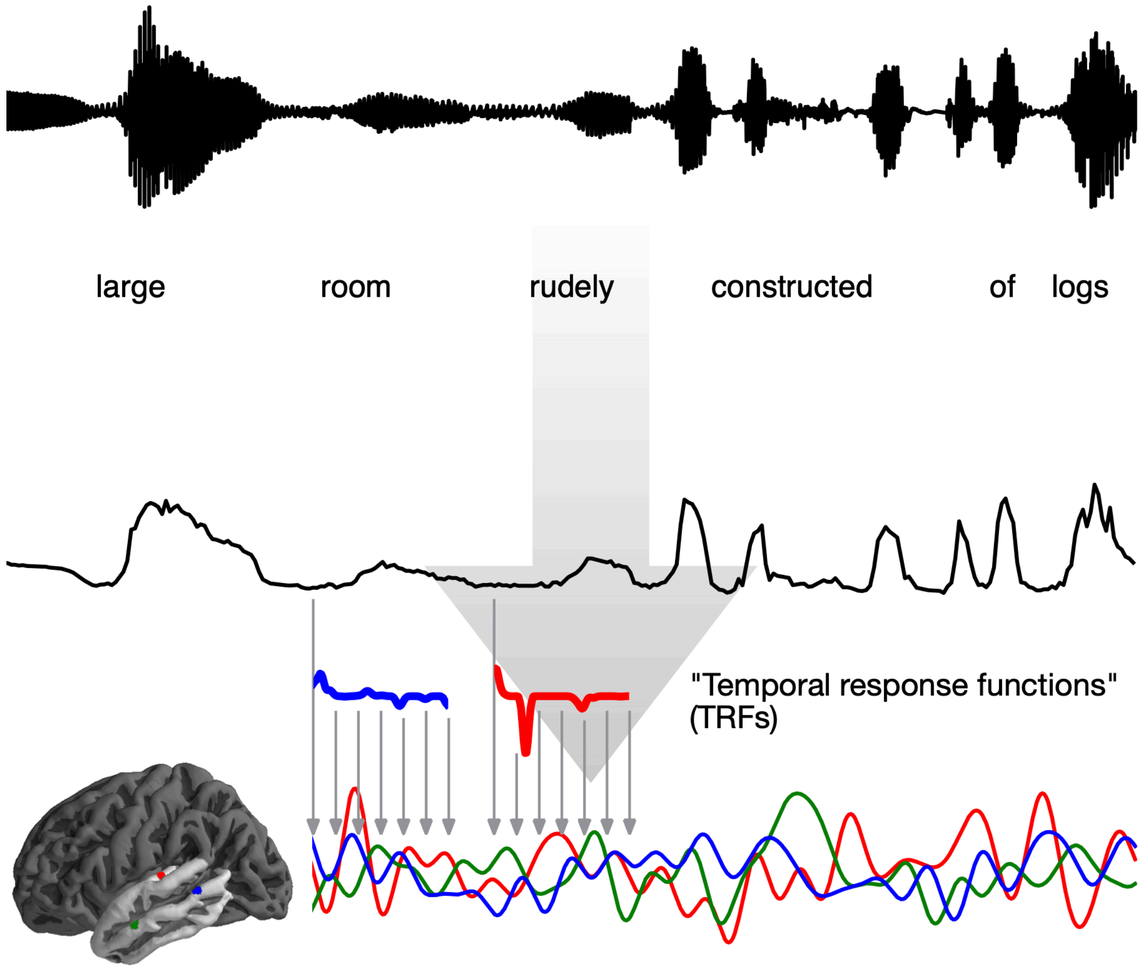
Neural Representations of Speech

- 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

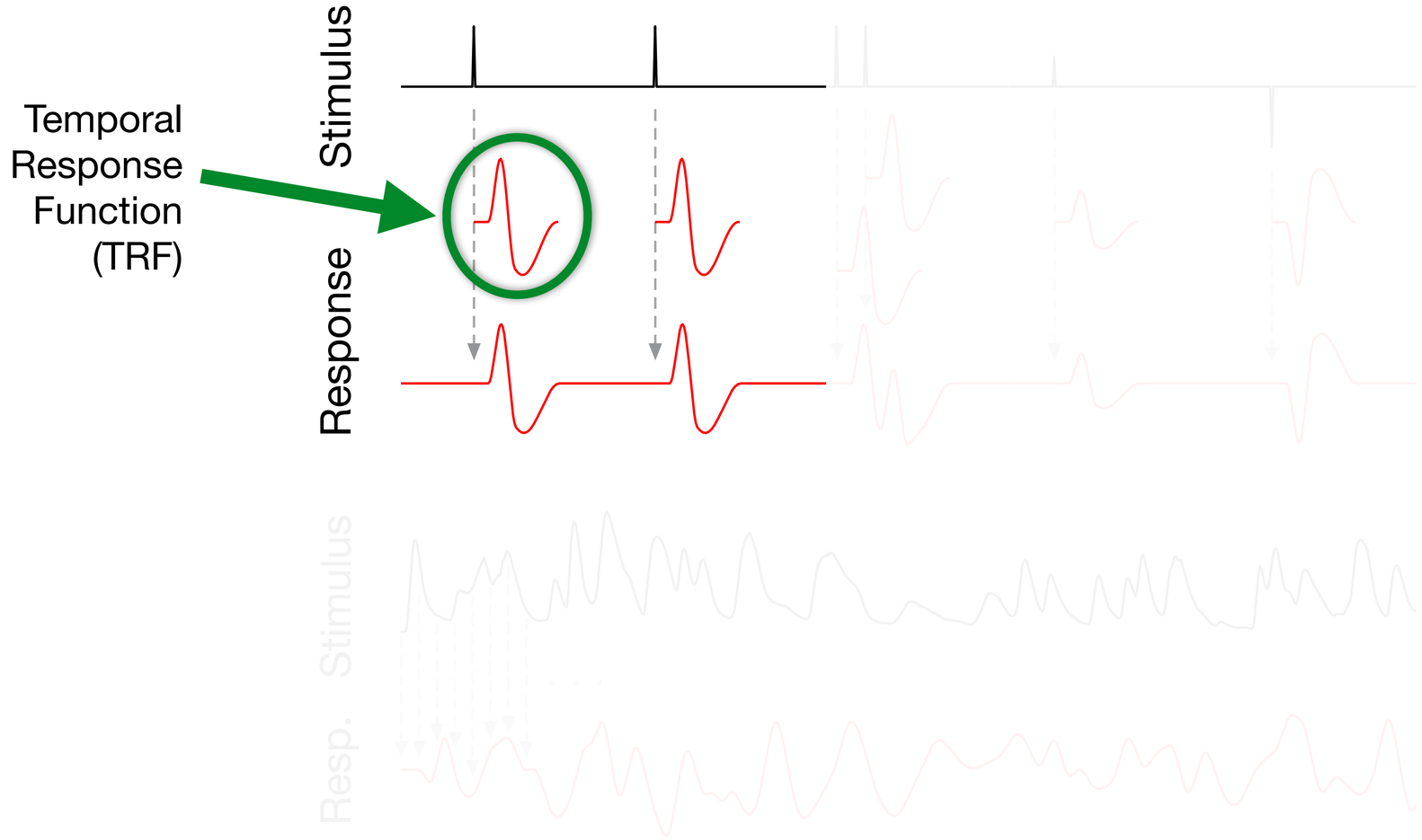
Cortical Representations: Encoding

- 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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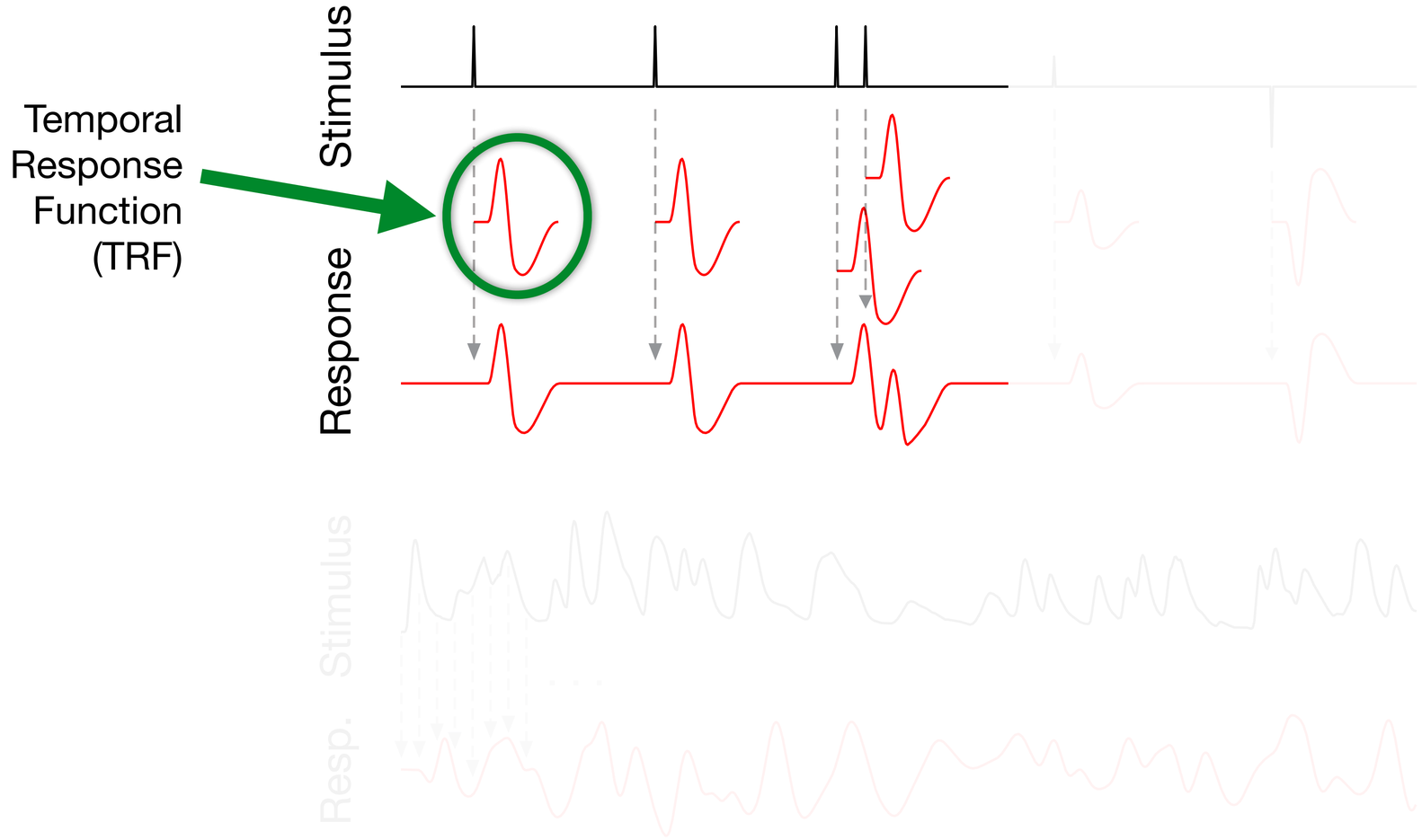

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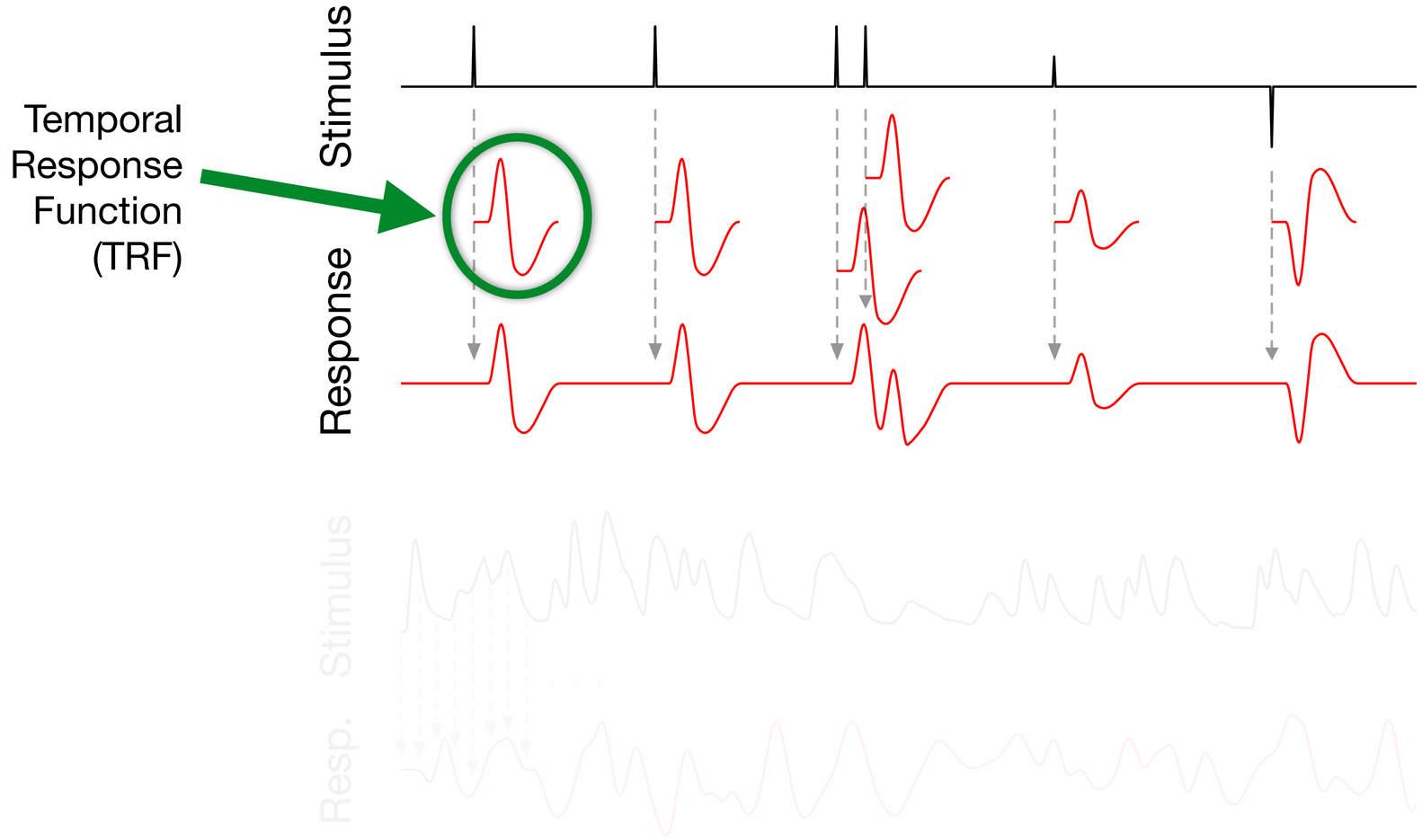

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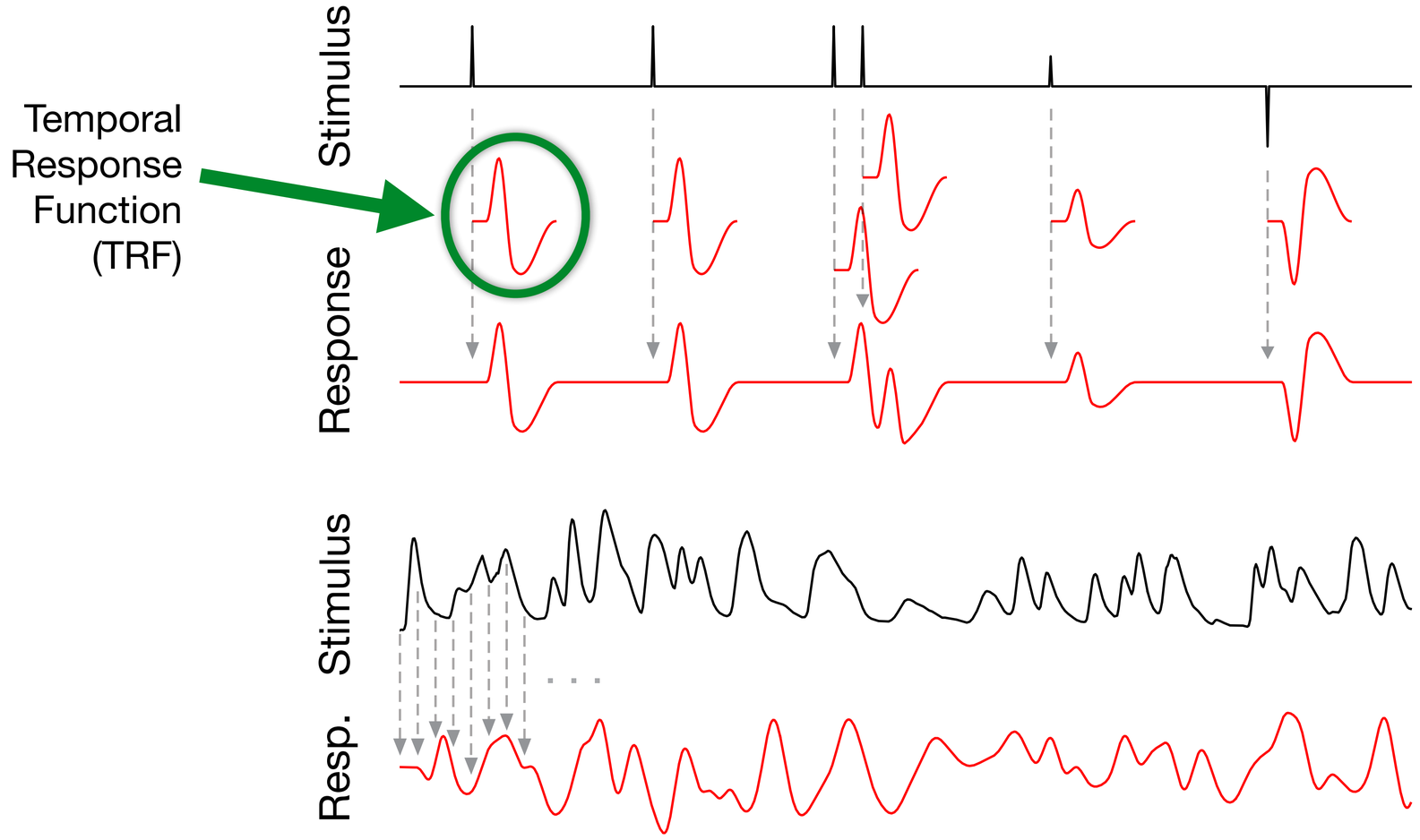
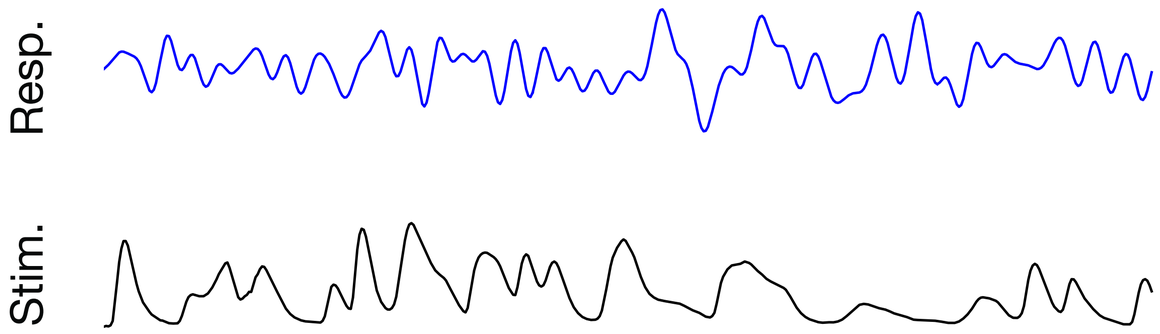


TRF Model Estimation & Fit

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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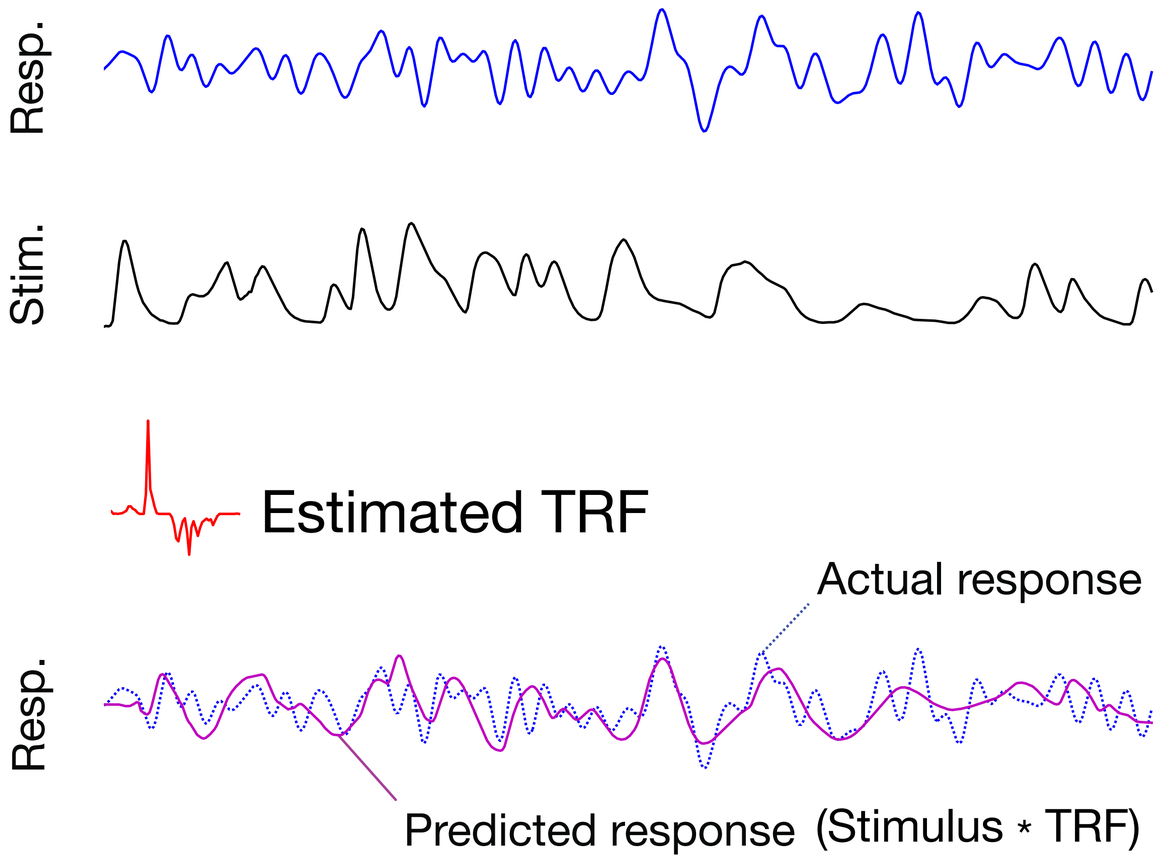
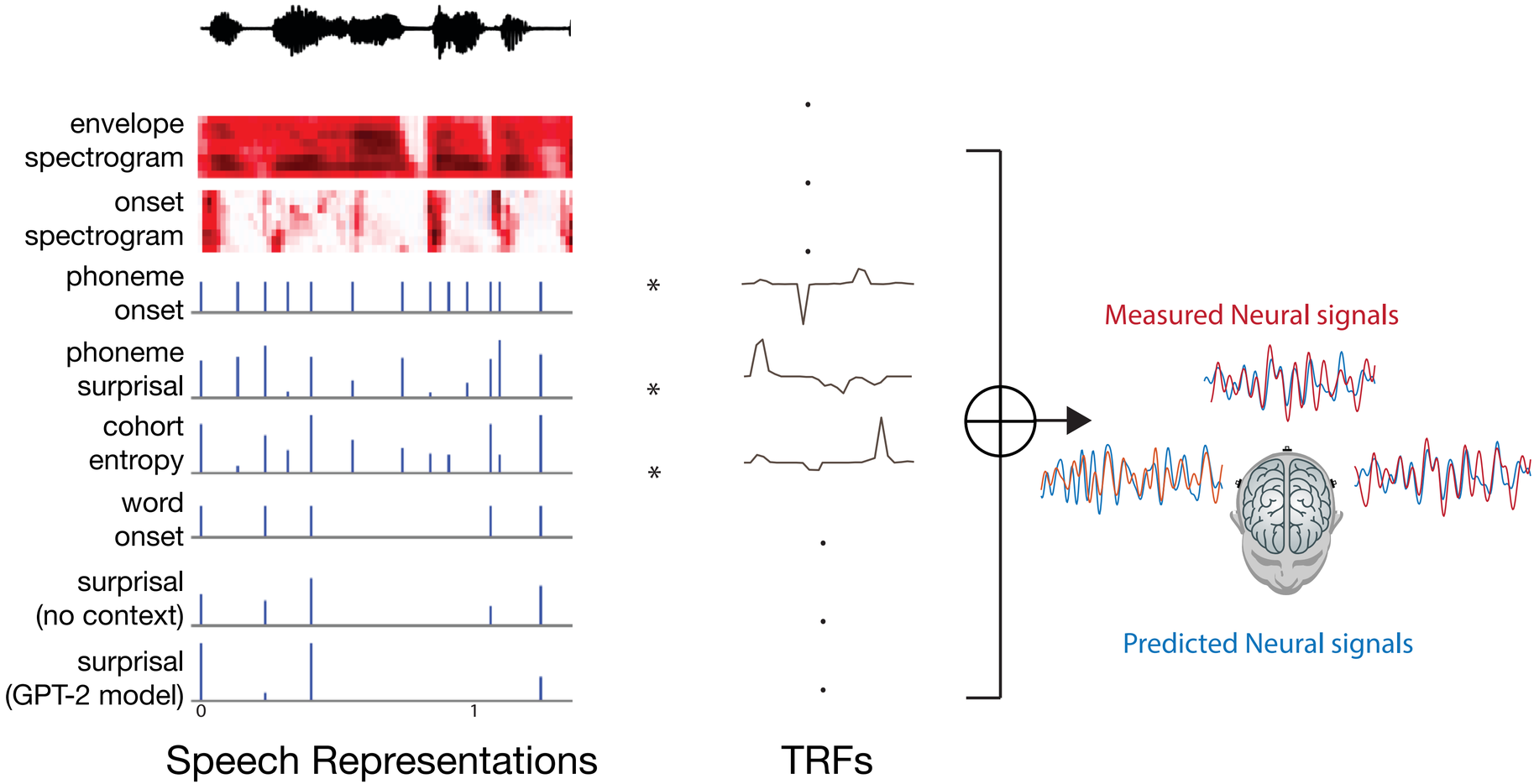


Lalor & Foxe (2010) *Neural Responses to Uninterrupted Natural Speech* … Eur J Neurosci
Ding & Simon (2012) *Neural Coding of Continuous Speech in Auditory Cortex* … , J Neurophys

Simultaneous Temporal Response Functions

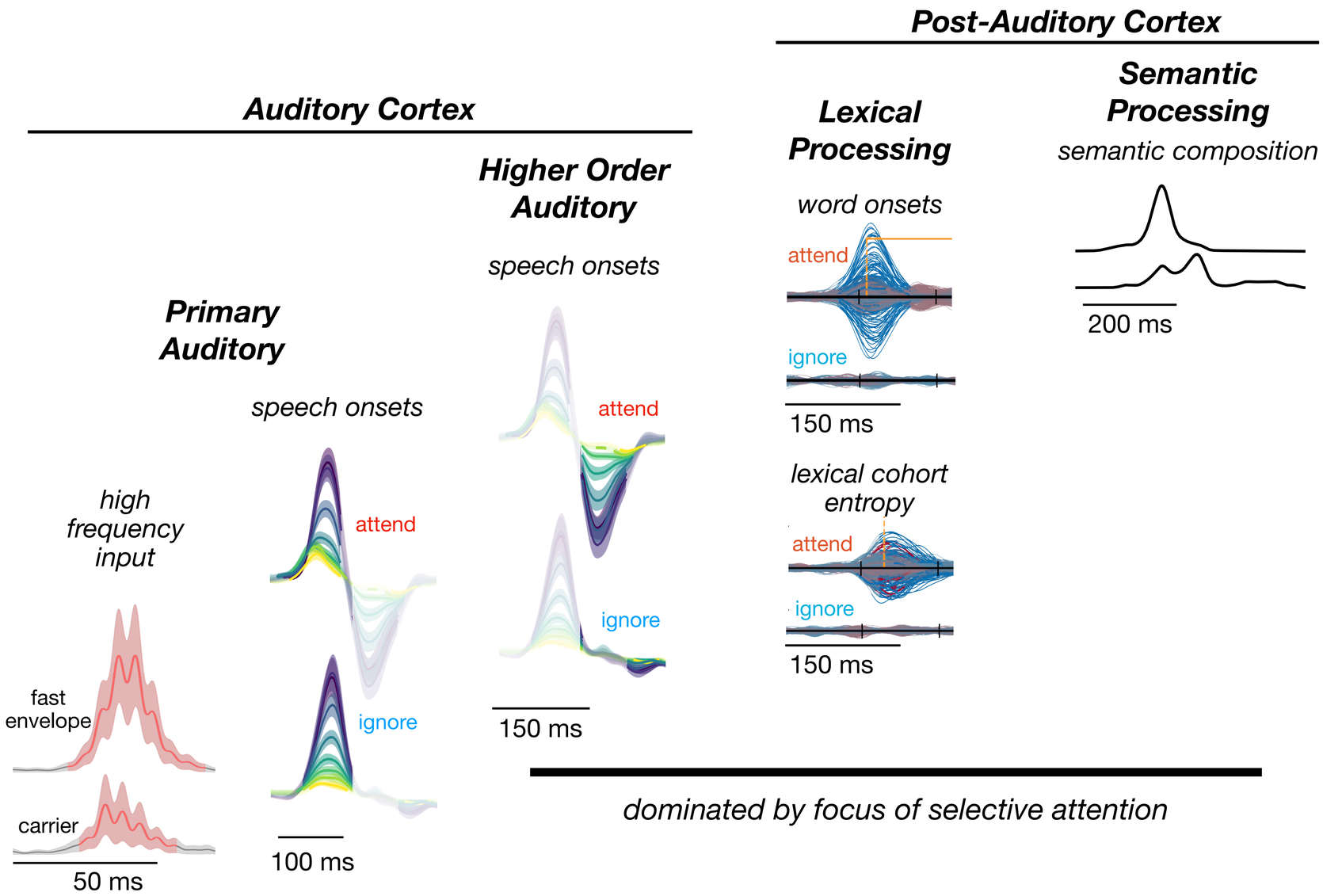
- TRFs predict neural response to speech
  - Analogous to evoked response
  - Peak amplitude ≈ processing intensity
  - Peak Latency ≈ source location
- Multiple TRFs estimated simultaneously
  - compete to explain variance (advantage over evoked response)



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

Brodbeck et al. (2023) *Eelbrain: A Python Toolkit for Time-Continuous Analysis* … , eLife

Cortical Representations Across Cortex



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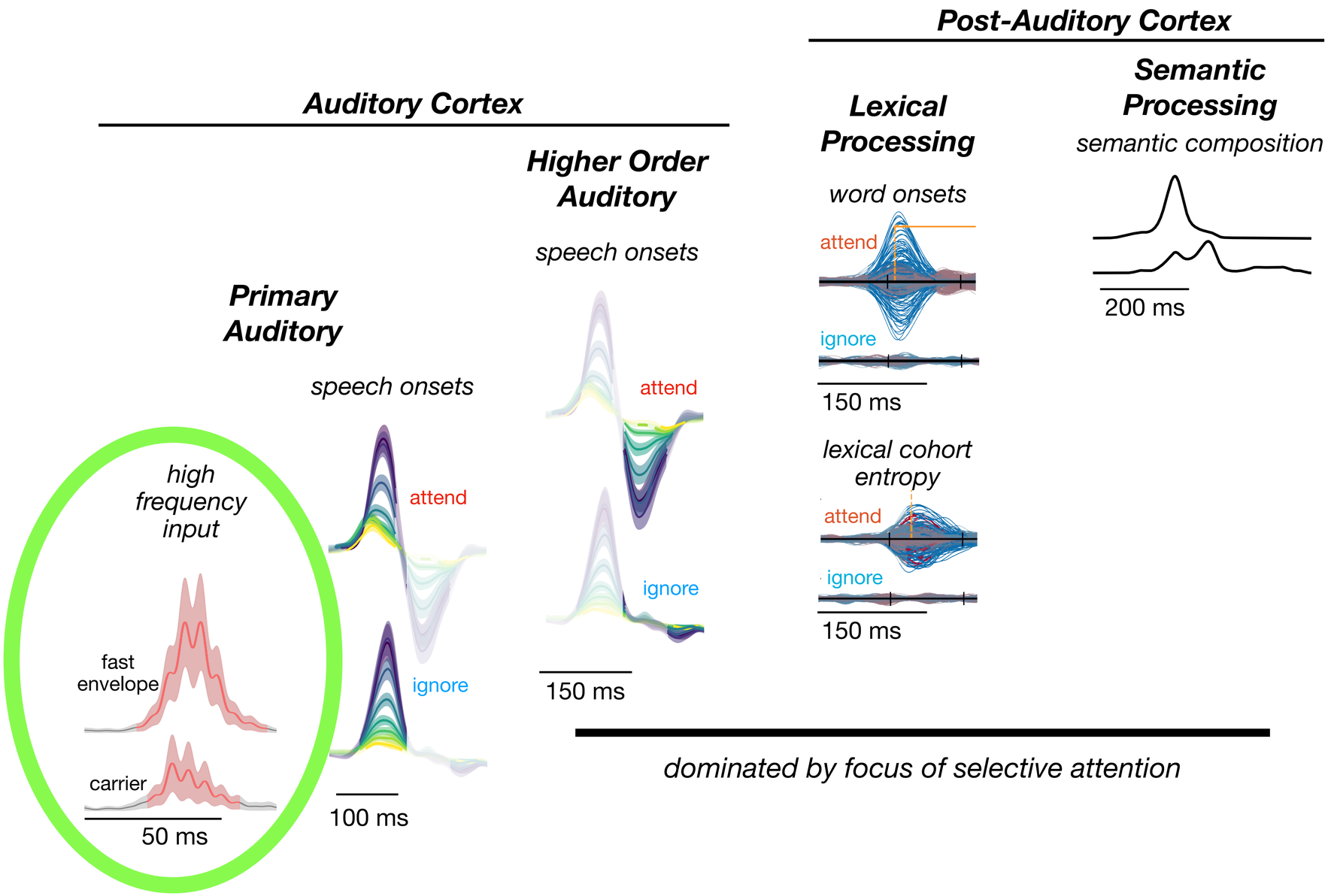

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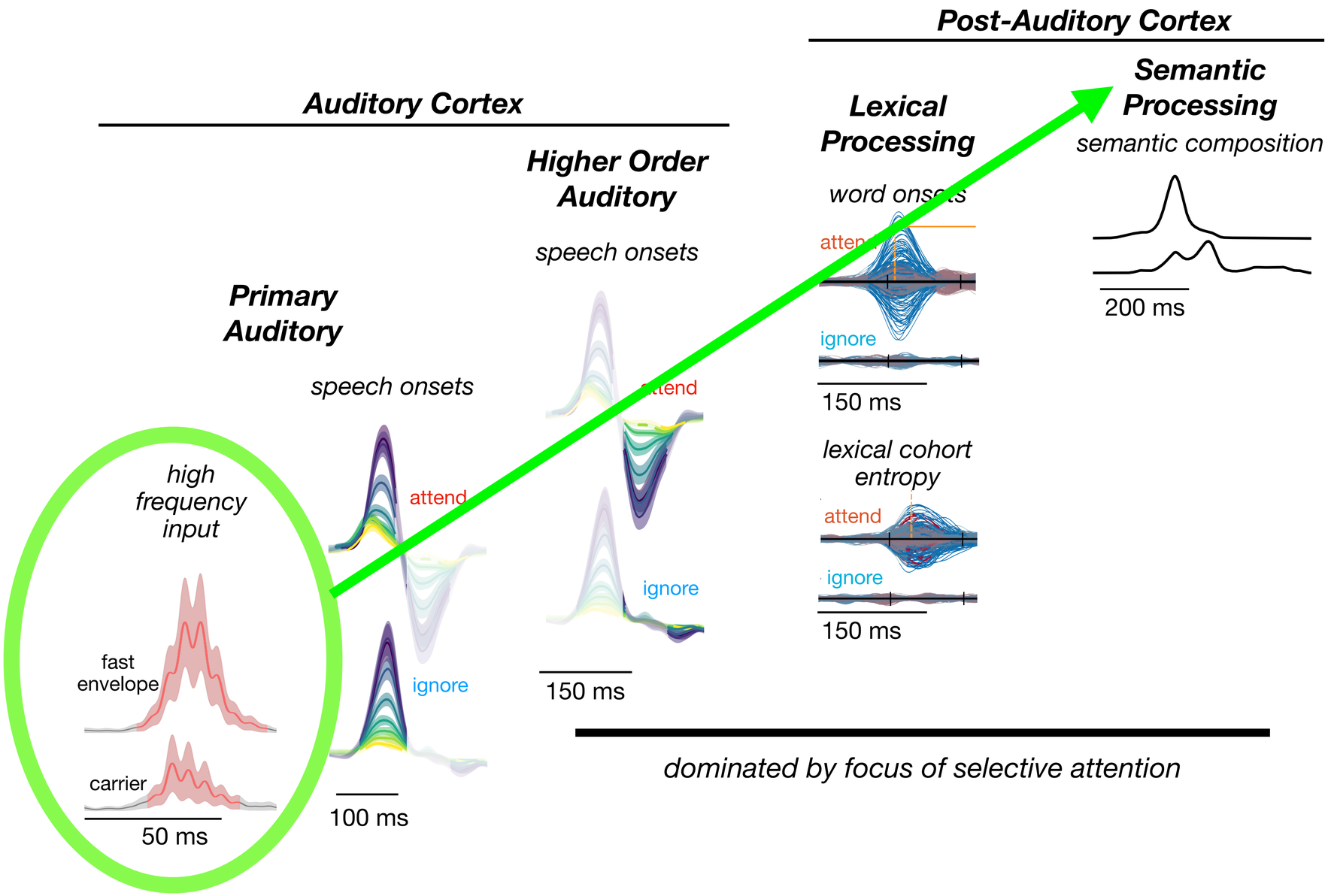

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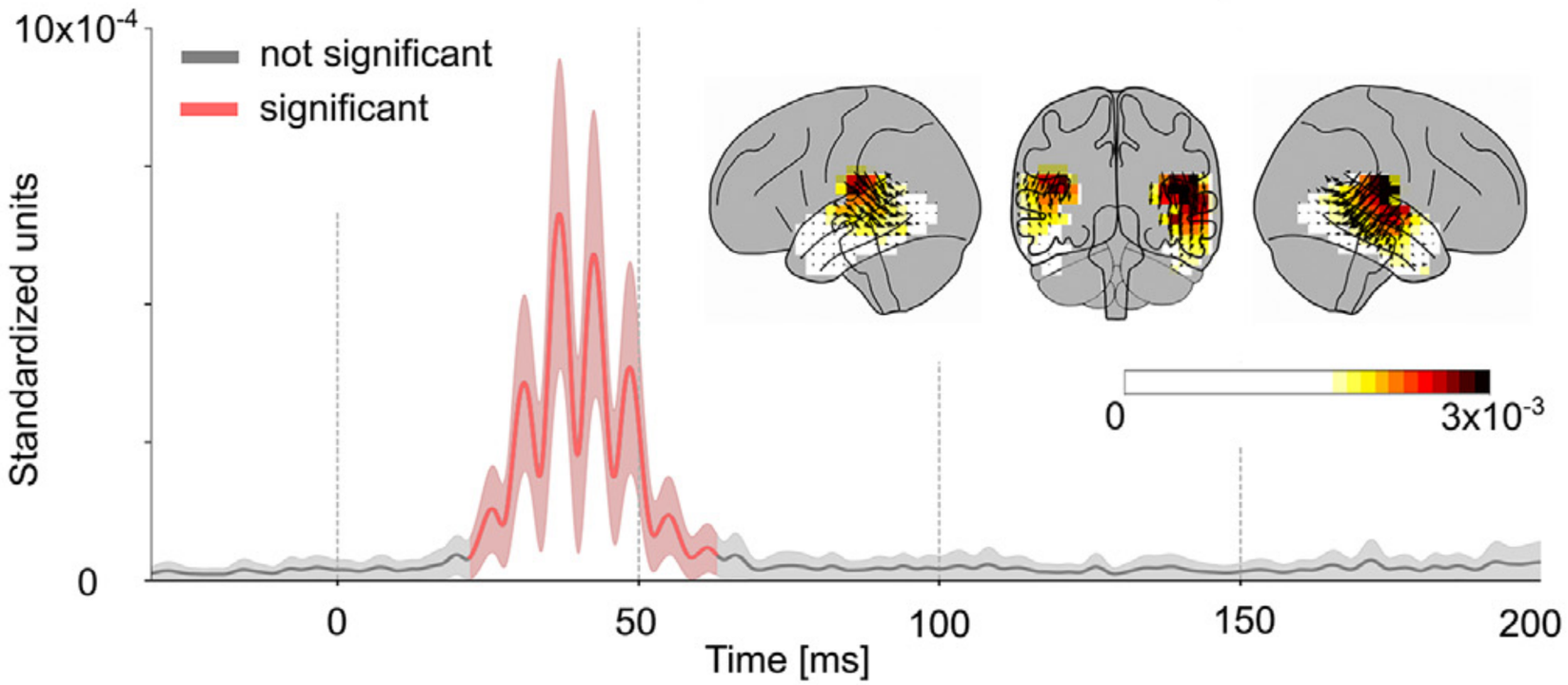
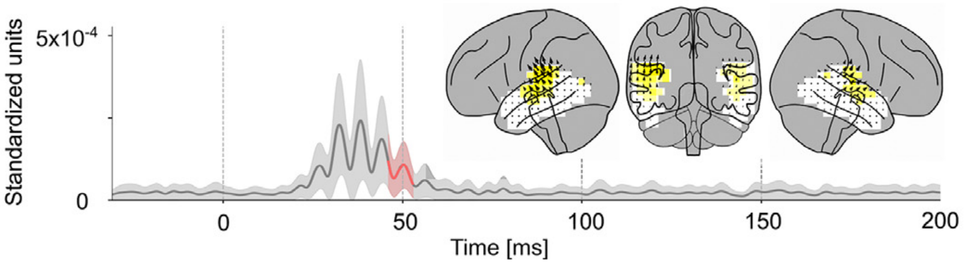
Fast & Early Cortical Representations



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

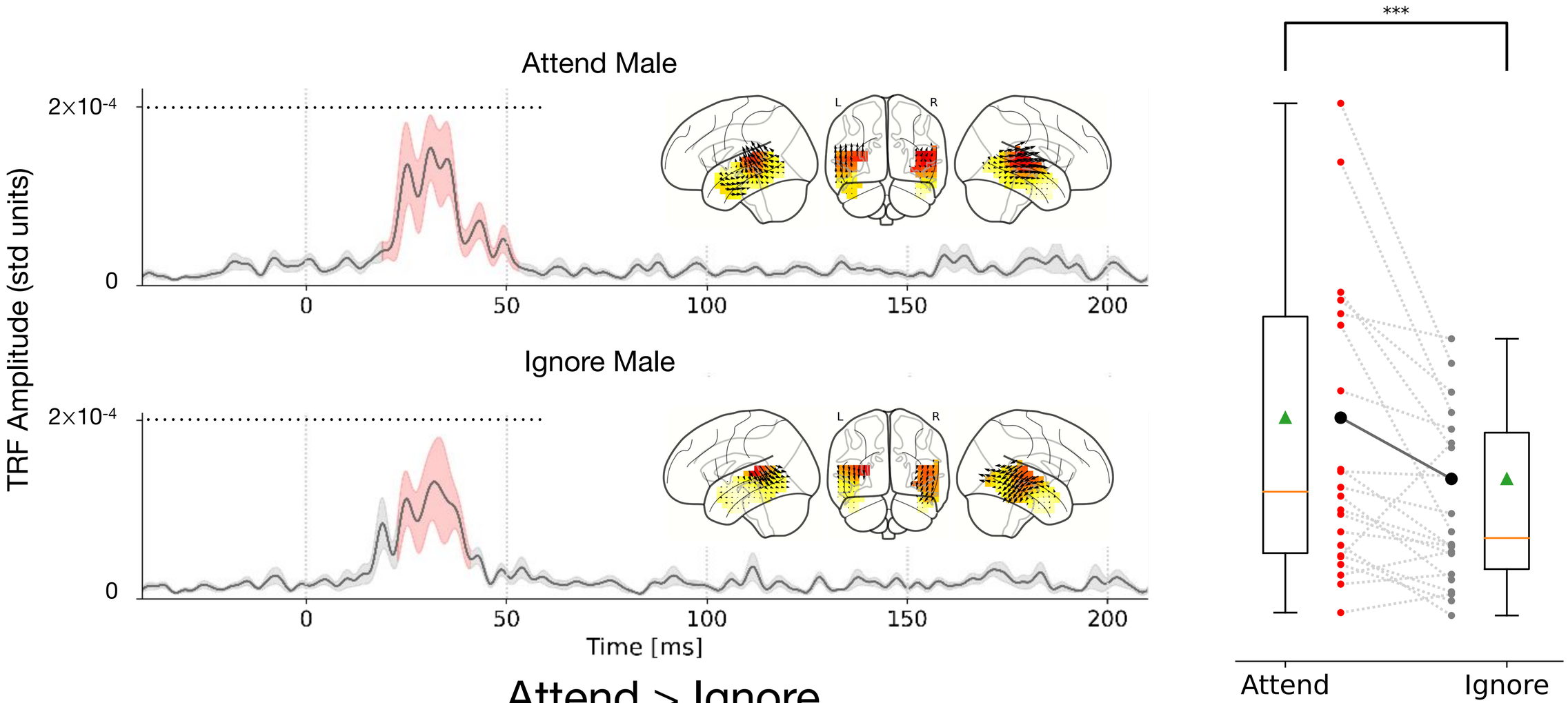


carrier

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. (2023) … *High-Gamma Band Depend on Selective Attention*, Front Neurosci

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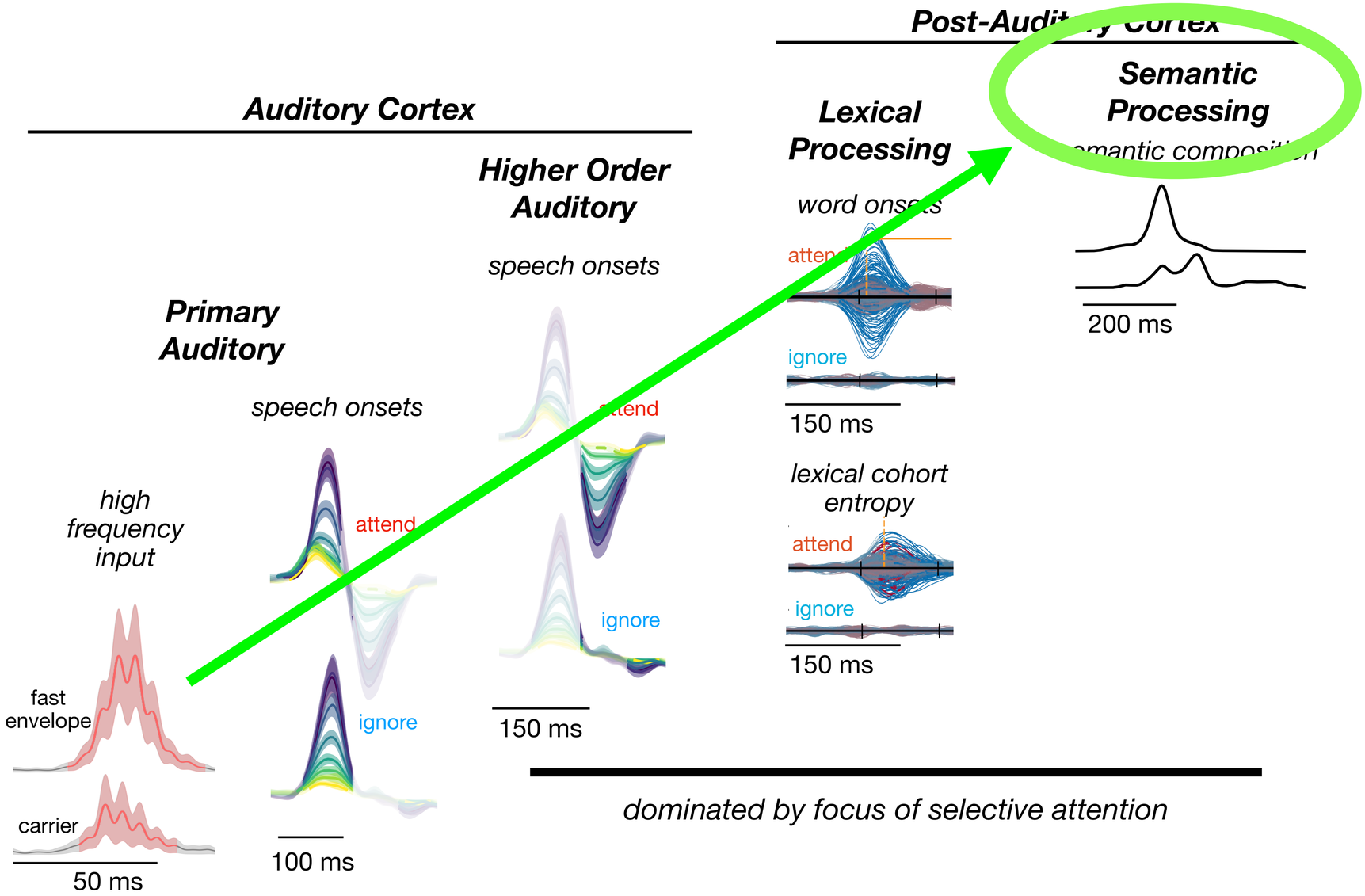

Speech Understanding/Meaning

- 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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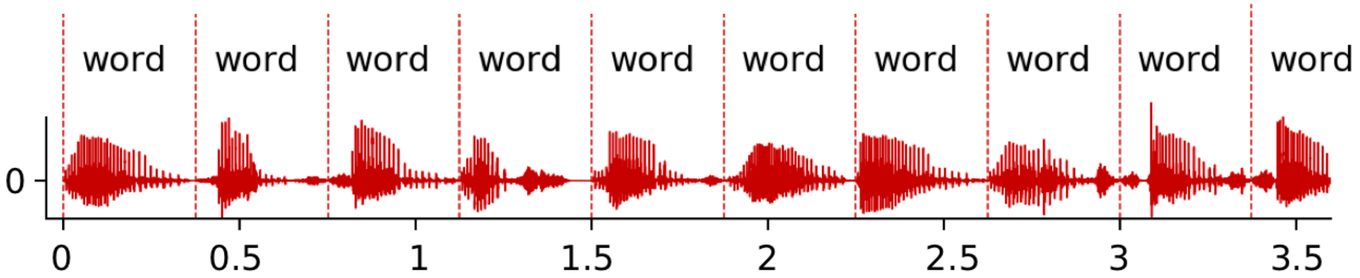
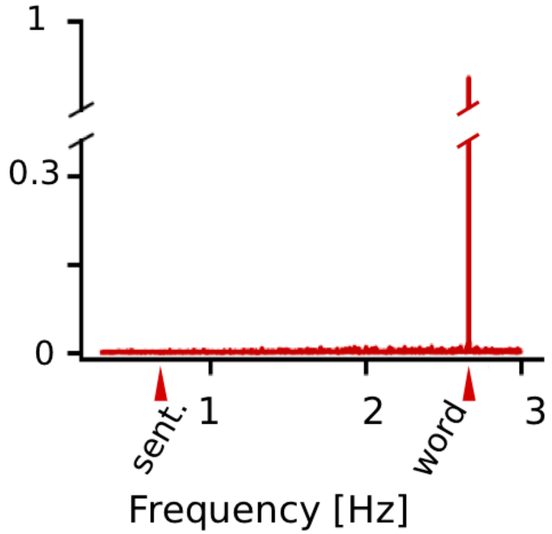
Isochronous Speech

Acoustics



Acoustical Spectrum (envelope)



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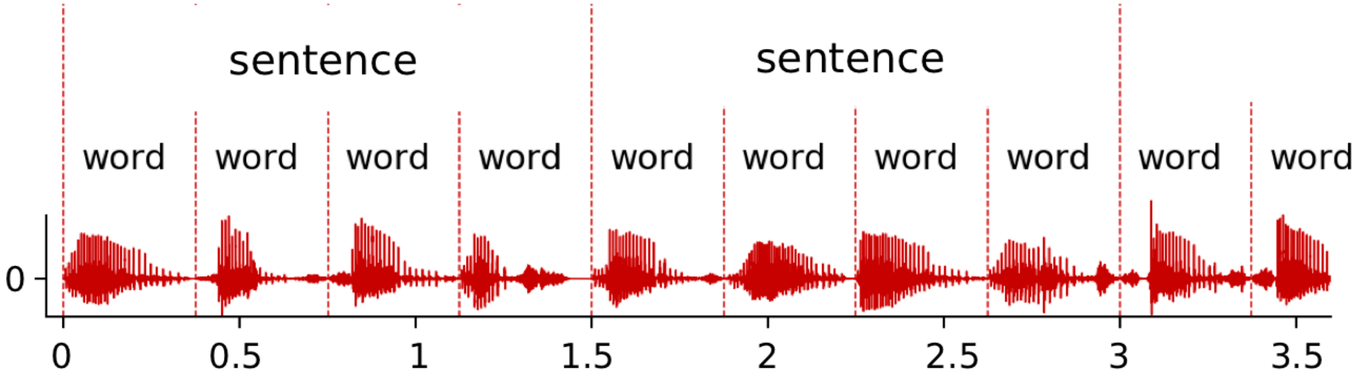

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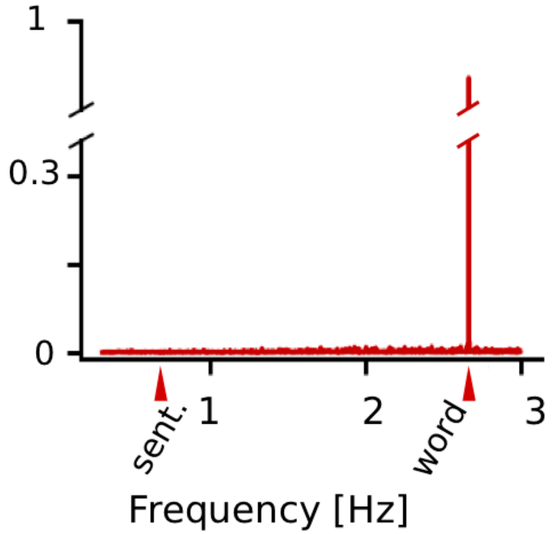

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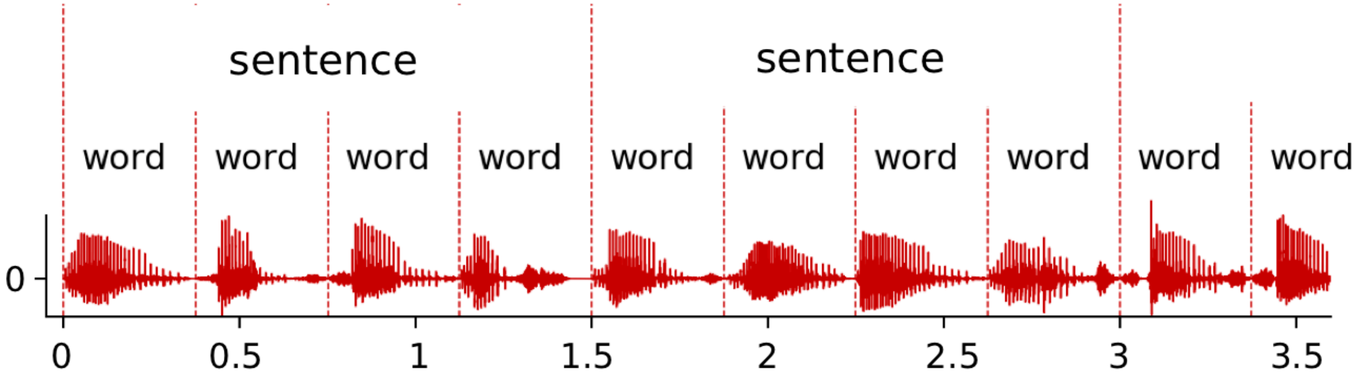

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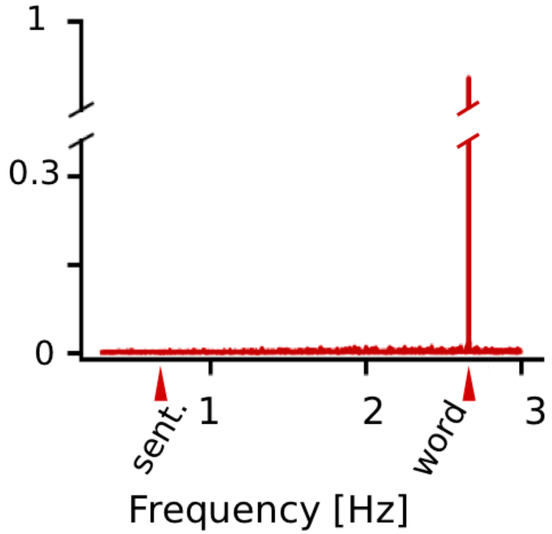

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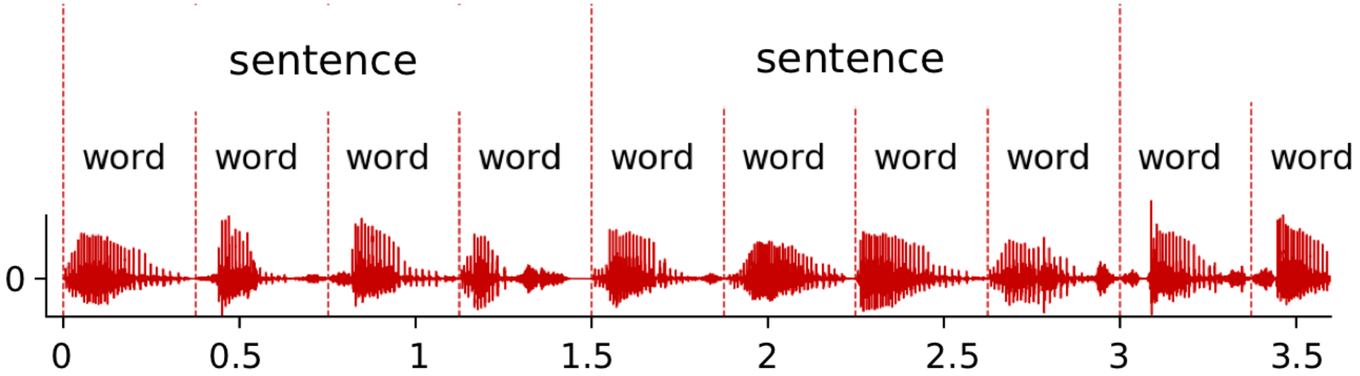

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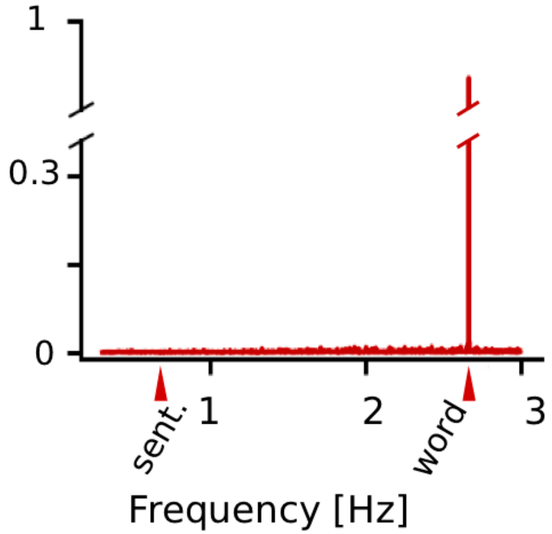

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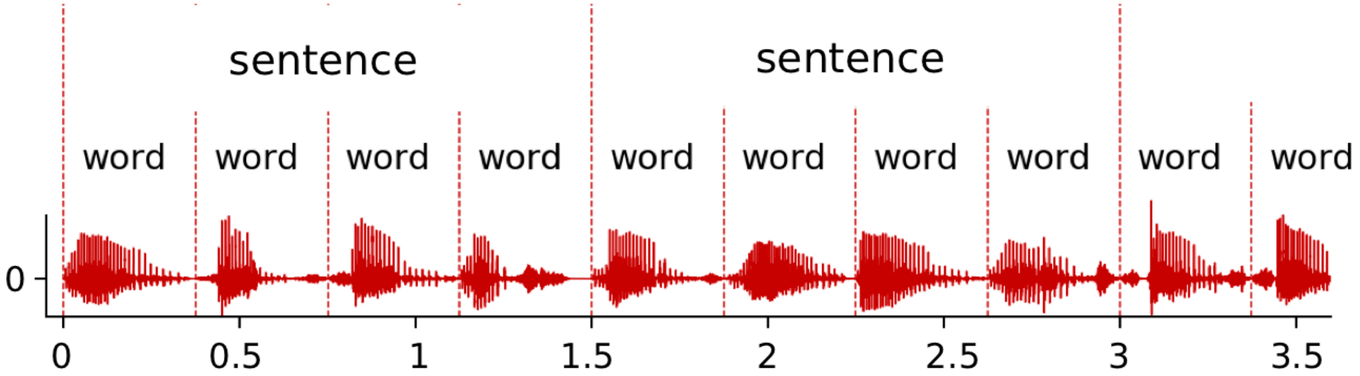

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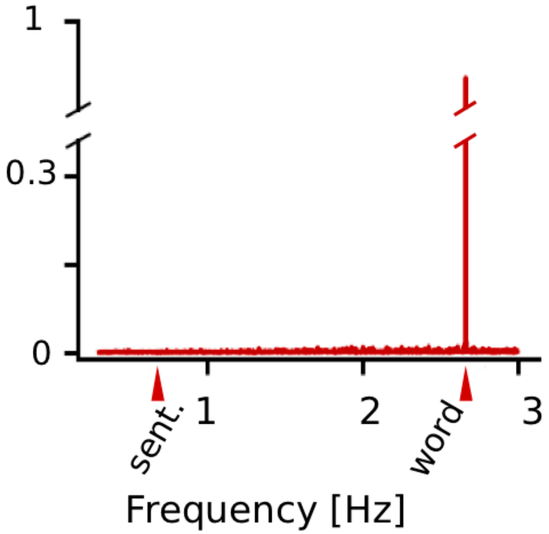
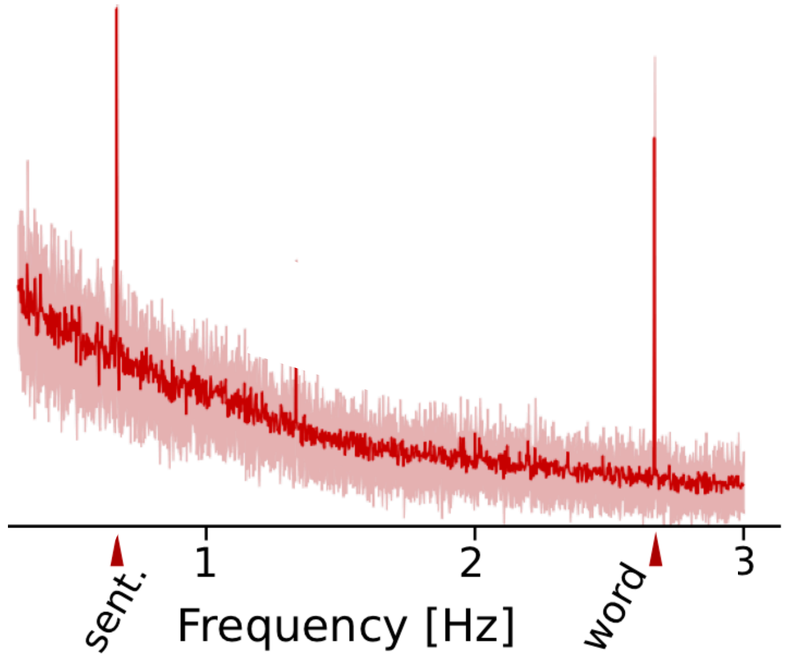


Perception?



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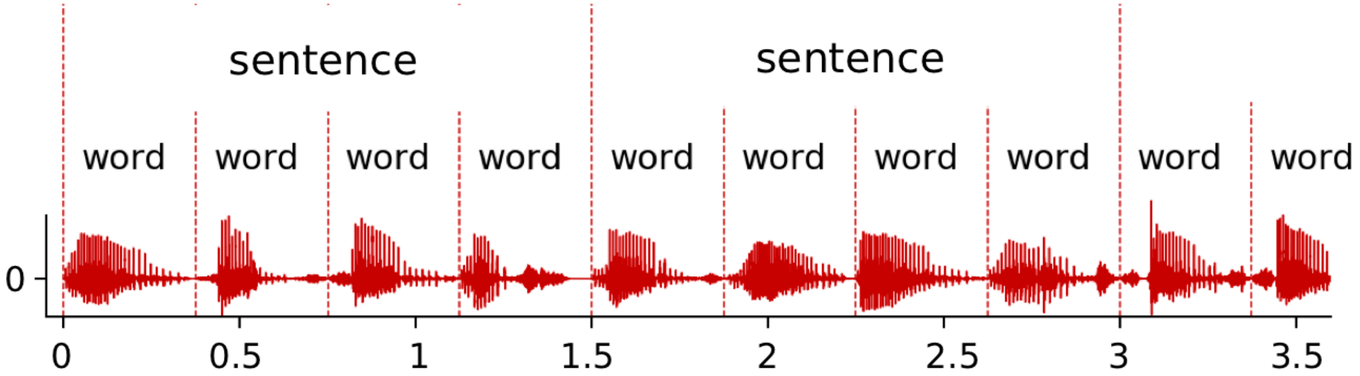

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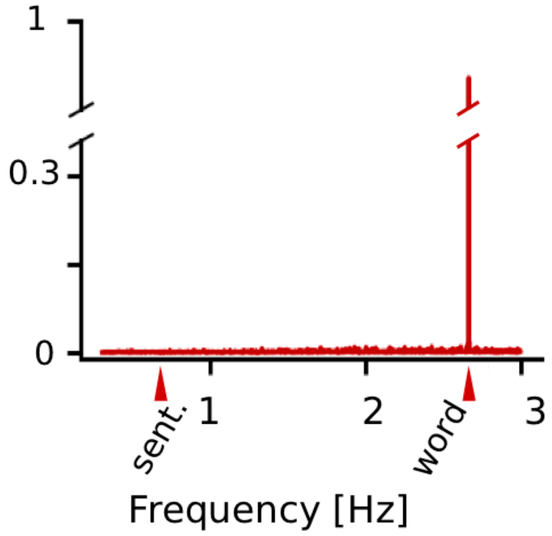
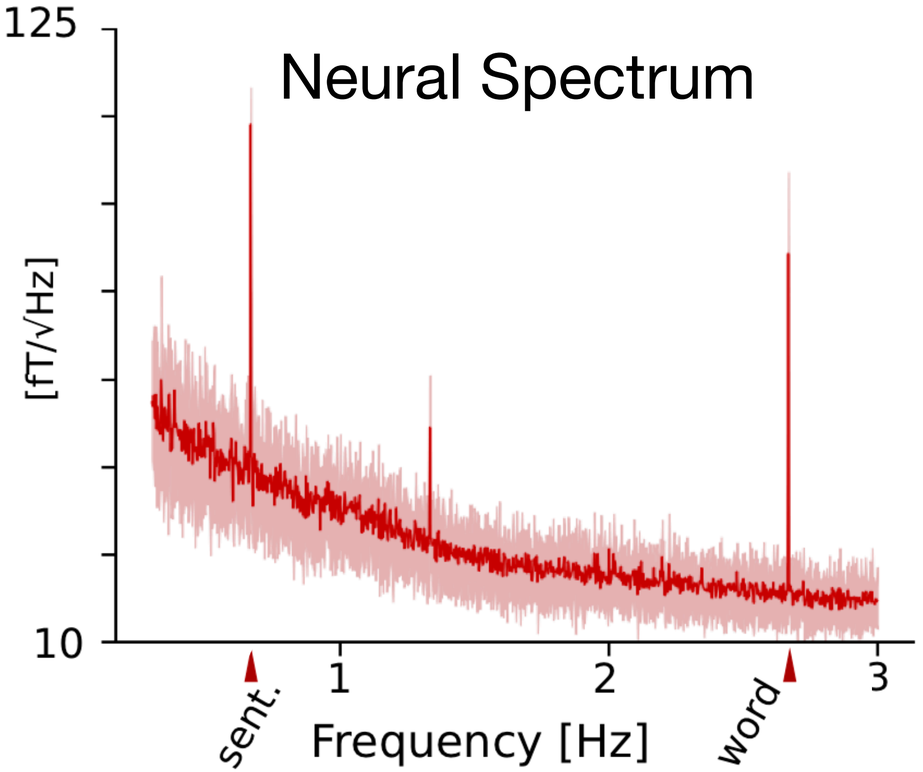
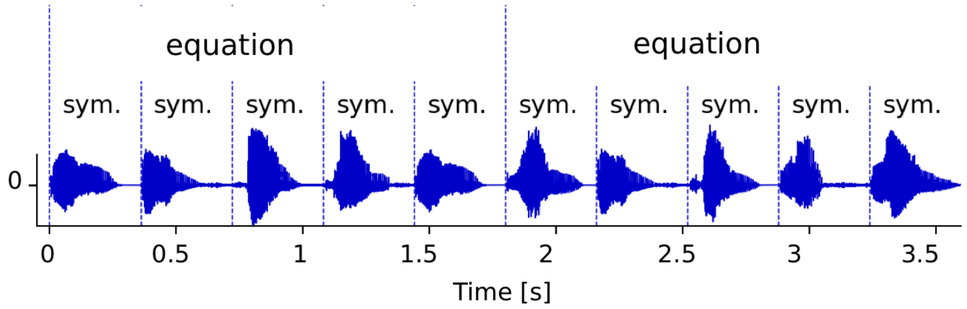


Neural Spectrum



Isochronous Arithmetic



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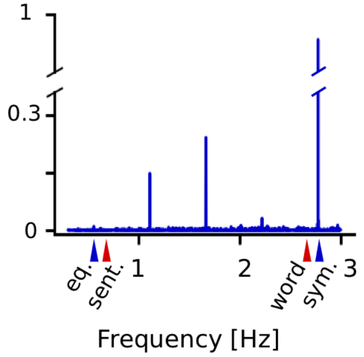

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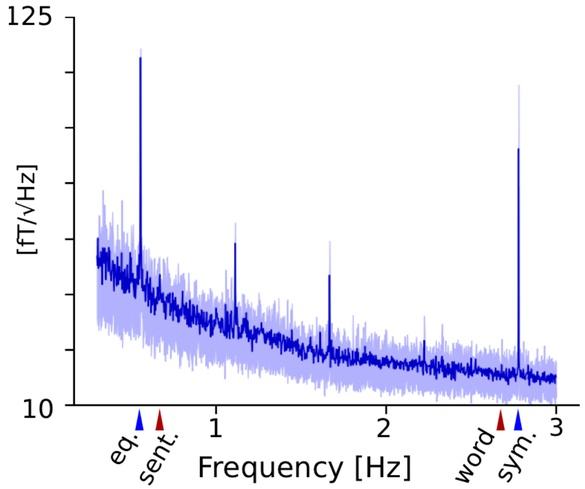
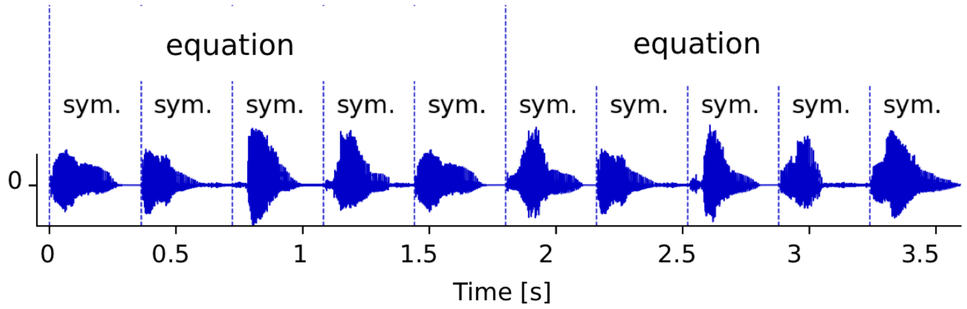


Neural Spectrum

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

Isochronous Arithmetic



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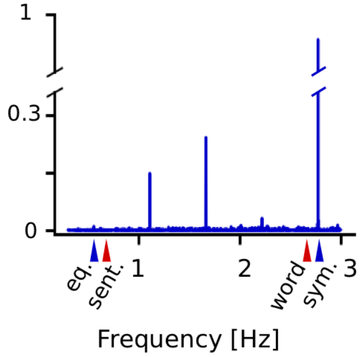

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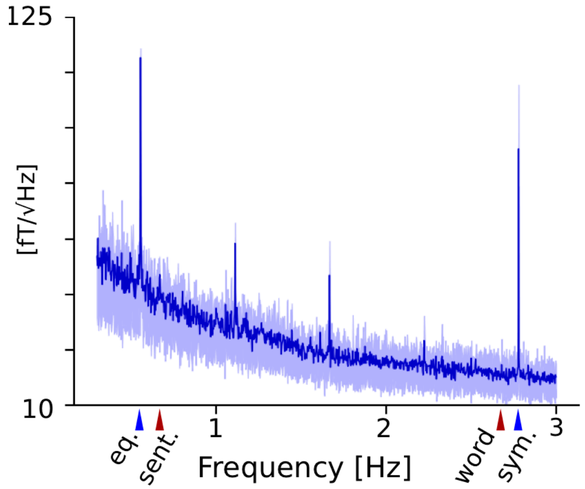

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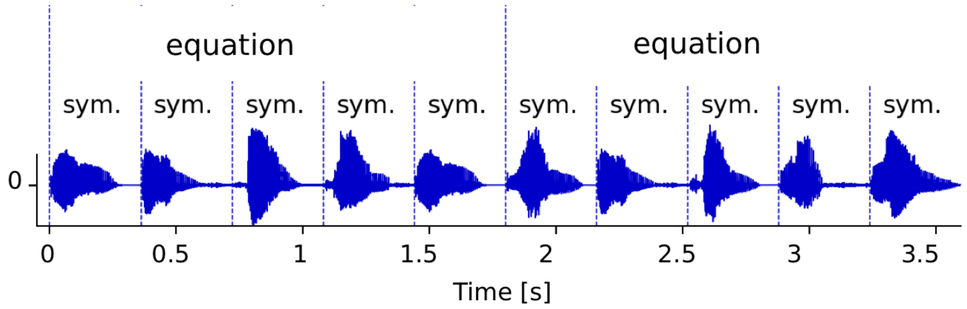

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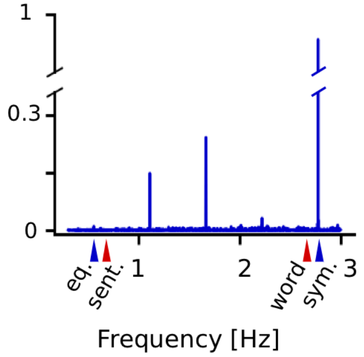

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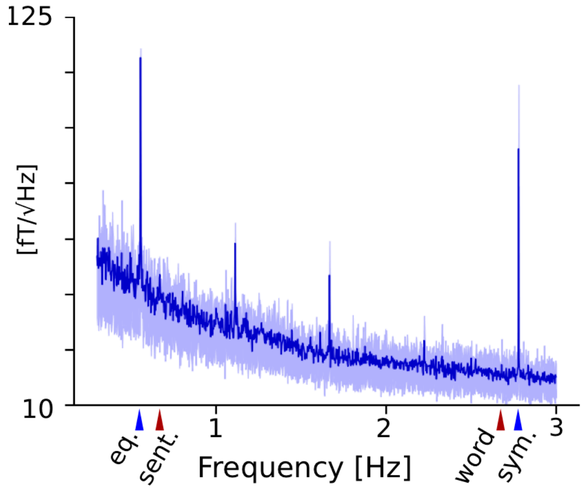

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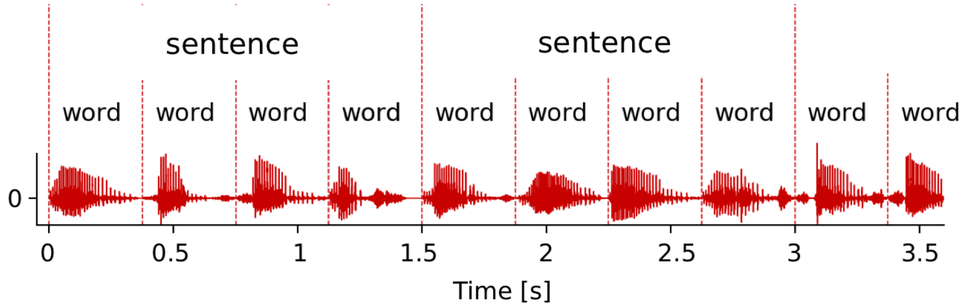
Isochronous Cocktail Party



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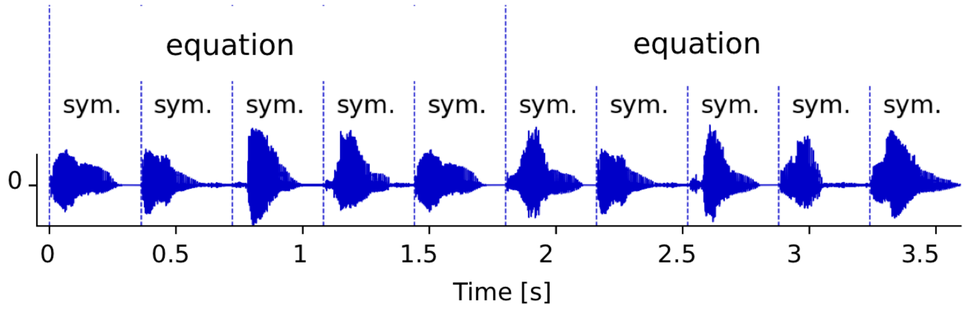

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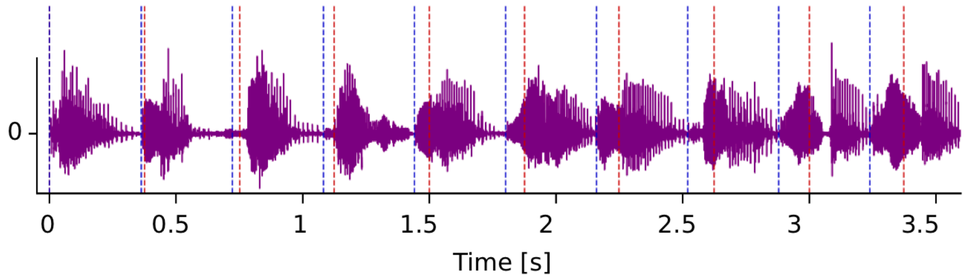

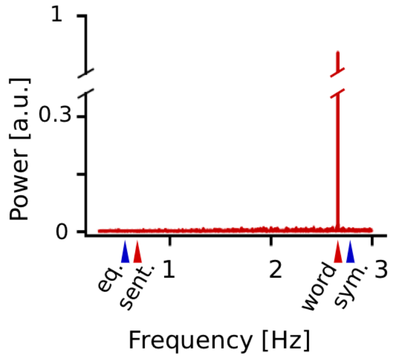

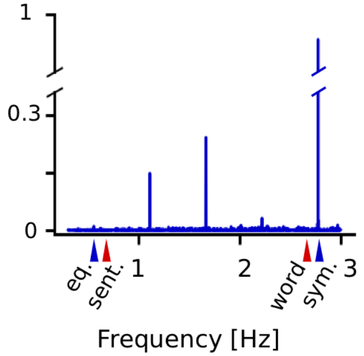

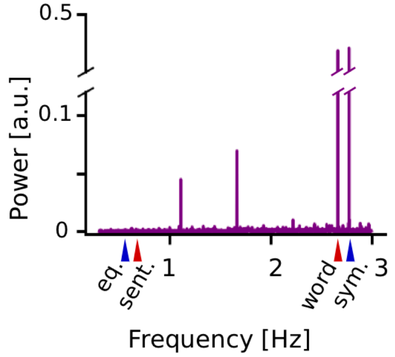

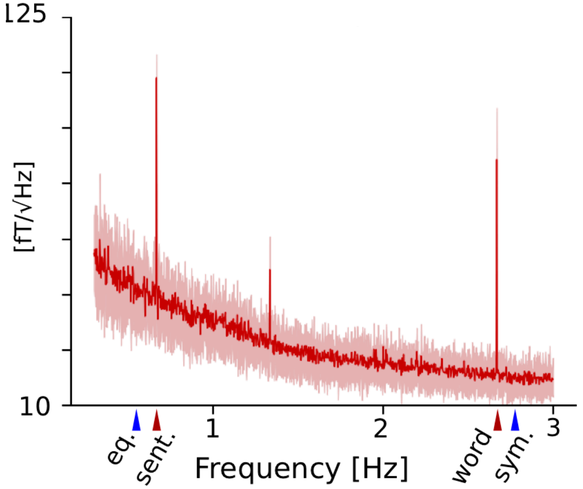

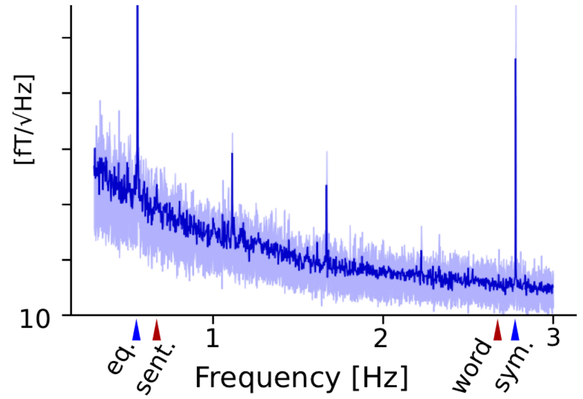

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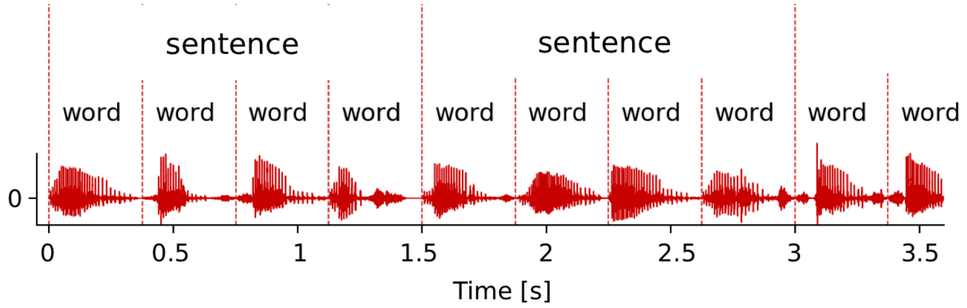
Isochronous Cocktail Party



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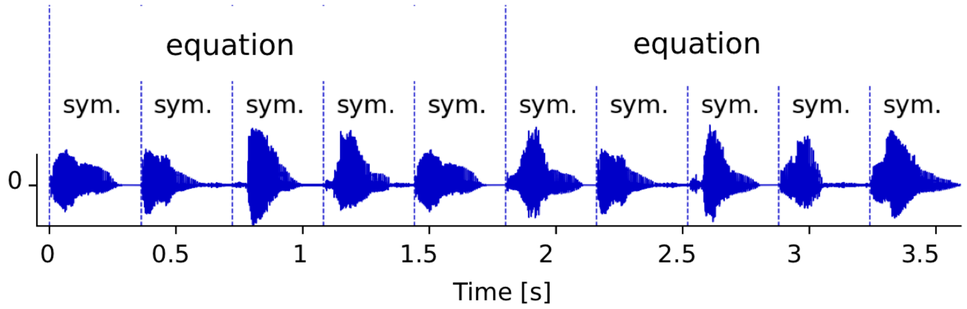

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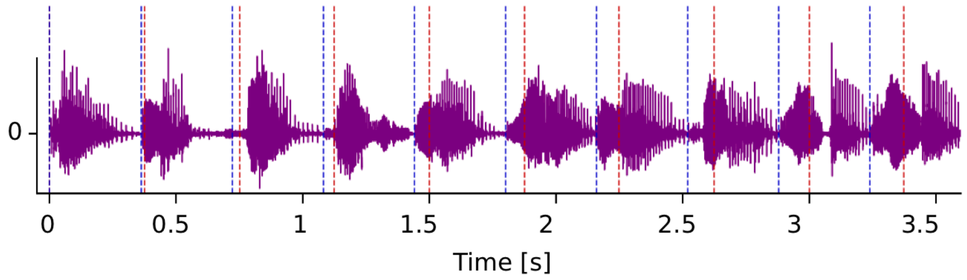

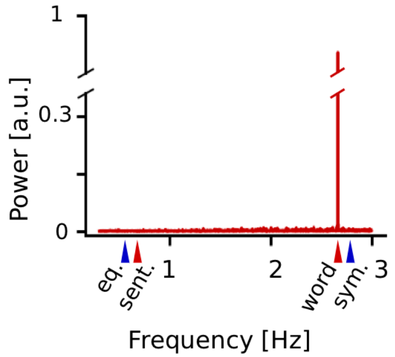

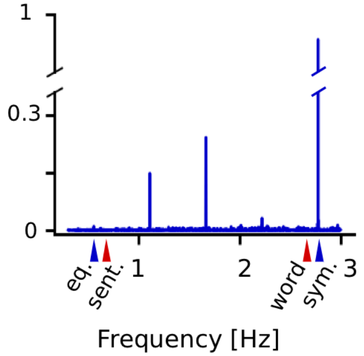

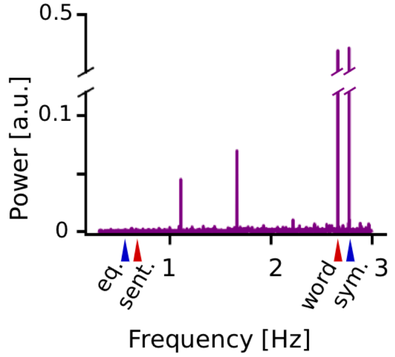

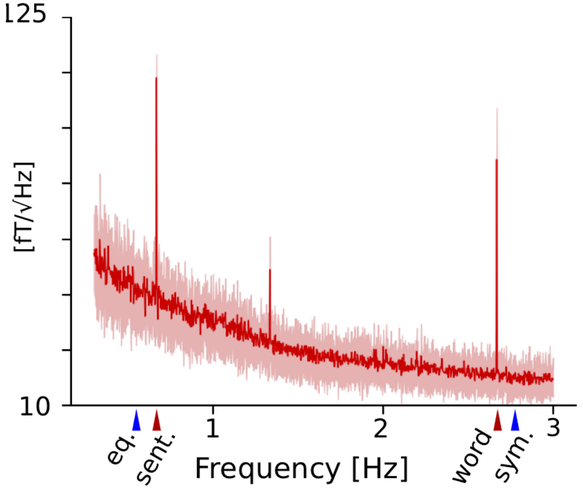

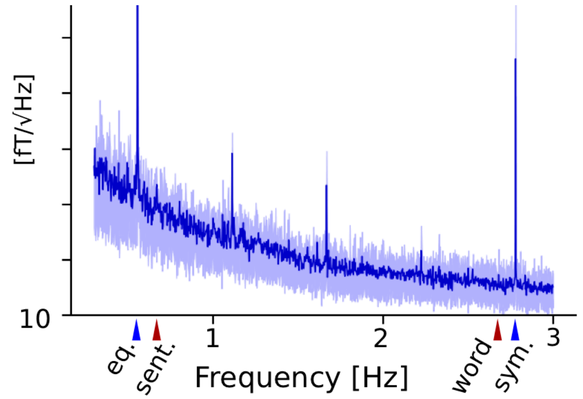

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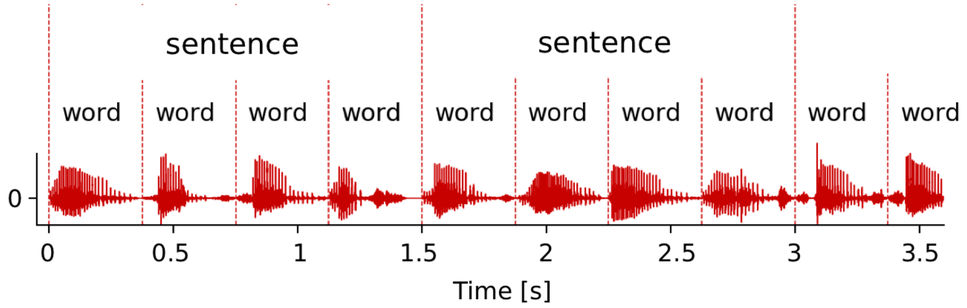

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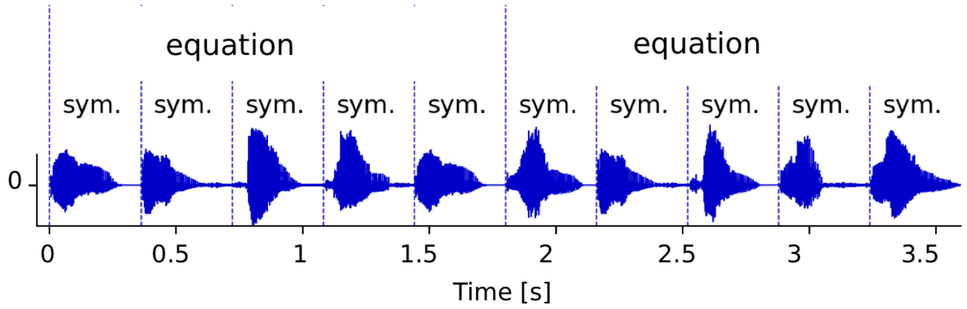

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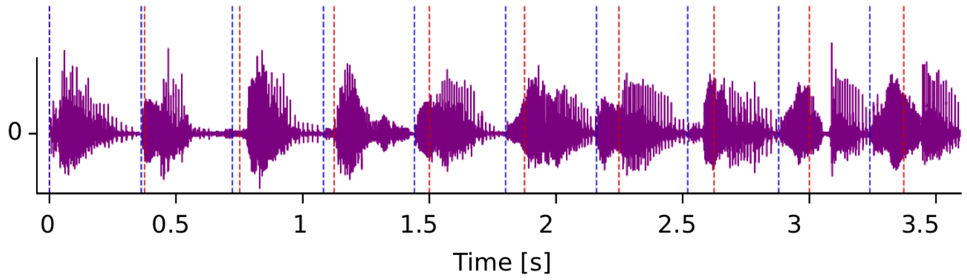

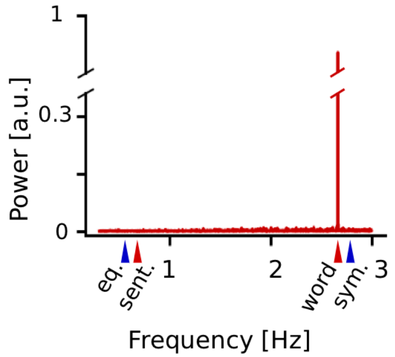

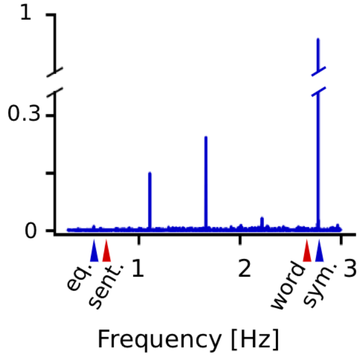

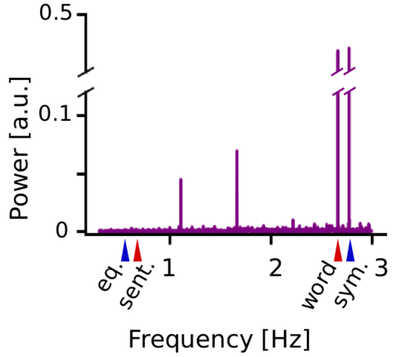

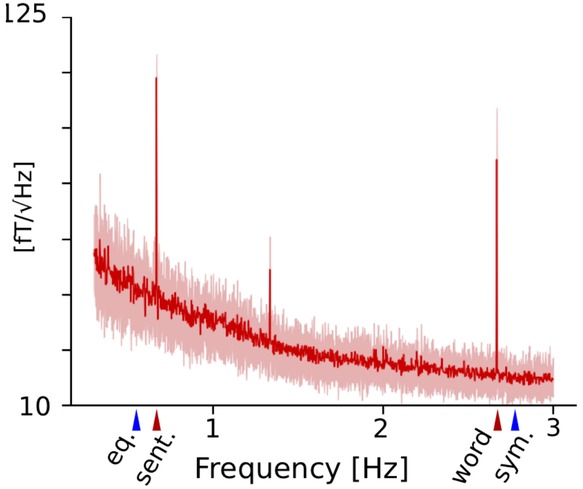

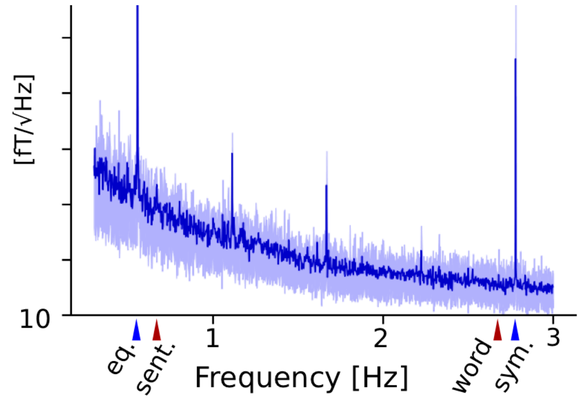

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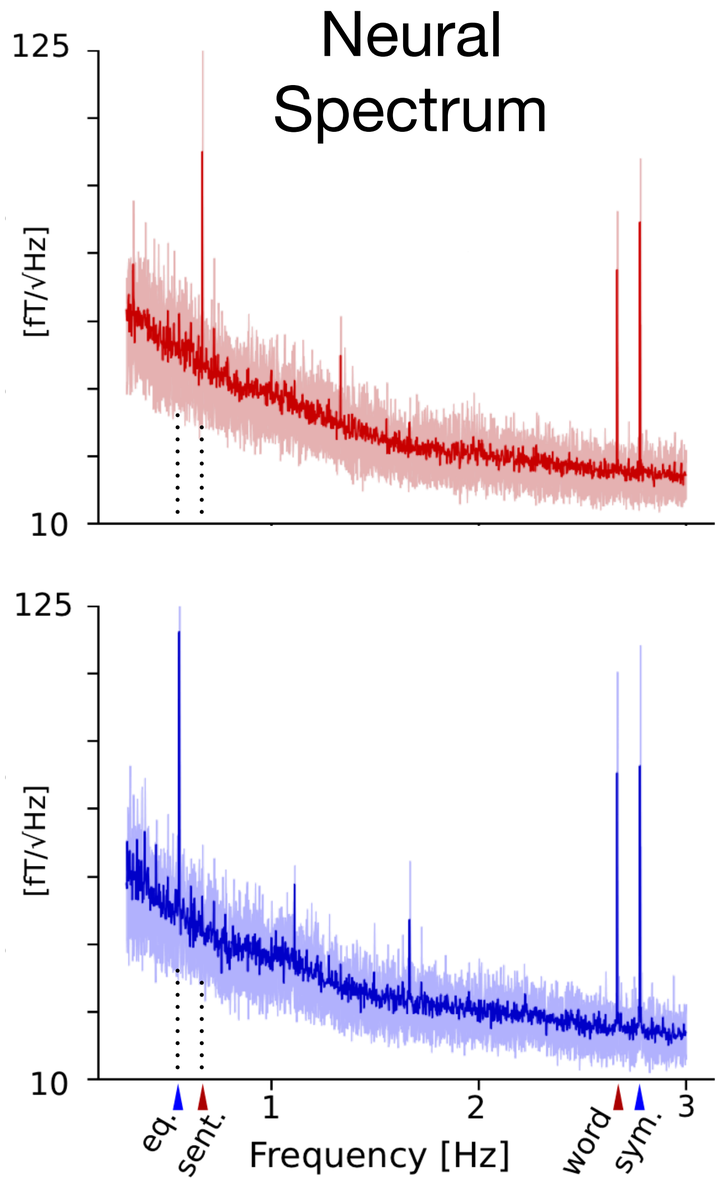
Isochronous Cocktail Party

Attend to Sentences

Attend to Equations



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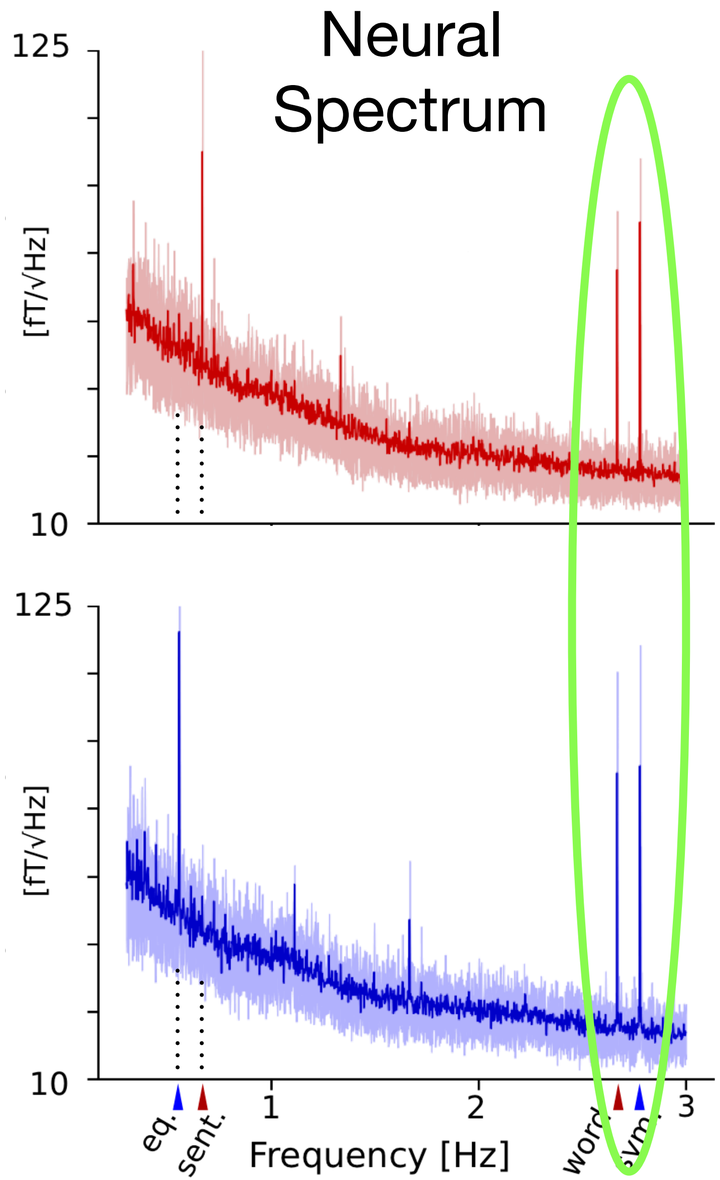

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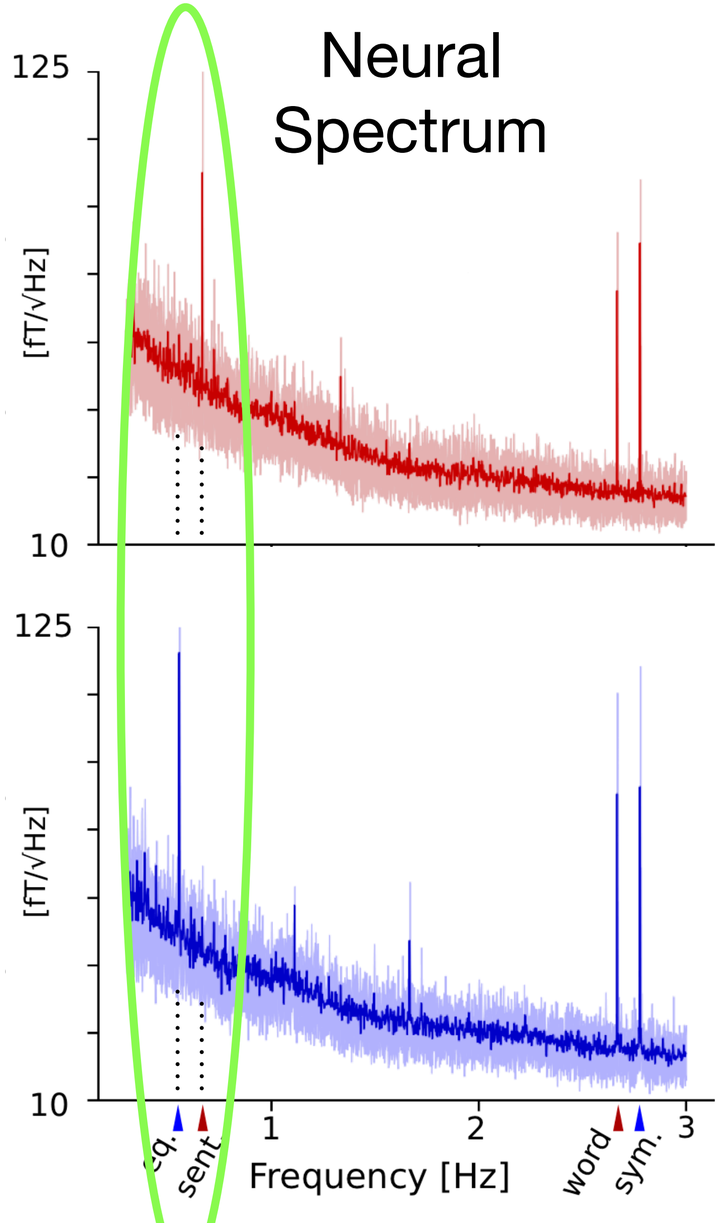

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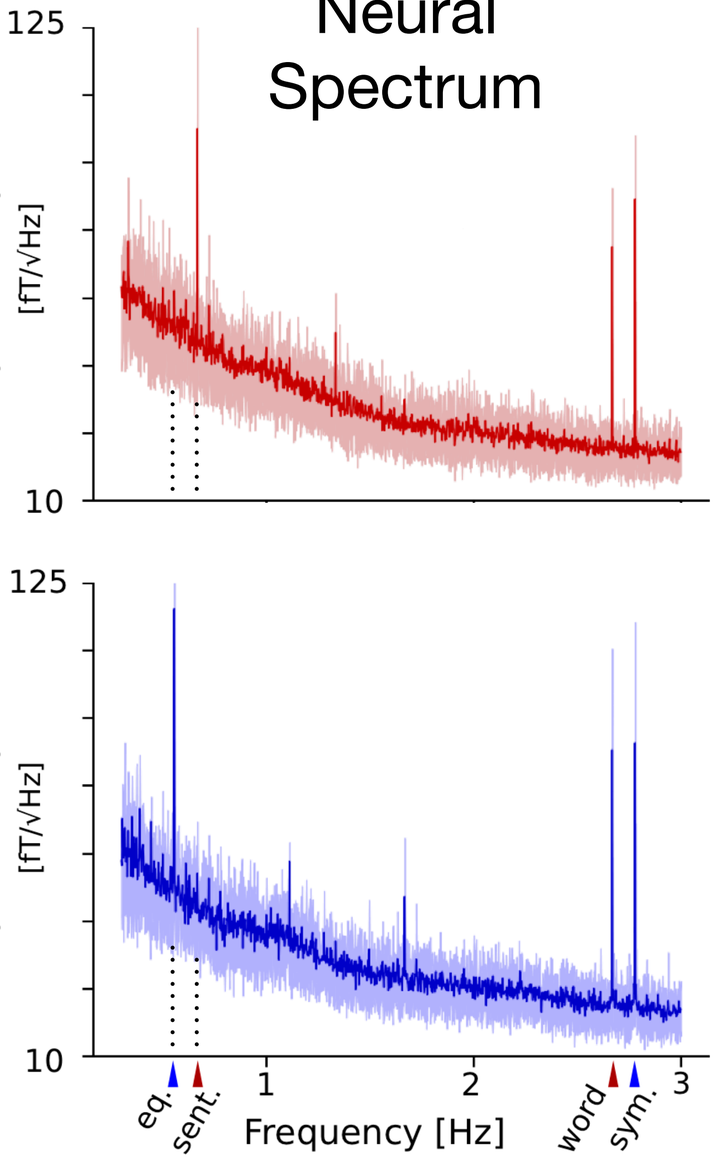
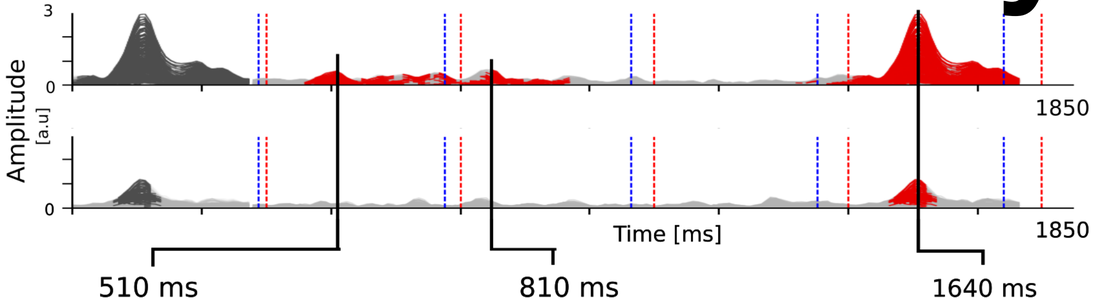
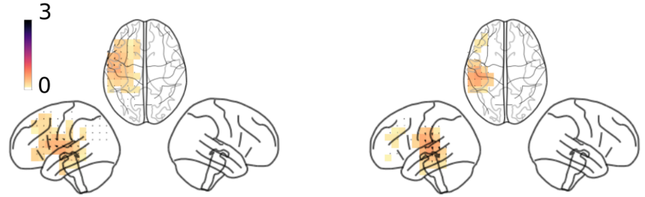
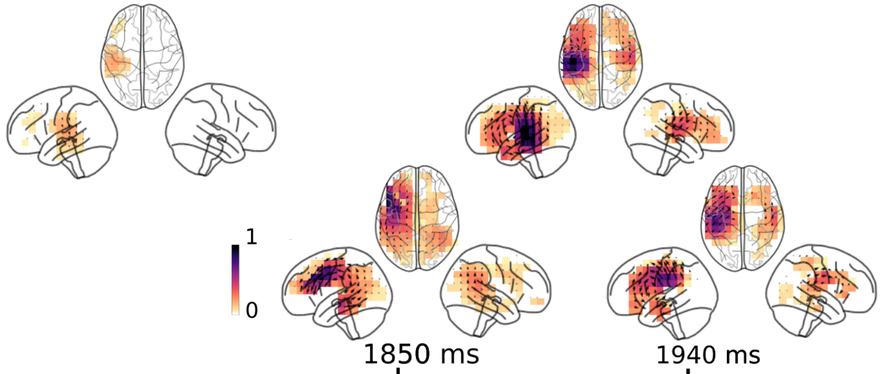




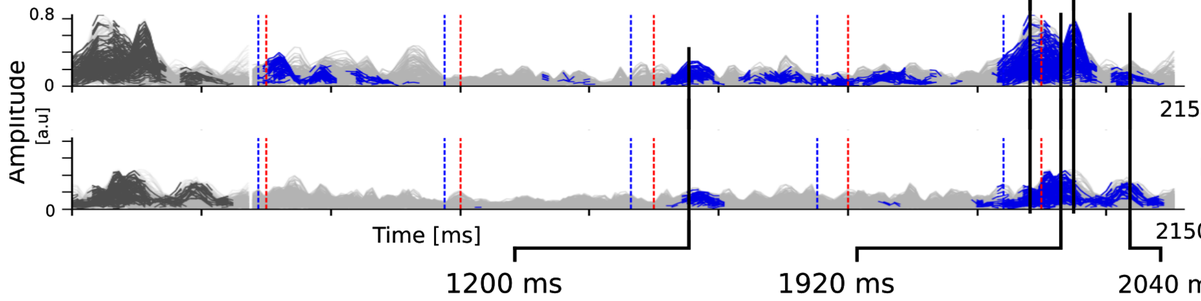
left hemisphere sources

right hemisphere sources





TRFs



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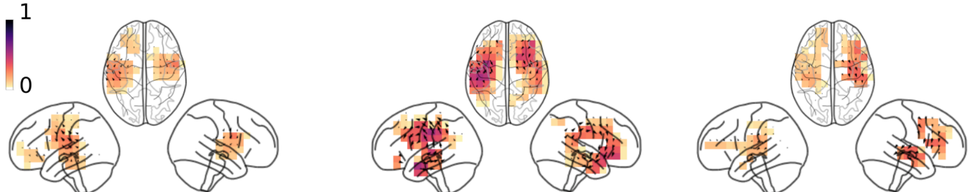

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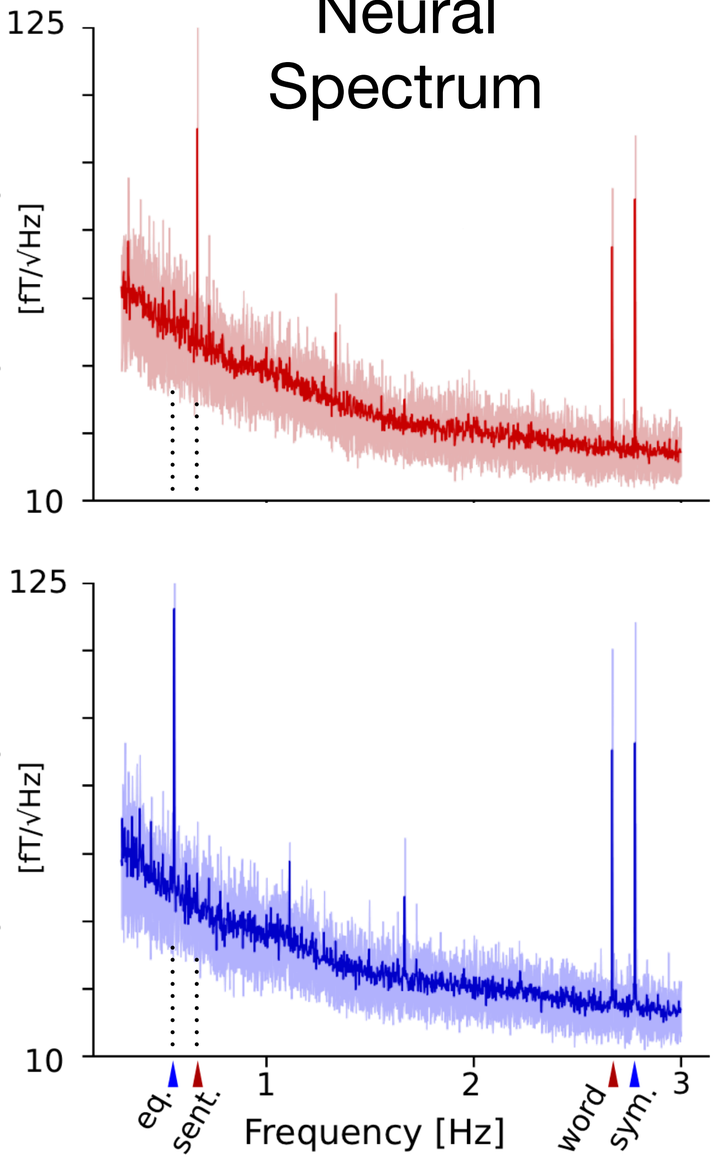

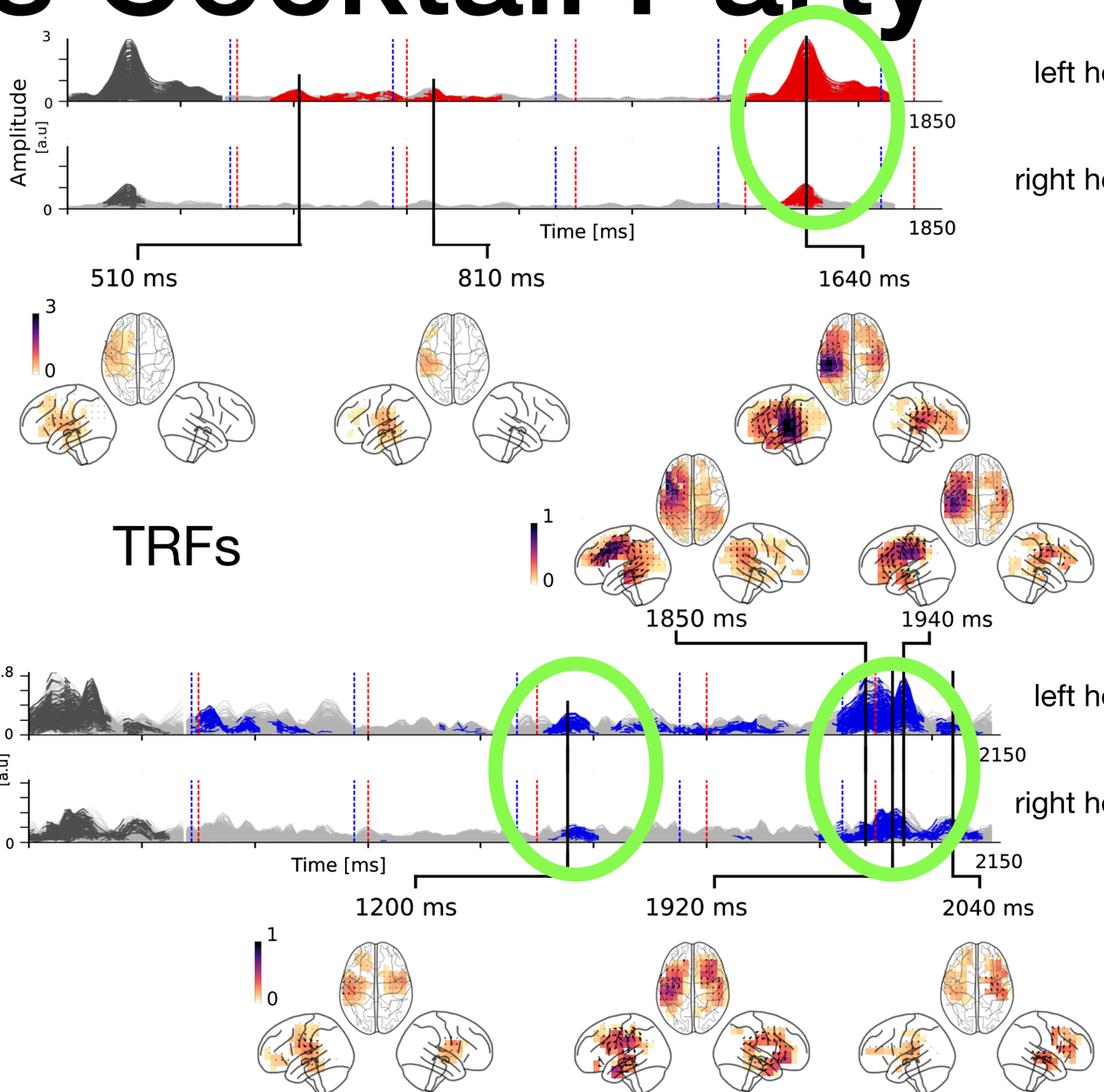

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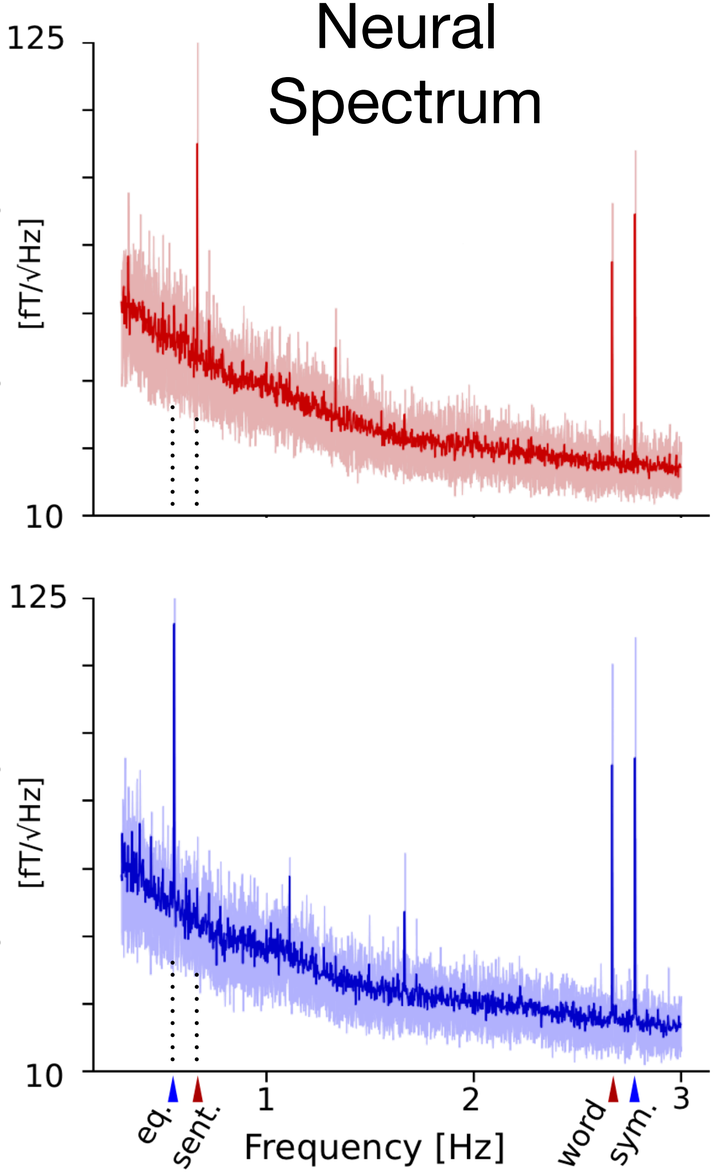

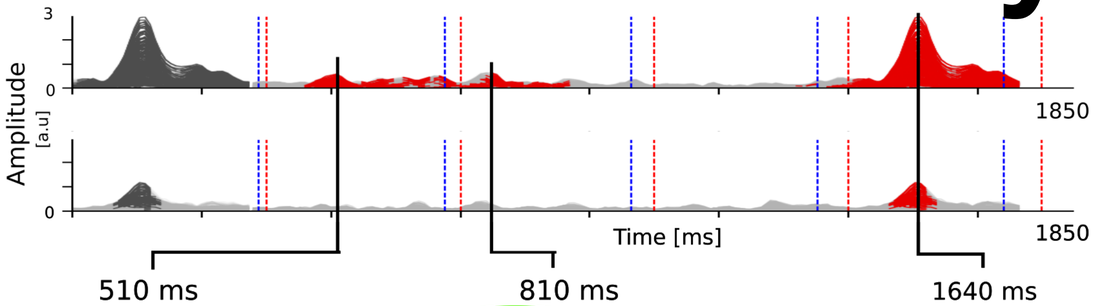

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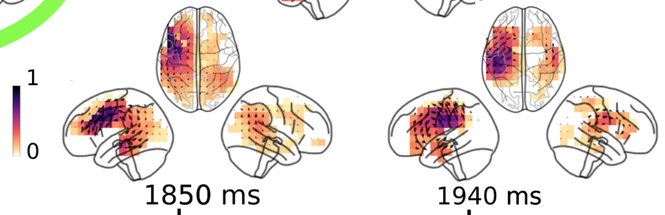
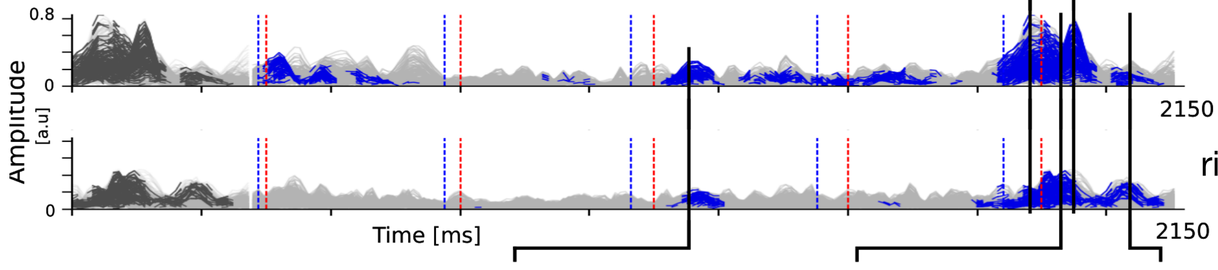
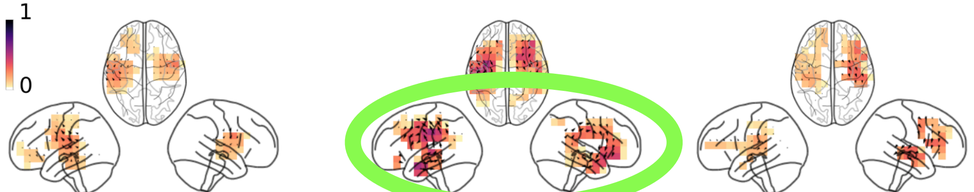
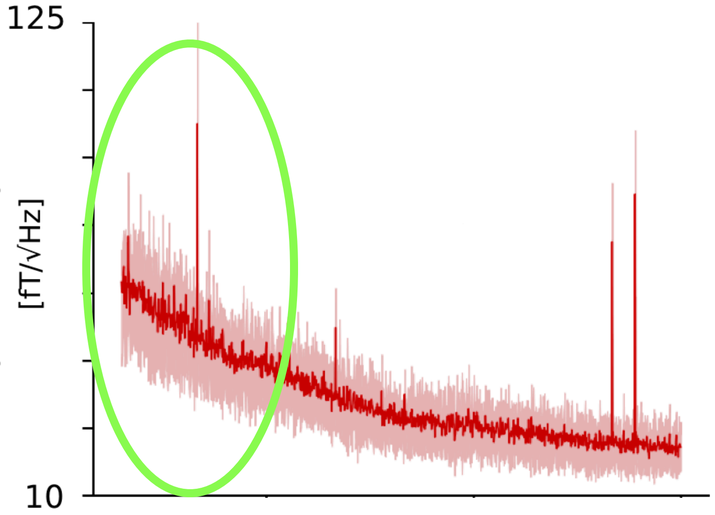




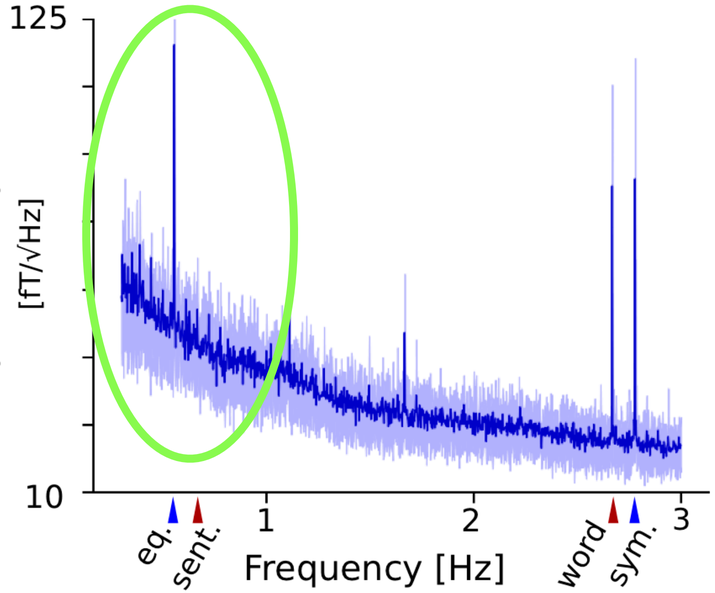


Representations of Understanding

Attend to Sentences



Attend to Equations



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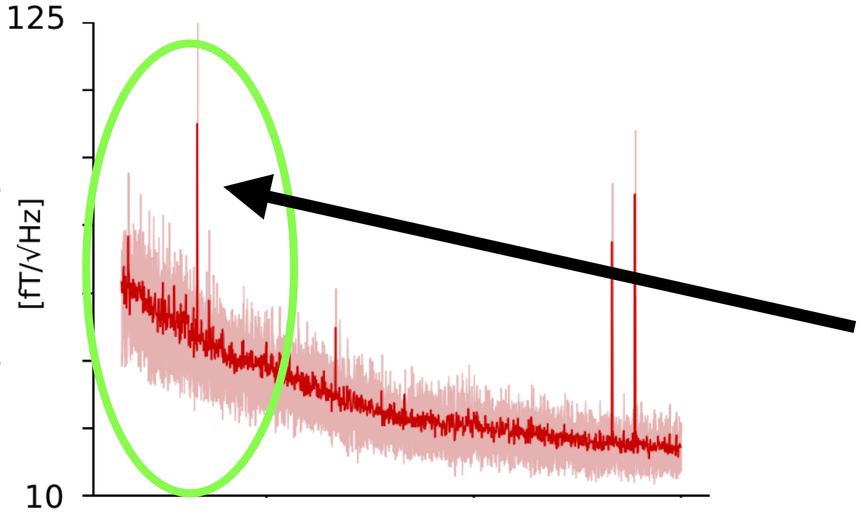

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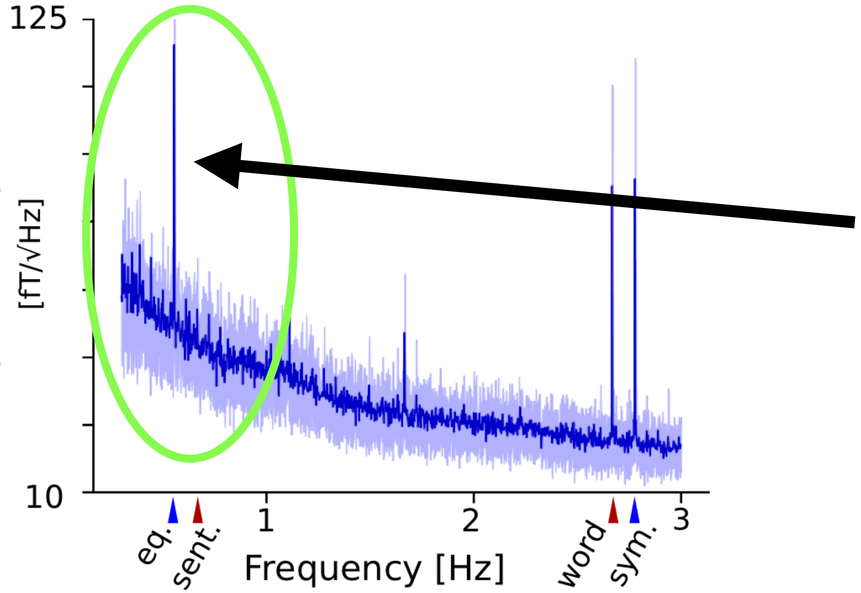
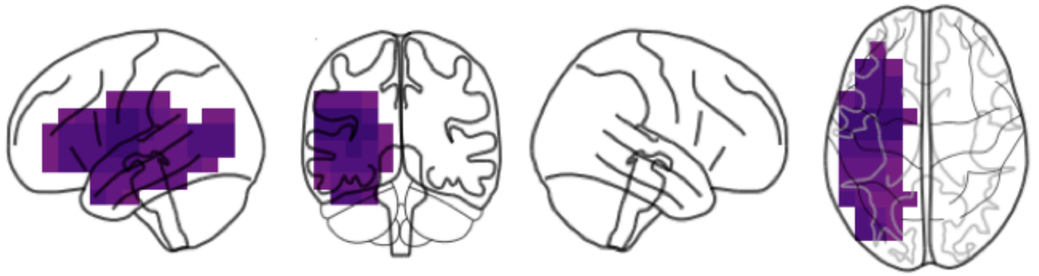
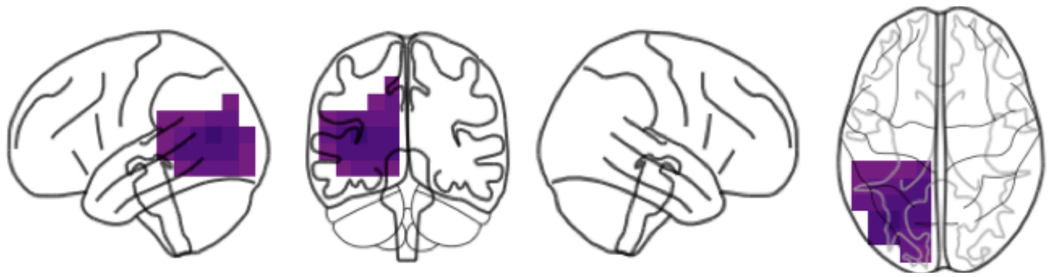


Neural Correlation with Behavior





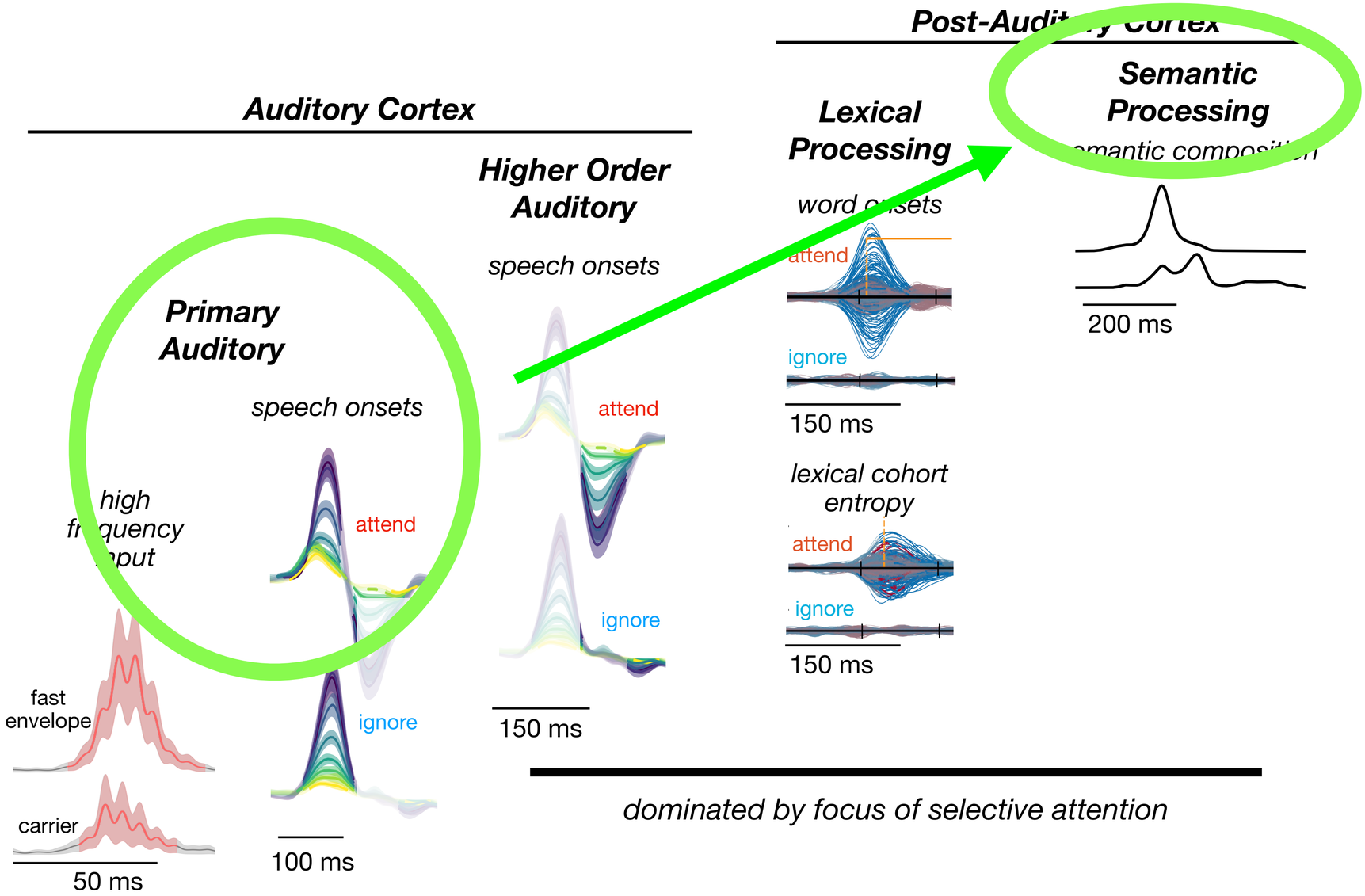
Neural Markers of Comprehension

- 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

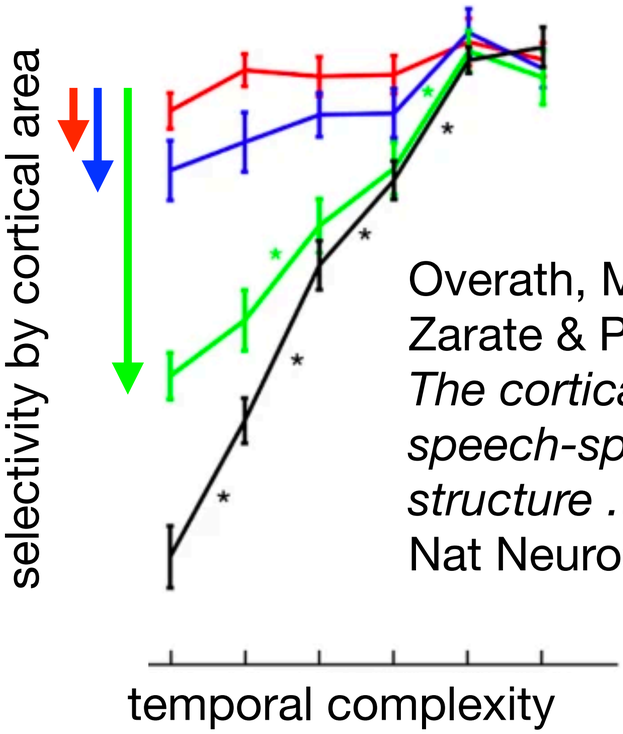
- Introduction—Cortical representations of continuous speech
- *Early & fast* cortical representation of continuous speech
- Cortical representations of speech *meaning*
- *Progression* of representations of continuous speech through cortex (bottom-up and top-down)

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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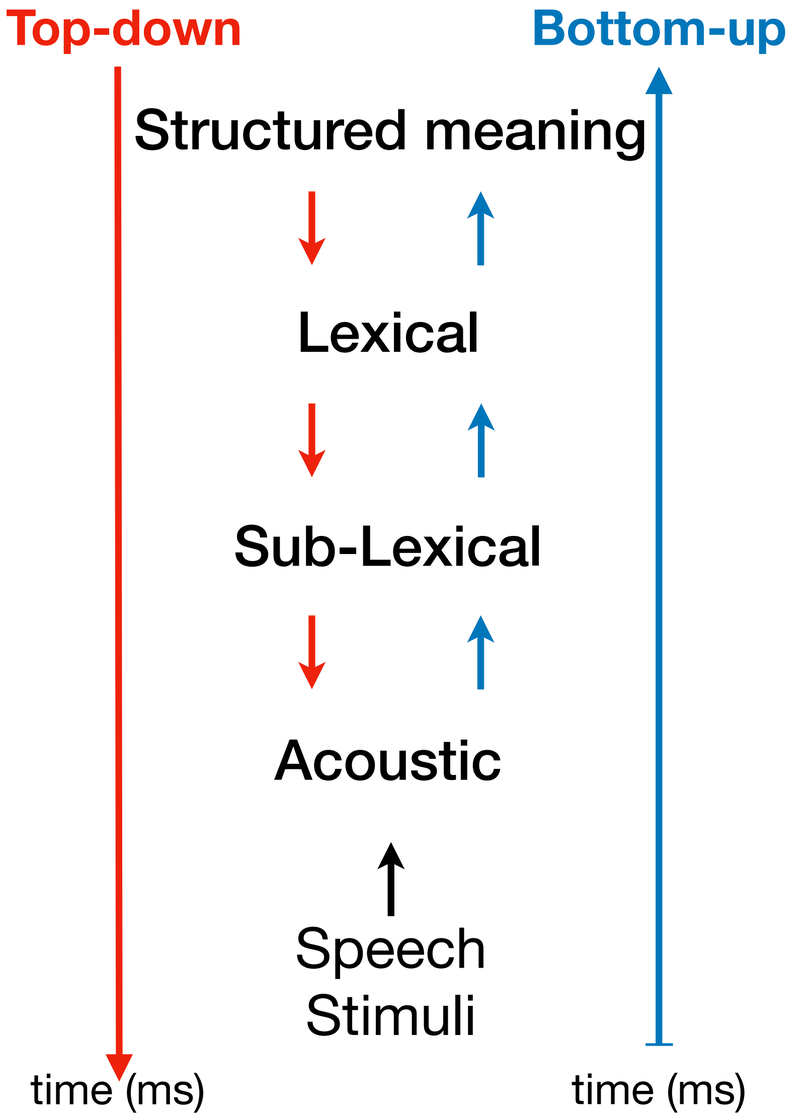


Brodbeck et al. (2022) *Parallel Processing in Speech Perception: Local and Global Representations…*, eLife

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*

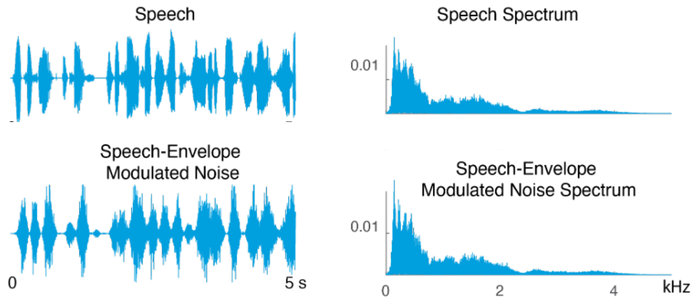
Experimental Design

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*

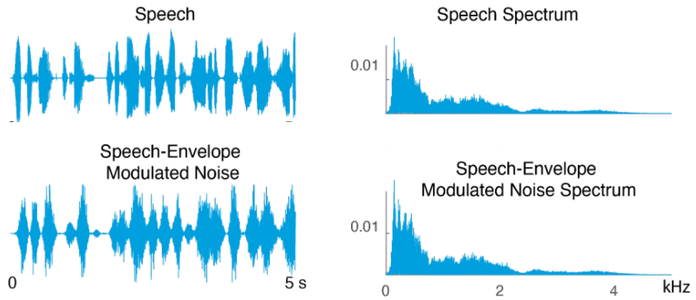
Experimental Design

Speech-envelope Modulated Noise

Non-words

Scrambled words

Narrative



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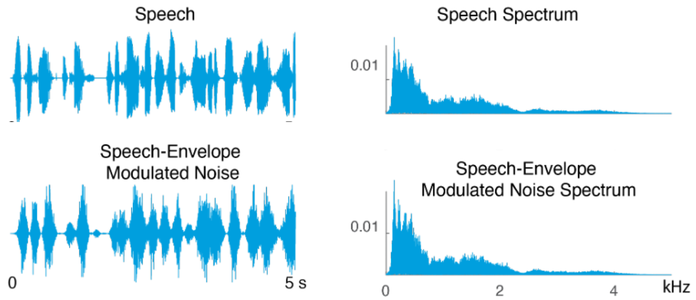

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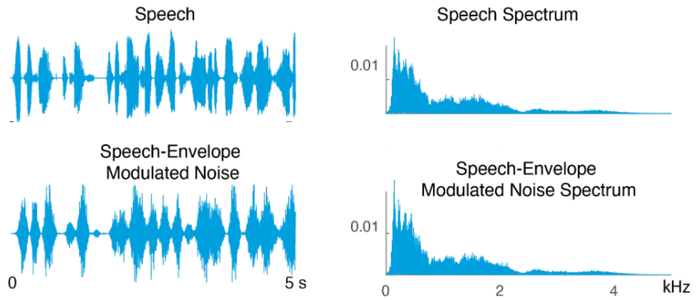
Scrambled words

Narrative



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continuous-speech-like prosody and rhythm

Karunathilake et al. *in preparation*

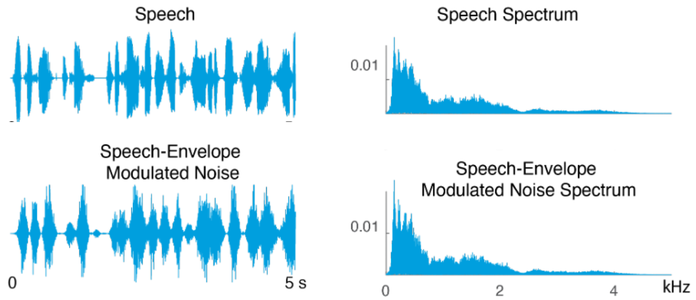
Experimental Design

Speech-envelope Modulated Noise

Non-words

Scrambled words

Narrative



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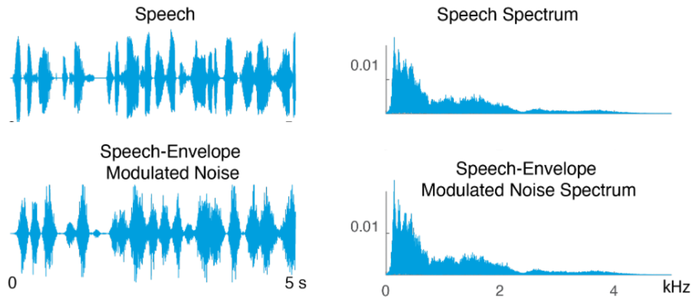

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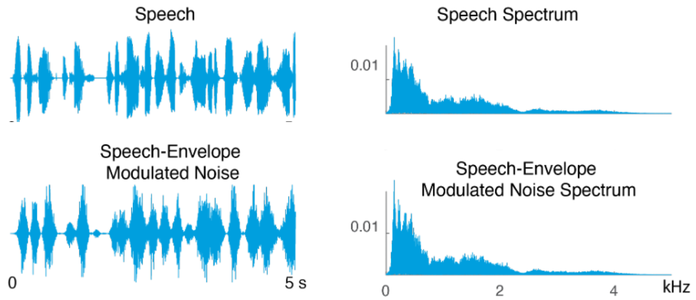

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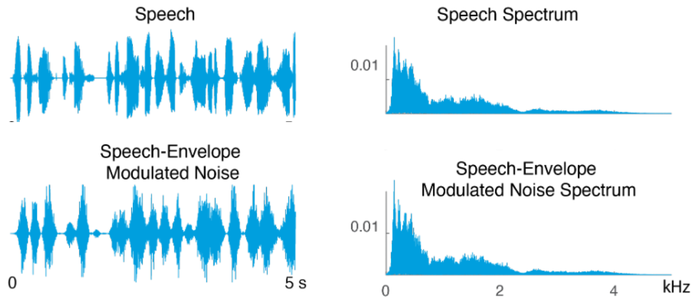

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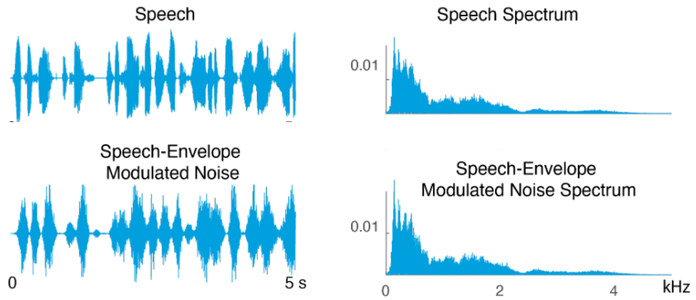

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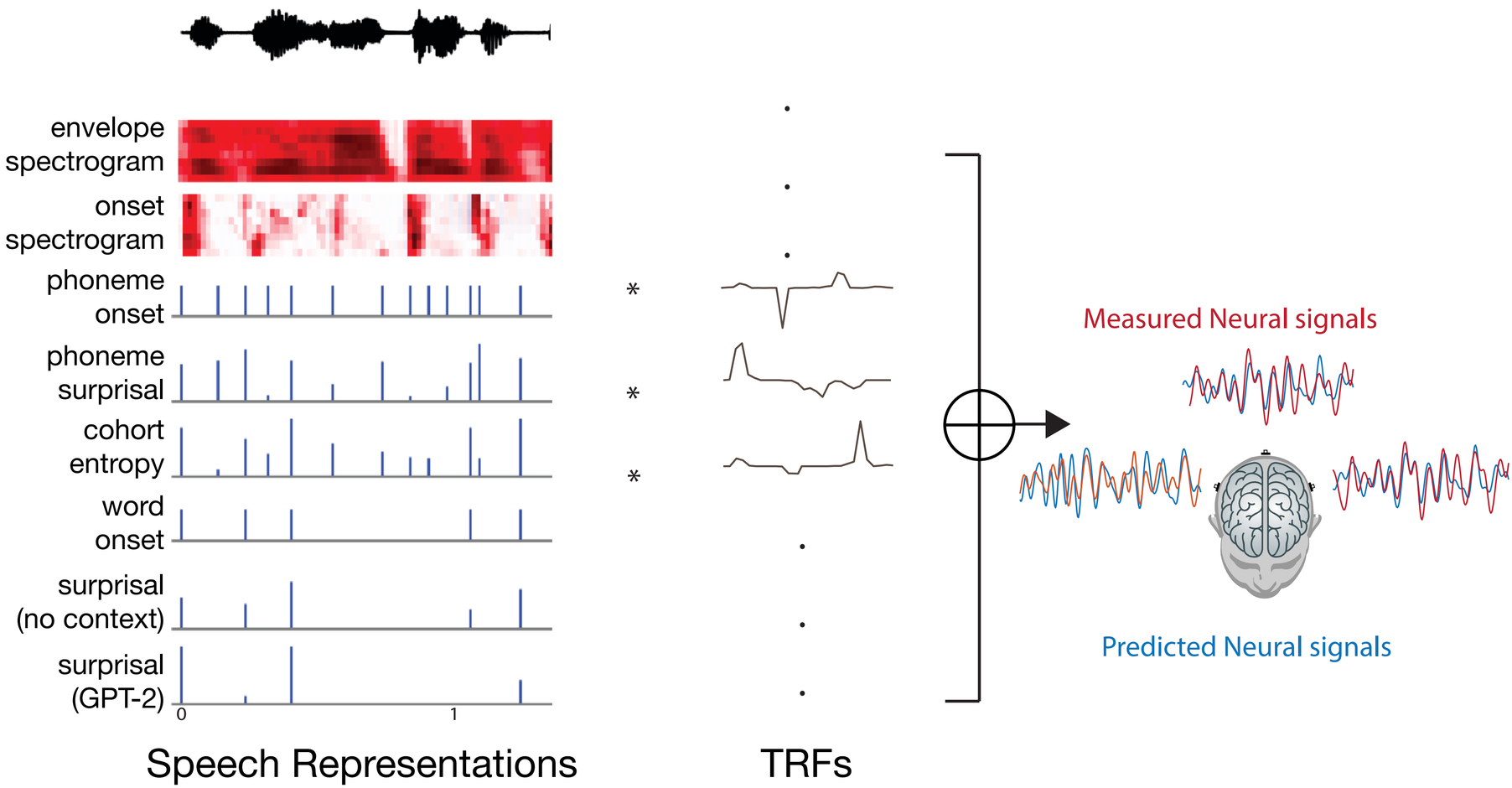
Simultaneous Temporal Response Functions

- 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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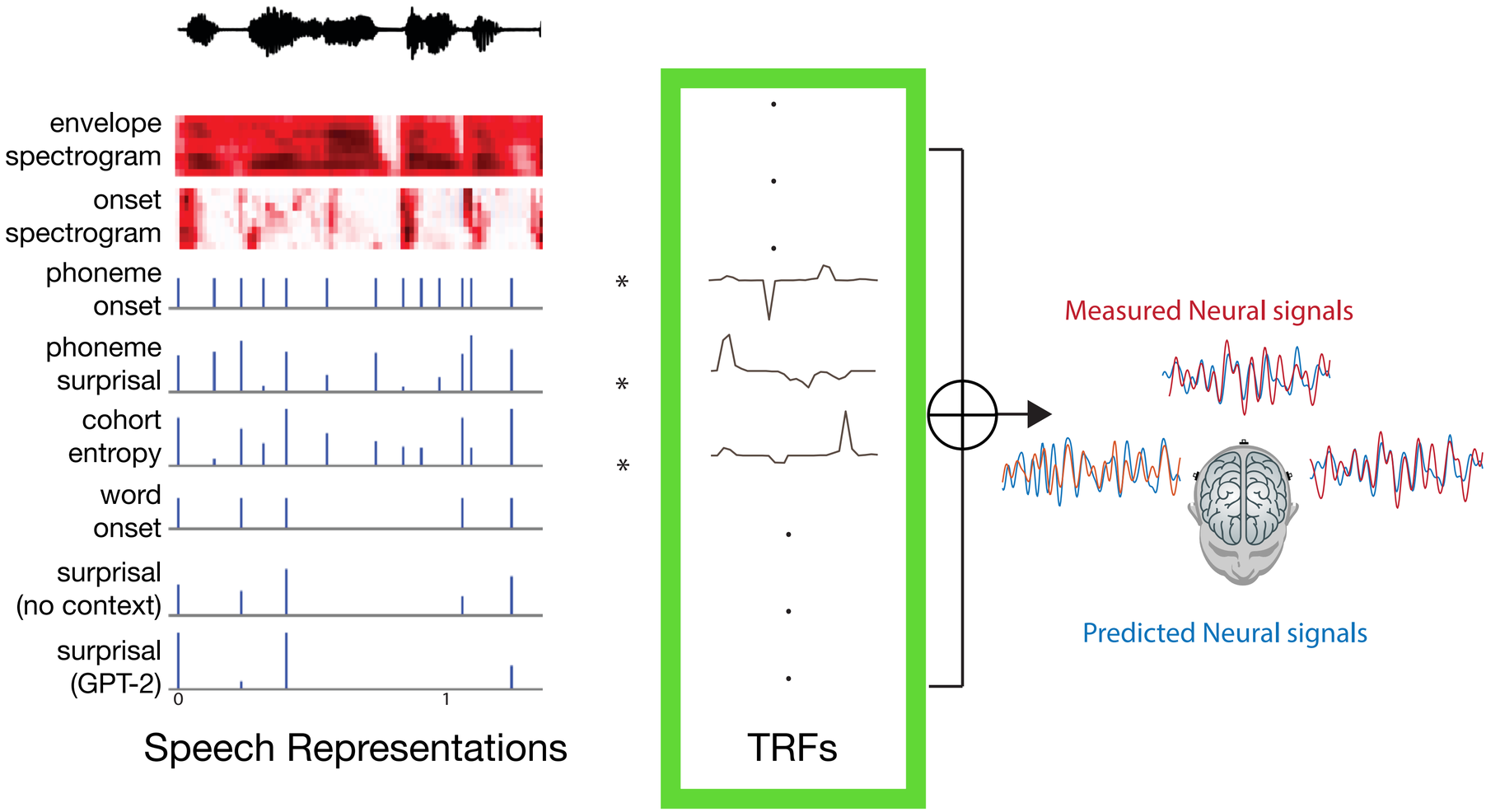
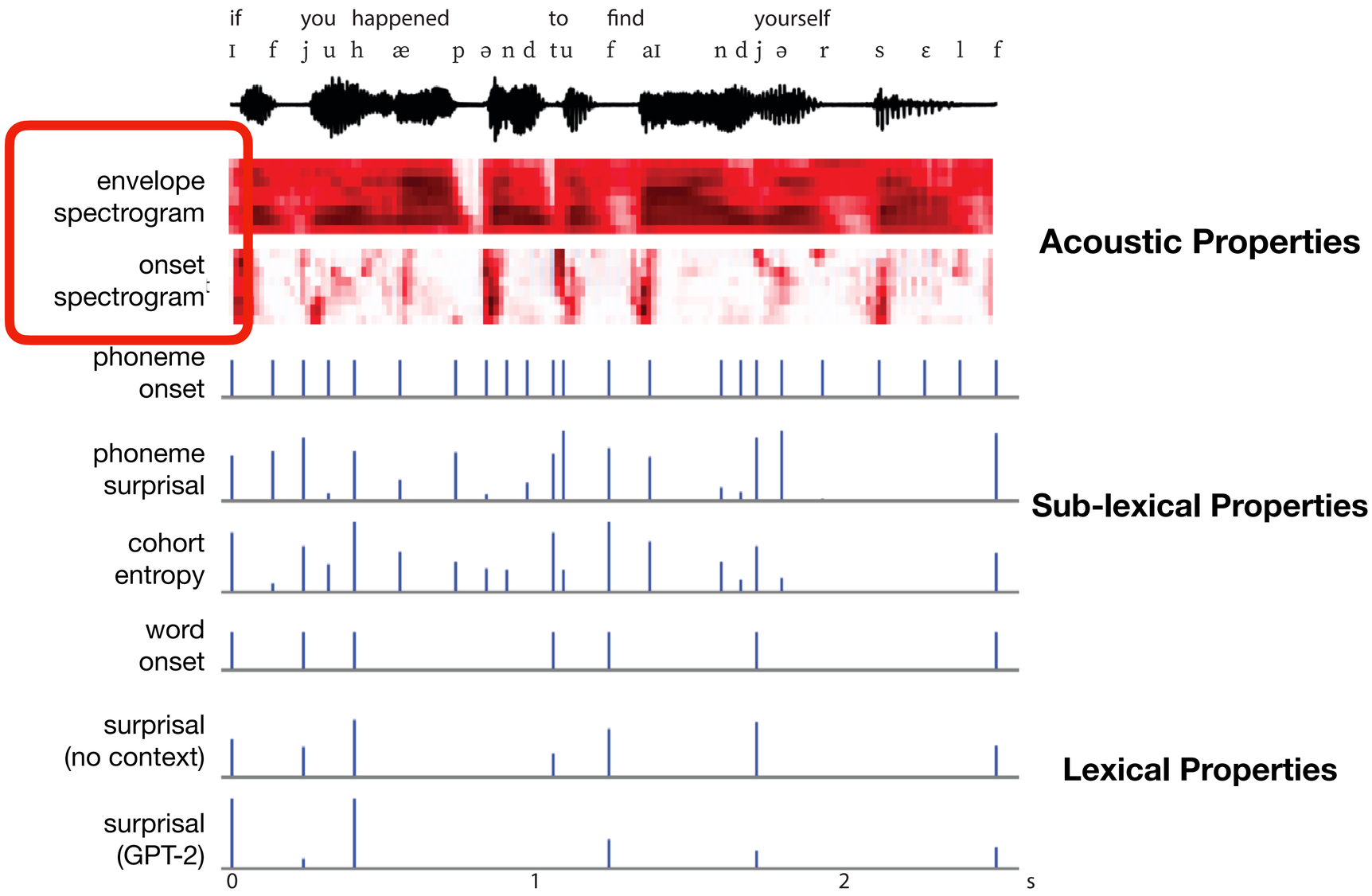


Speech Representations



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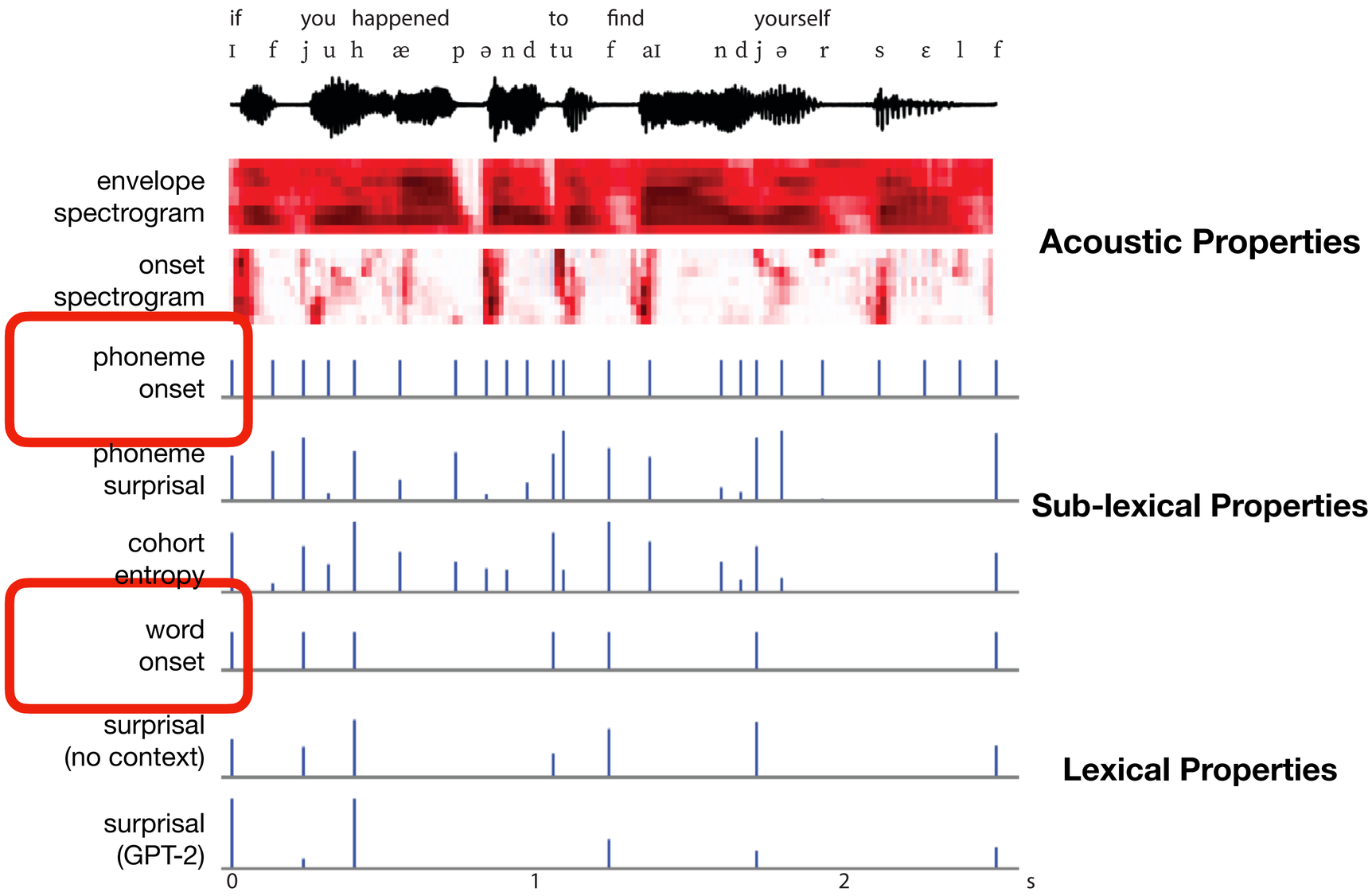

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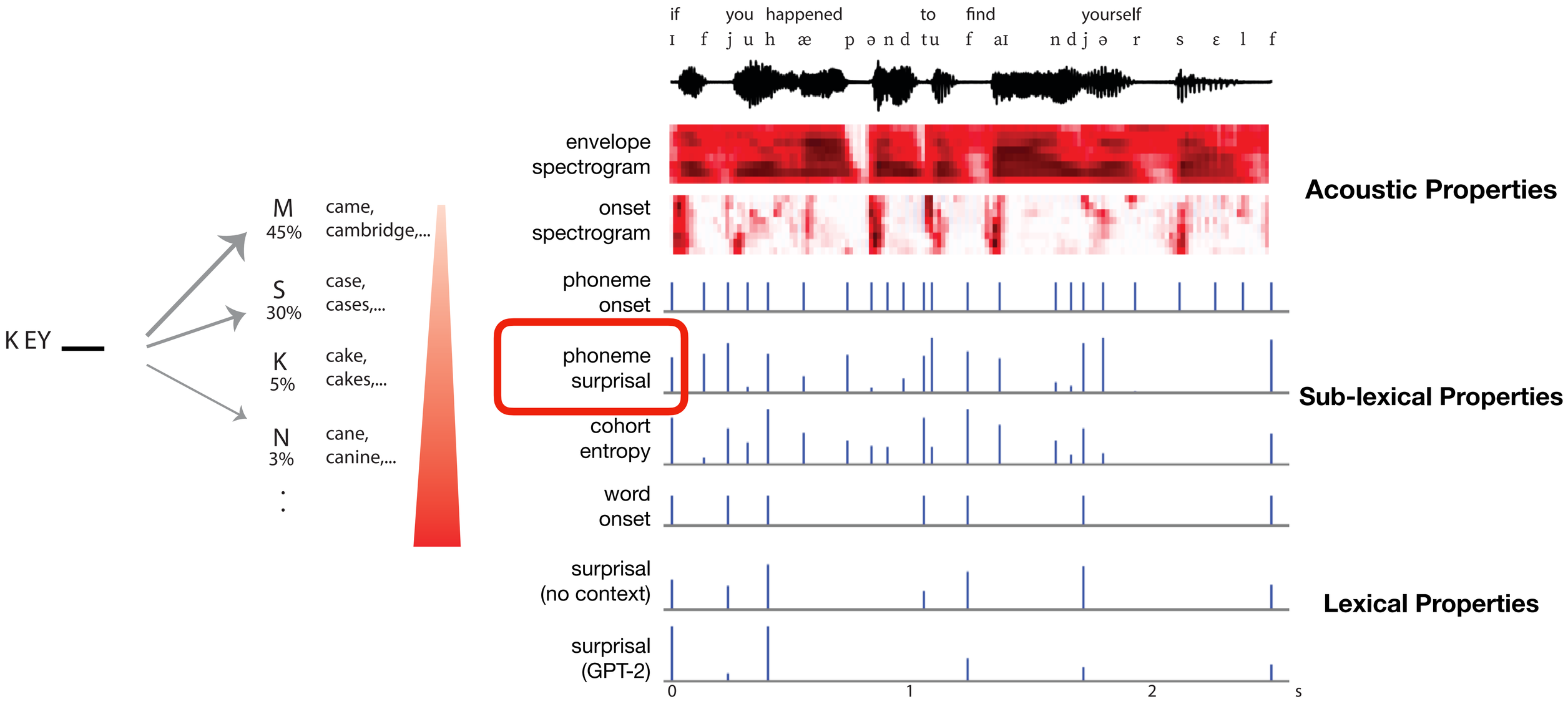

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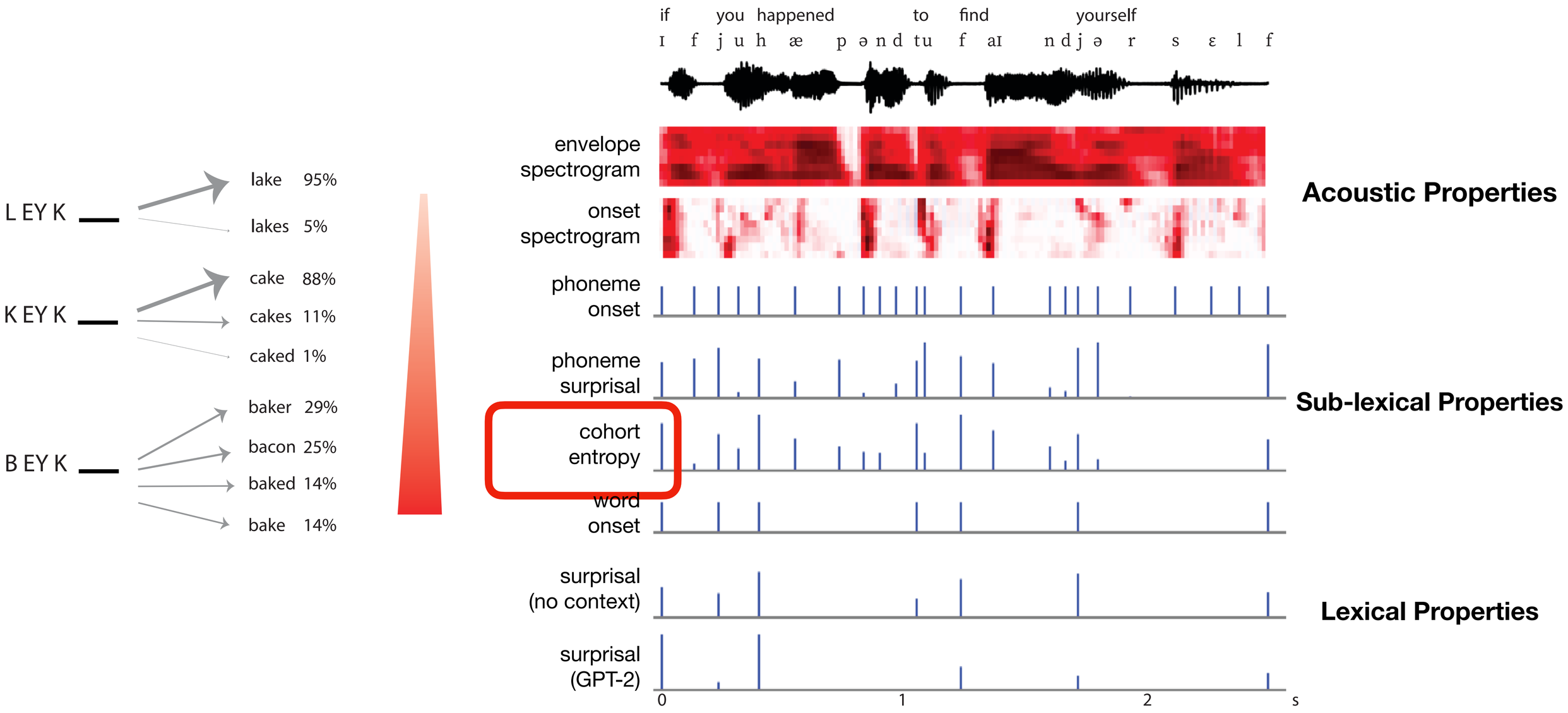

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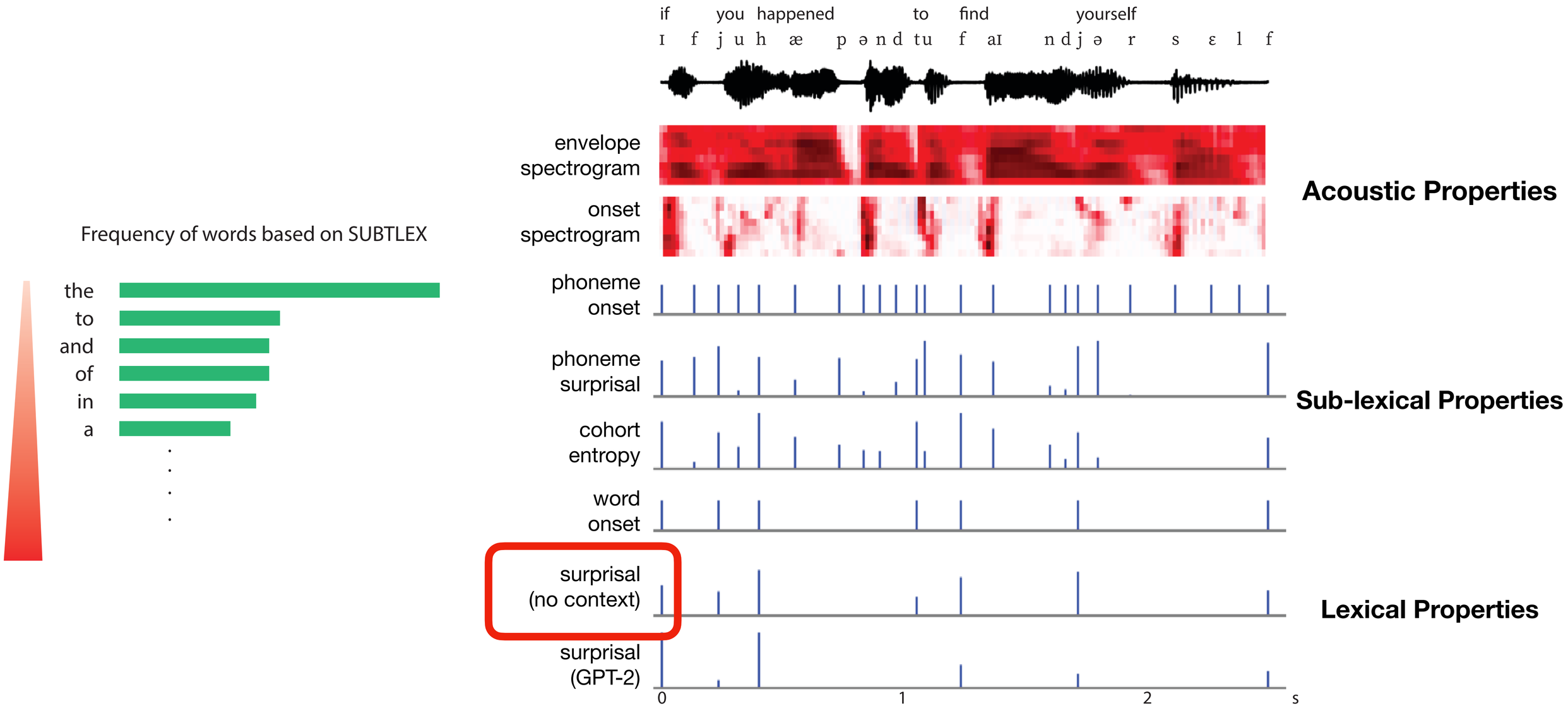

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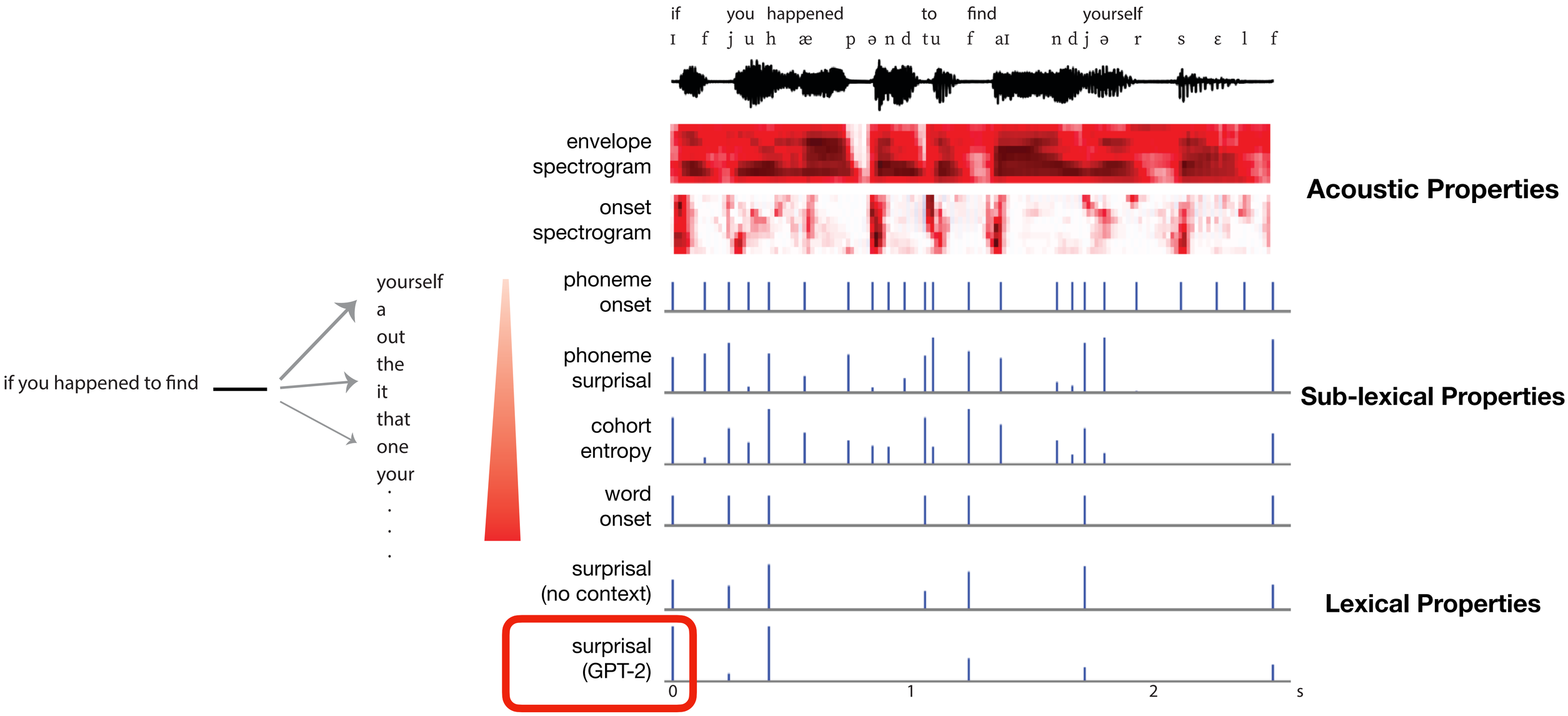
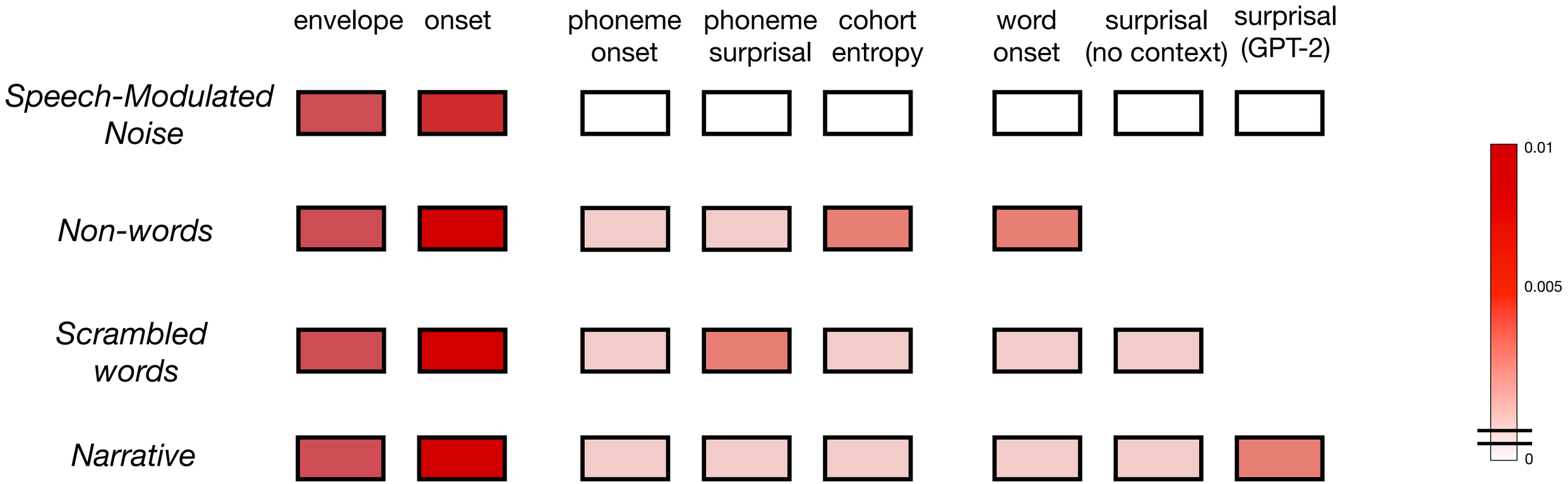


Neural Prediction Results

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
- Context based word surprisal emerges for narrative passage
- When context supports, context based surprisal is better tracked compared to naive surprisal

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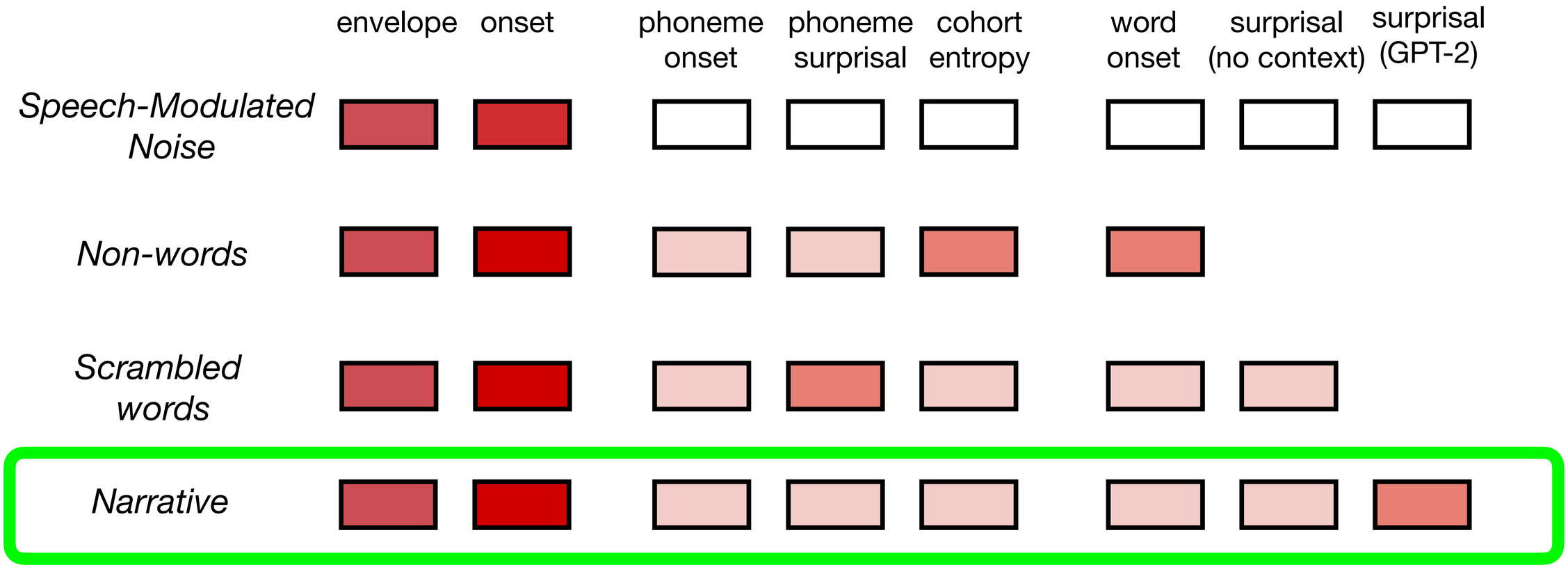

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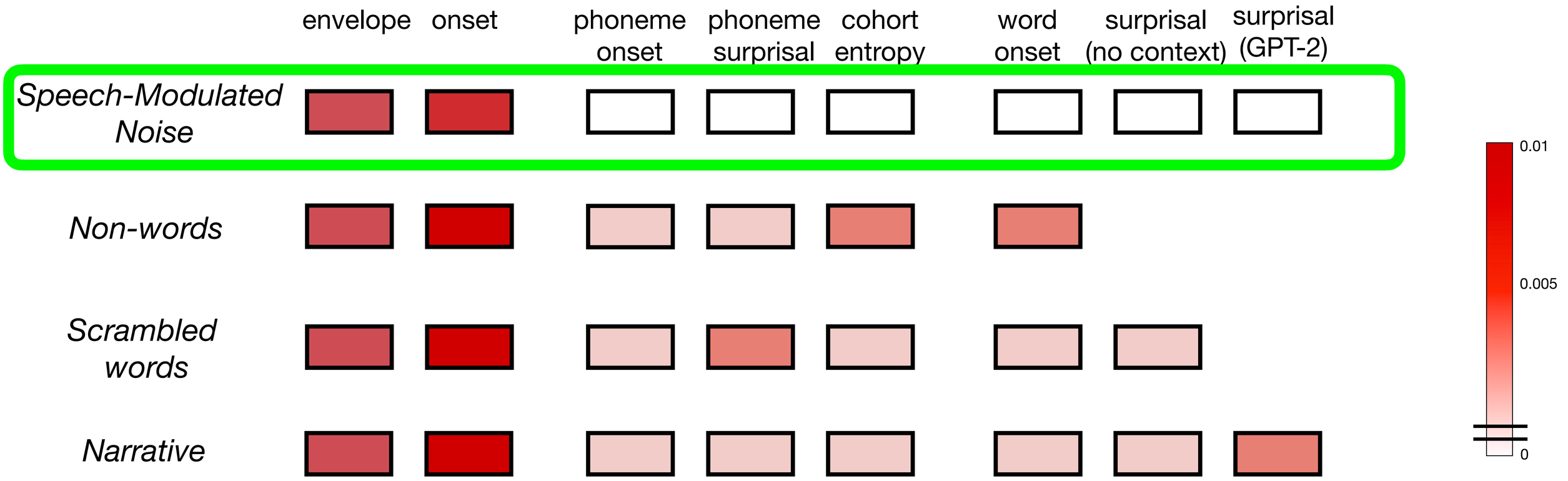

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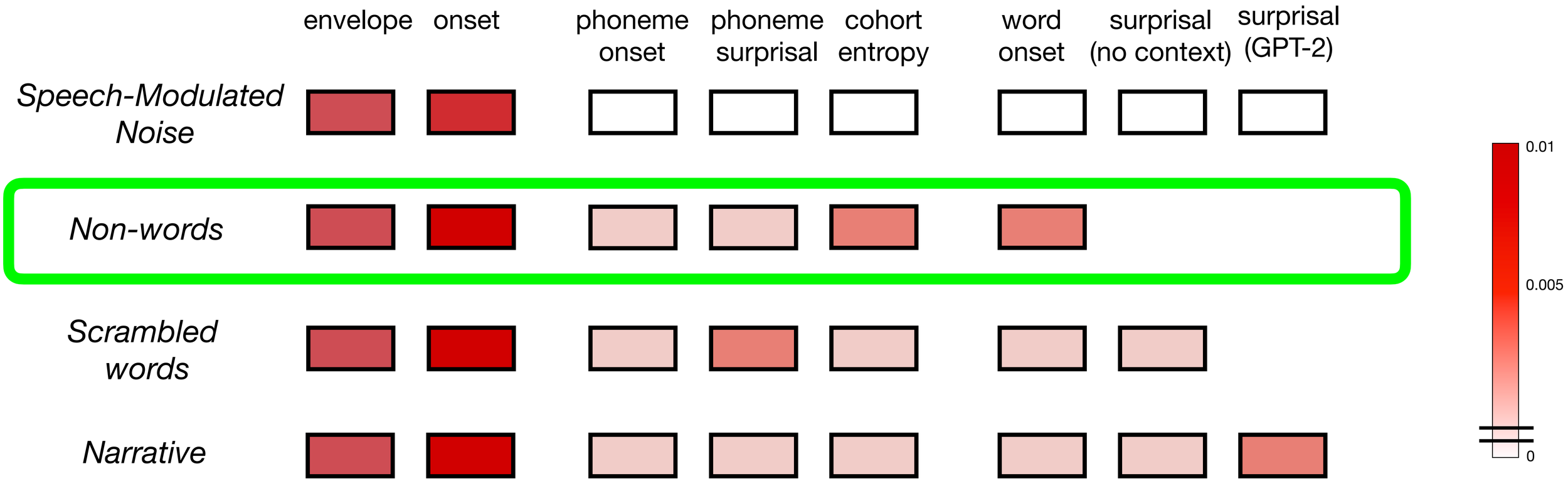

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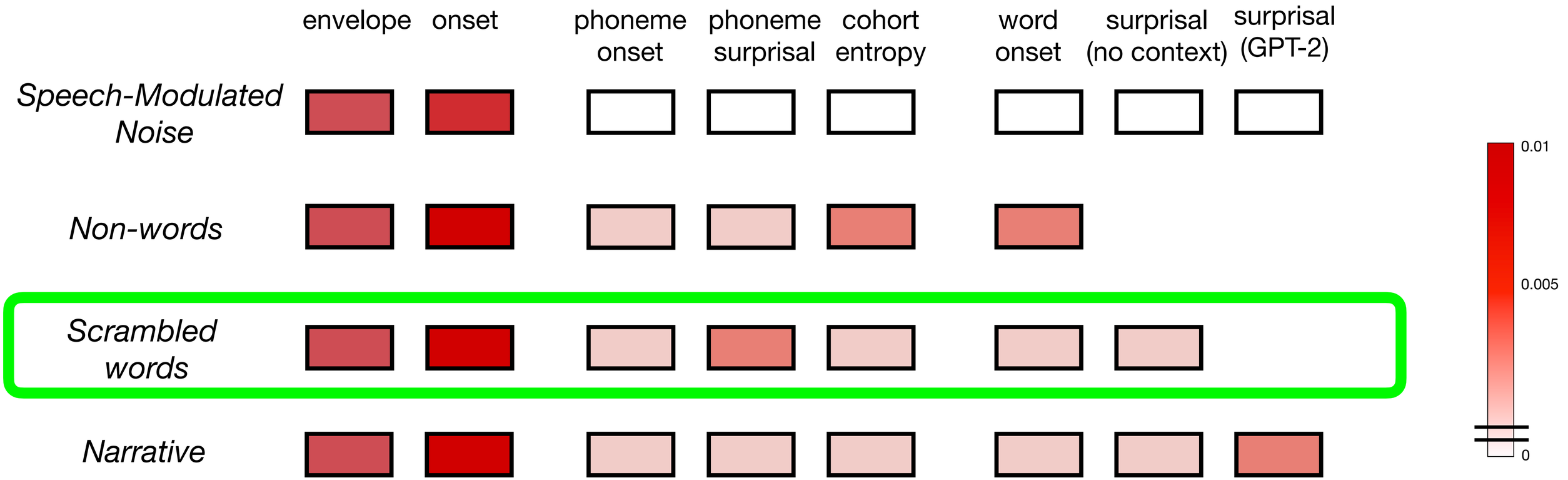

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Hemispheric Lateralization Results

Speech feature

Envelope Onset

Envelope

Phoneme Onset

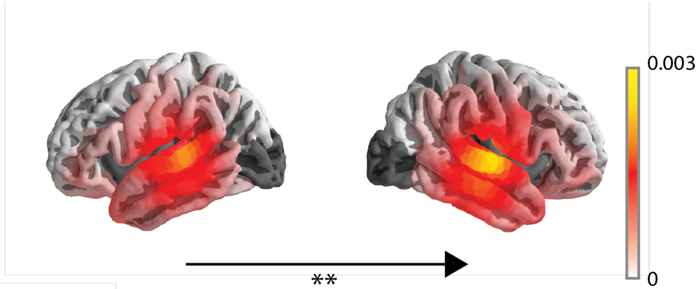
Phoneme Surprisal

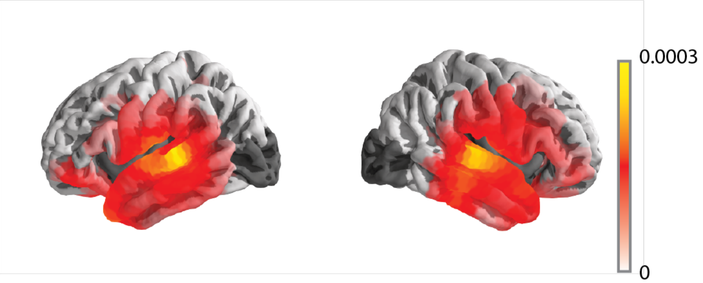
Cohort Entropy

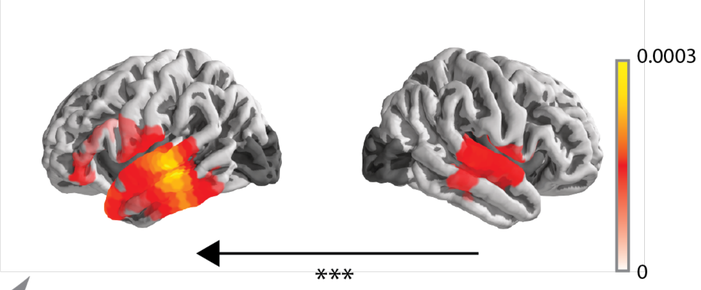
Word Onset

Unigram Surprisal

GPT2 Surprisal





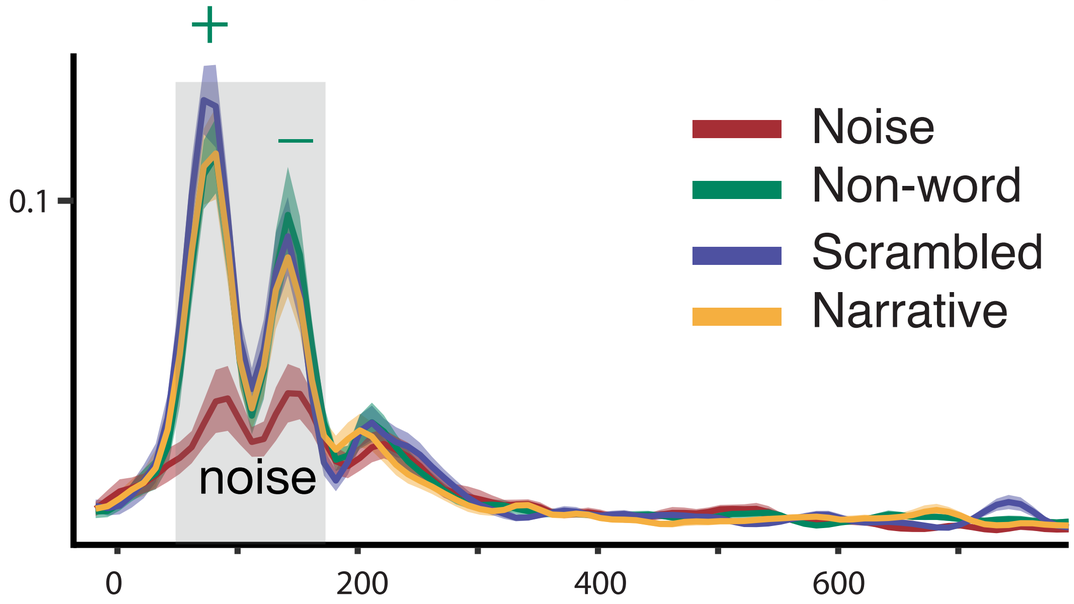


Left Lateralized **Bilateral** **Right Lateralized**

Note: lateralization results can be task dependent

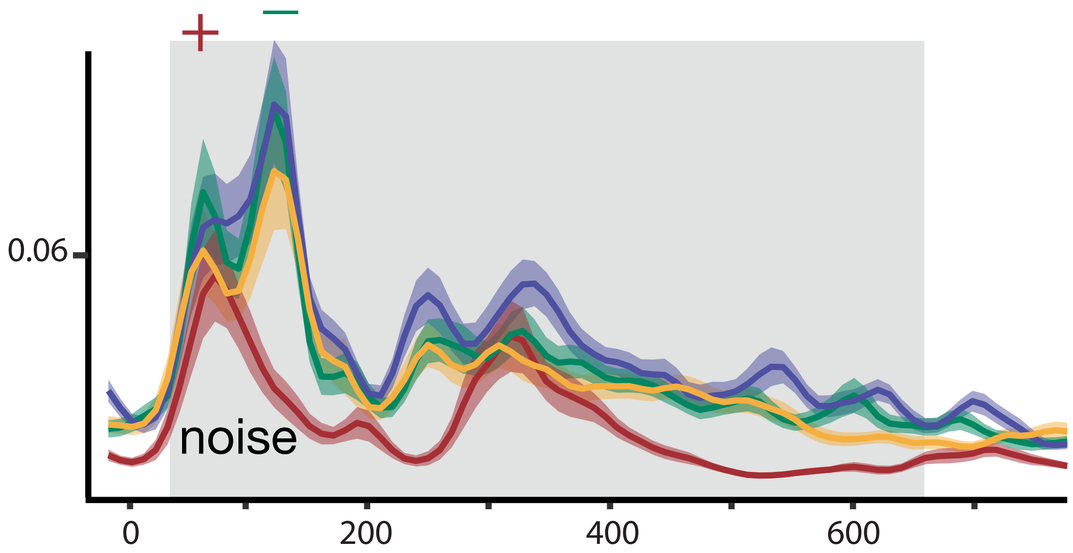
Acoustic TRF Results

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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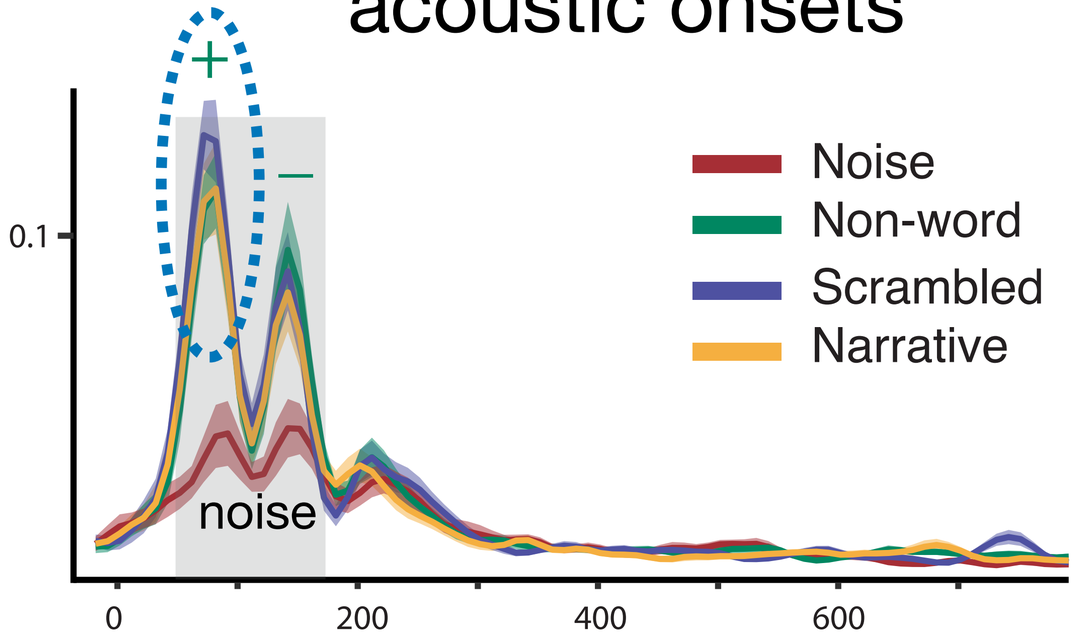

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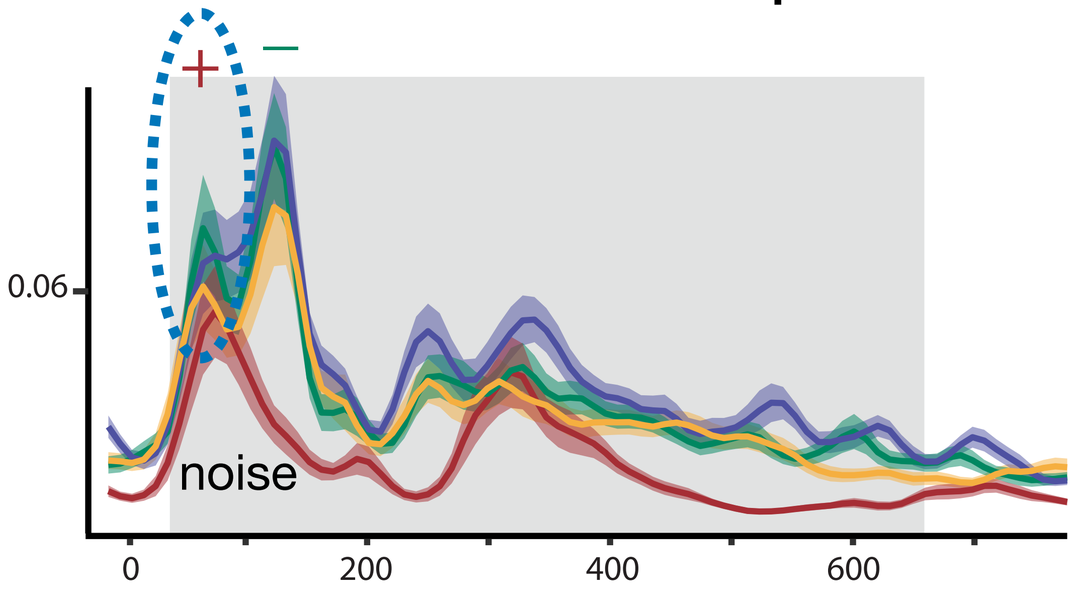

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60 ms: acoustic bottom-up processing

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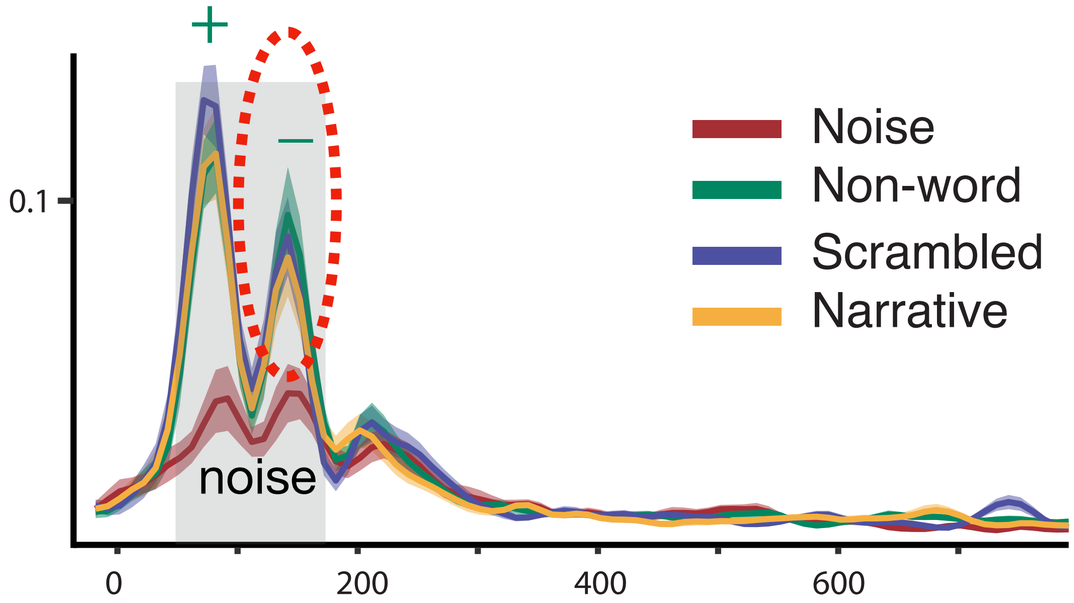

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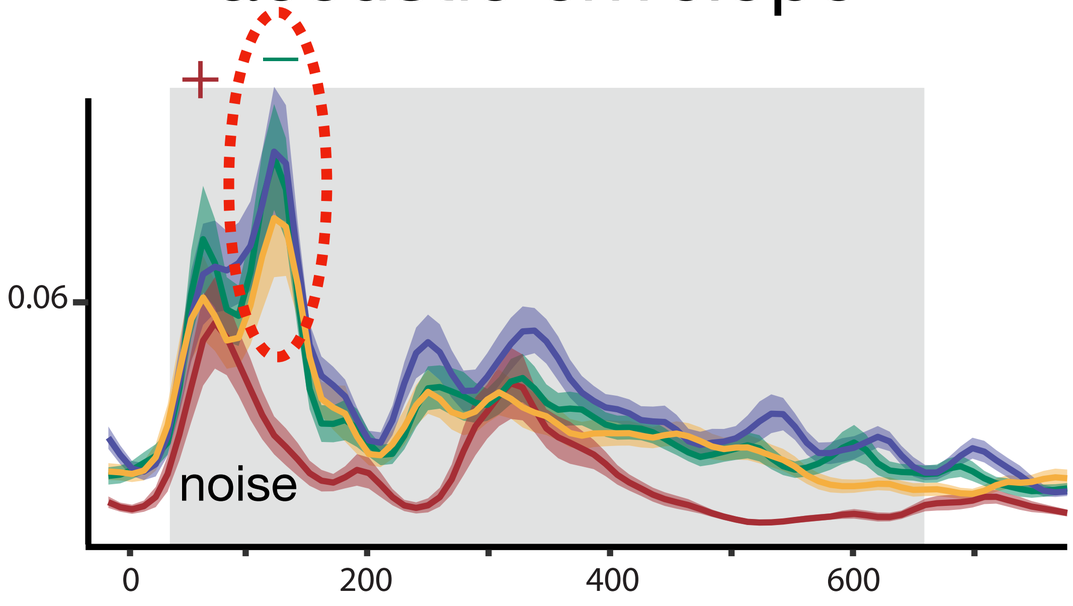

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60 ms: acoustic bottom-up processing

120 ms: acoustic but attention-dependent

right hemisphere shown
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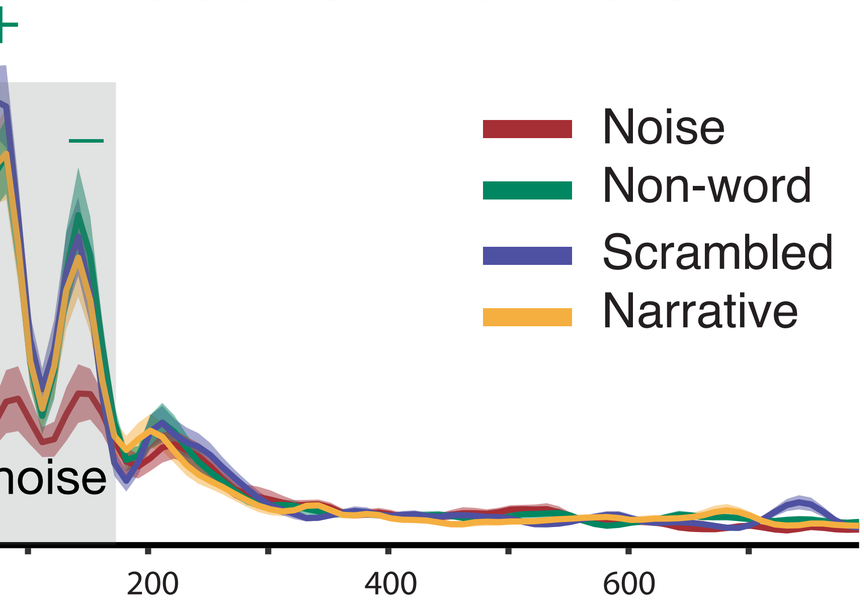
Acoustic TRF Results

acoustic onsets



Noise
Non-word
Scrambled
Narrative

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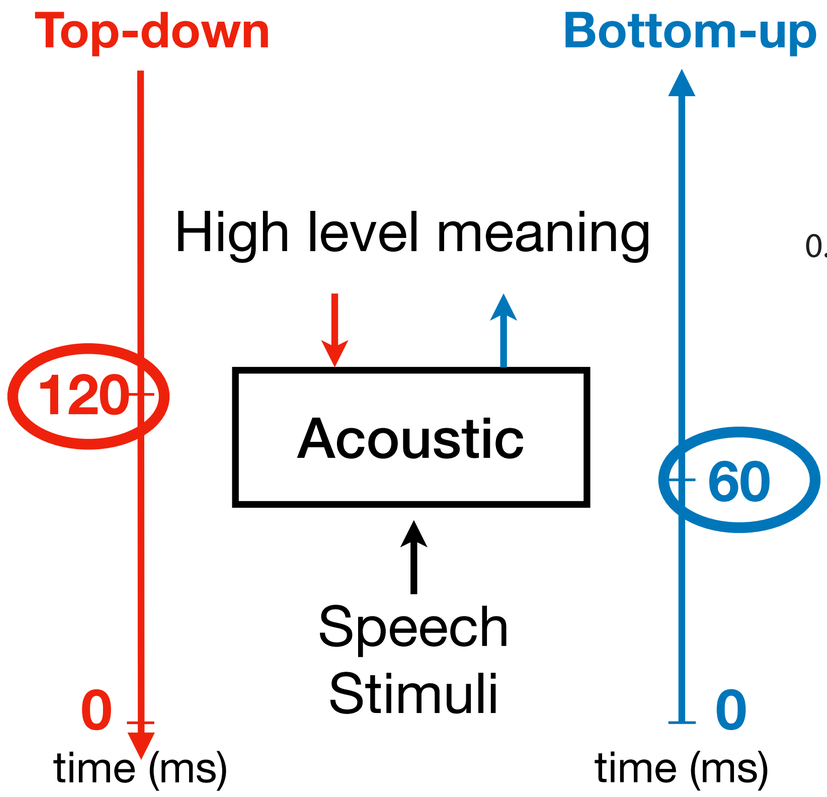

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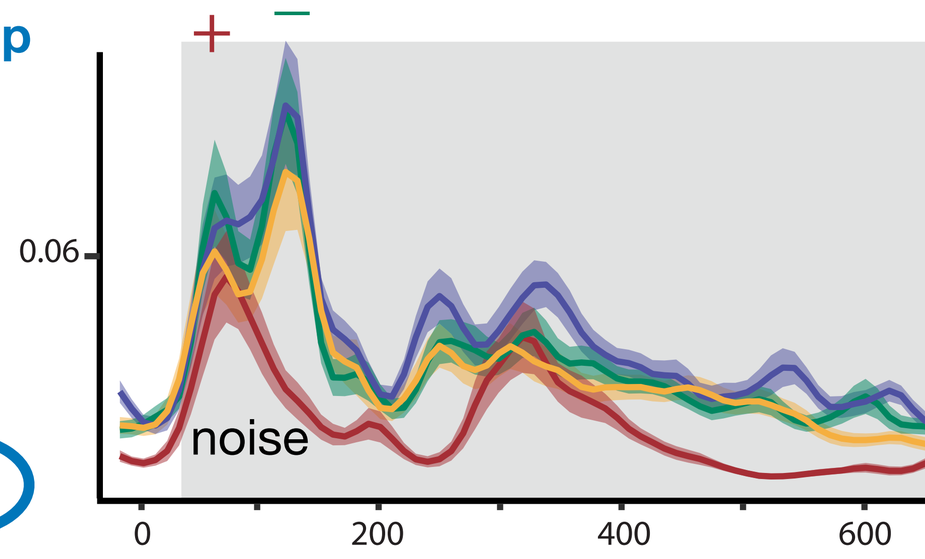

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Phonemic TRF Results

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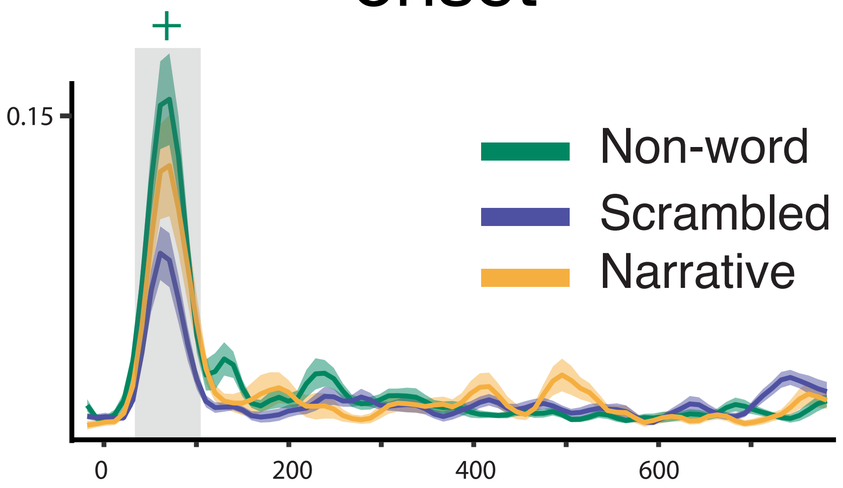
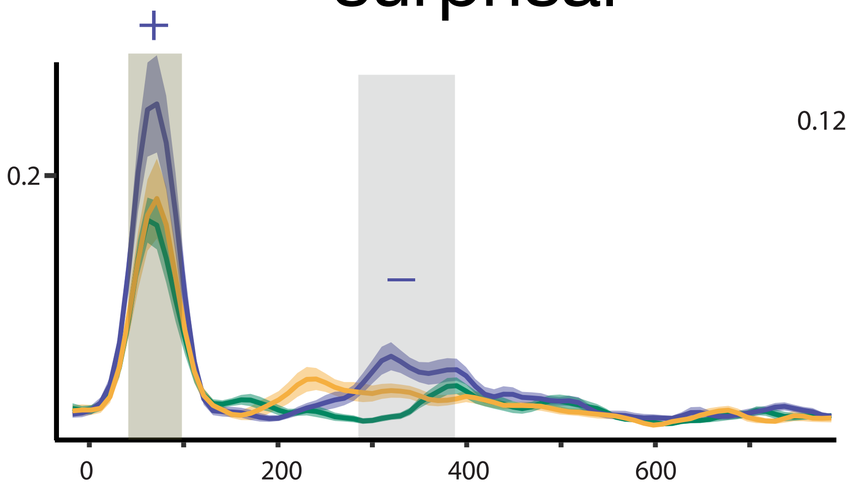


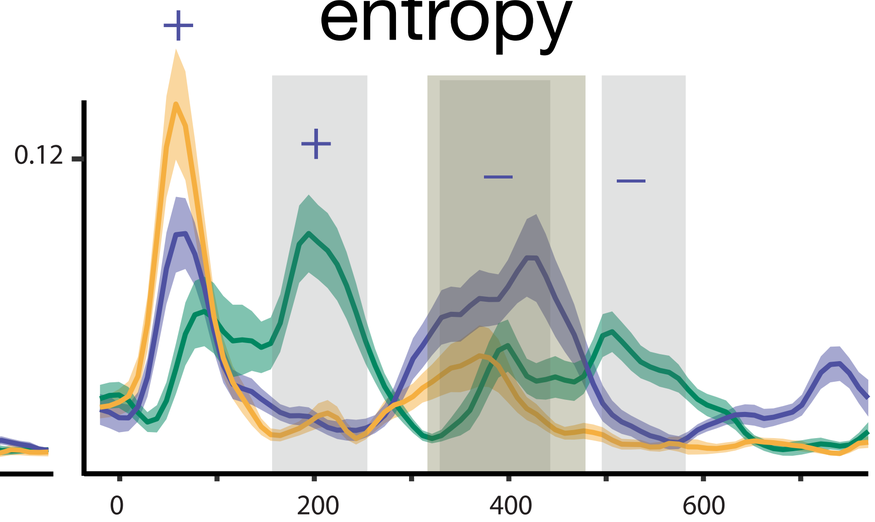
- Non-words largest
- No later processing

phoneme surprisal



- Early phone processing ~80 ms (scrambled > narrative)
- Late phone processing ~350 ms) (words > non-words)

cohort entropy

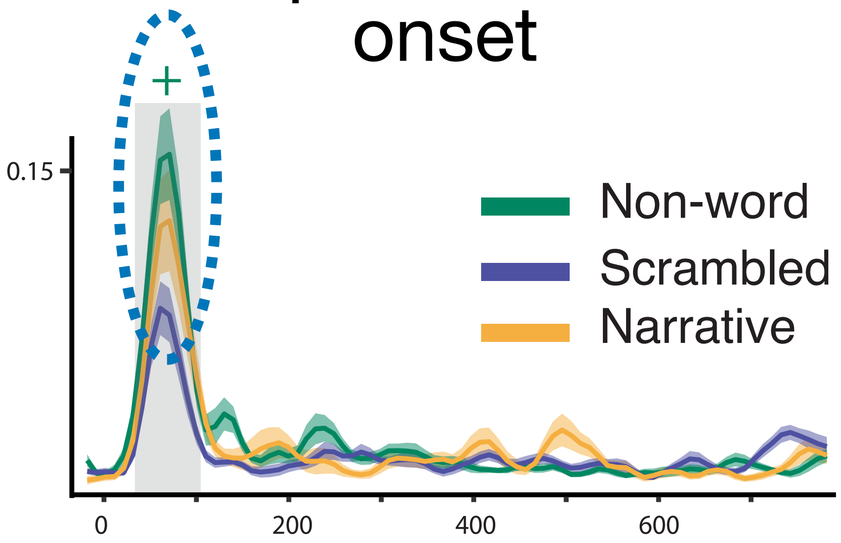


- Late context processing
- N400-like response (reduced for narrative)
- Additional/delayed peaks in non-words (difference in stimulus distributions)

left hemisphere shown (right similar)

Phonemic TRF Results

phoneme onset



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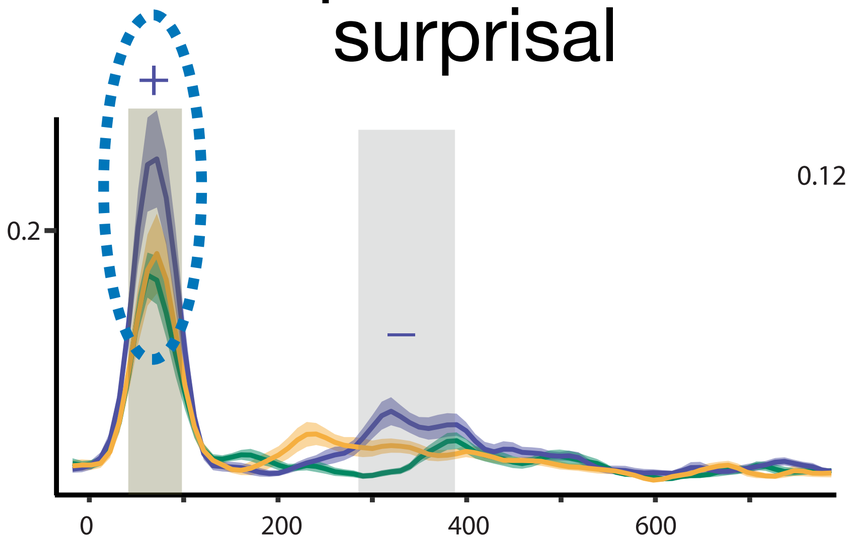
phoneme surprisal



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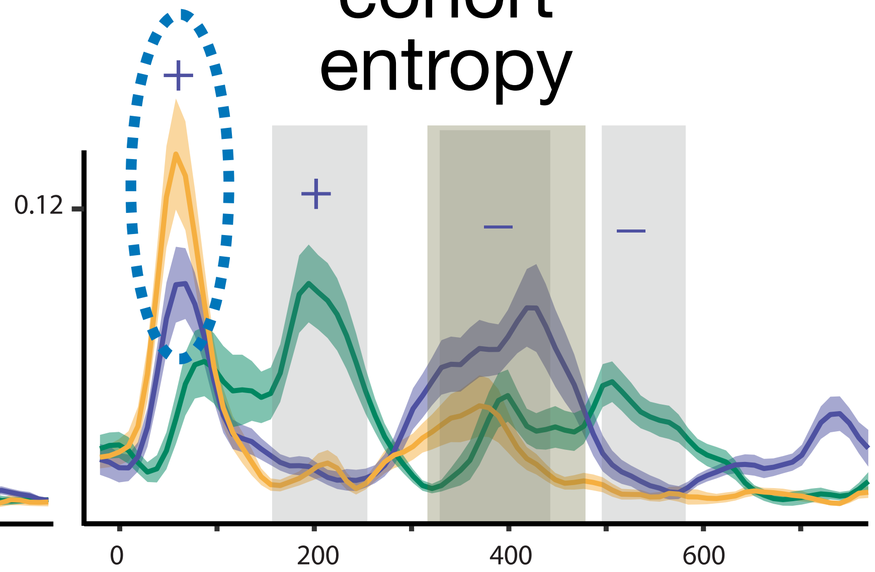

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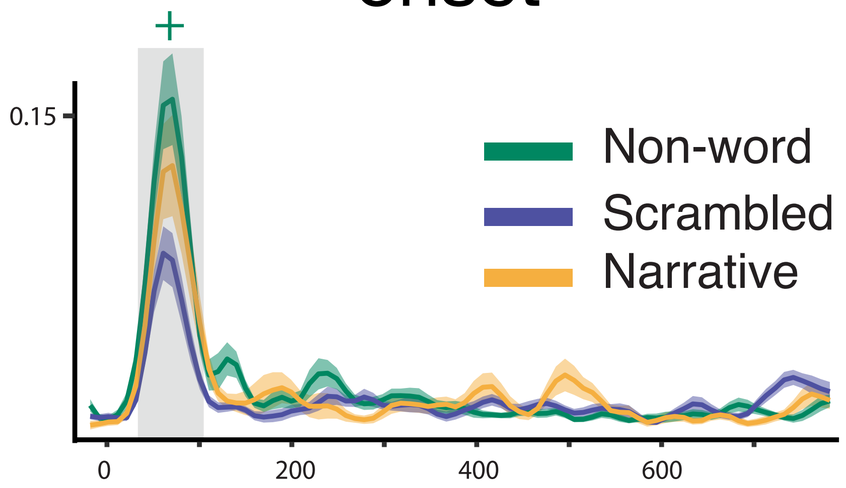
80 ms: simple phoneme processing

left hemisphere shown (right similar)

Phonemic TRF Results

phoneme onset



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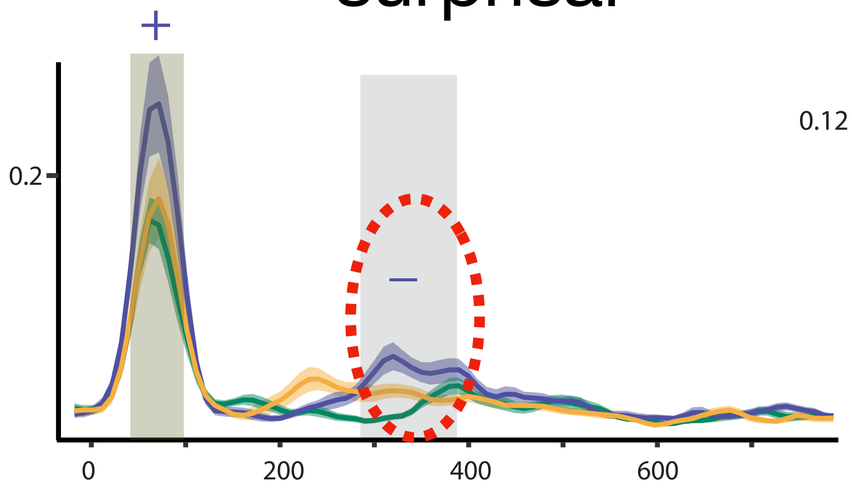

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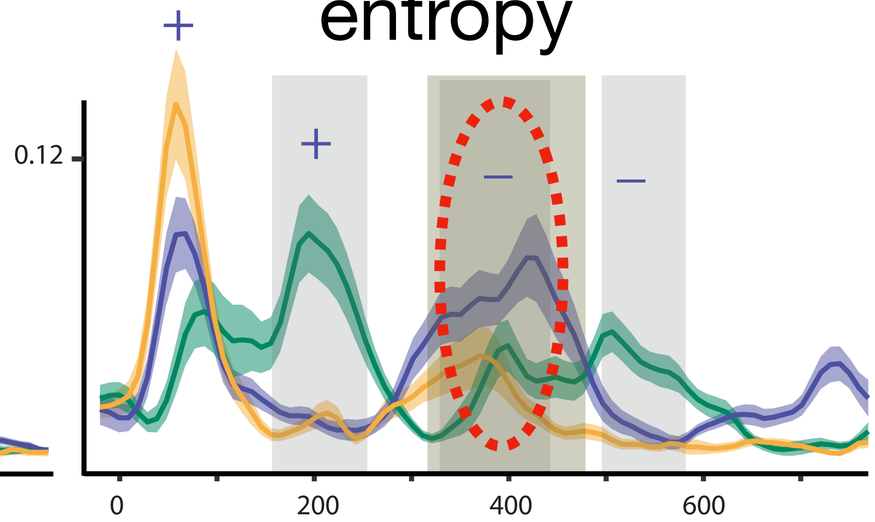
- Late phone processing ~350 ms) (words > non-words)

cohort entropy



- Late context processing
- N400-like response (reduced for narrative)
- Additional/delayed peaks in non-words (difference in stimulus distributions)

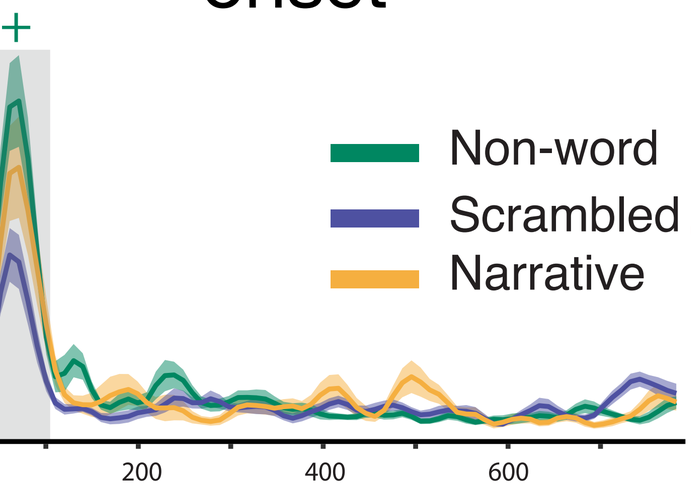
80 ms: simple phoneme processing

350 ms: additional further processing

left hemisphere shown (right similar)

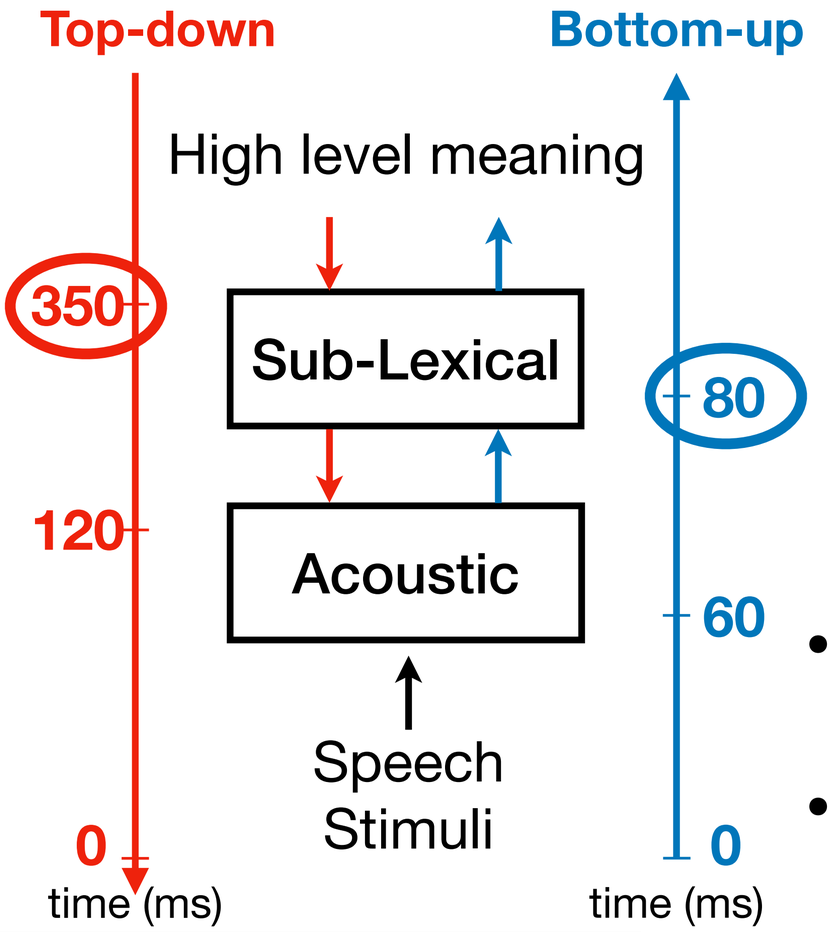
Phonemic TRF Results

phoneme onset

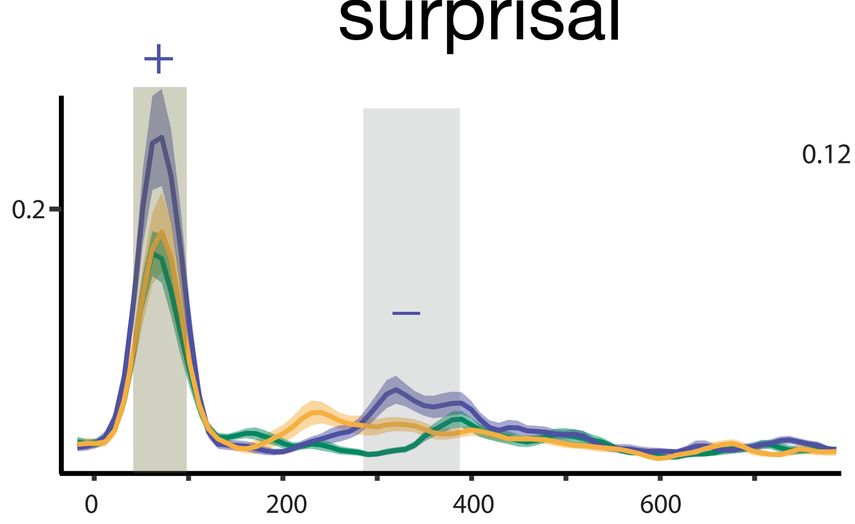


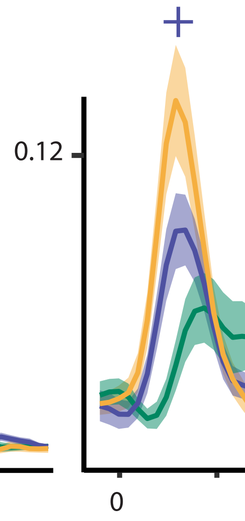
Non-words largest

No later processing



phoneme surprisal





- Early phone processing ~80 ms (scrambled > narrative)
- Late phone processing ~350 ms) (words > non-words)

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

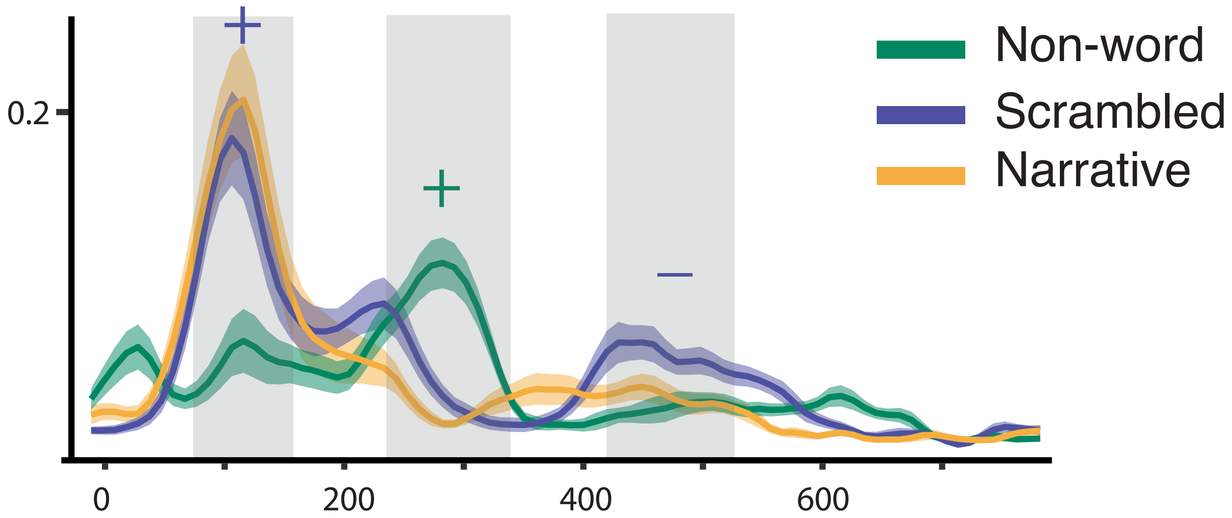
left hemis

80 ms: simple phoneme processing

350 ms: additional further processing

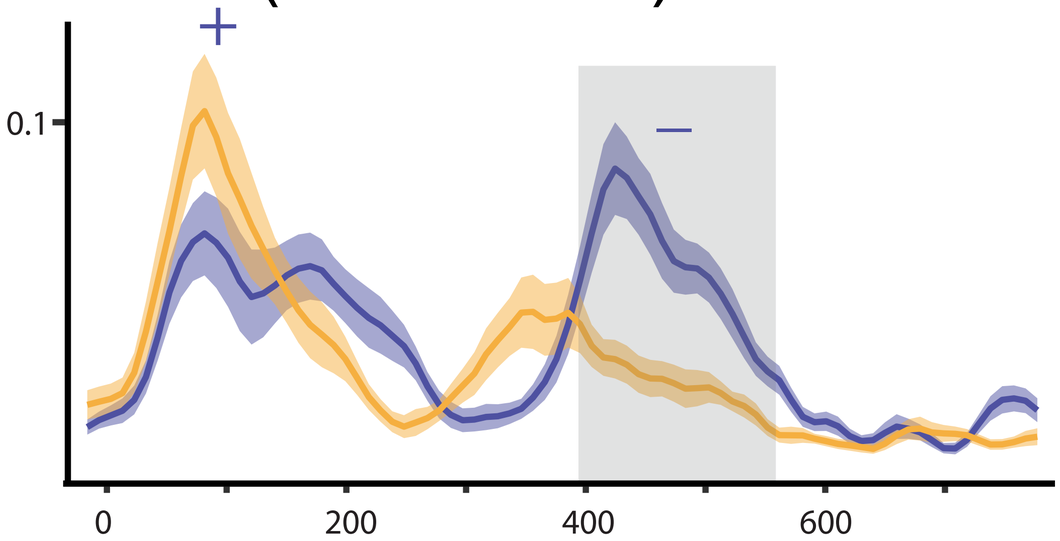
Word-based TRF Results

word onset



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

surprisal (no context)

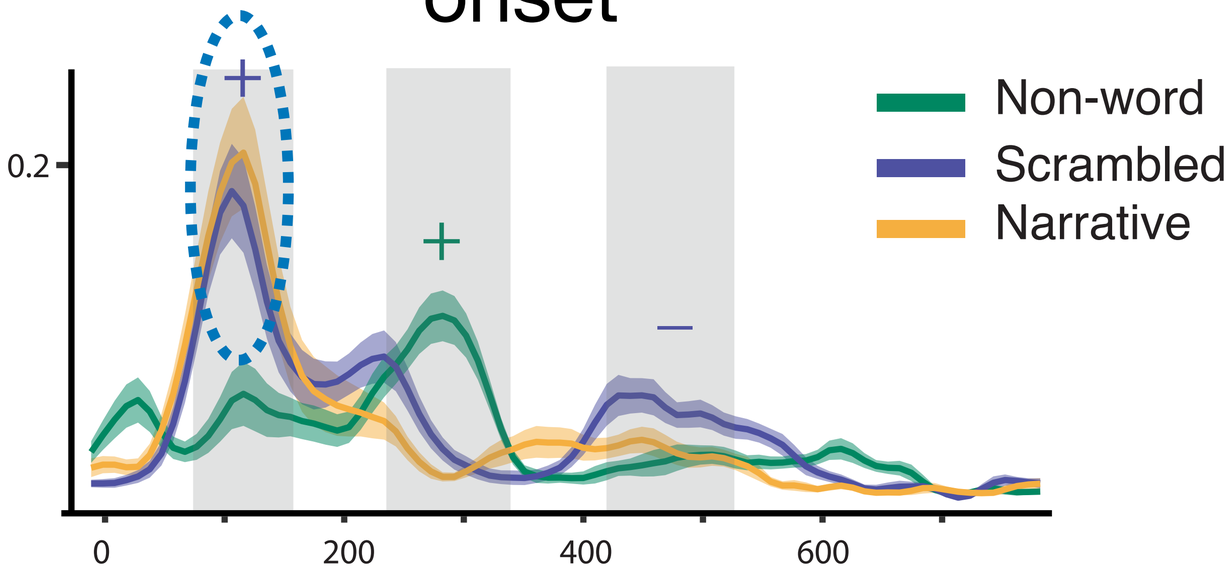


- N400 like response
- Reduction in surprisal when context
- Left hemi > Right hemi
- Right hemisphere: Scrambled ≈ Narrative

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

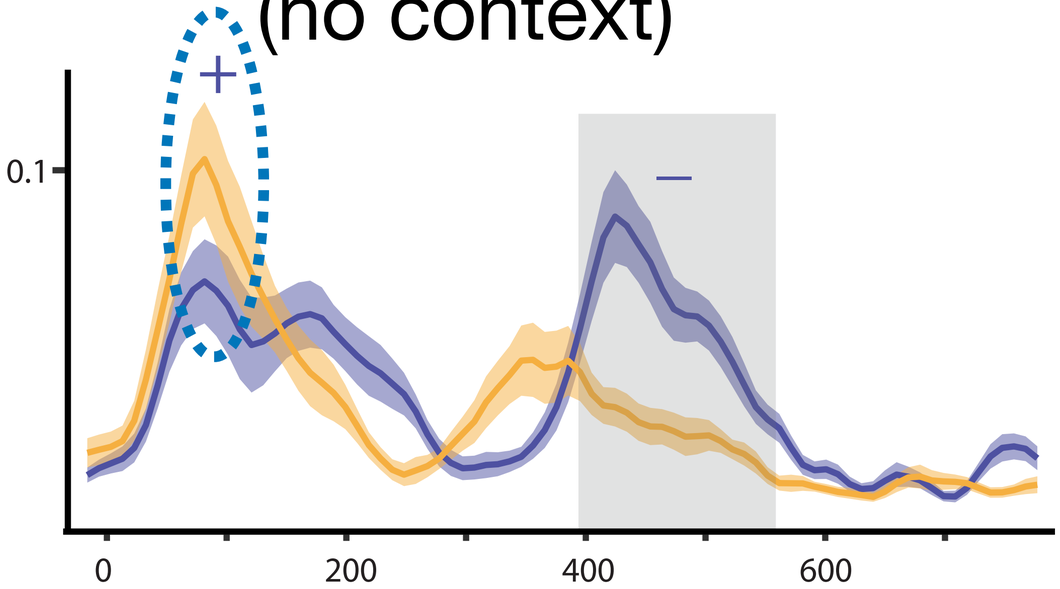
Word-based TRF Results

word onset



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

surprisal (no context)



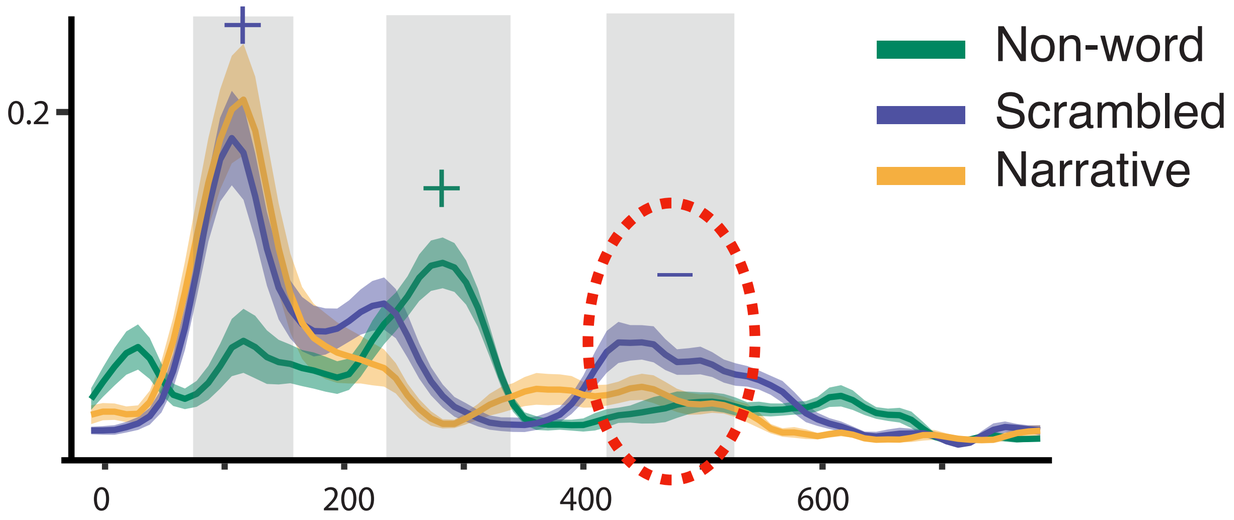
- N400 like response
- Reduction in surprisal when context
- Left hemi > Right hemi
- Right hemisphere: Scrambled ≈ Narrative

100 ms: simple word processing

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

Word-based TRF Results

word onset

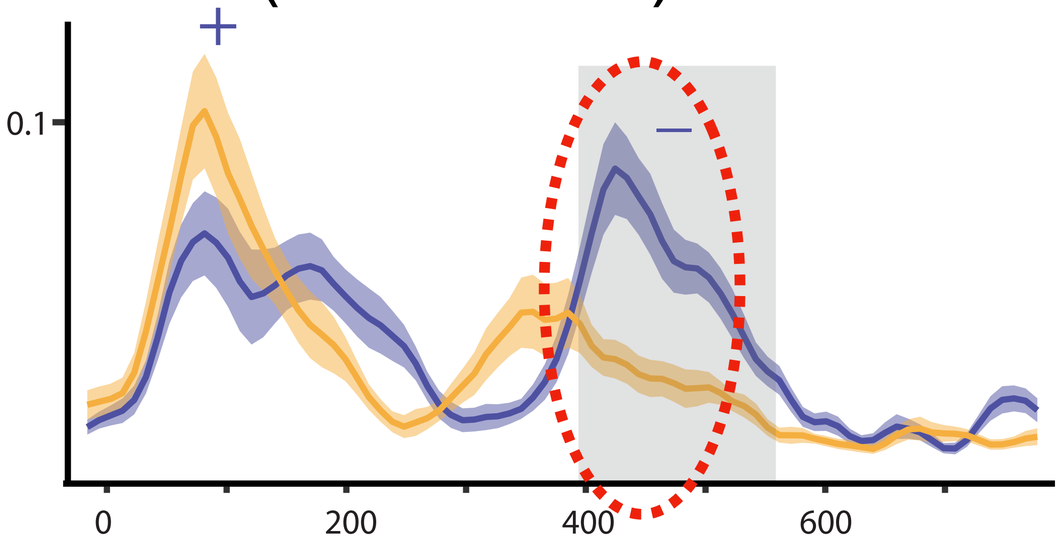


- Scrambled ≈ narrative for rapid processing
- Scrambled words > narrative at ~450 ms
- words: Left hemi > Right (non-words: L ≈ R)

100 ms: simple word processing

450 ms: “error” correction processing

surprisal (no context)

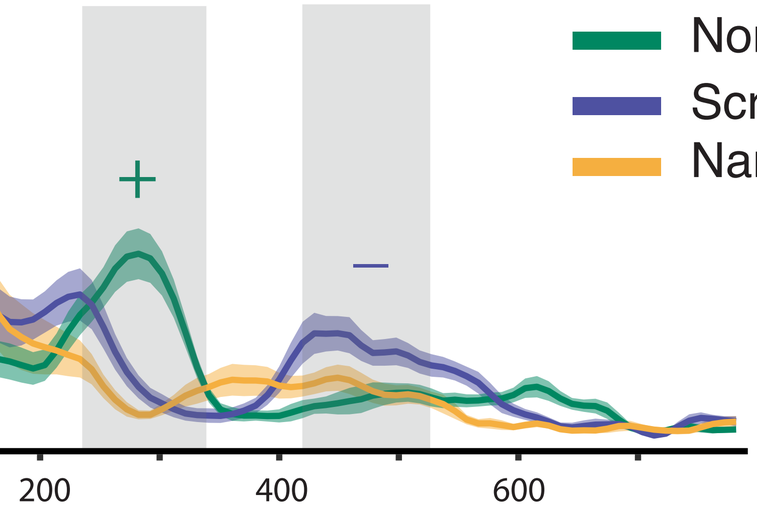


- N400 like response
- Reduction in surprisal when context
- Left hemi > Right hemi
- Right hemisphere: Scrambled ≈ Narrative

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

Word-based TRF Results

word onset



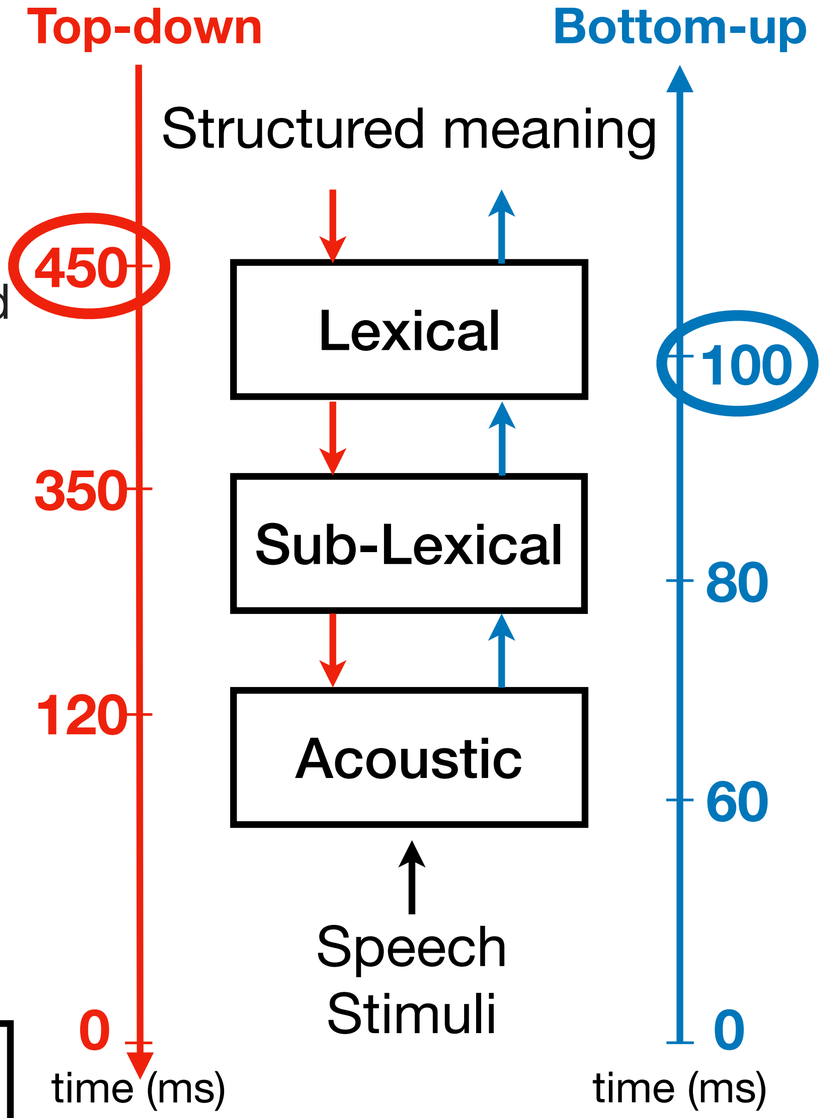
ed ≈ narrative for rapid processing

ed words > narrative at ~450 ms

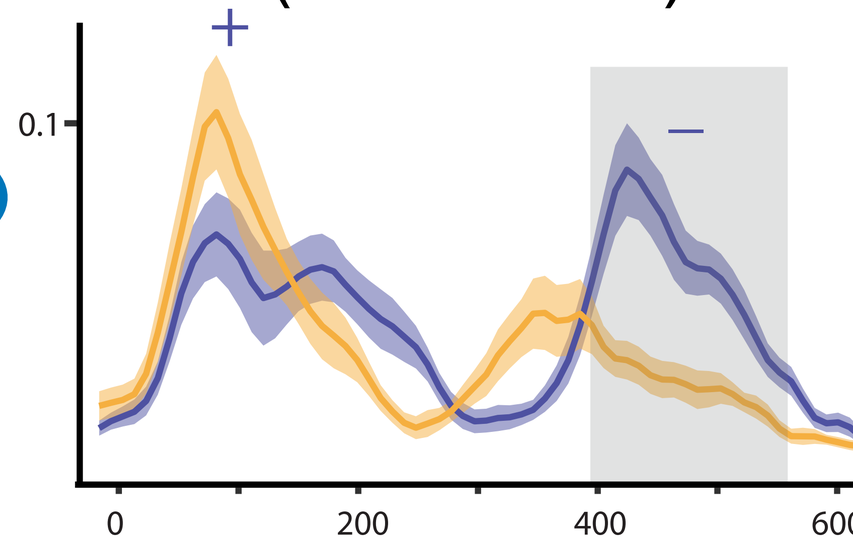
eft hemi > Right (non-words: L ≈ R)

simple word processing

ror" correction processing



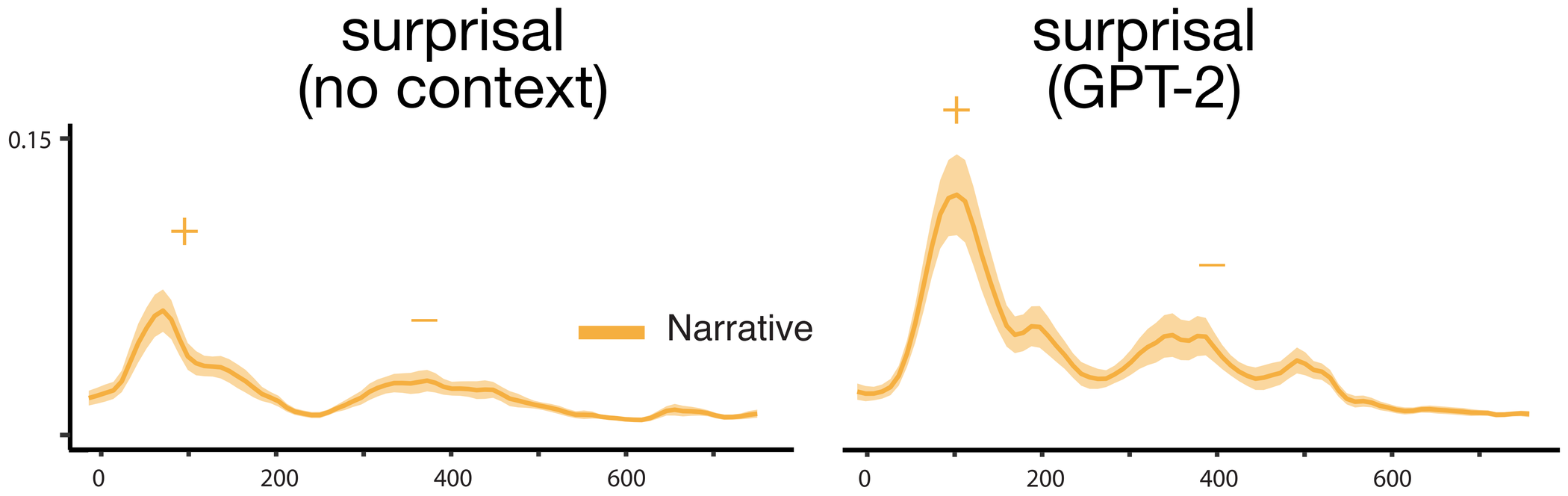
surprisal (no context)



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

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

Contextual Word Surprisal Results

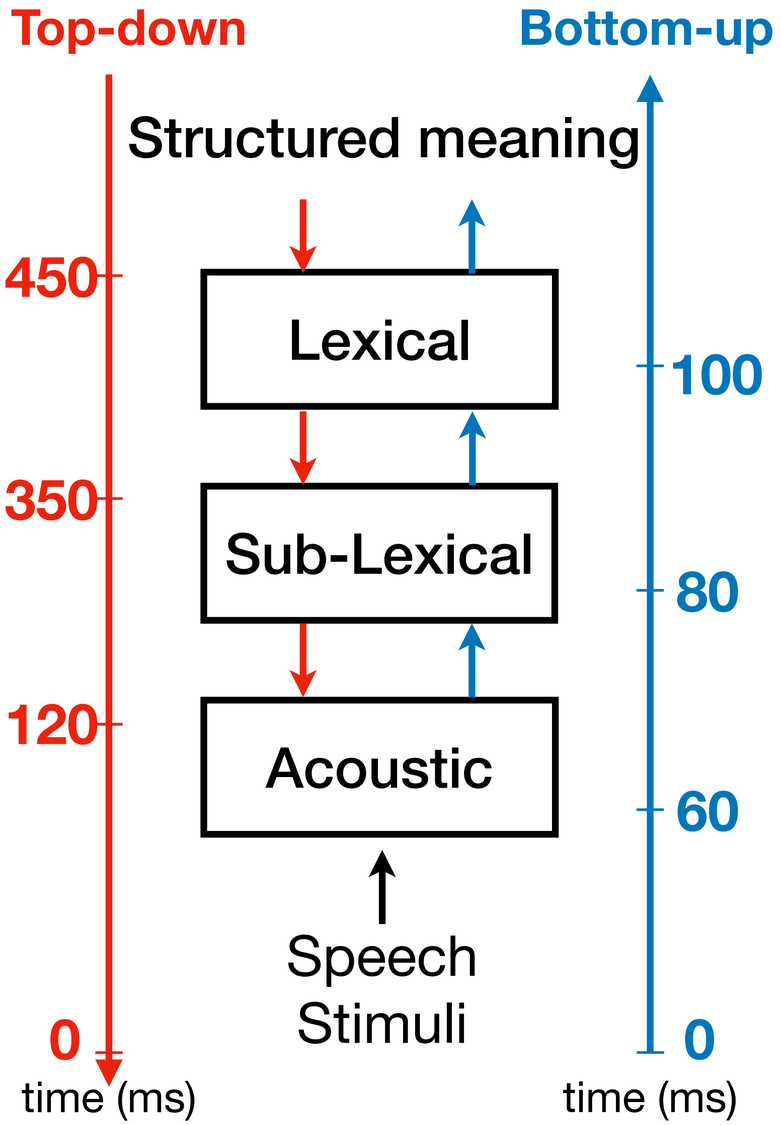


- When context helps, context-based surprisal is better tracked than raw surprisal
- N400 like response in both predictors

left hemisphere shown
(right much weaker)

Neural Speech Processing Progression

- Cortical responses time-lock to emergent features, from acoustics to context: multiple individual steps in the processing of speech input
- Bottom-up processing has quite short latencies, supporting models of predictive processing
- Top-down mechanisms can augment bottom-up speech processing, supporting models of corrections to predictive processing
- Lower-level acoustic responses bilateral (but right lateralized); context-based responses left lateralized



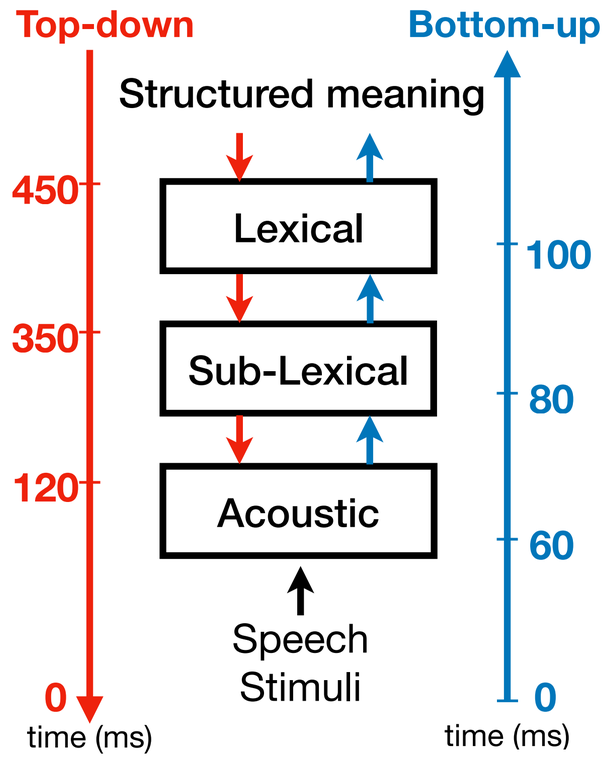
Karunathilake et al. *in preparation*

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, from acoustics to context: multiple individual steps in the processing of speech input
- Higher level processing / top-down mechanisms distinct from lower level/bottom up mechanisms



thank you

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