

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

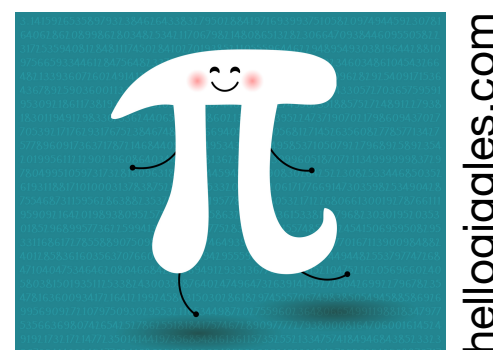
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<http://www.isr.umd.edu/Labs/CSSL/simonlab>



U. Rochester, 3.14 2023

Acknowledgements

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Funding & Support



NIDCD



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

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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 \Leftrightarrow 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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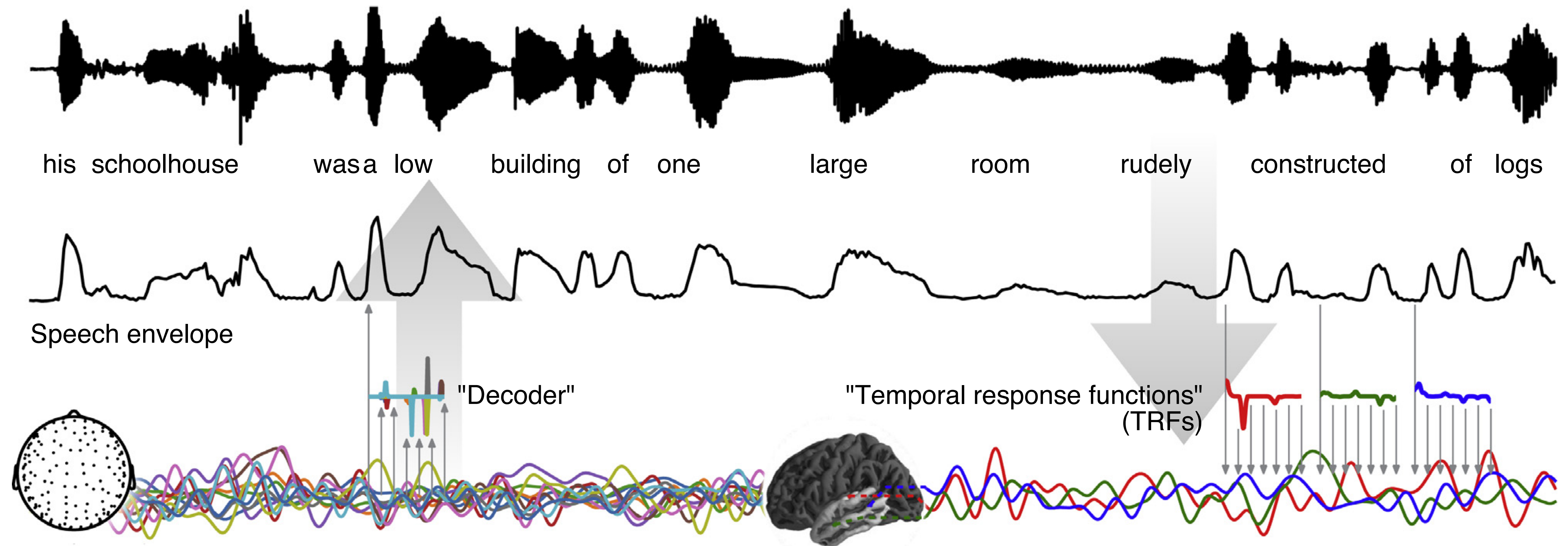
Cortical Representations of Continuous Speech

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**

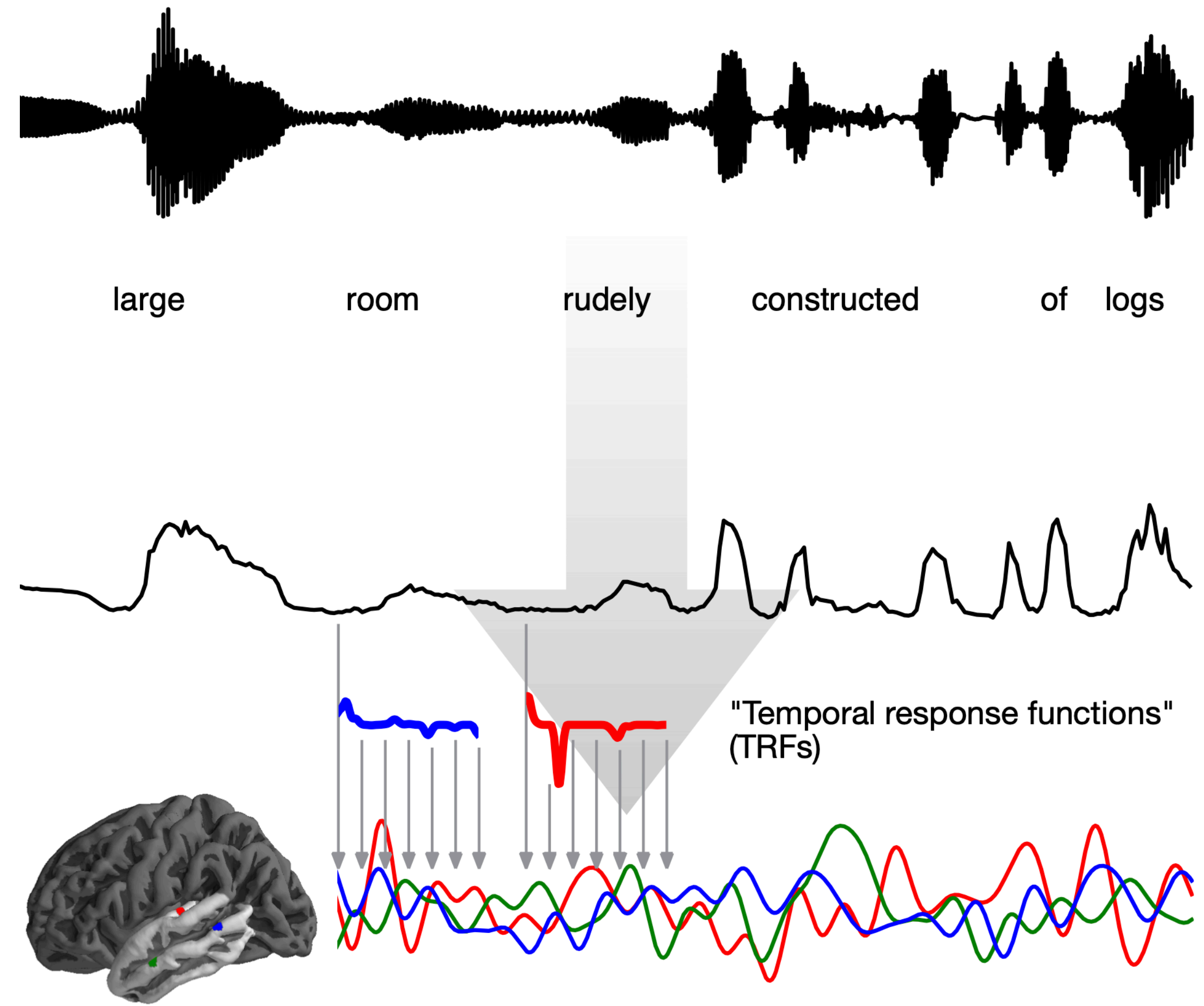
Cortical Representations of Speech

- 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



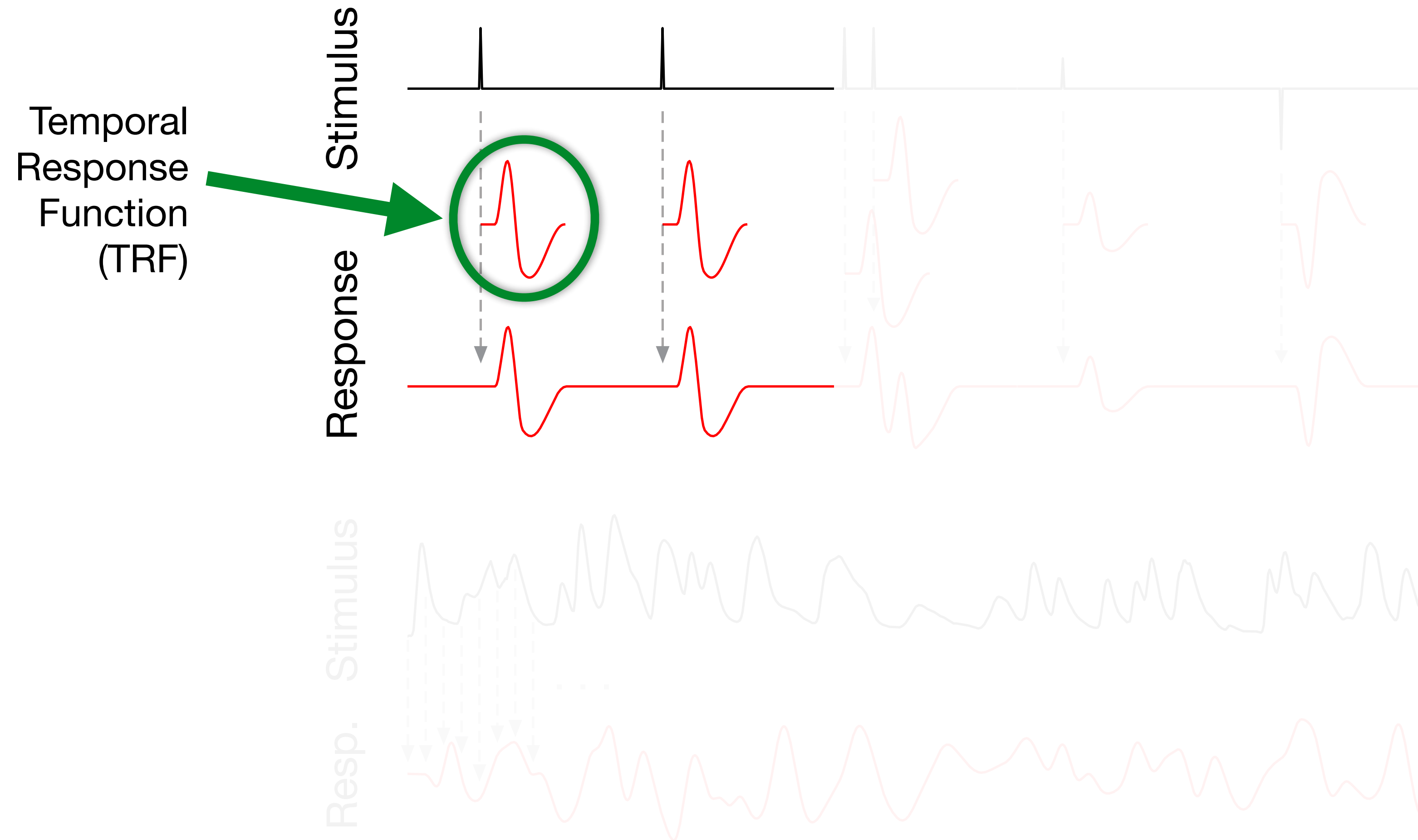
Cortical Representations: Encoding

- 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 \approx processing intensity
 - peak latency \approx source location
 - multiple TRFs simultaneously

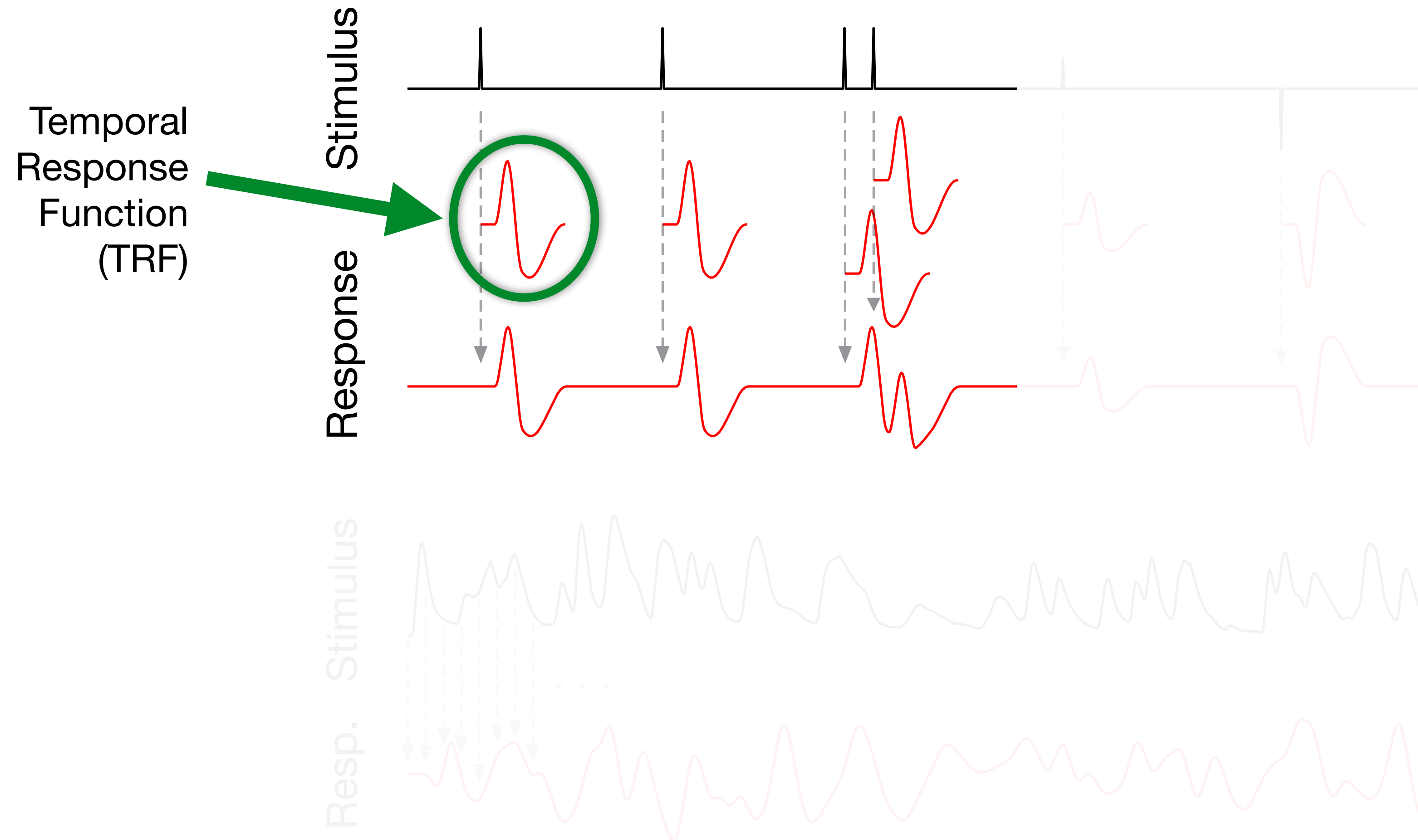


Example: MEG Prediction of Voxel Responses

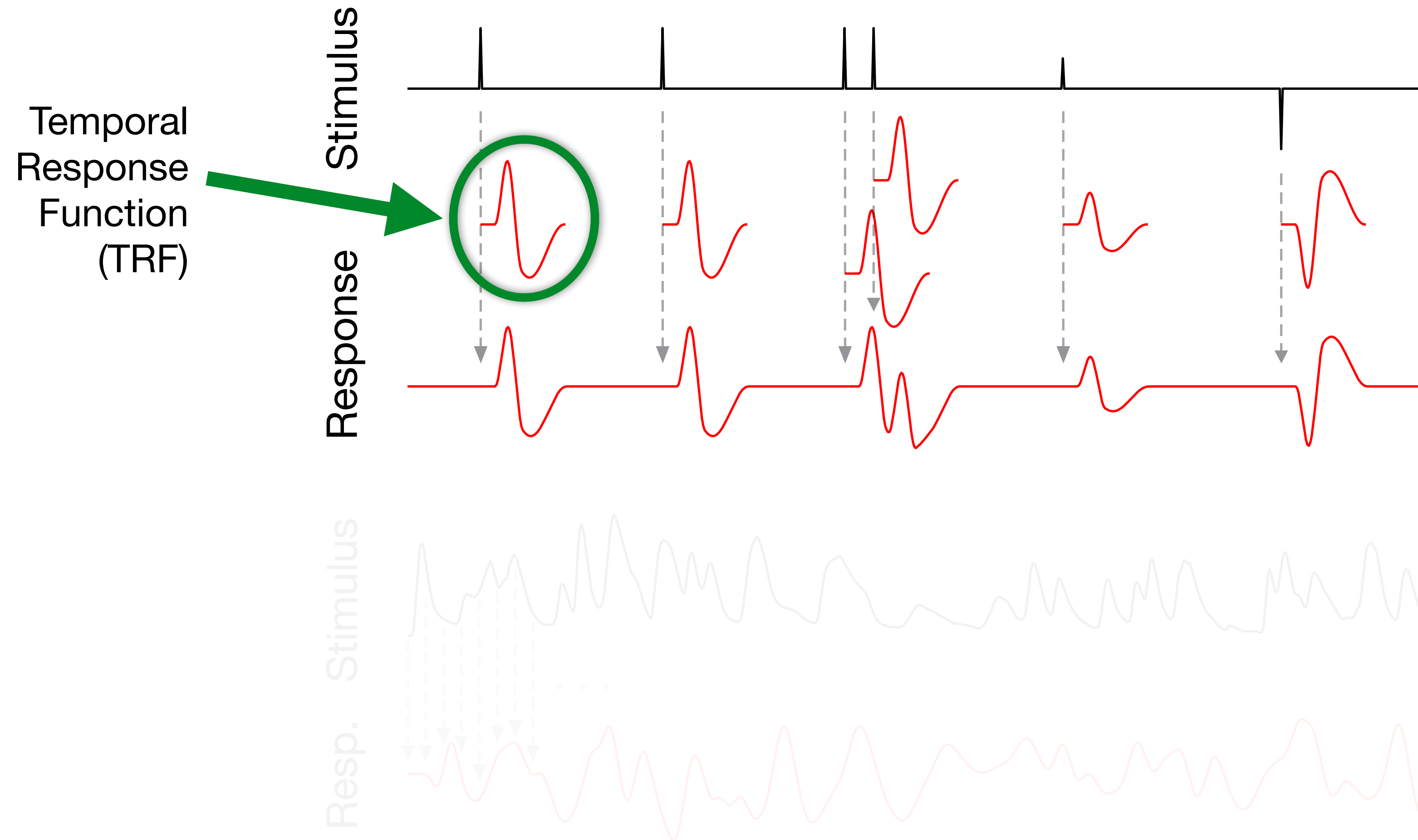
Temporal Response Functions



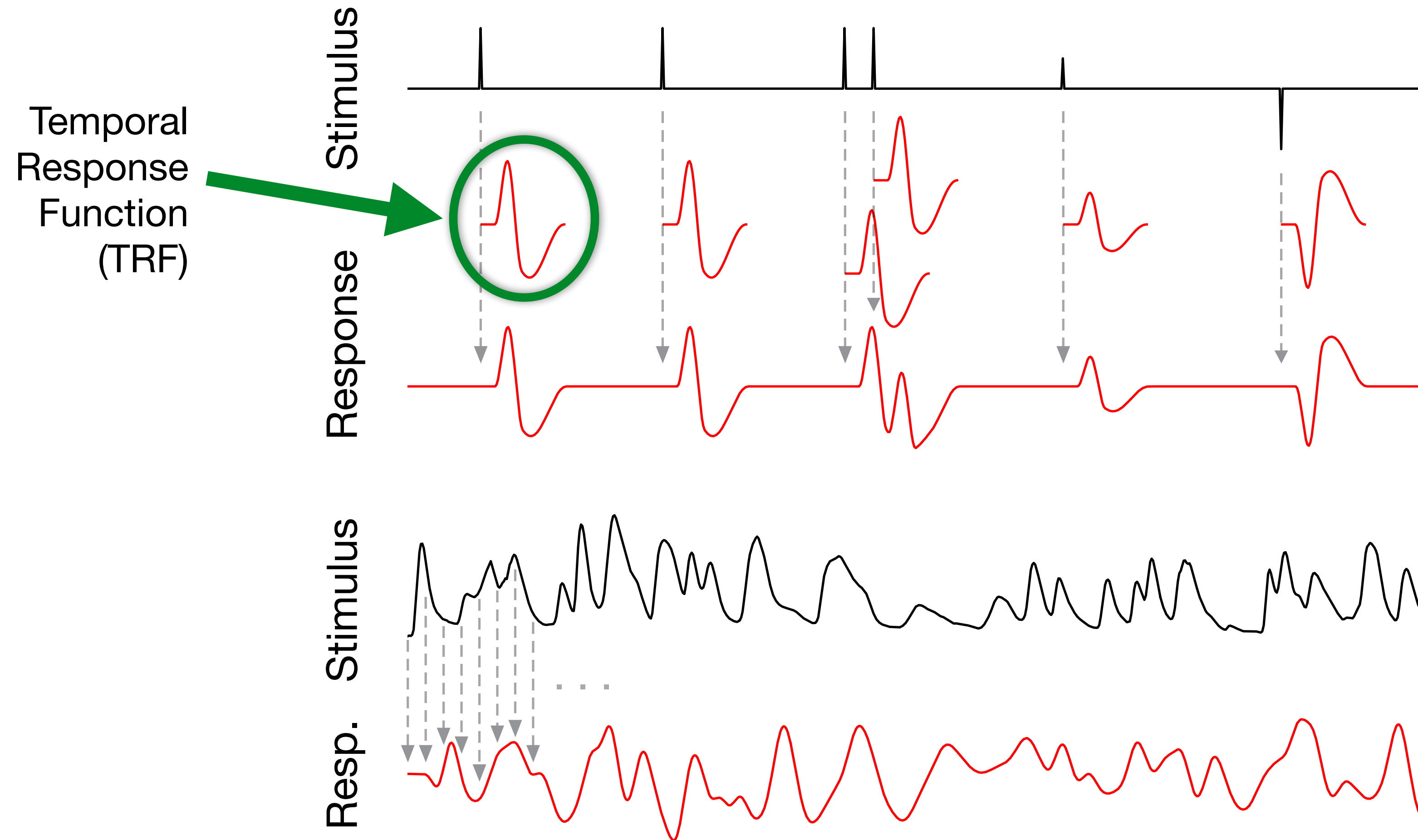
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Temporal Response Functions



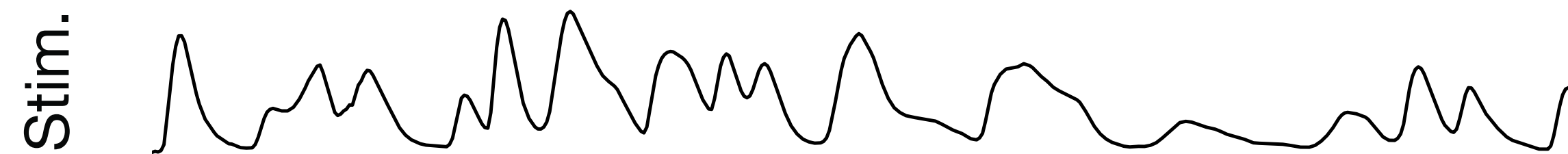
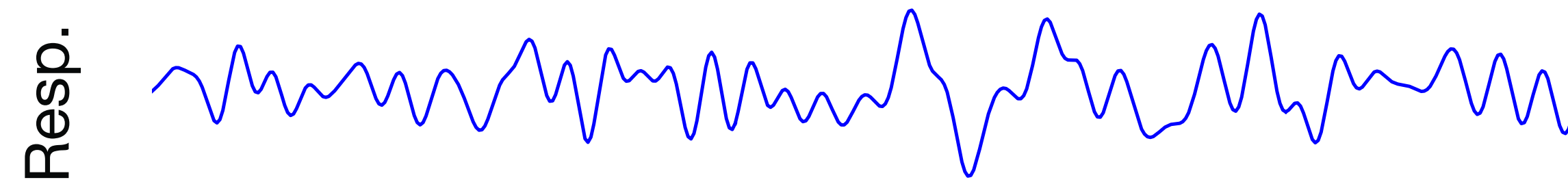
Temporal Response Functions



TRF Model Estimation & Fit

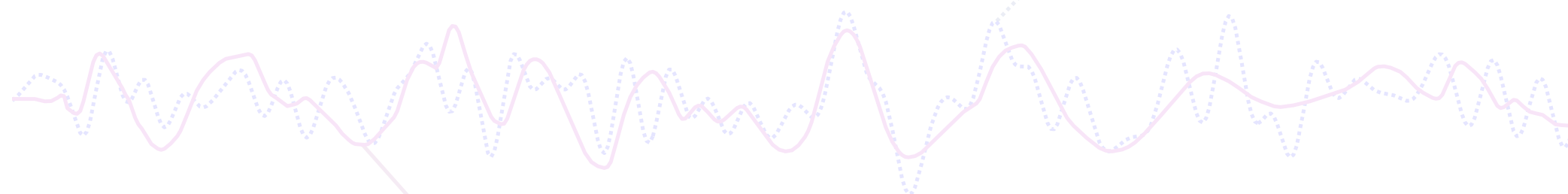
Temporal Response Function (TRF) estimation:

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



Estimated TRF

Resp.



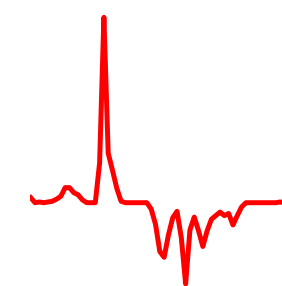
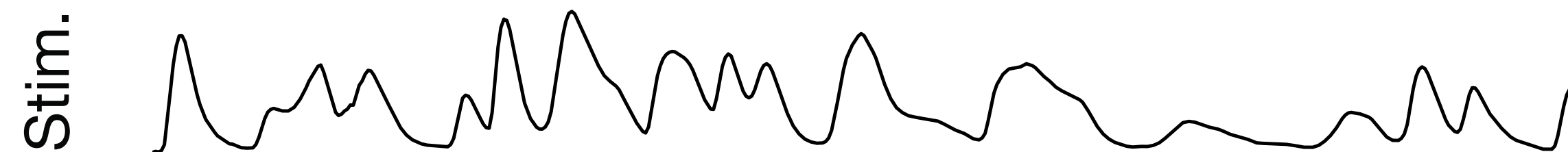
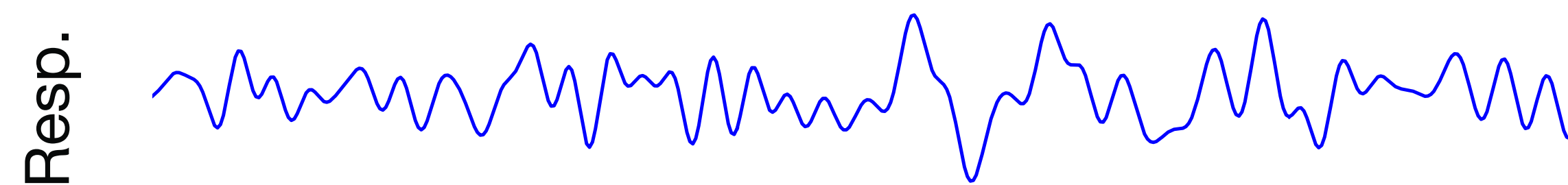
Actual response

Predicted response (Stimulus * TRF)

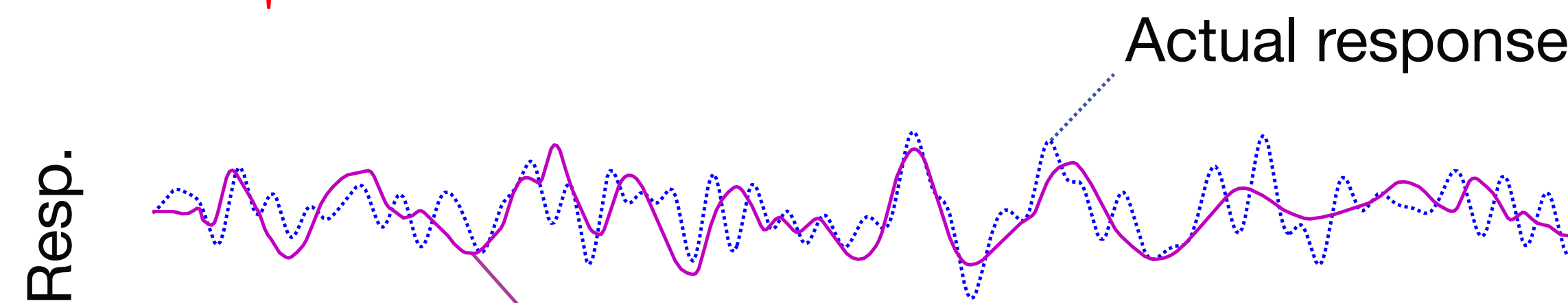
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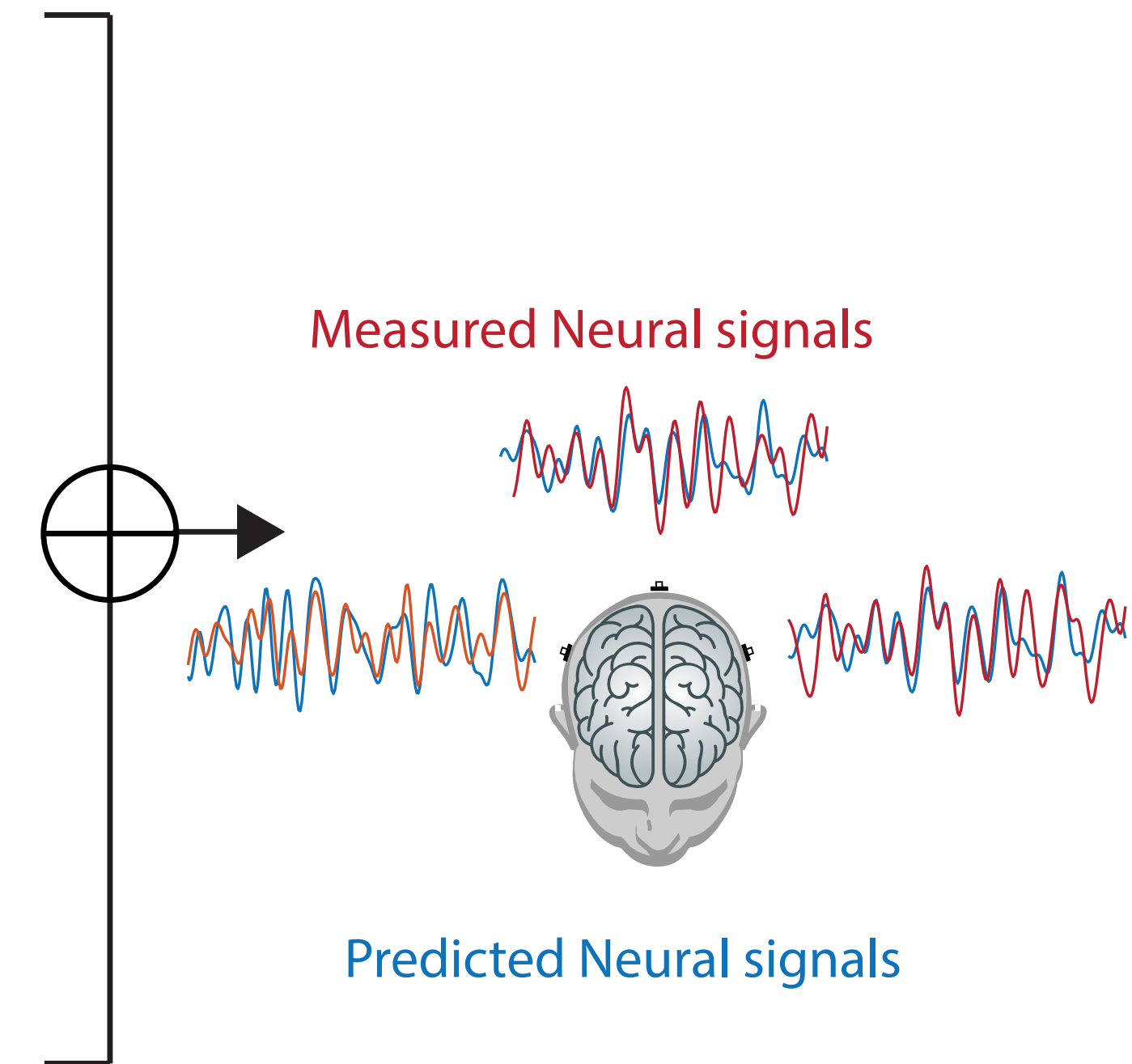
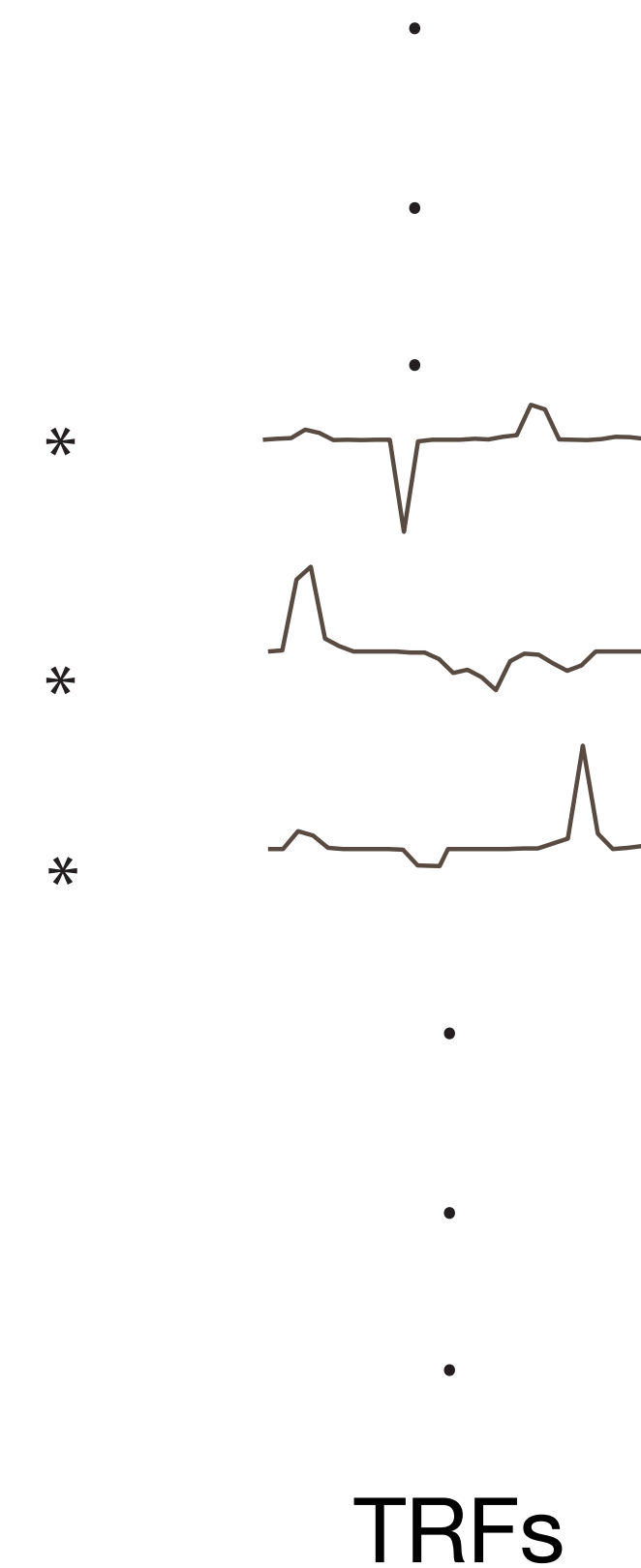
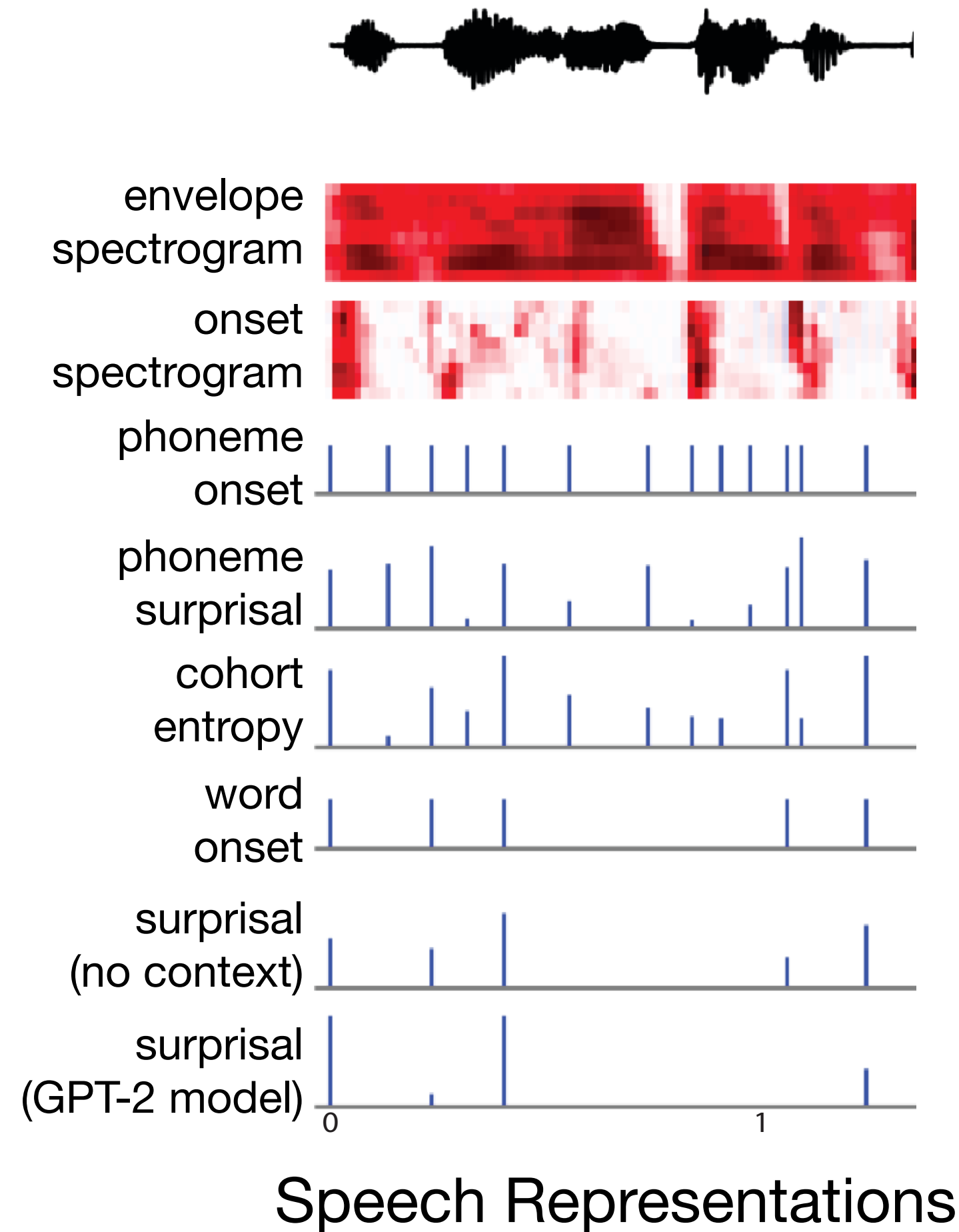


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Simultaneous Temporal Response Functions

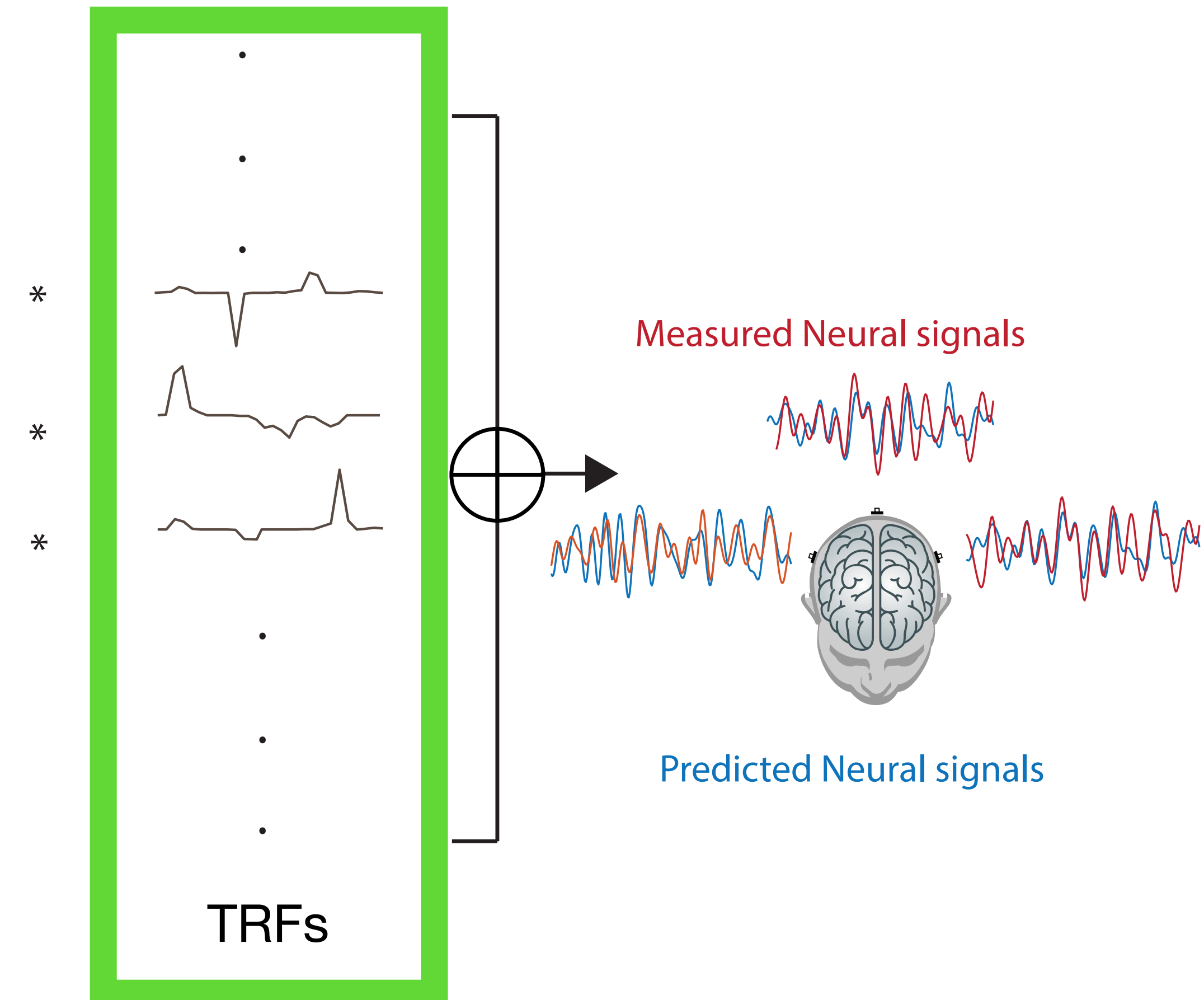
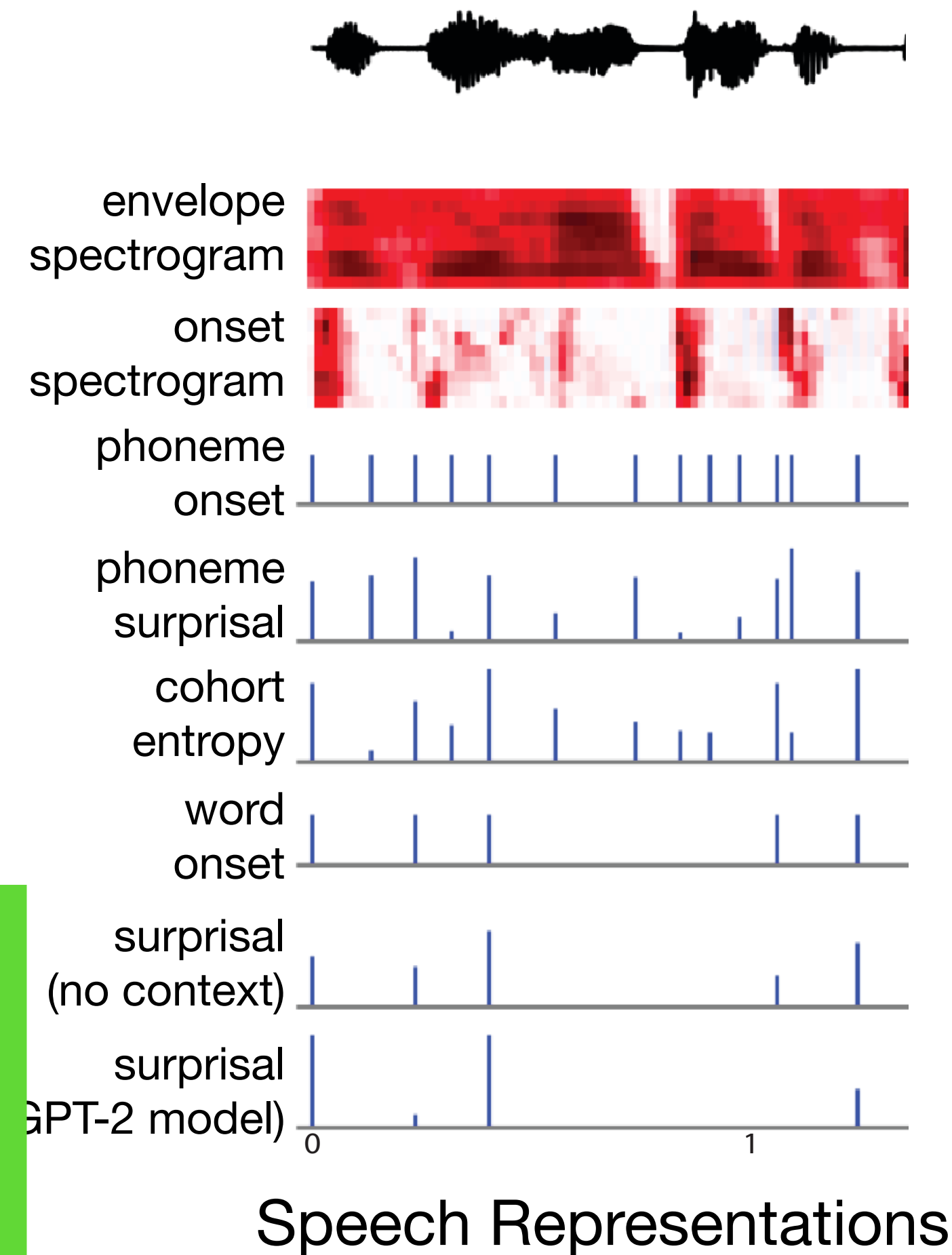
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 - Analogous to evoked response
 - Peak amplitude \approx processing intensity
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- Multiple TRFs estimated simultaneously
 - compete to explain variance (advantage over evoked response)



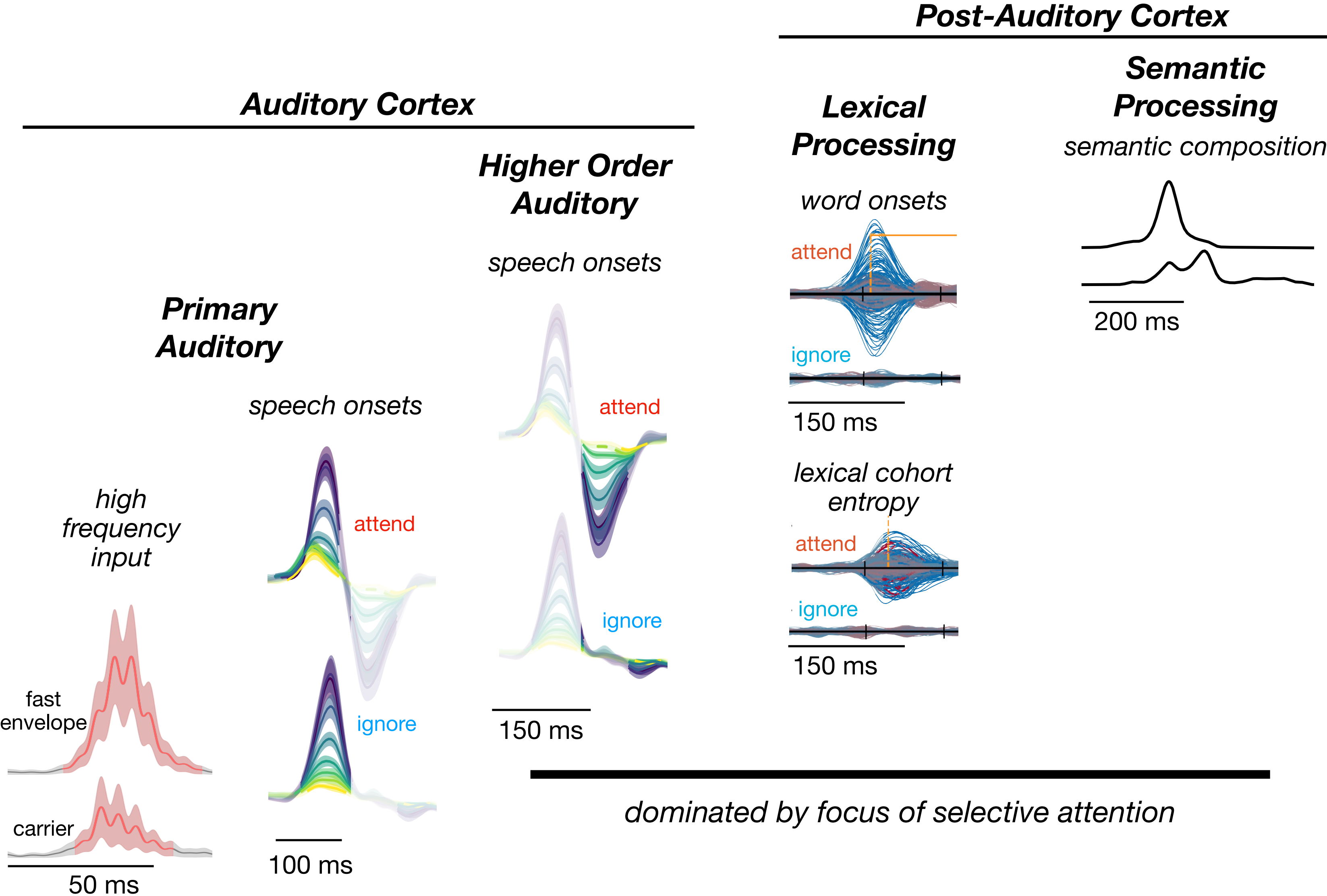
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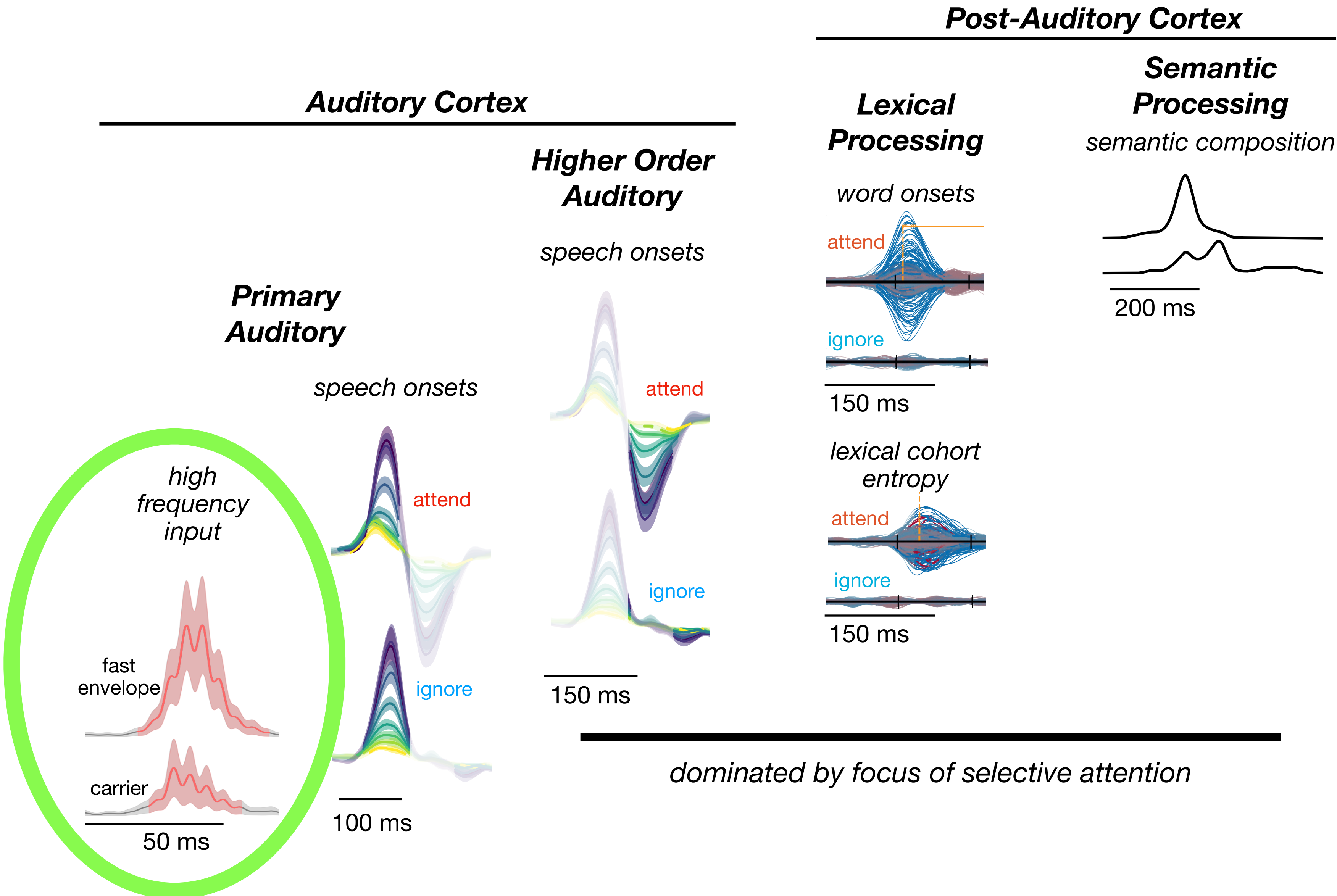
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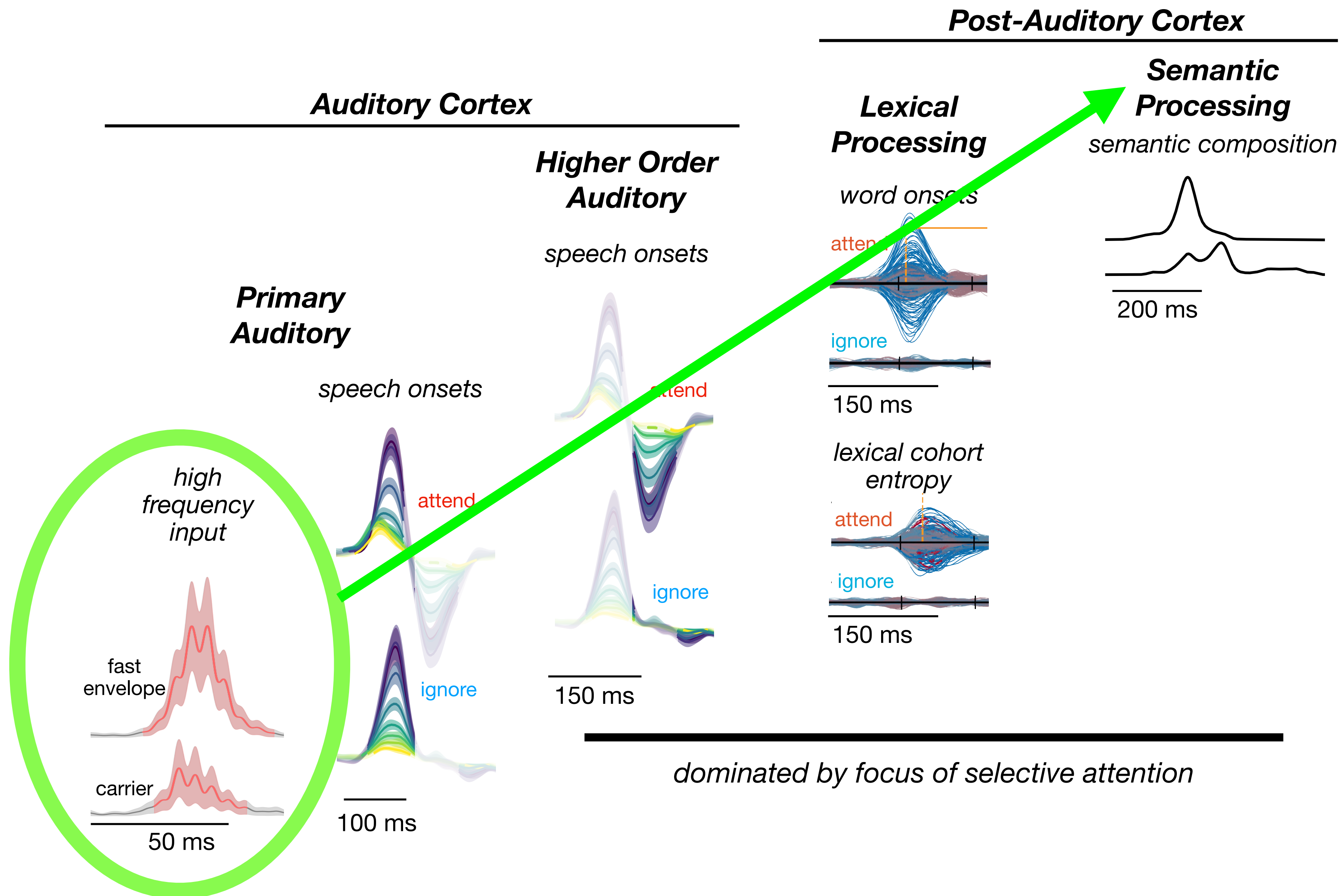
Cortical Representations Across Cortex



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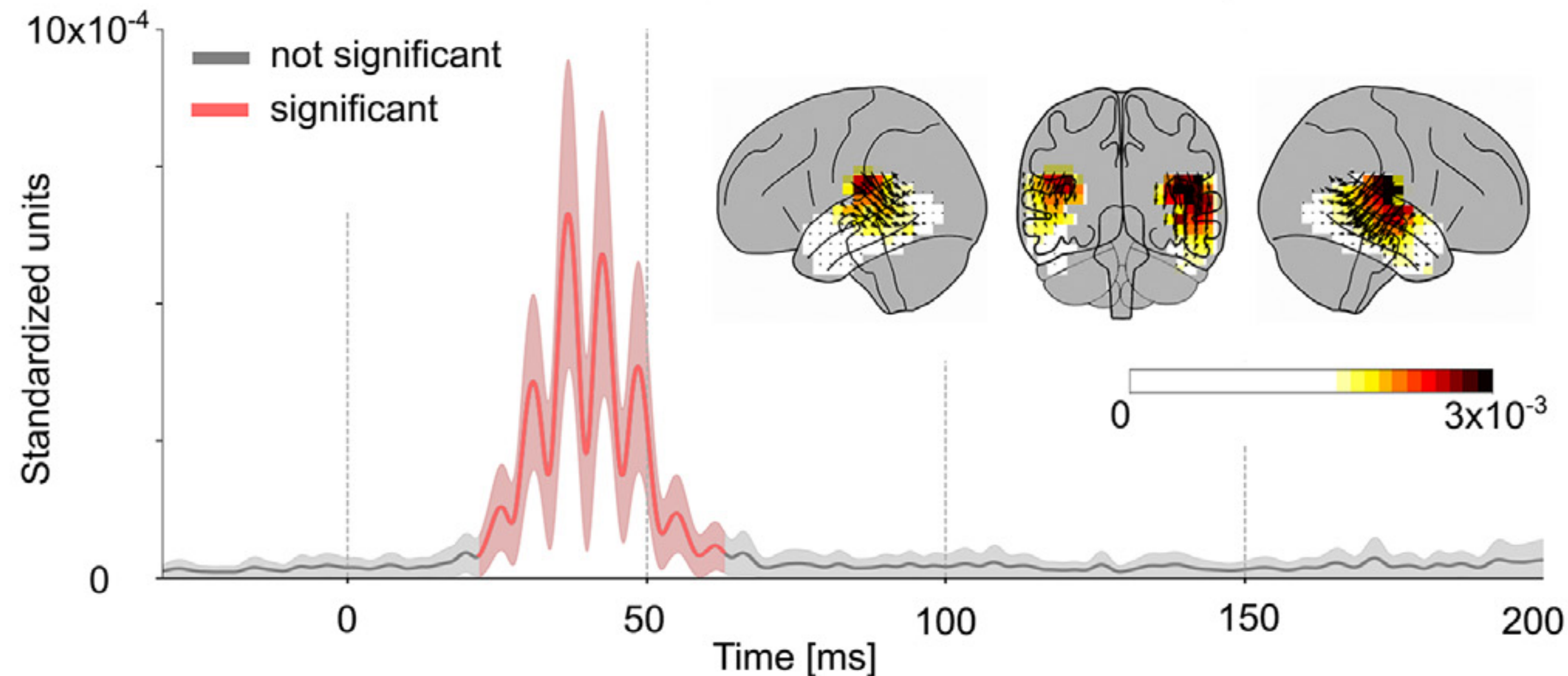
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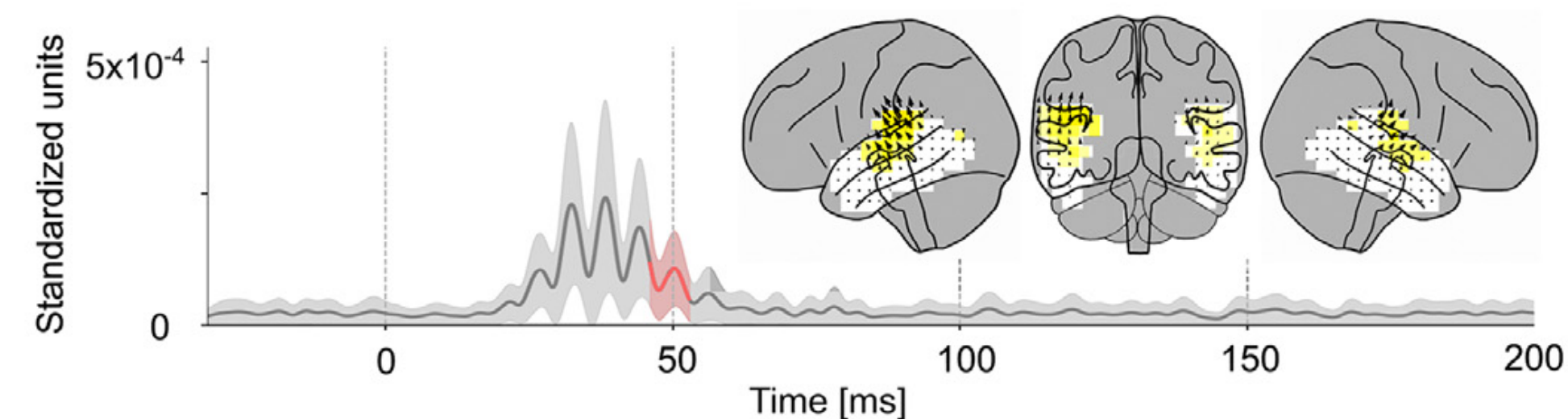
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Fast & Early Cortical Representations



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

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



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



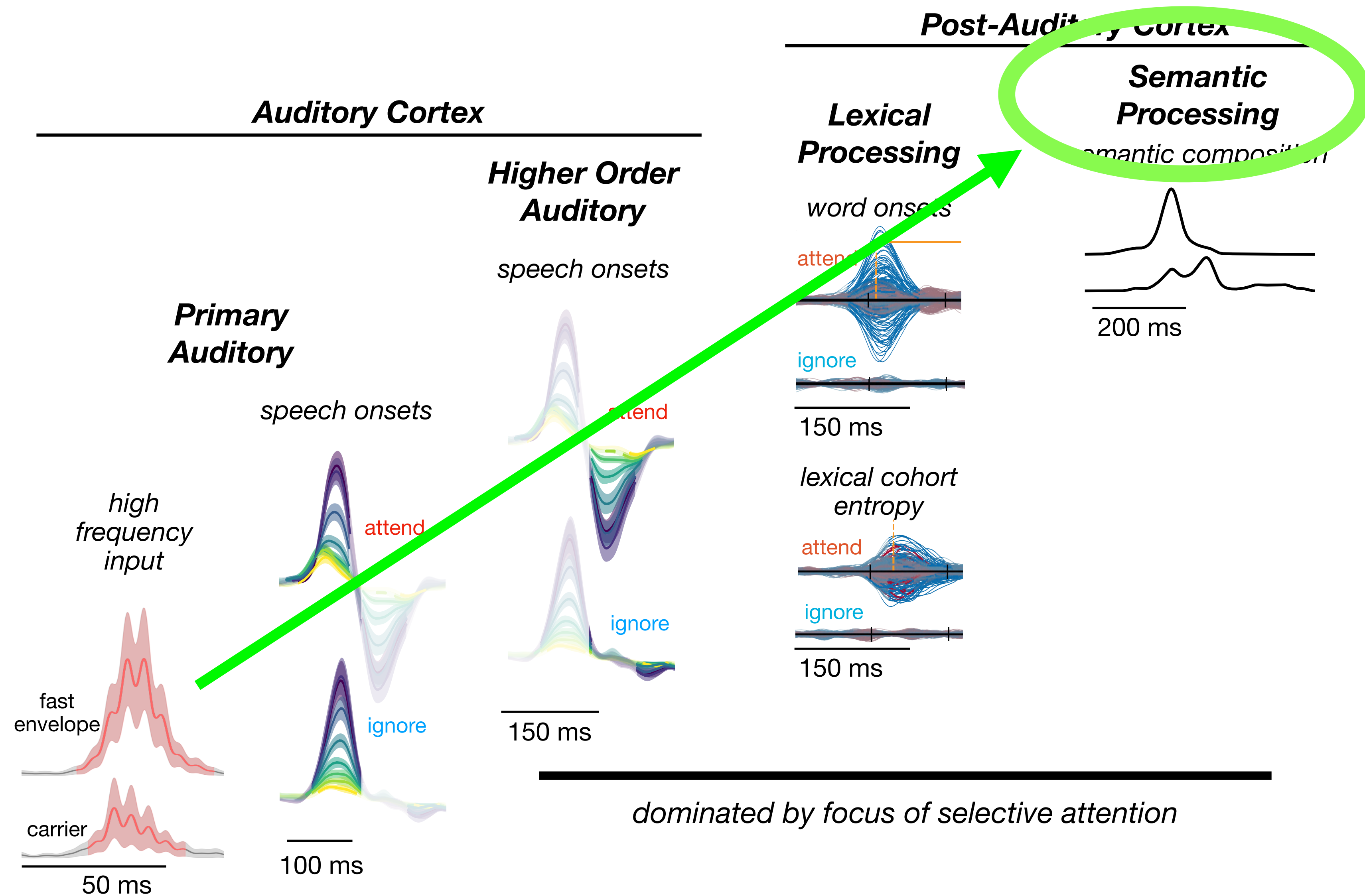
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Cortical Representations Across Cortex



Speech Understanding/Meaning

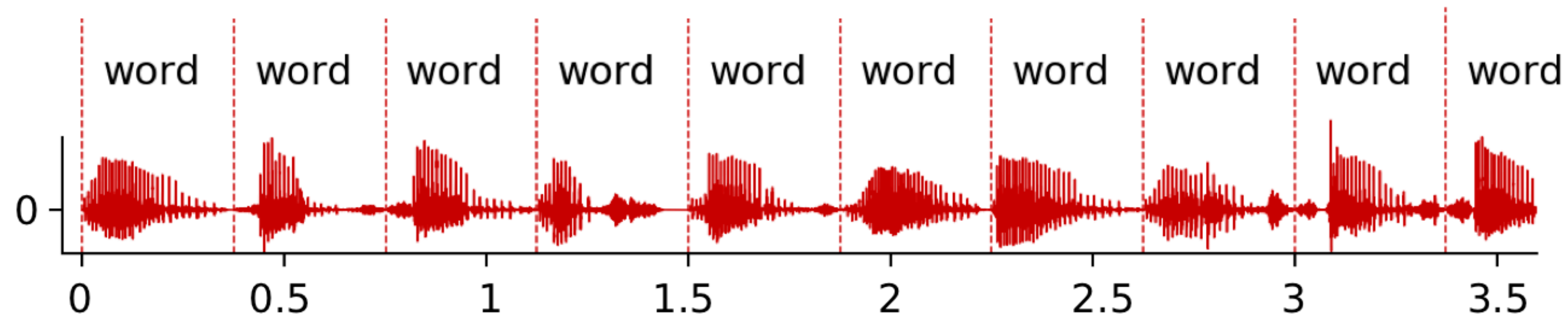
- Behavioral correlates of speech understanding
 - implies language comprehension
 - structural comprehension
 - sentence structure
 - other structures, e.g. poetic, logical
- Neural correlates of speech understanding
 - rhythms of structural comprehension/meaning, even if *fully absent in the acoustics*
 - sentence structures Ding et al., Nat Neurosci 2016
 - poetic structures Teng et al., Curr Biol 2020
 - mathematical structures

Speech Understanding/Meaning

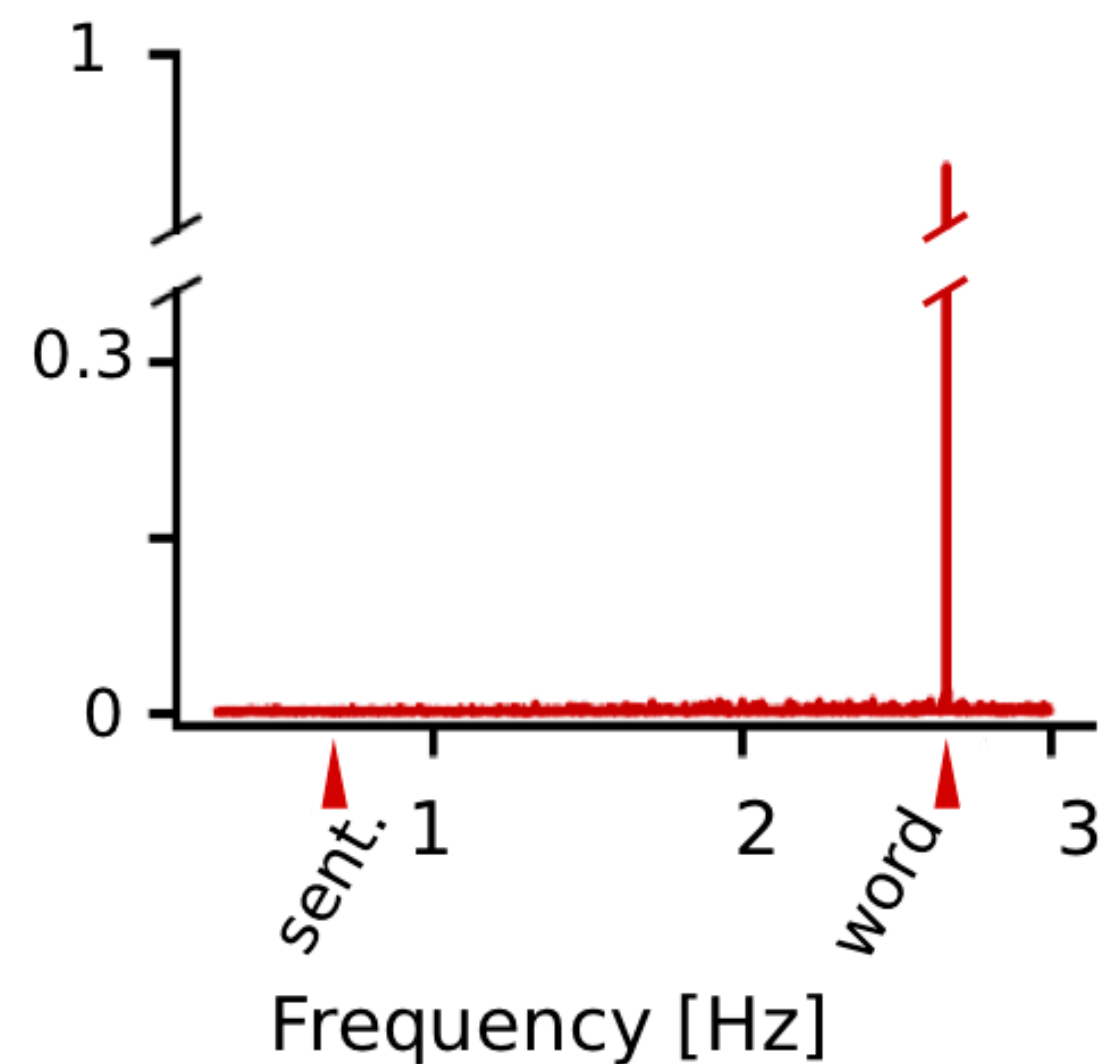
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Isochronous Speech

Acoustics

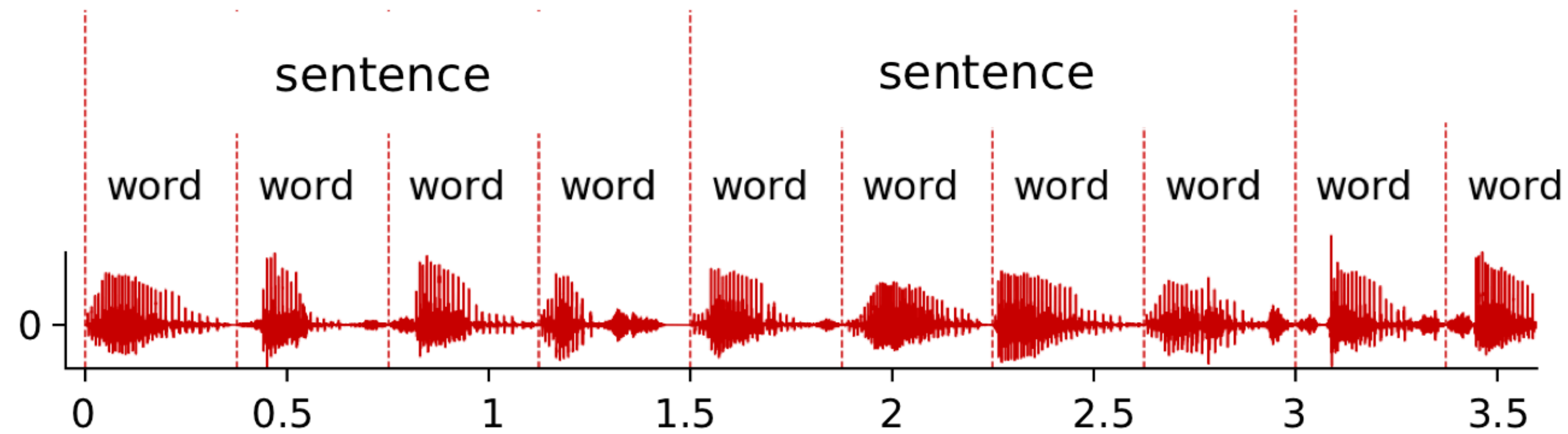


Acoustical
Spectrum
(envelope)

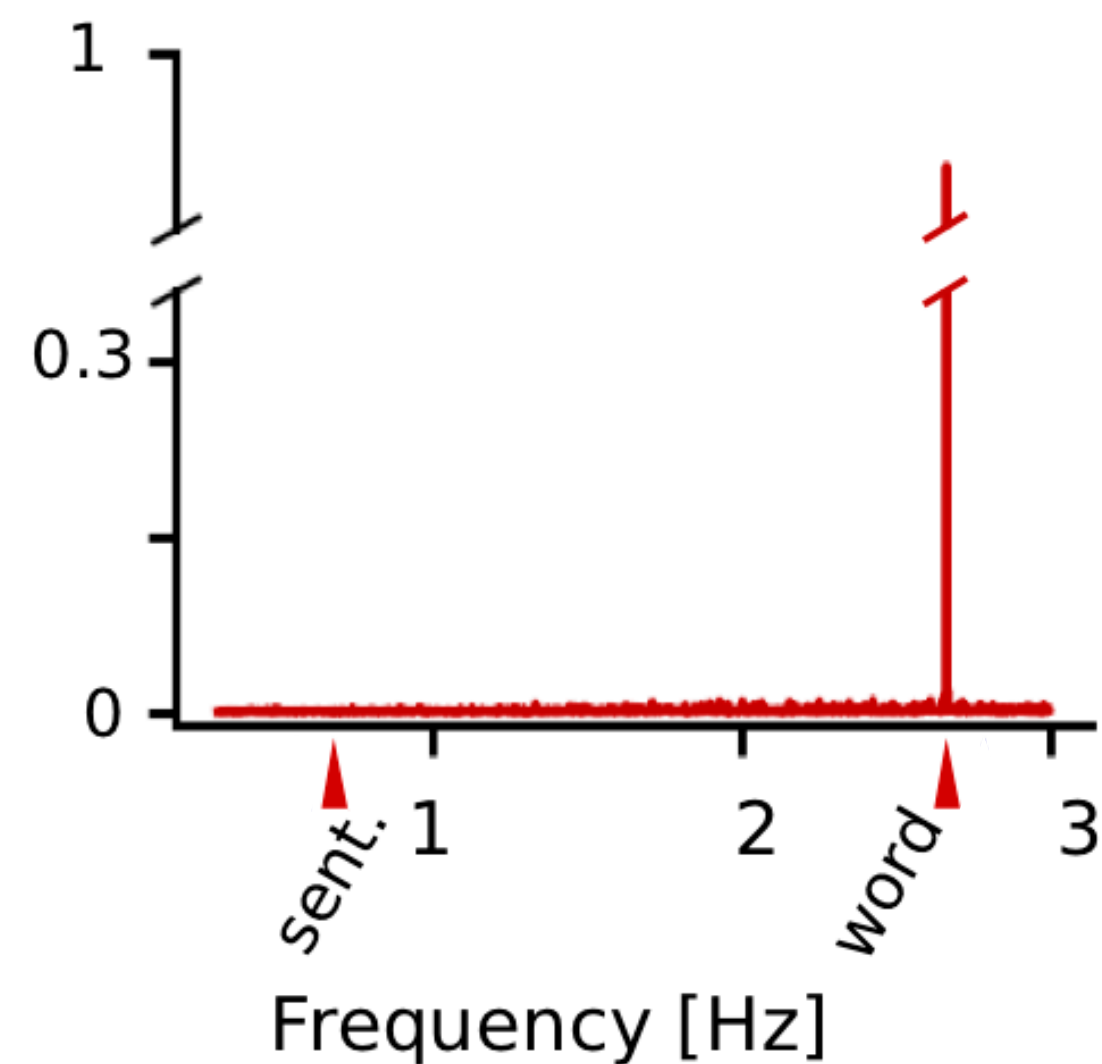


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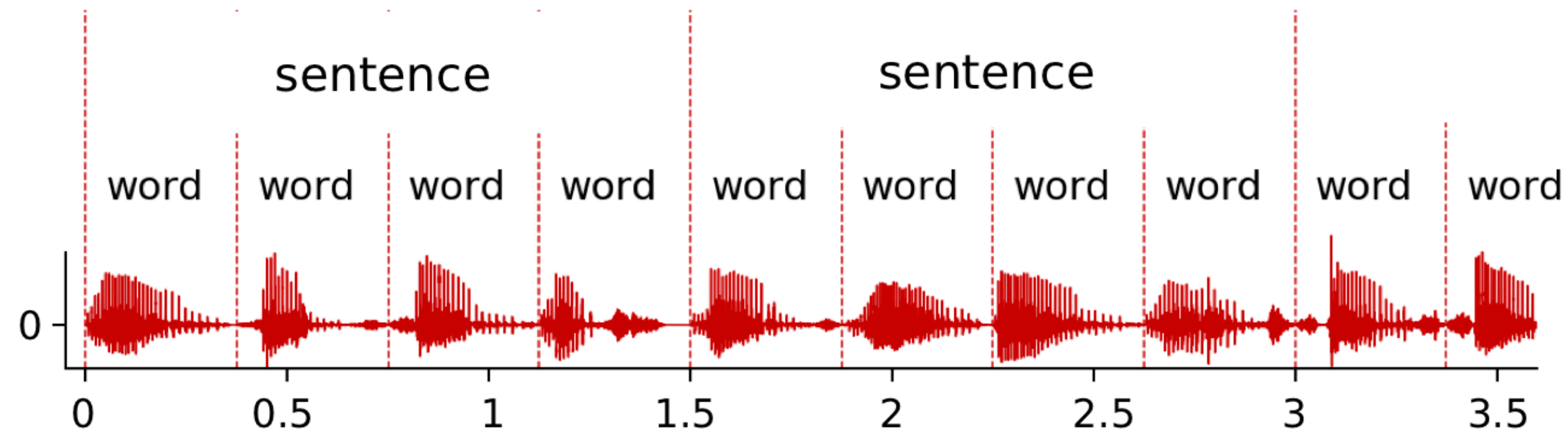


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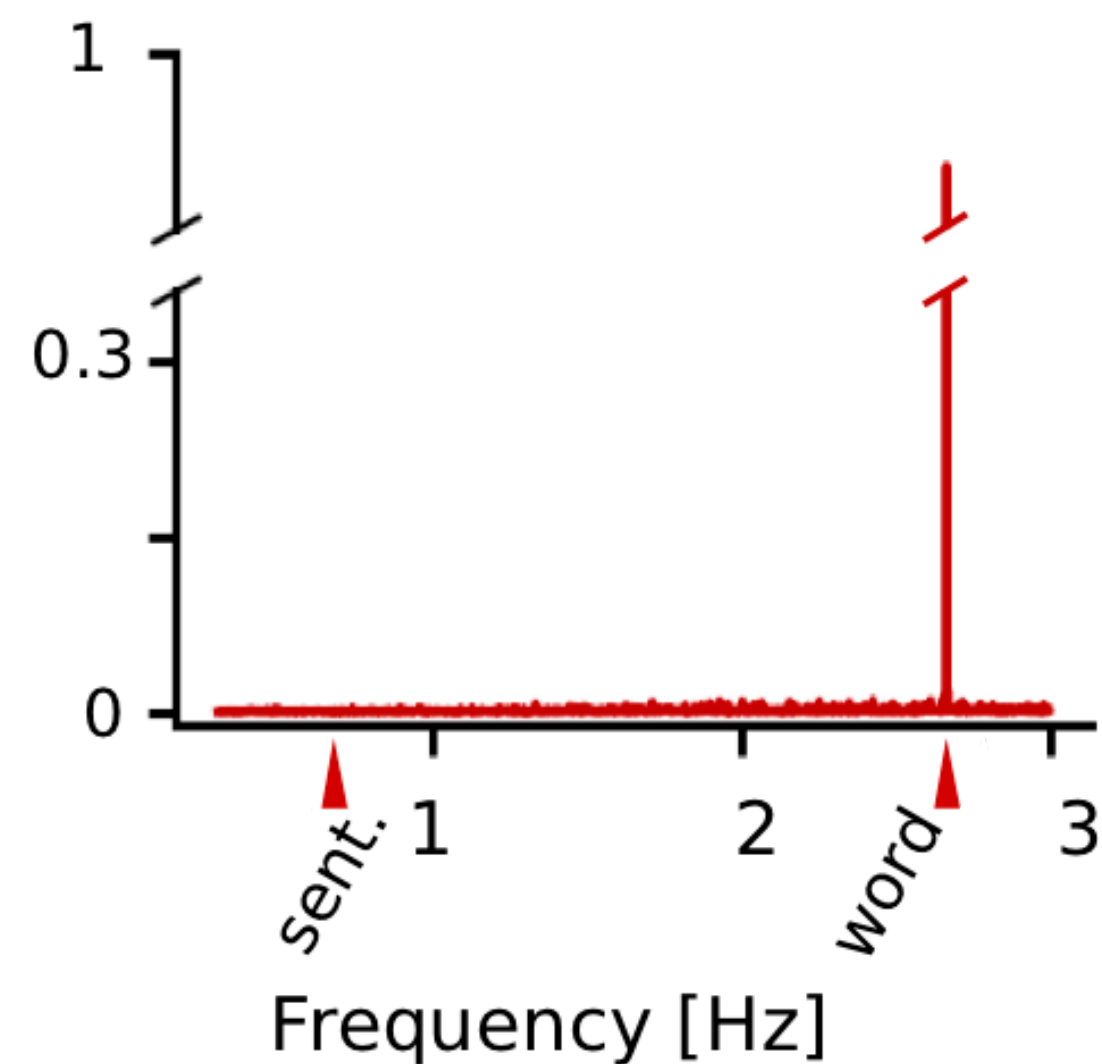


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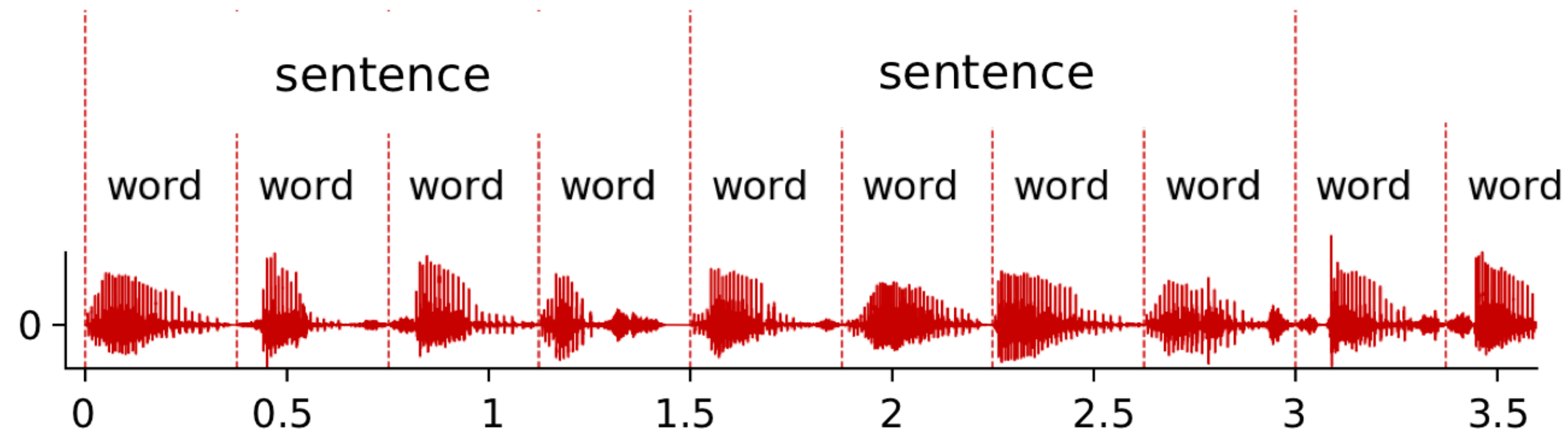


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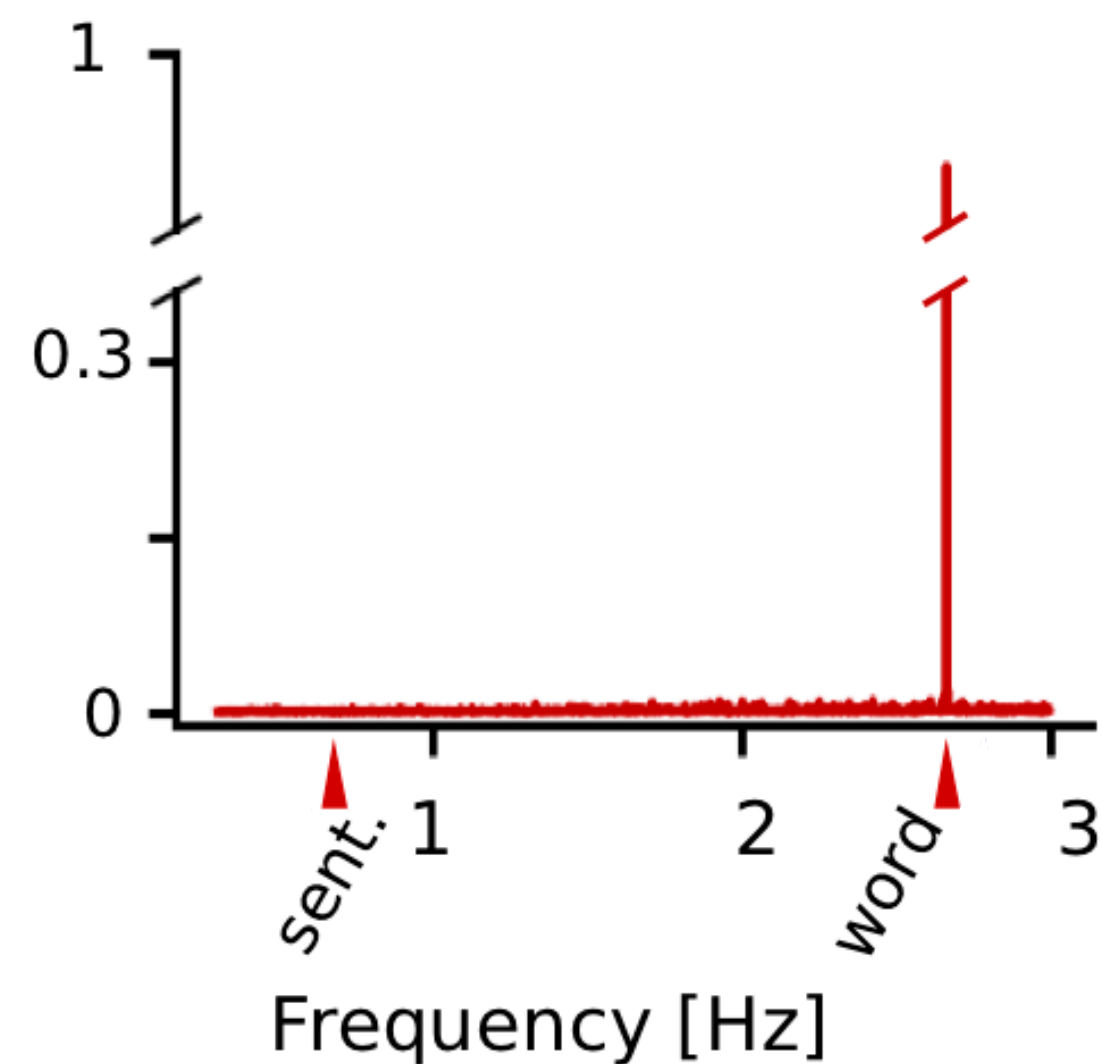


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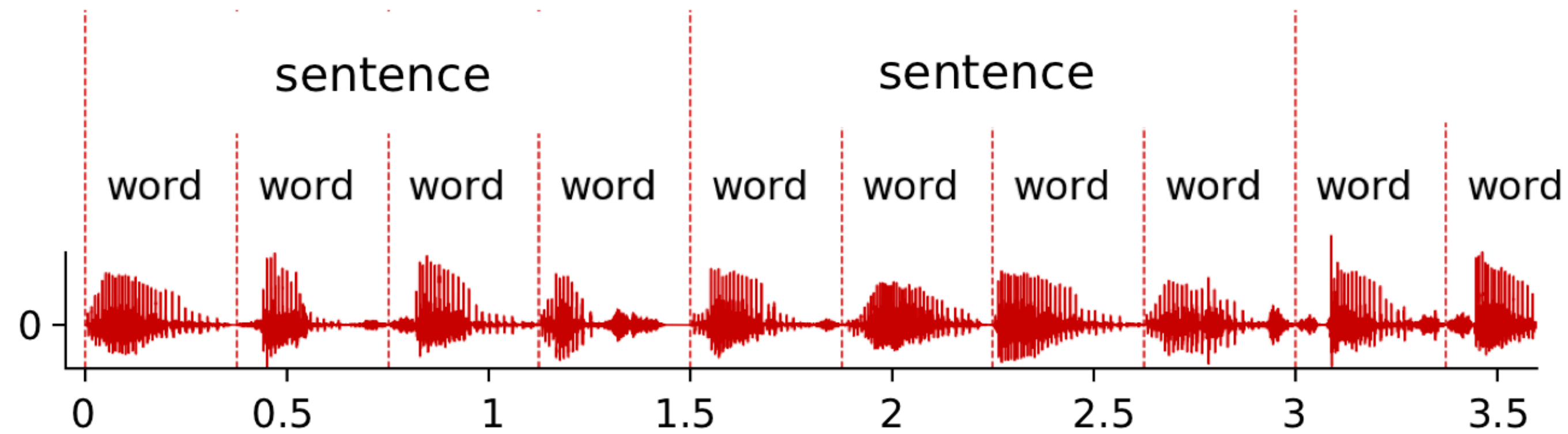


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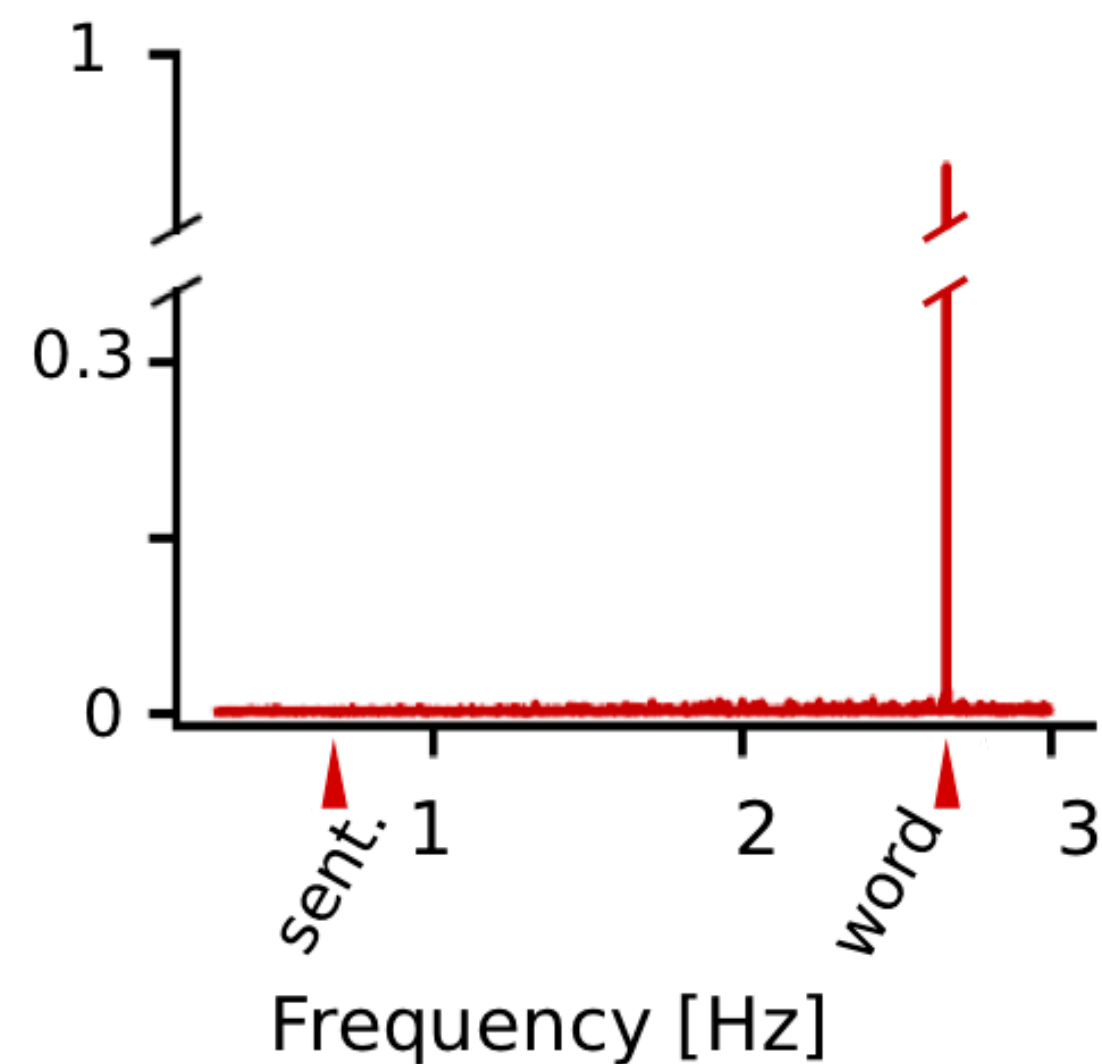


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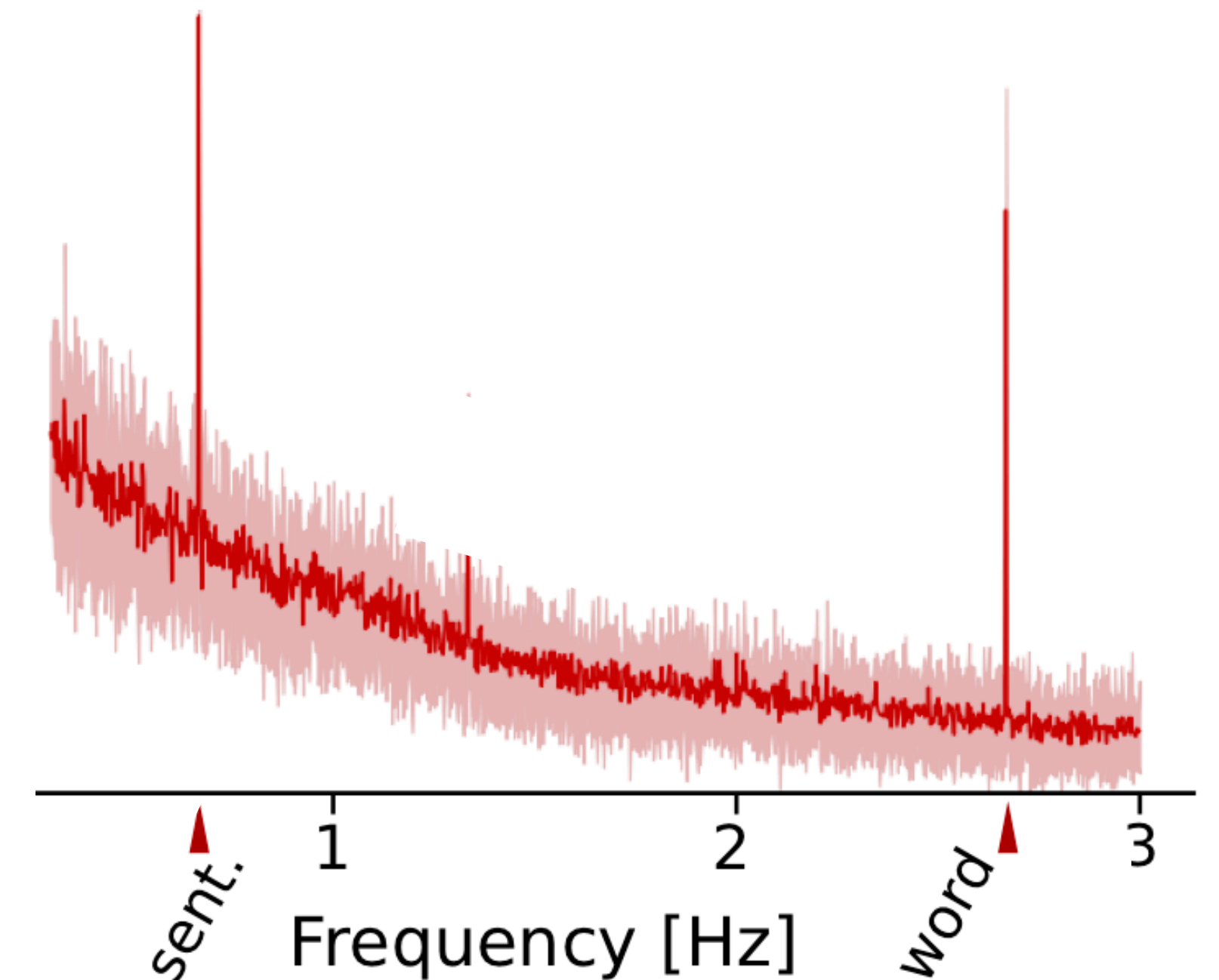
Acoustics



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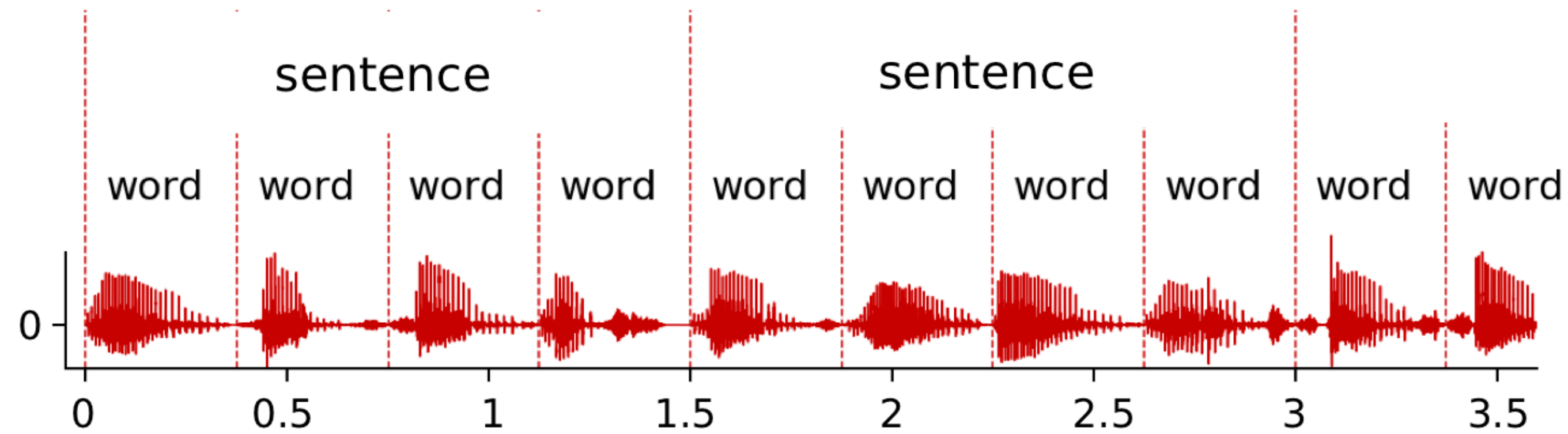


Perception?

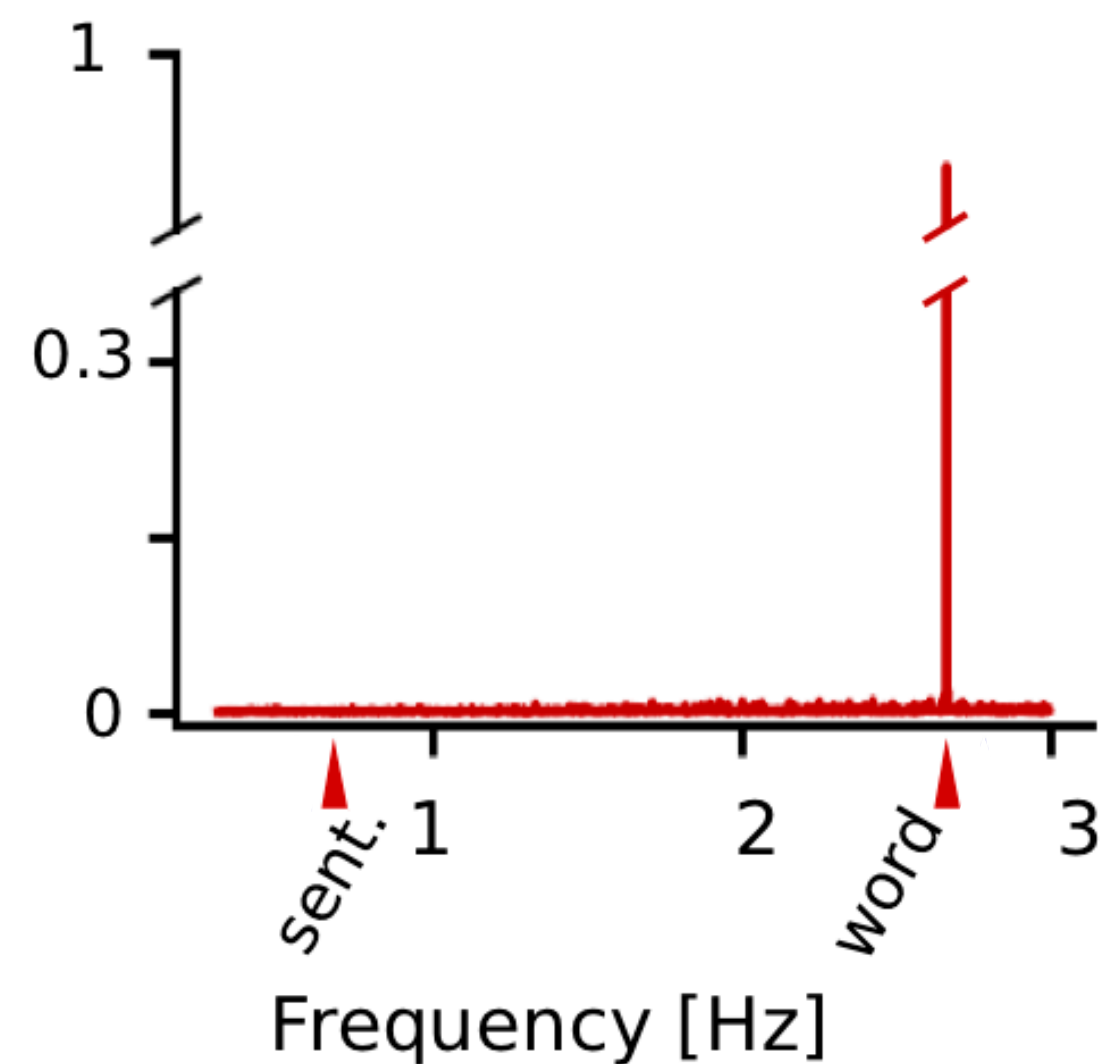


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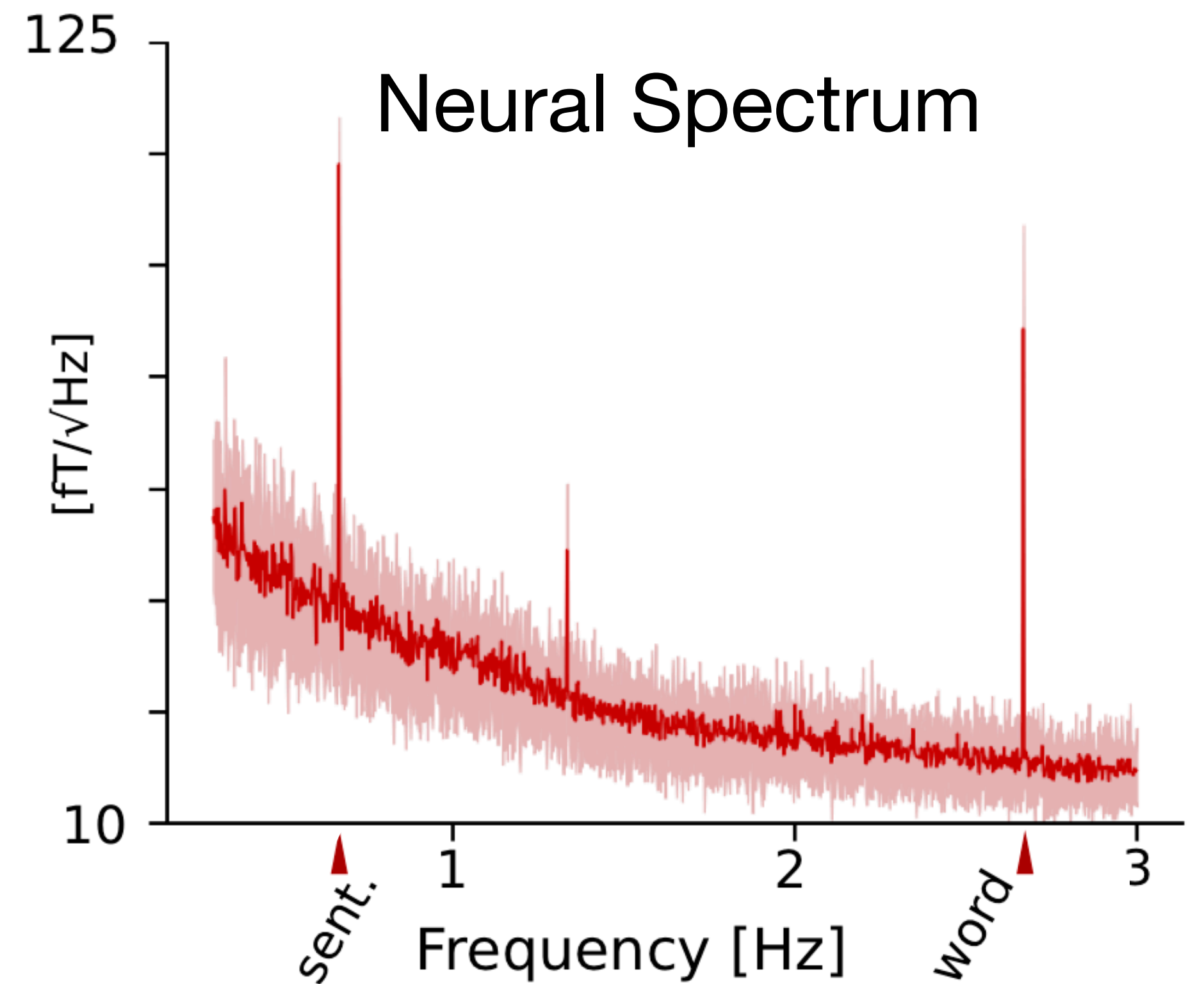
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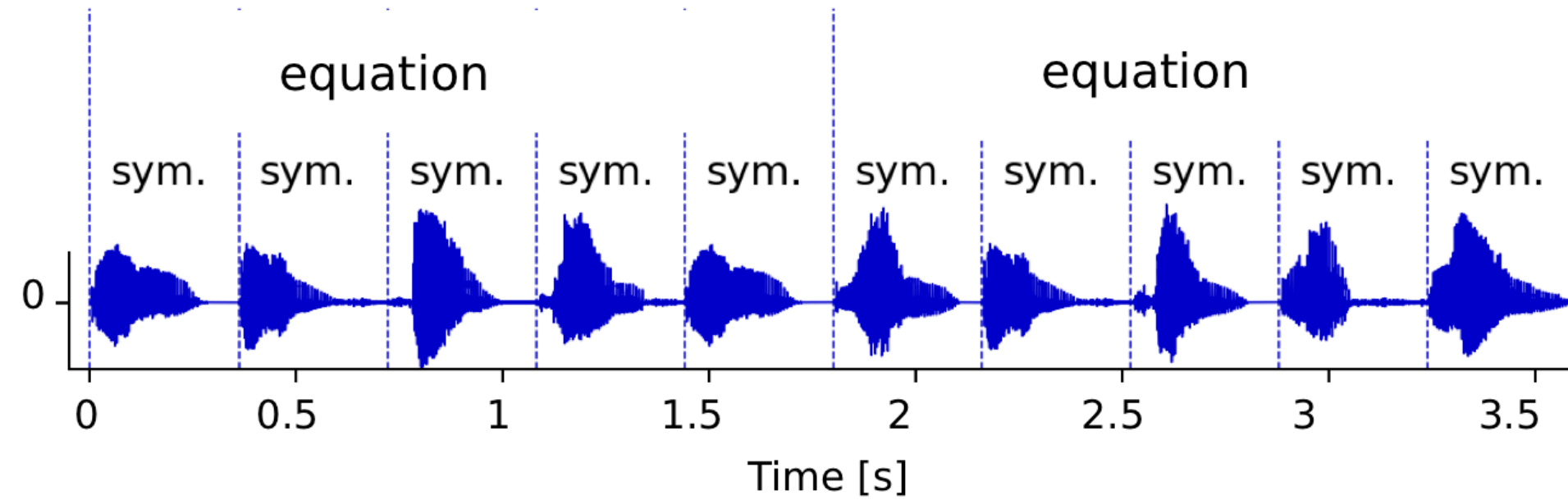
Acoustical
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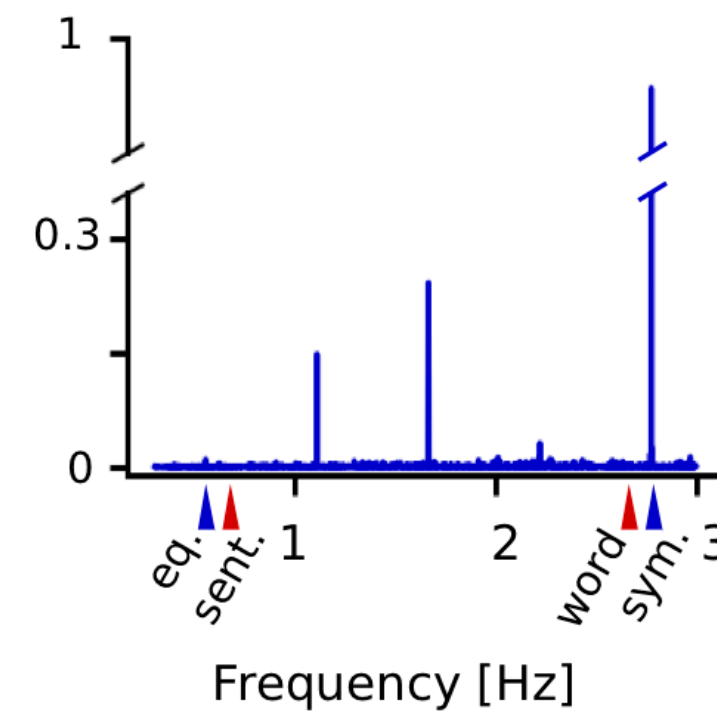
Neural Spectrum



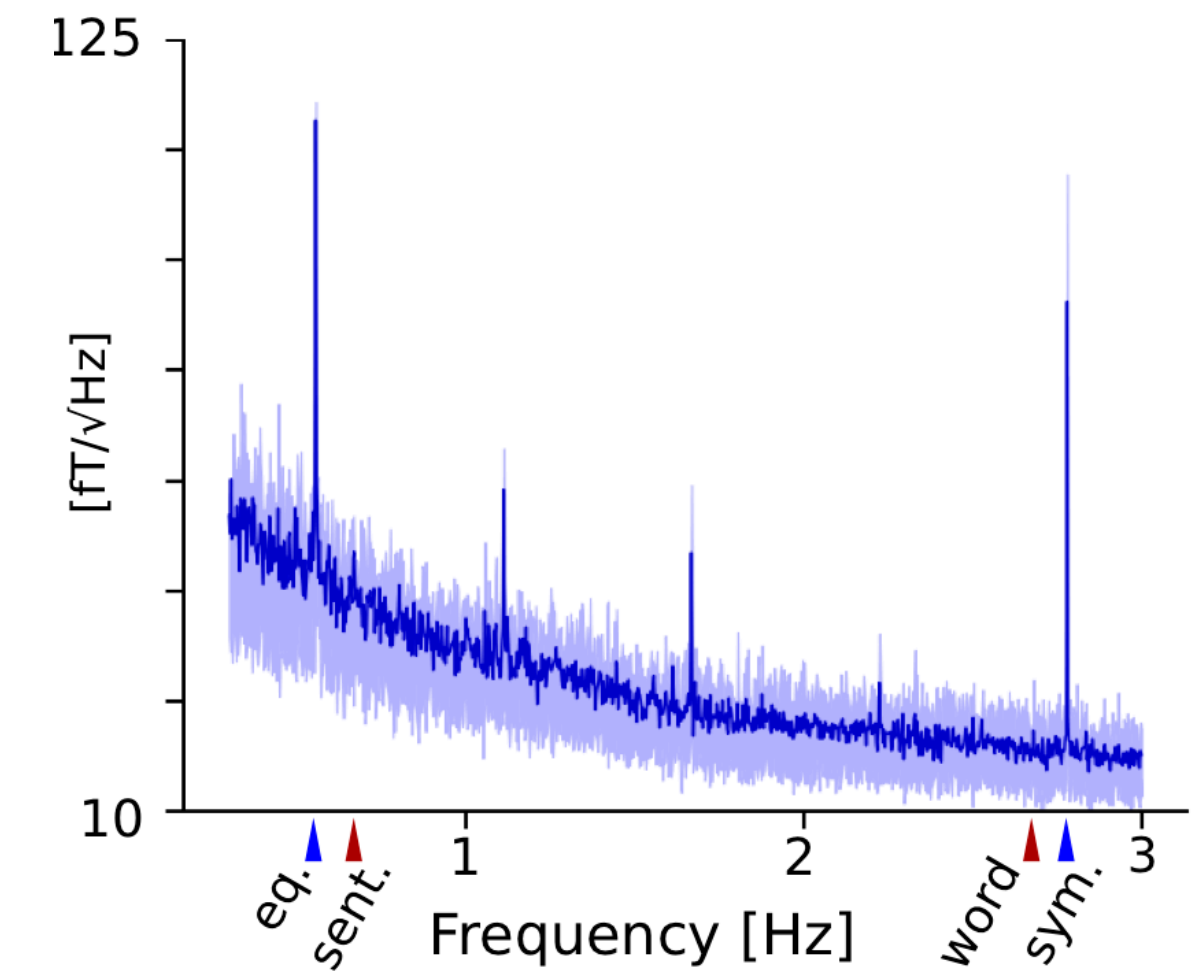
Isochronous Arithmetic



Acoustics



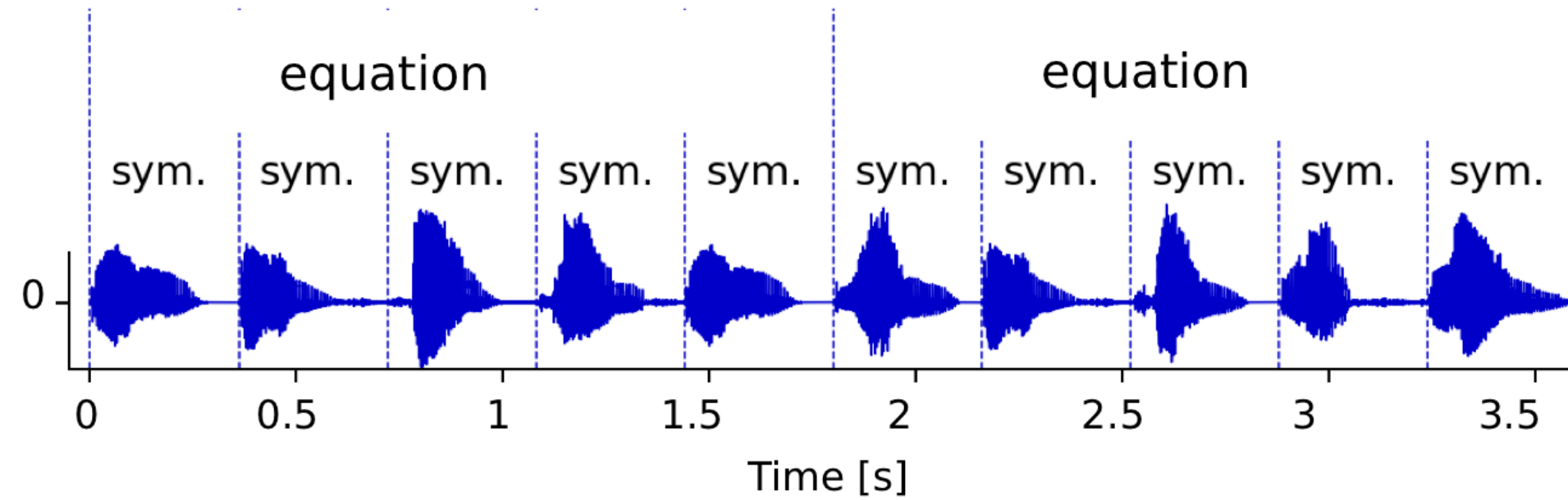
Acoustical Spectrum



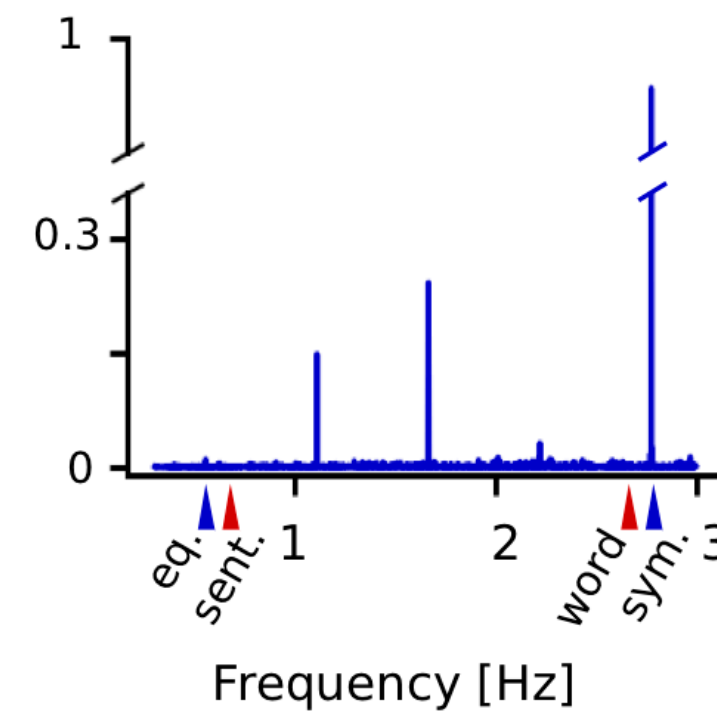
Neural Spectrum



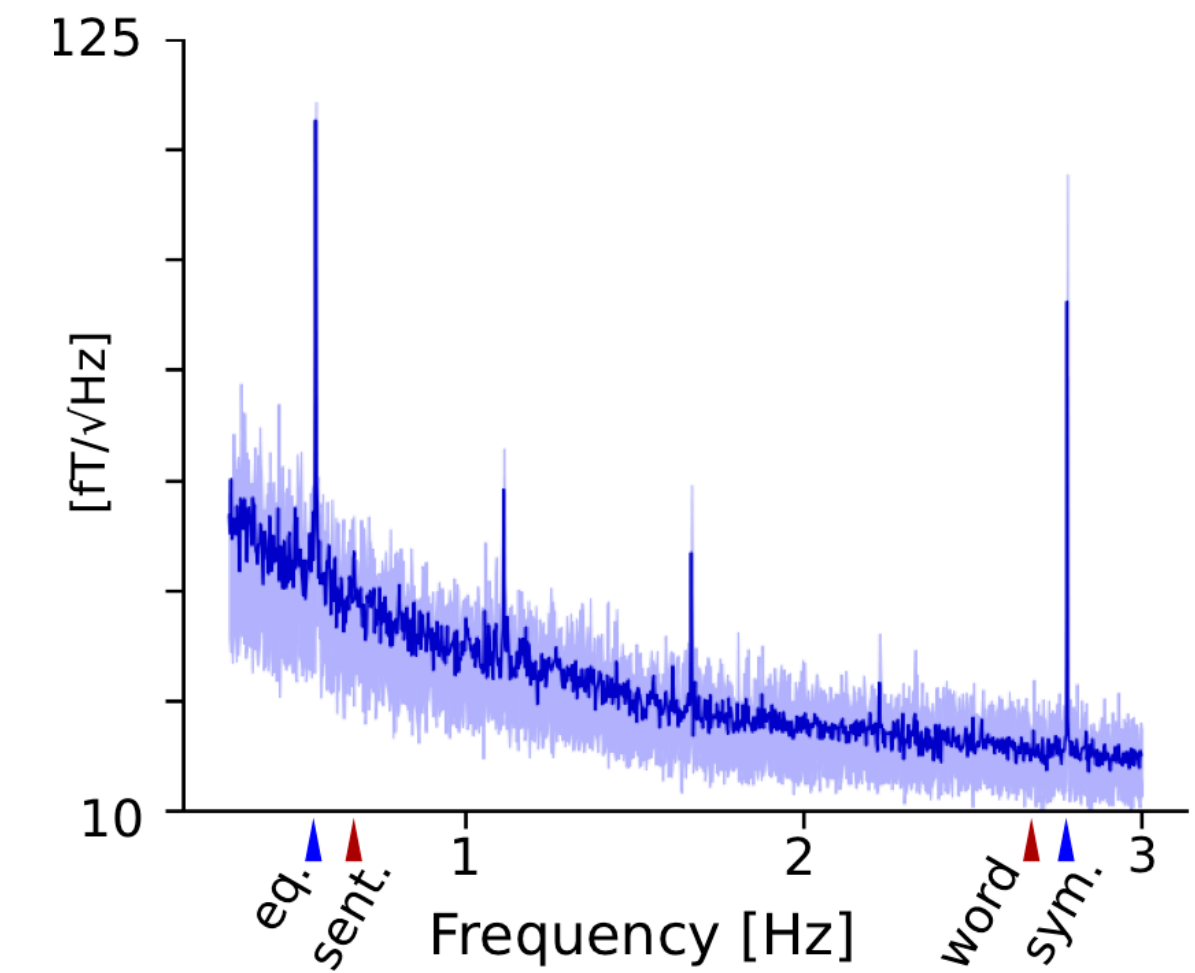
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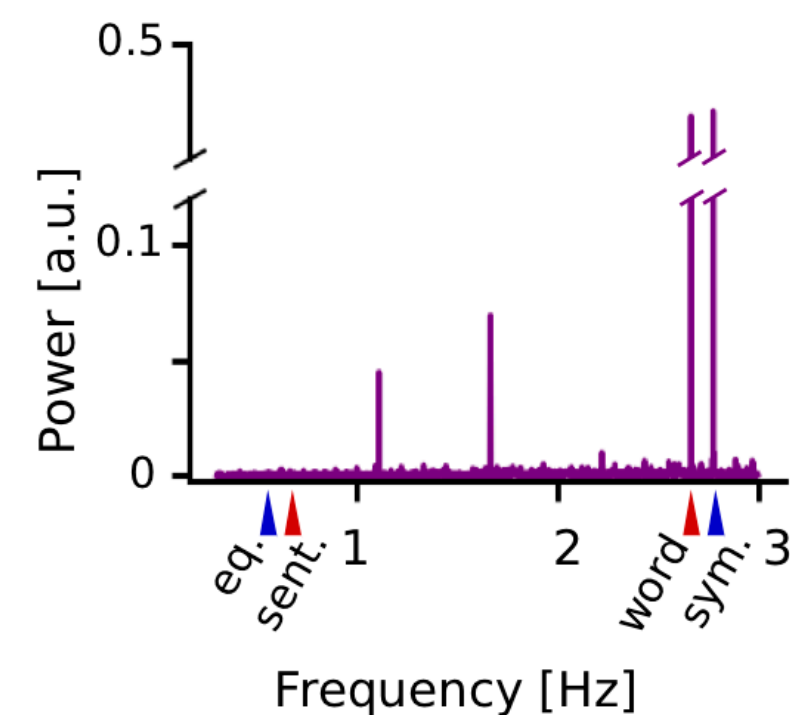
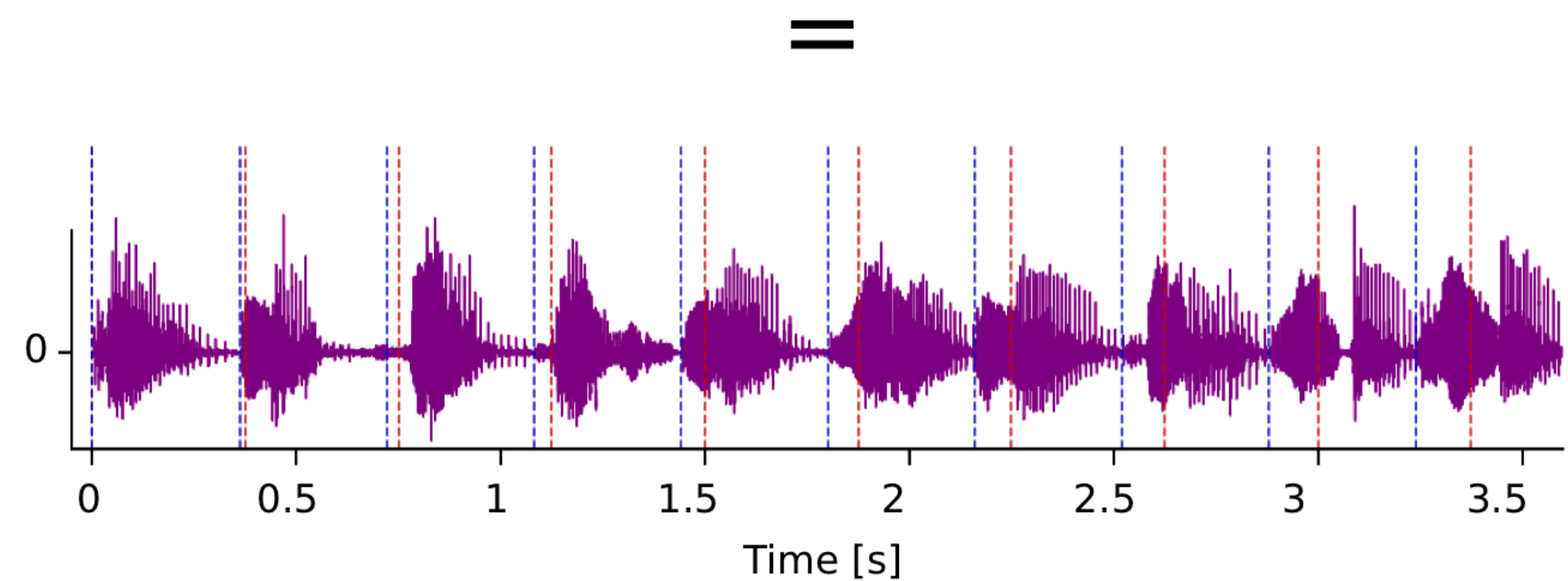
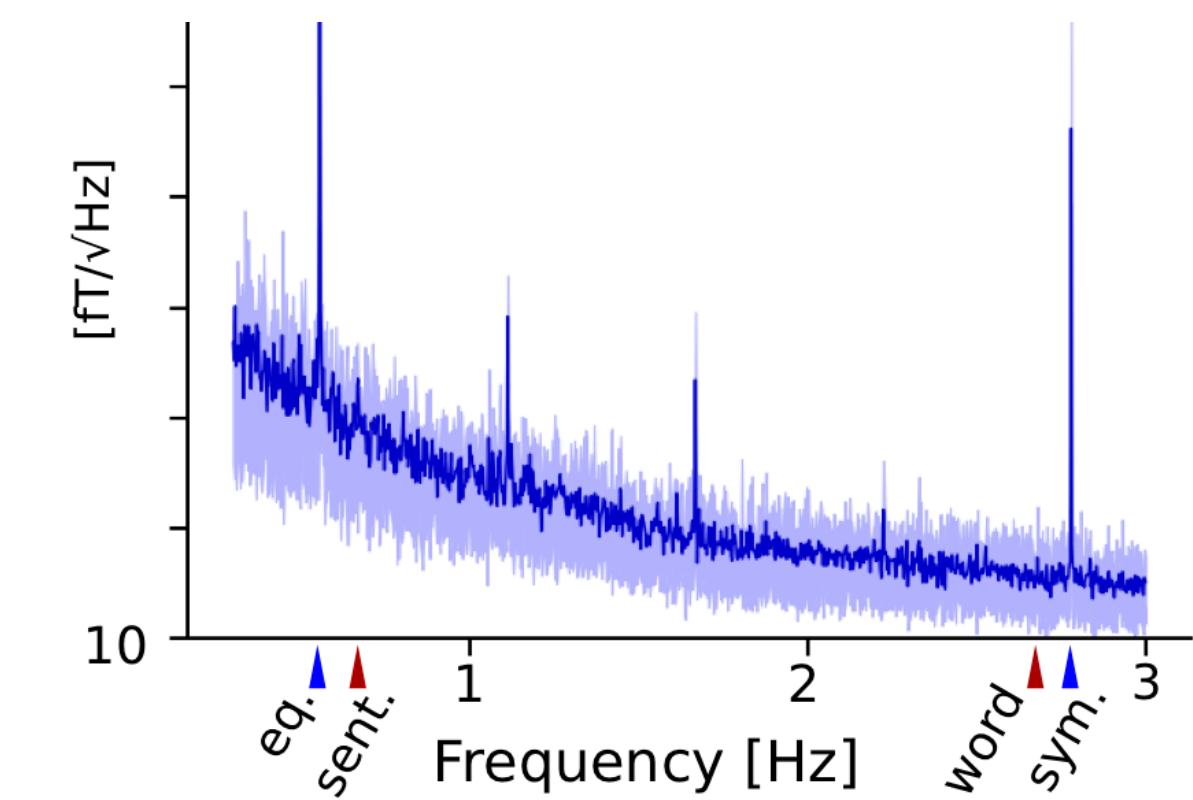
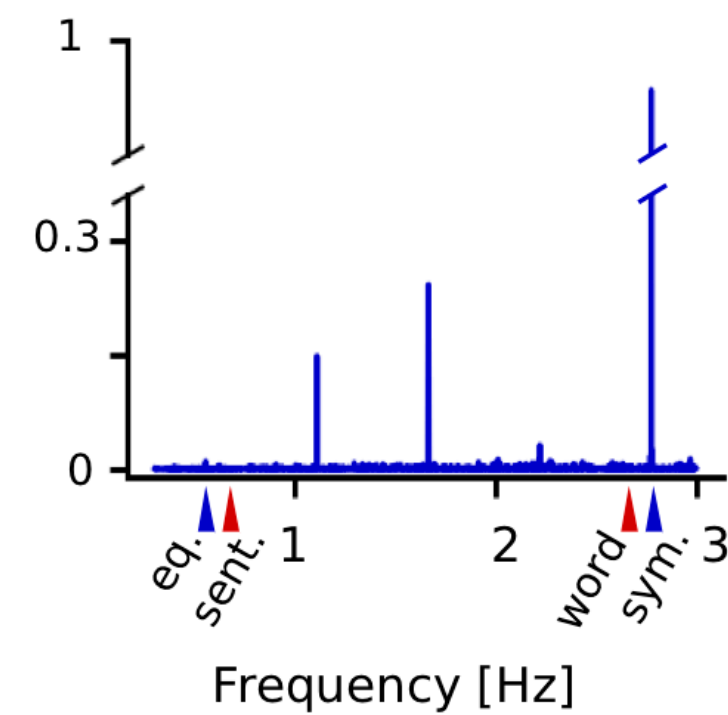
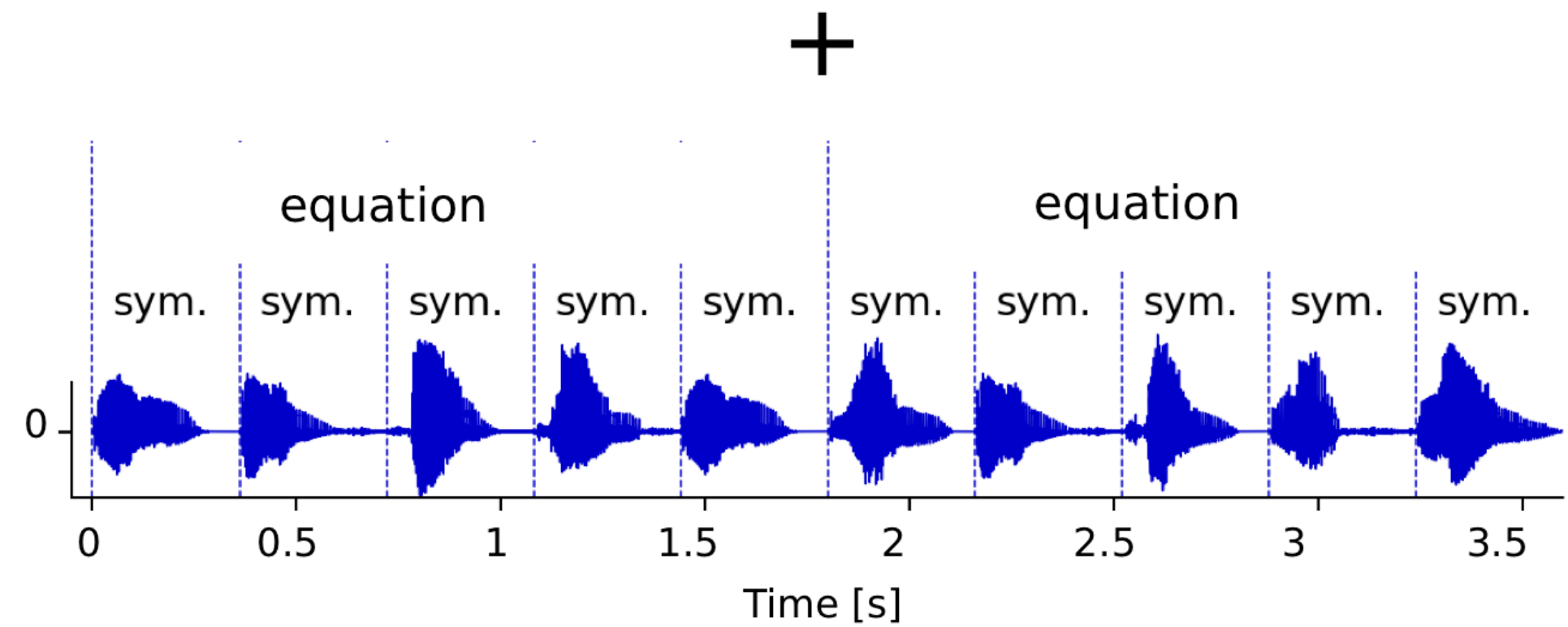
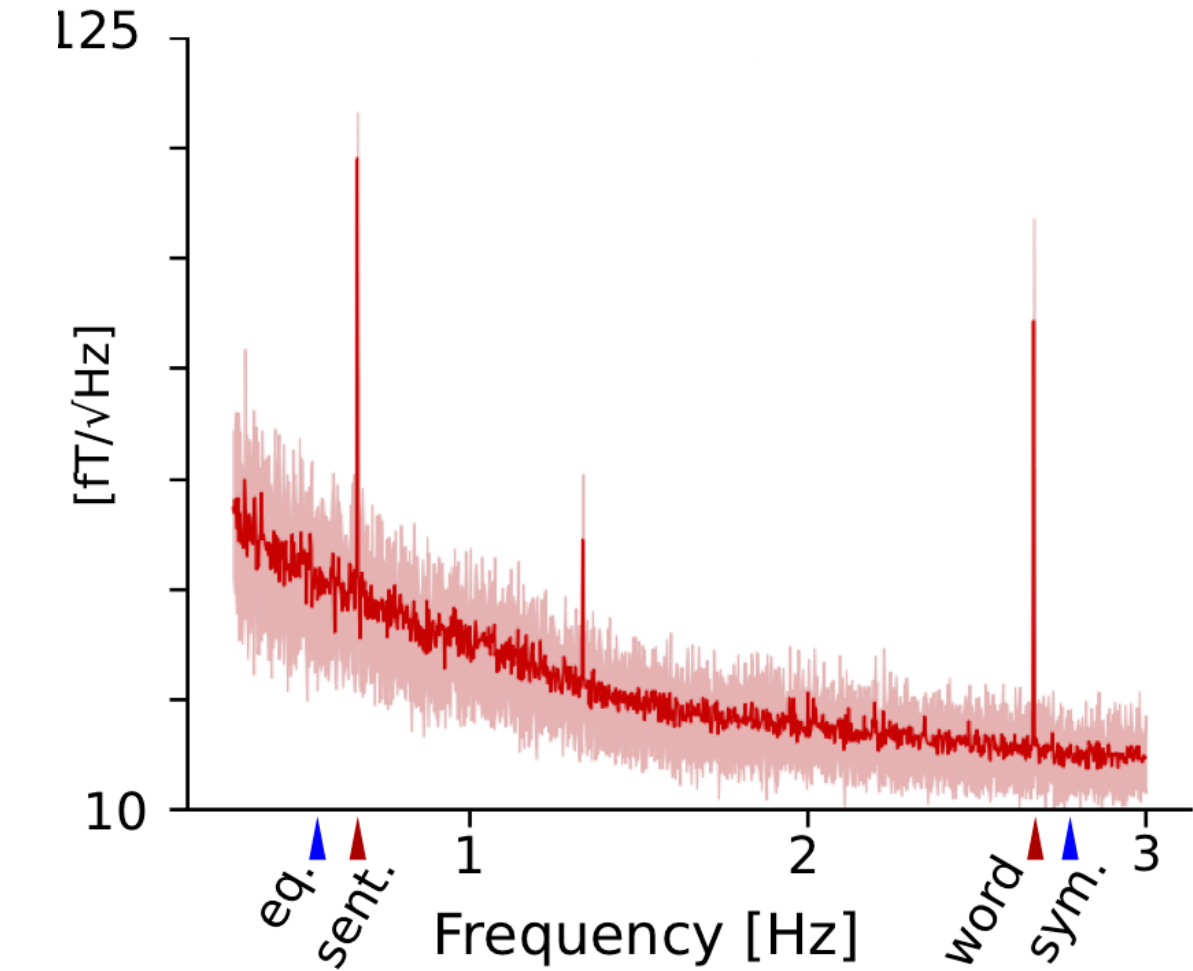
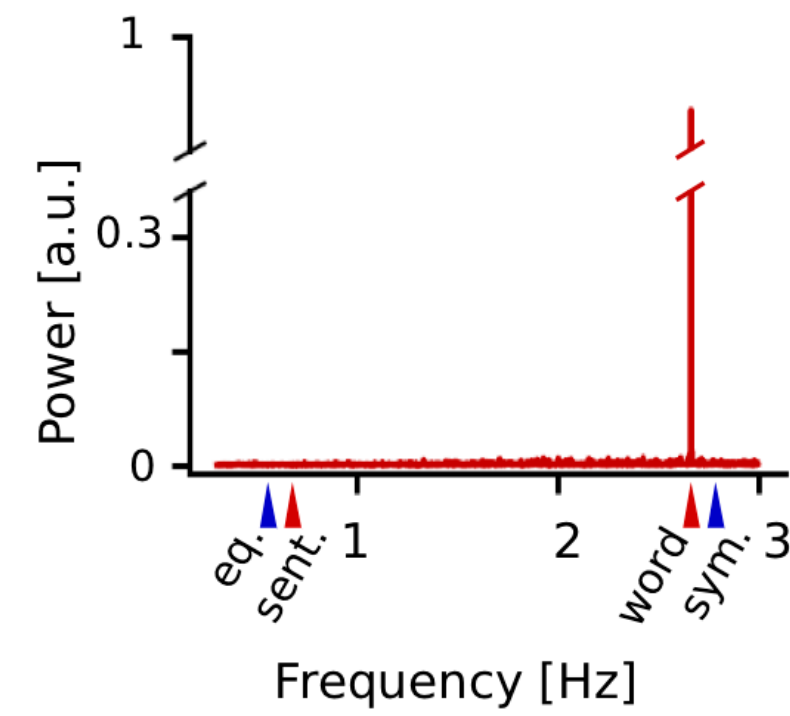
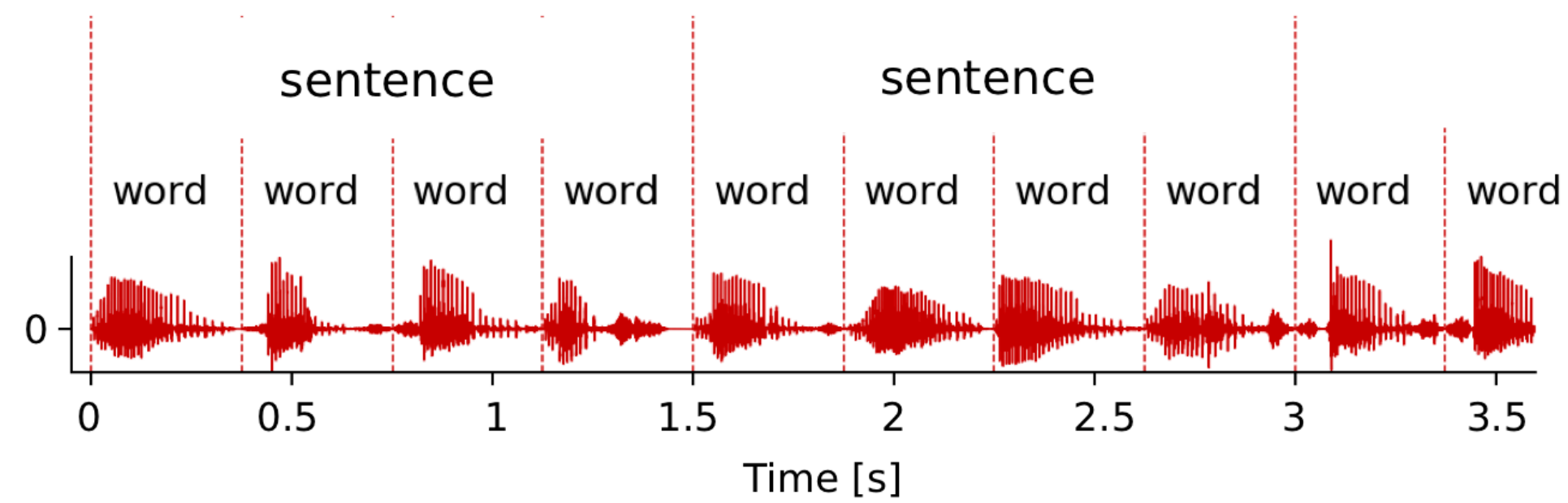
Acoustical Spectrum



Neural Spectrum



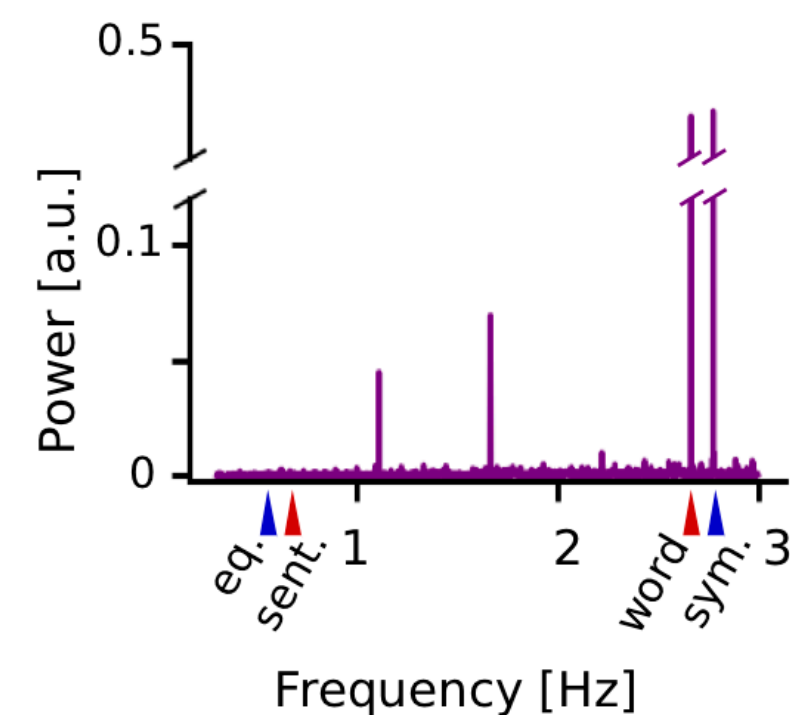
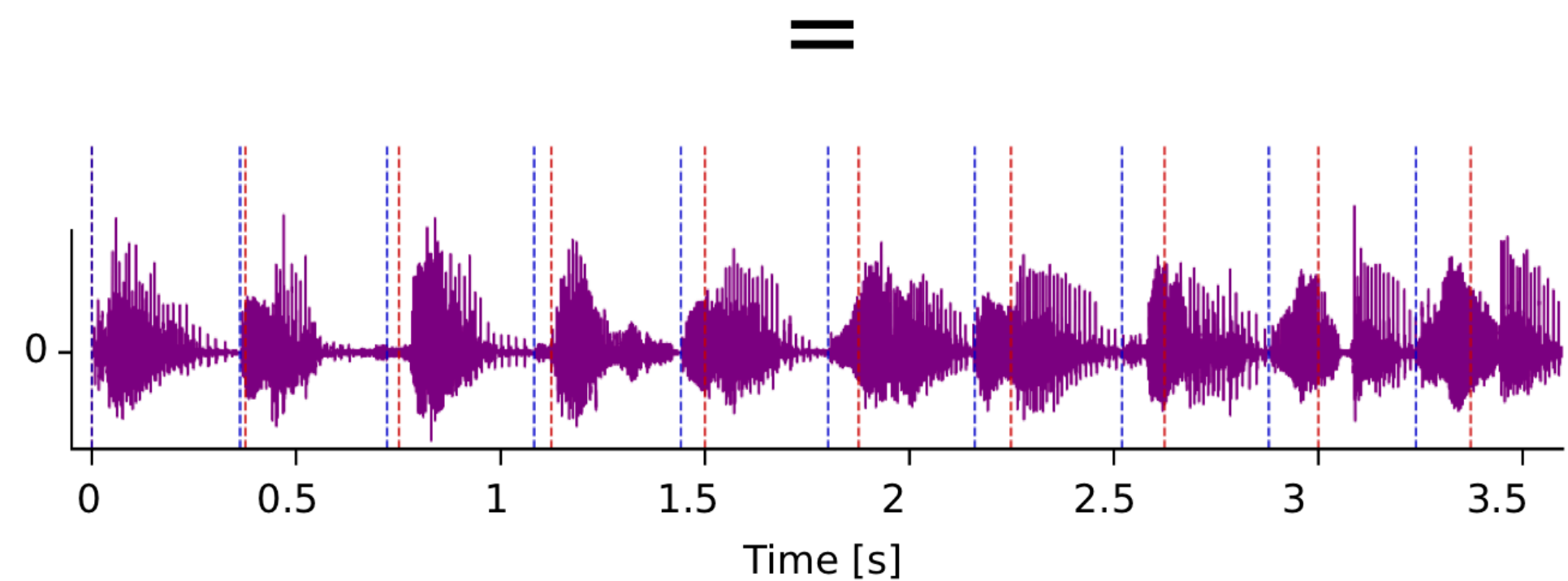
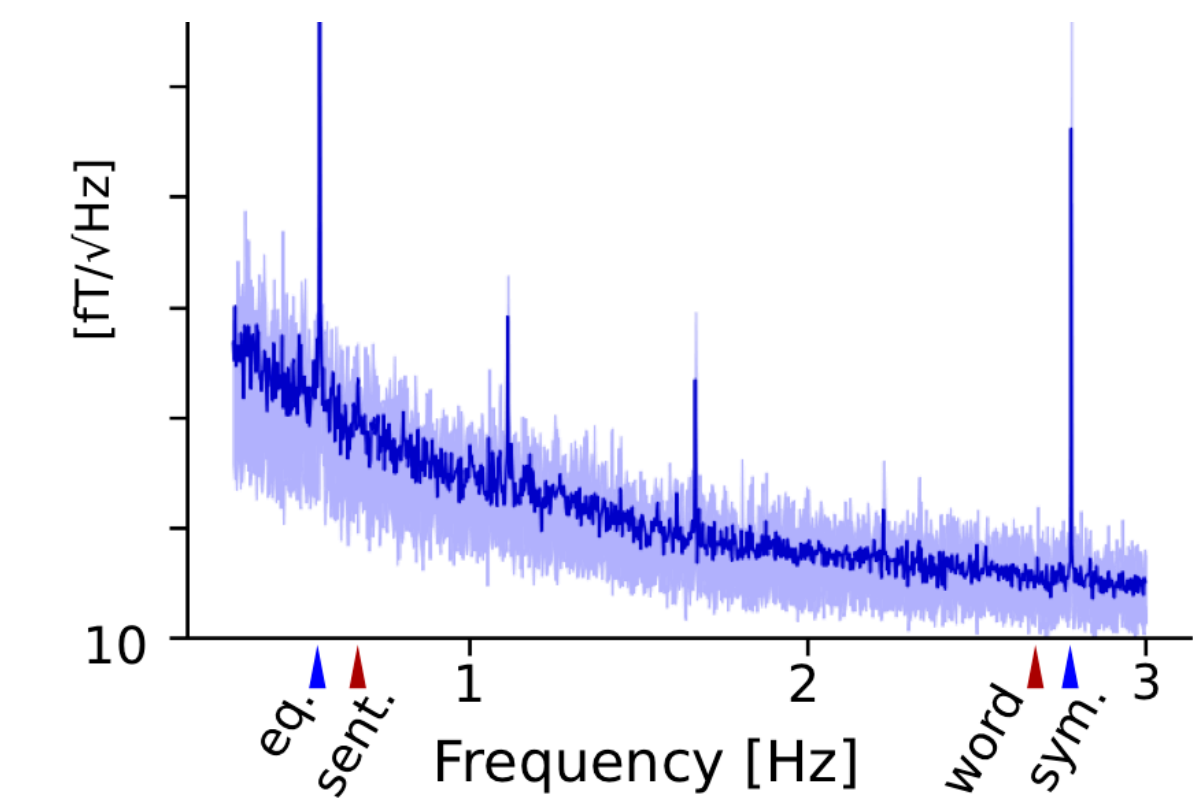
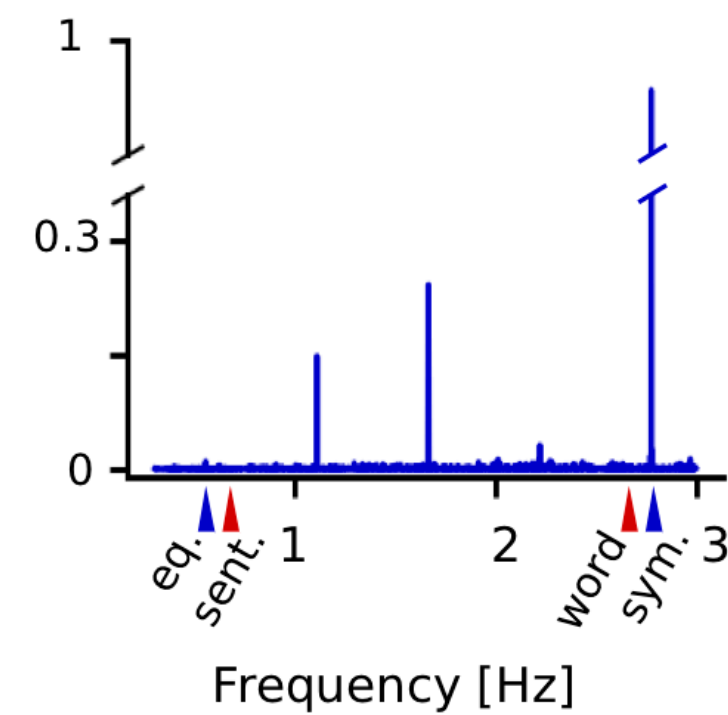
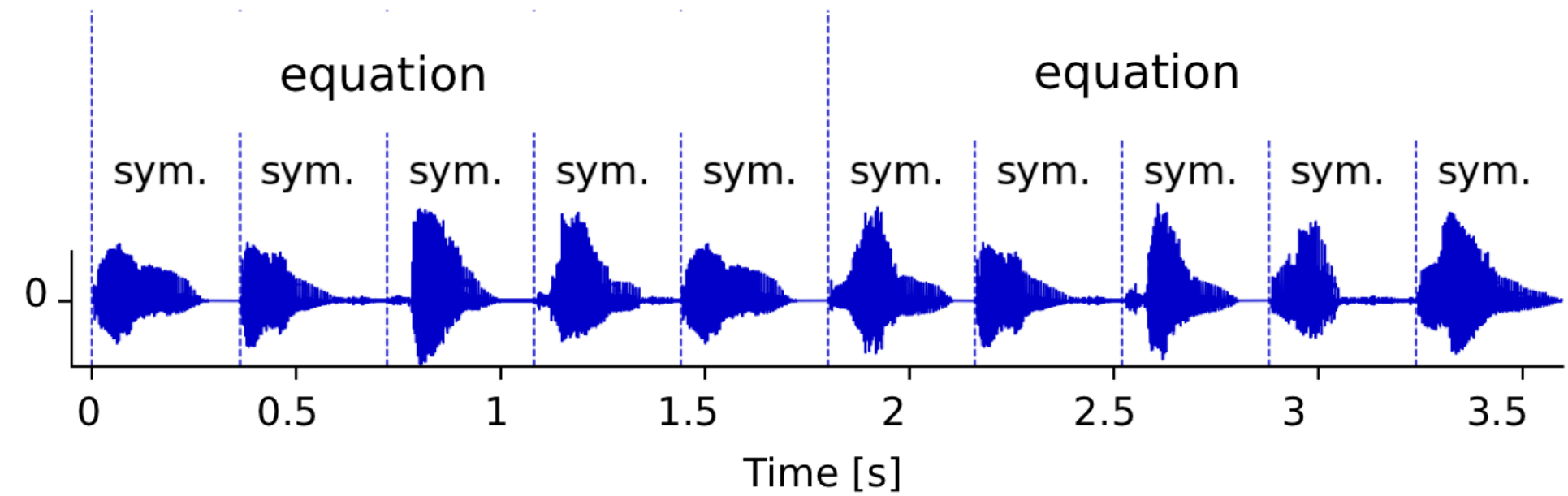
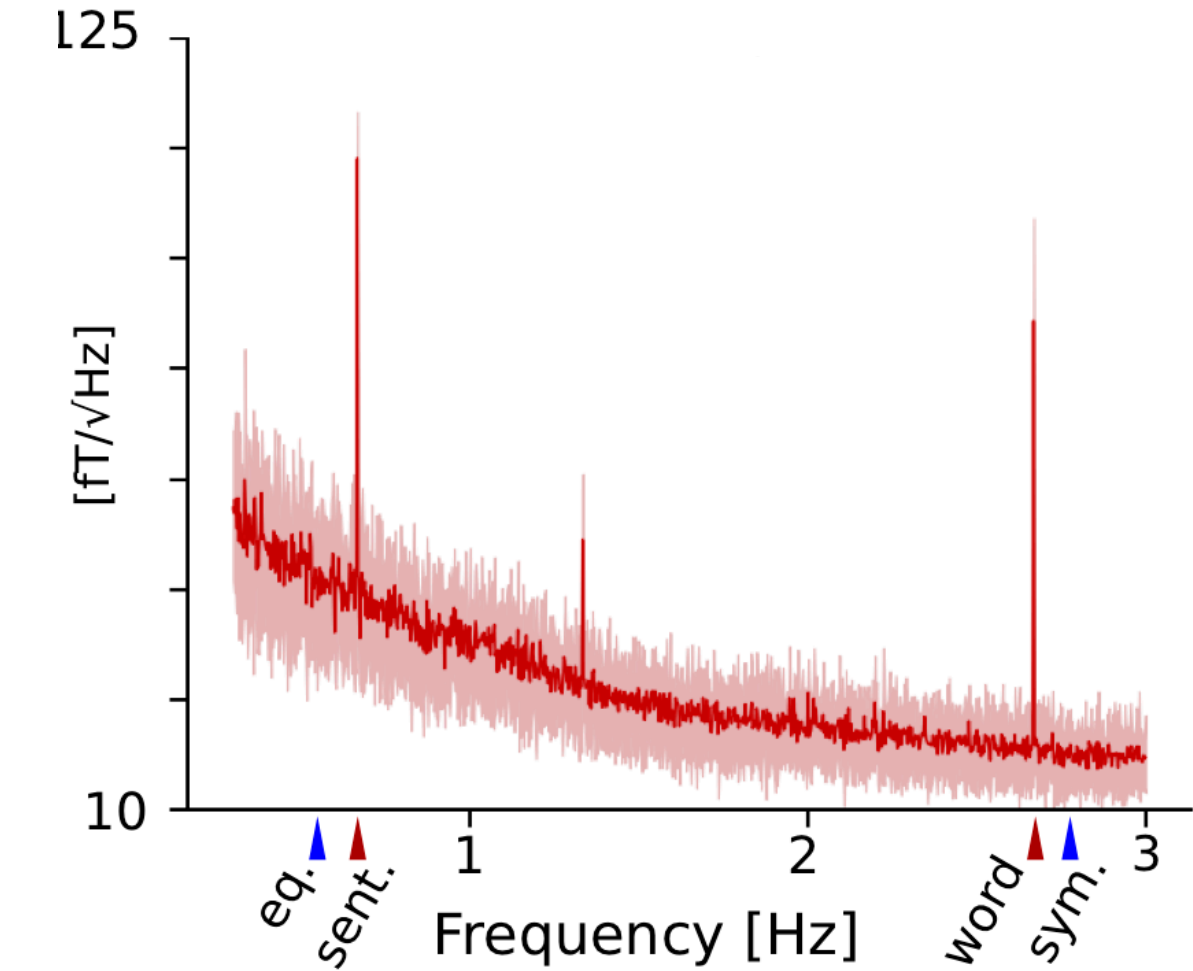
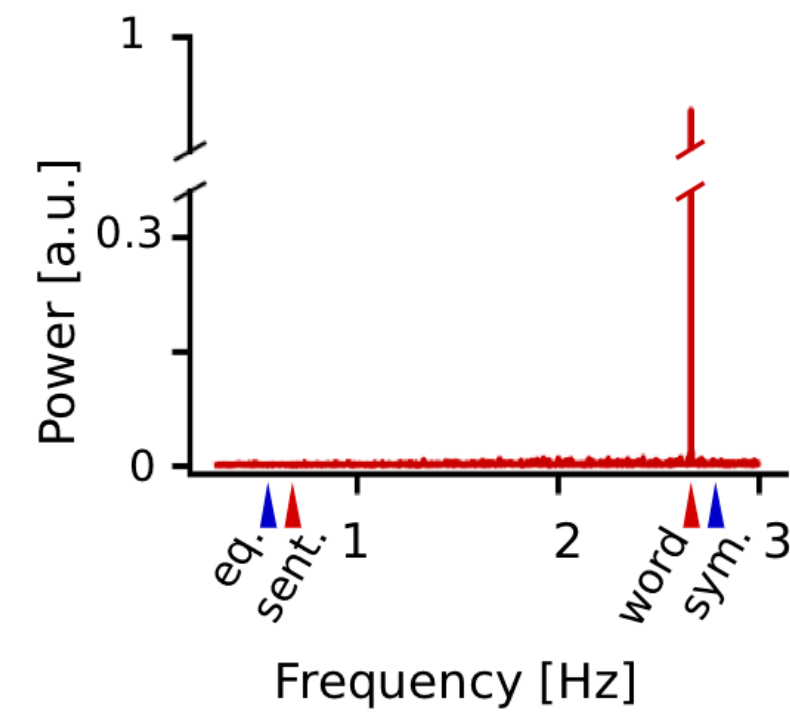
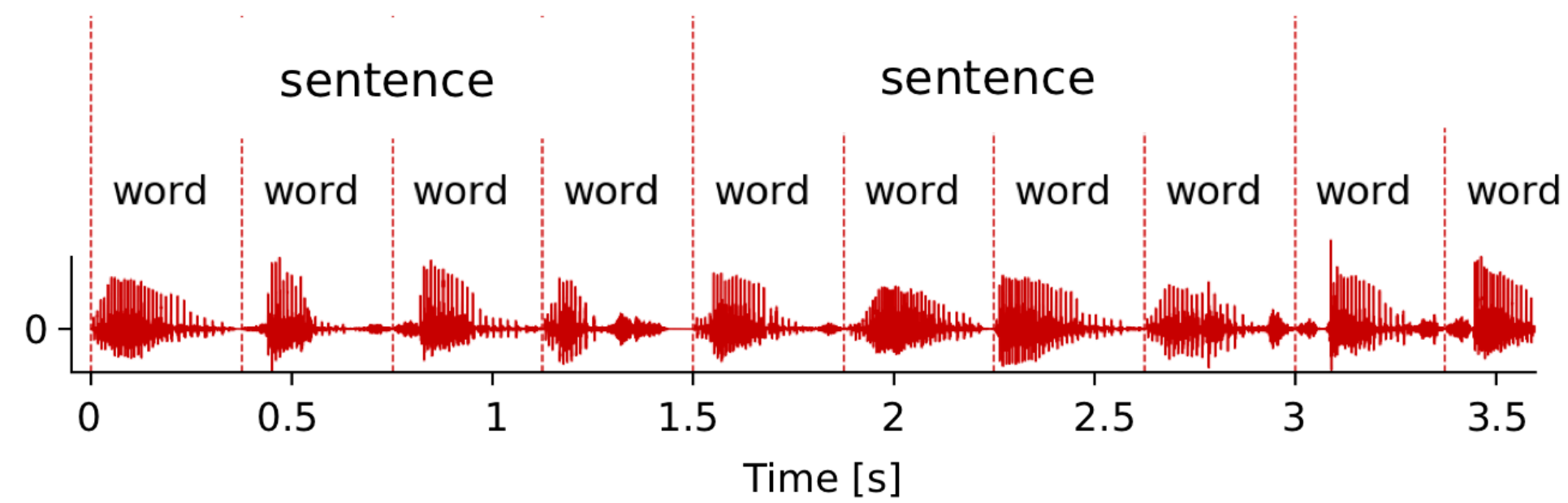
Isochronous Cocktail Party



?



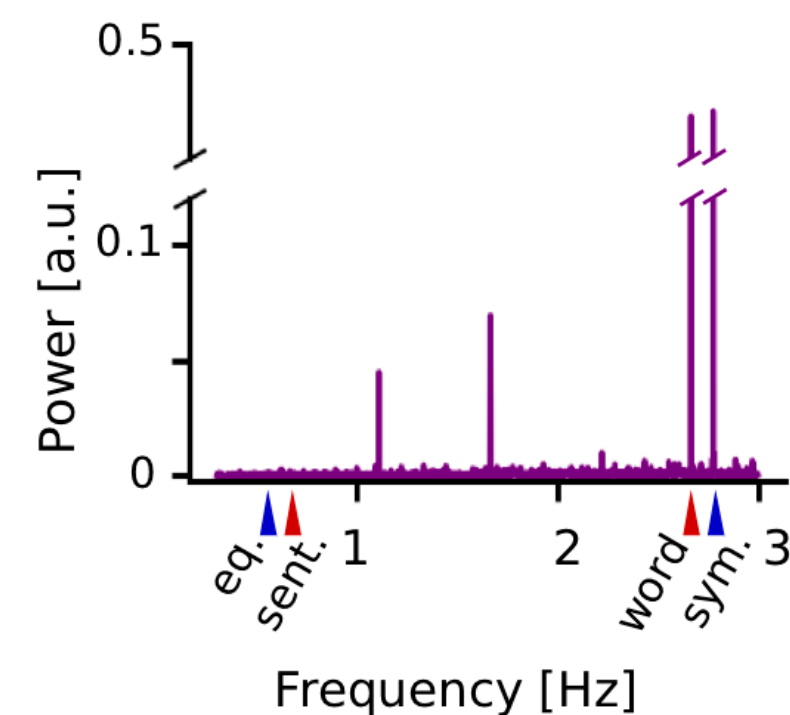
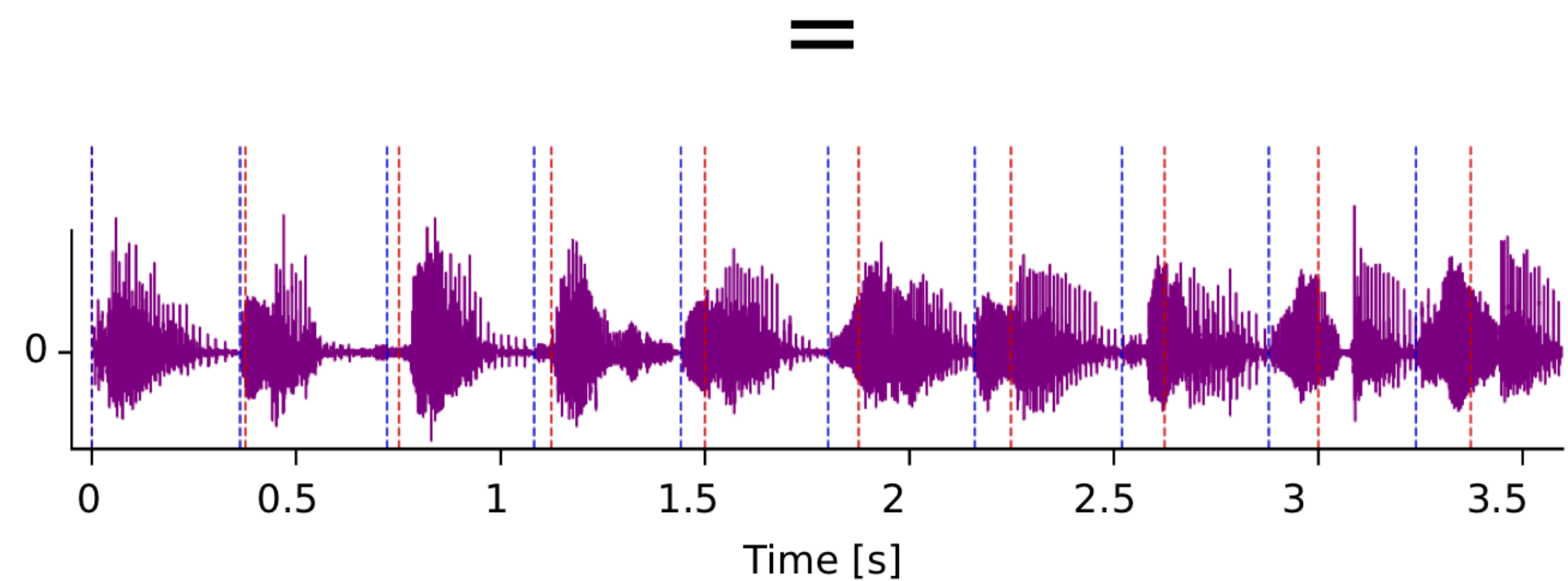
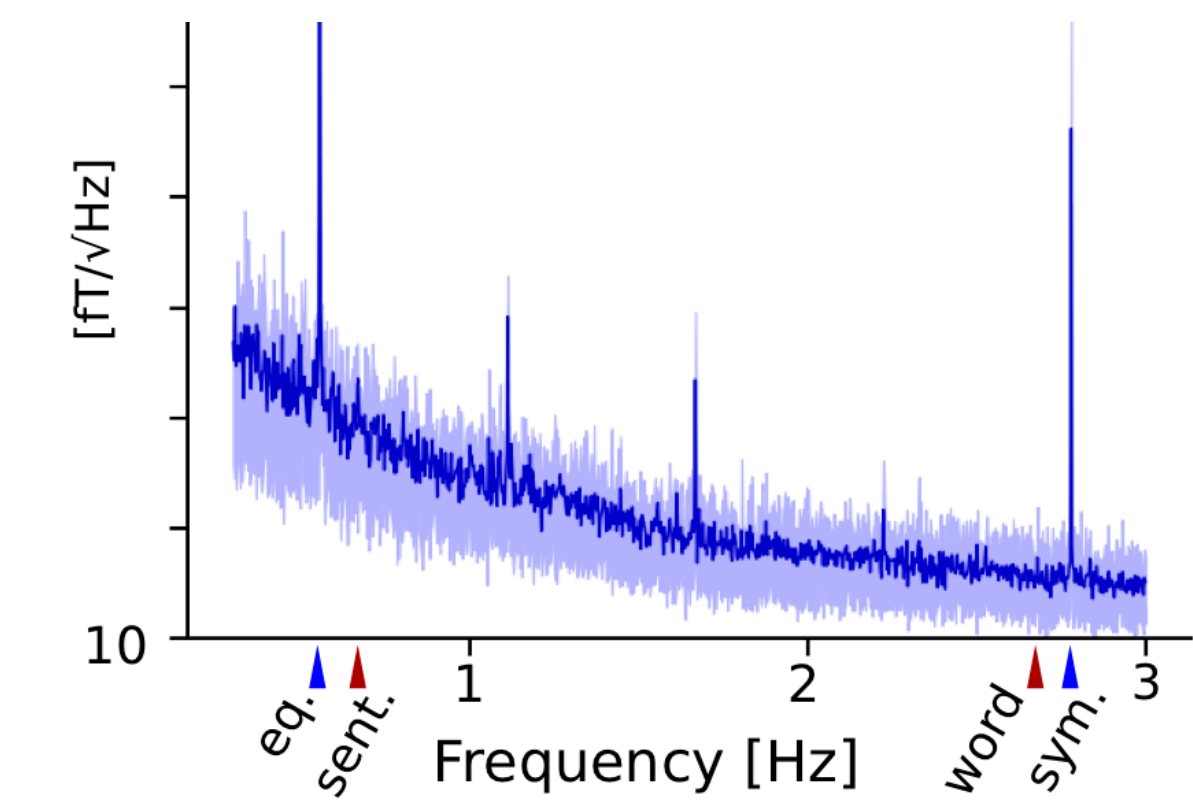
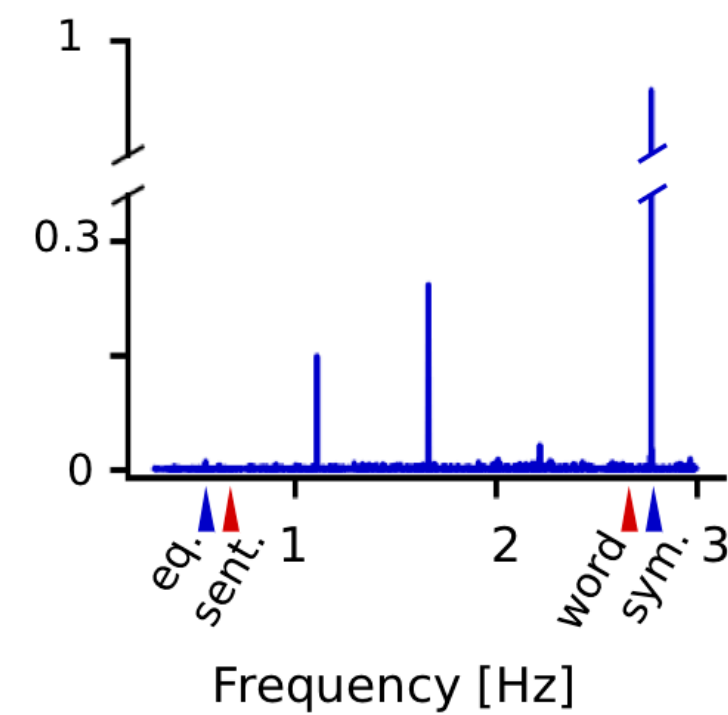
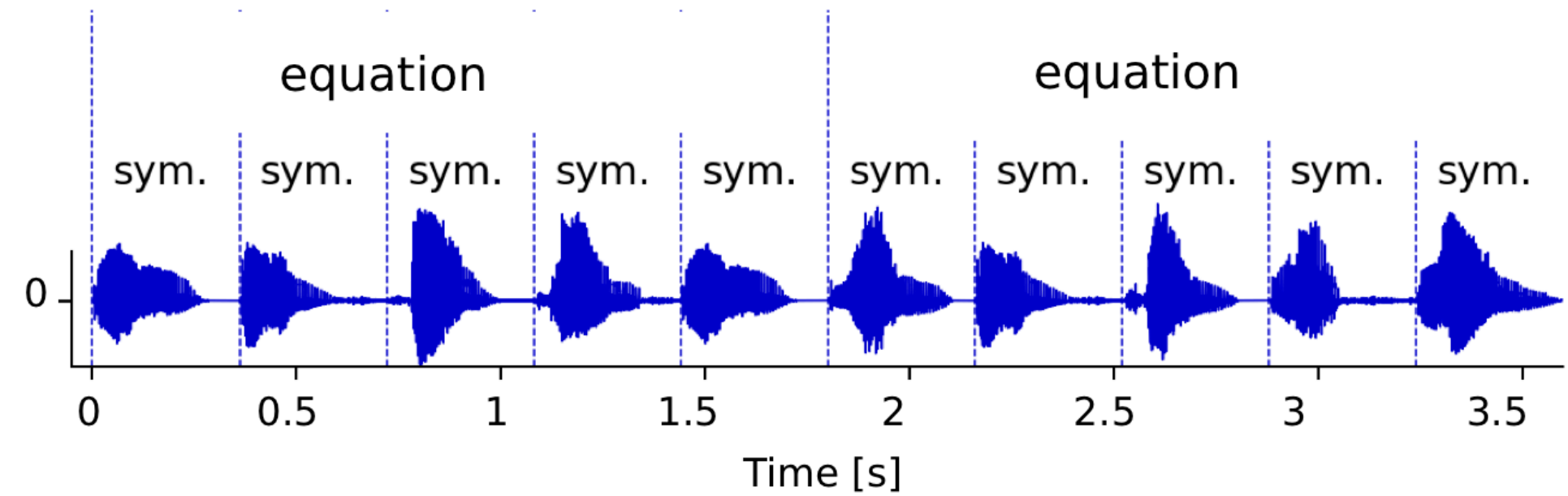
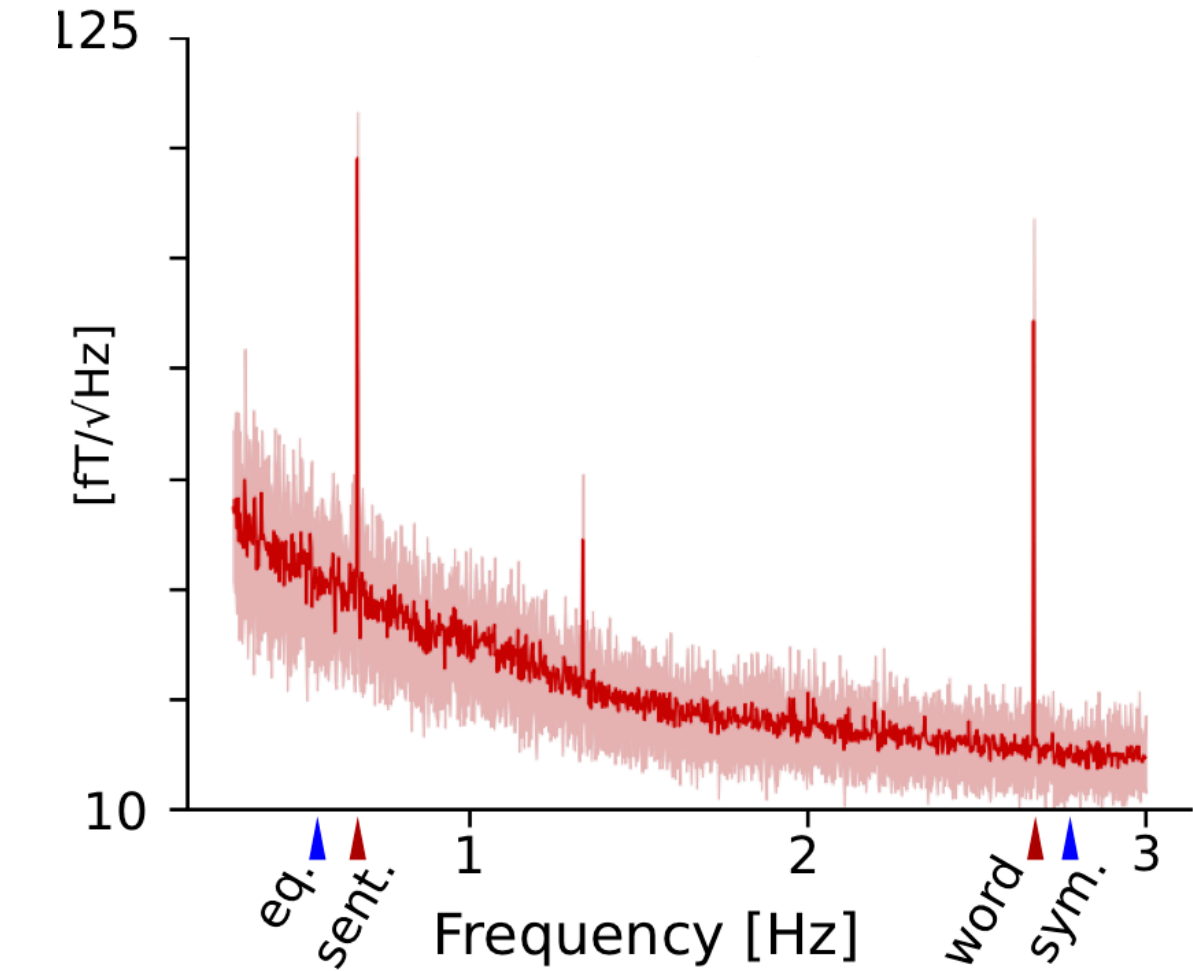
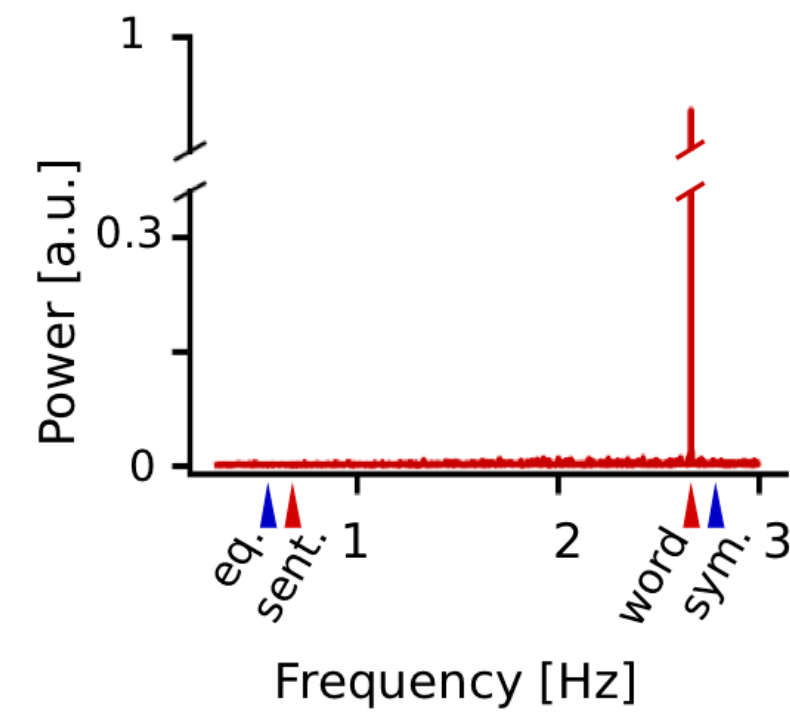
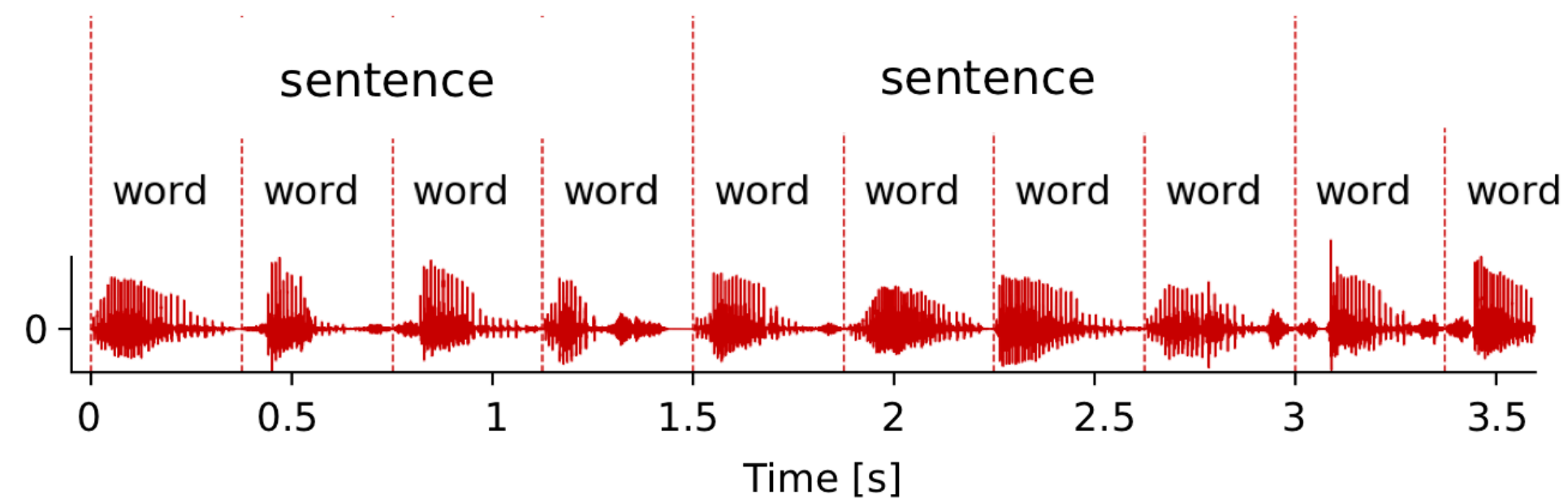
Isochronous Cocktail Party



?



Isochronous Cocktail Party



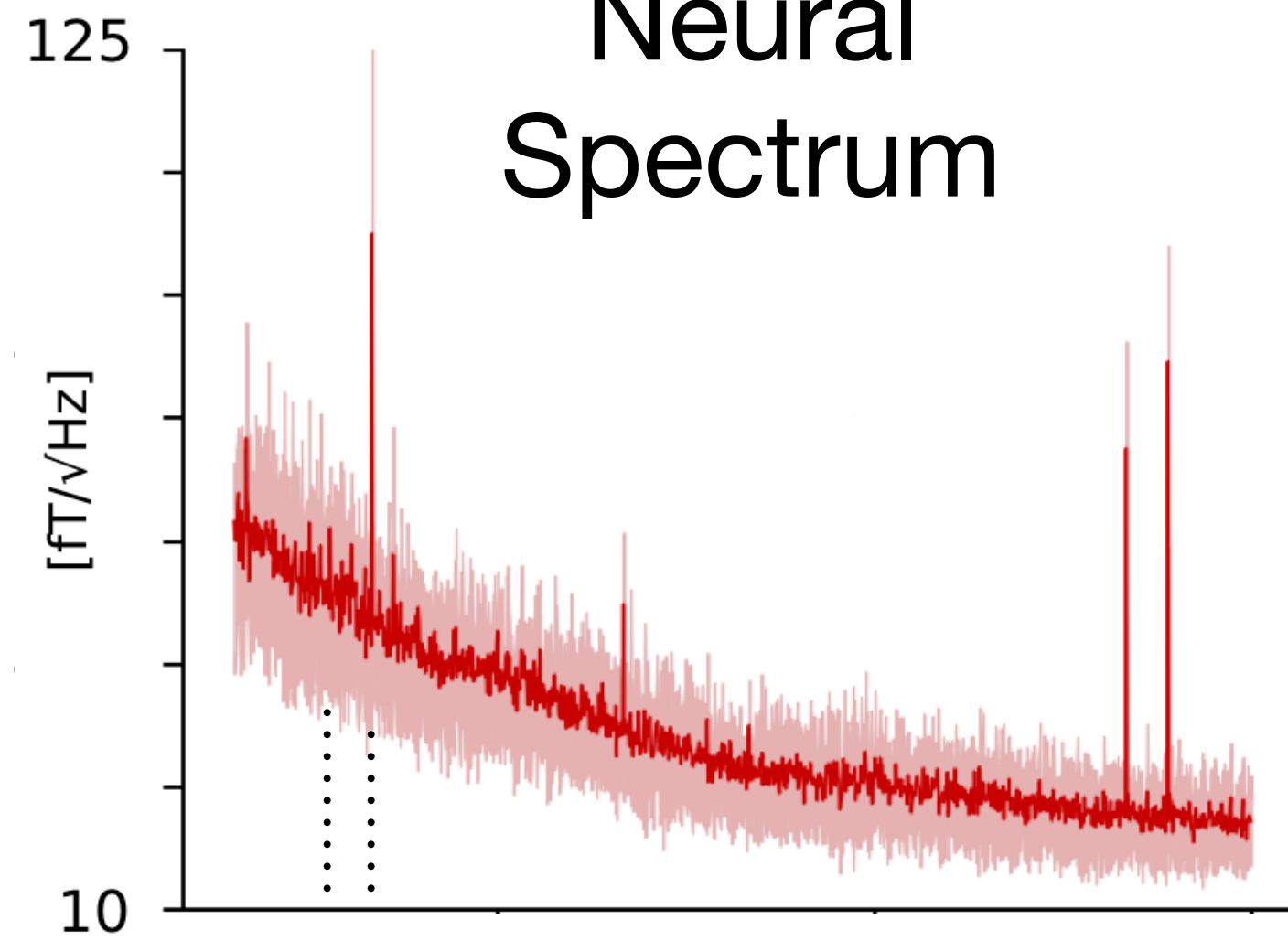
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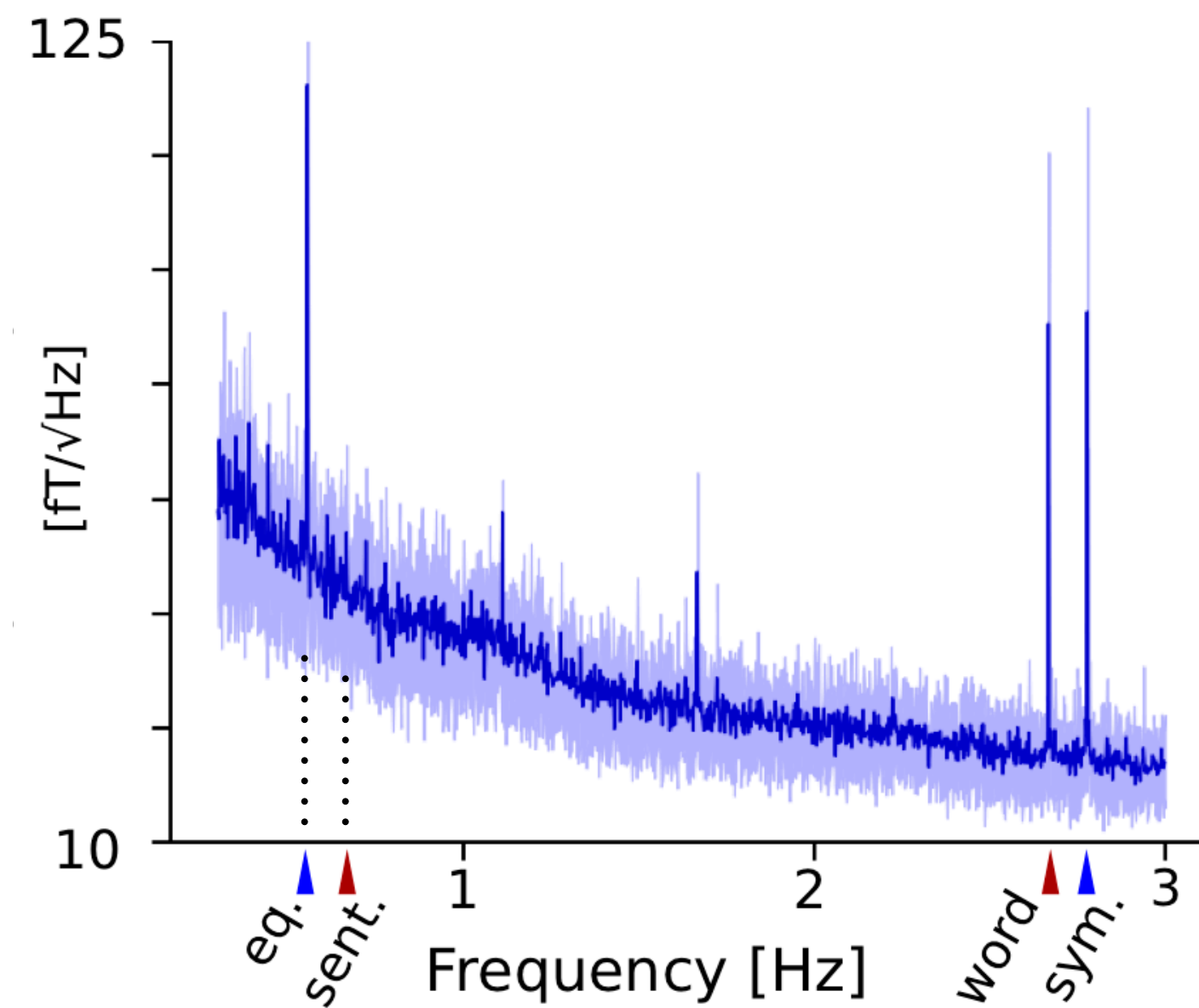
Isochronous Cocktail Party

Neural
Spectrum

Attend to
Sentences



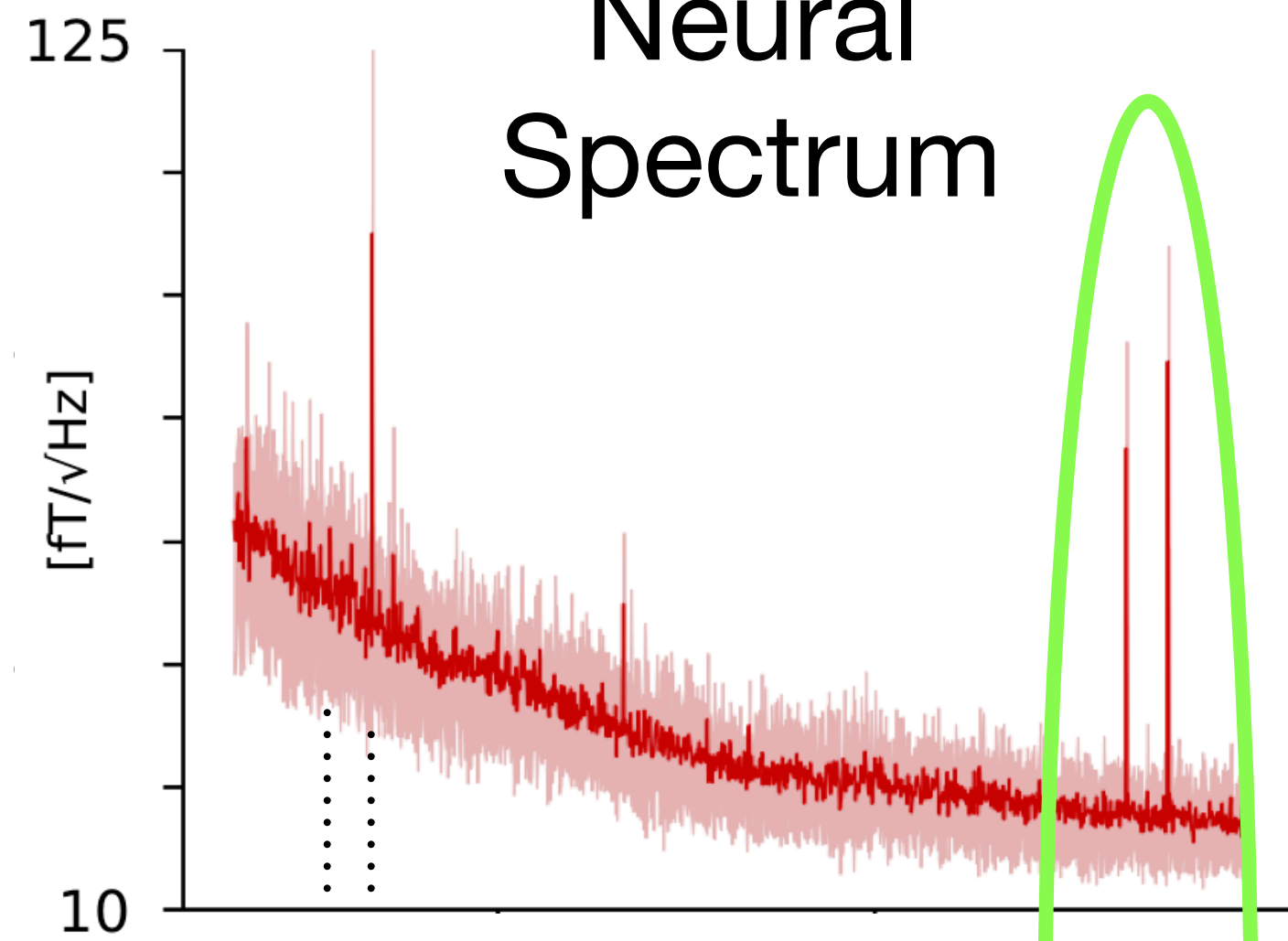
Attend to
Equations



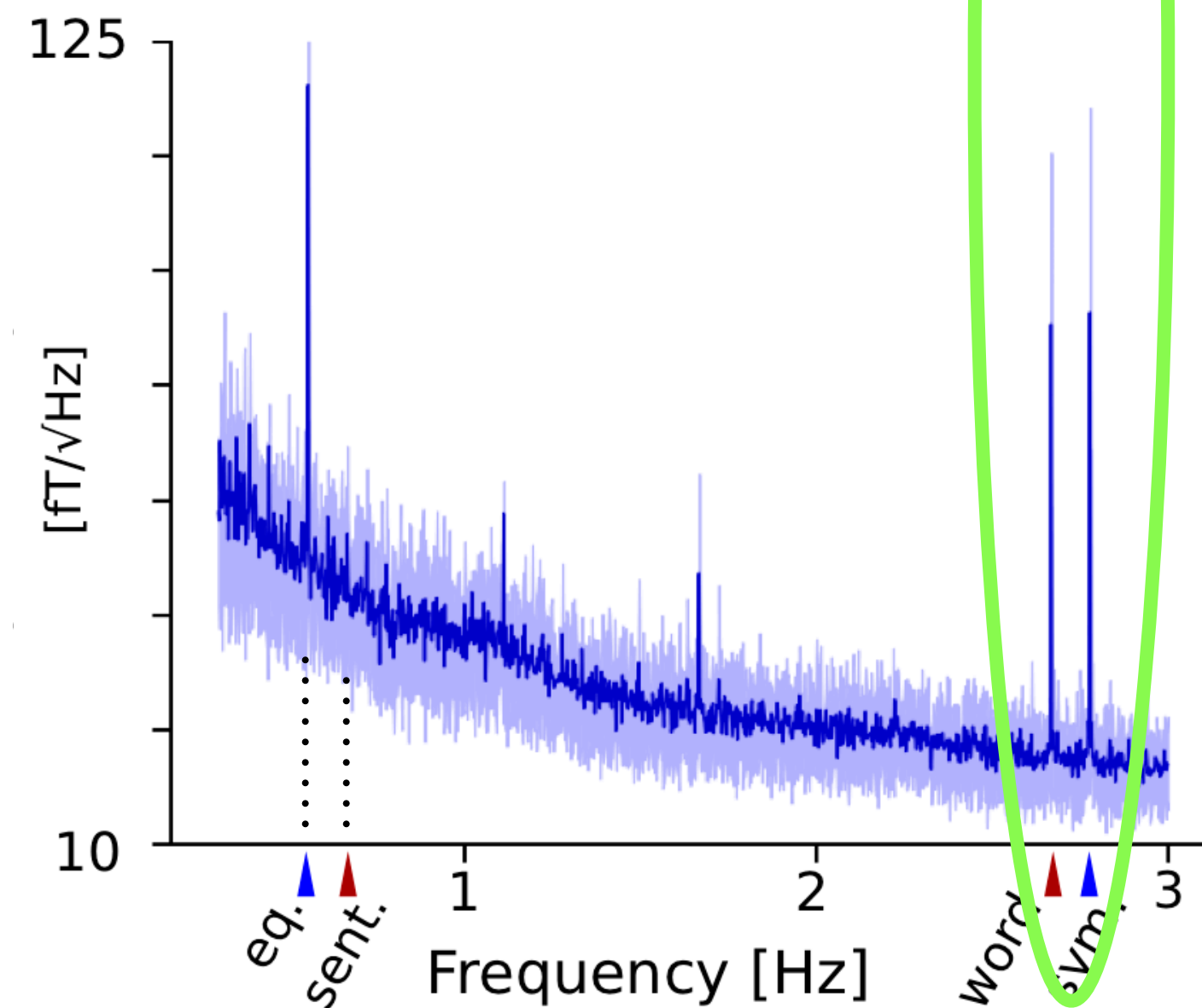
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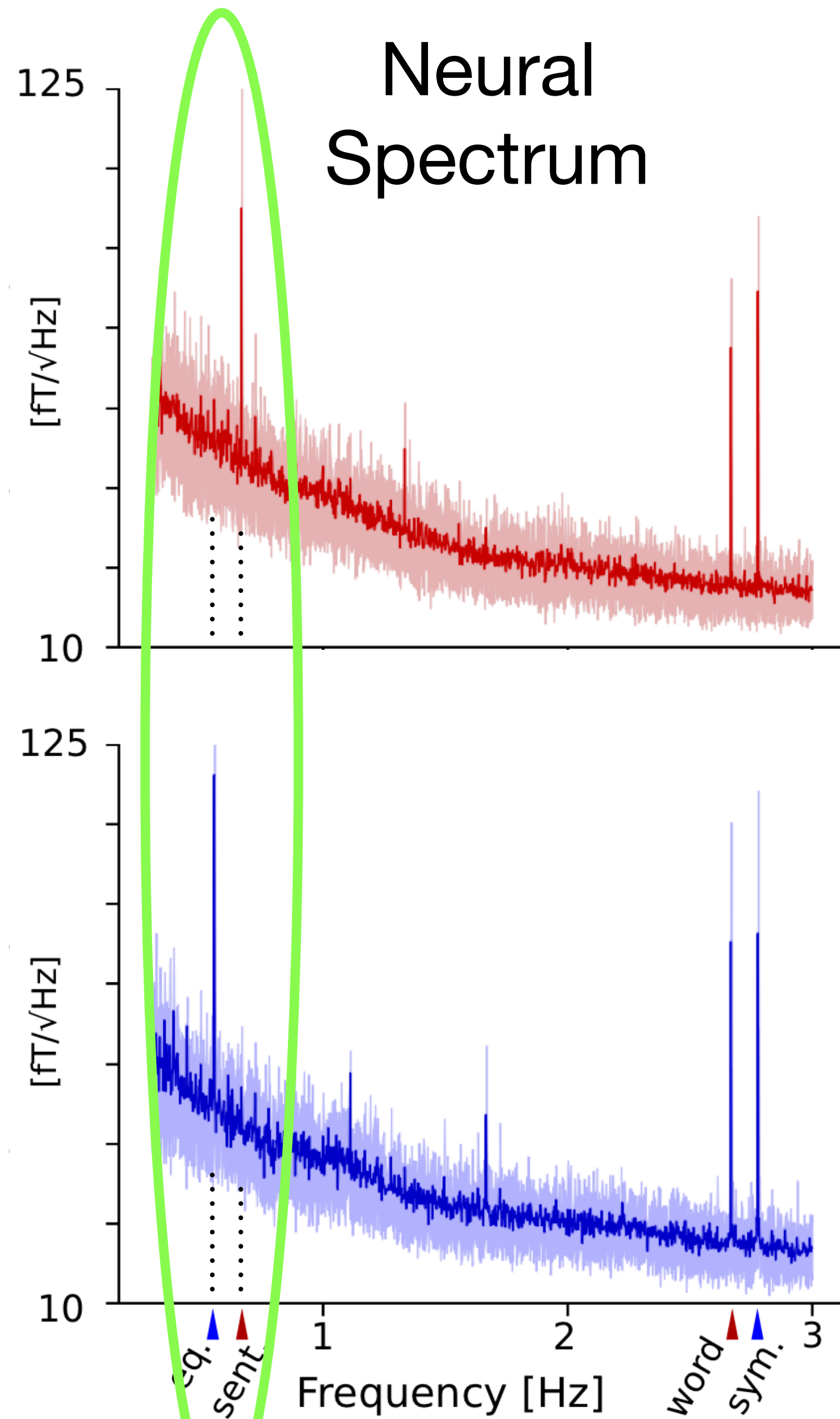


Attend to
Equations



Isochronous Cocktail Party

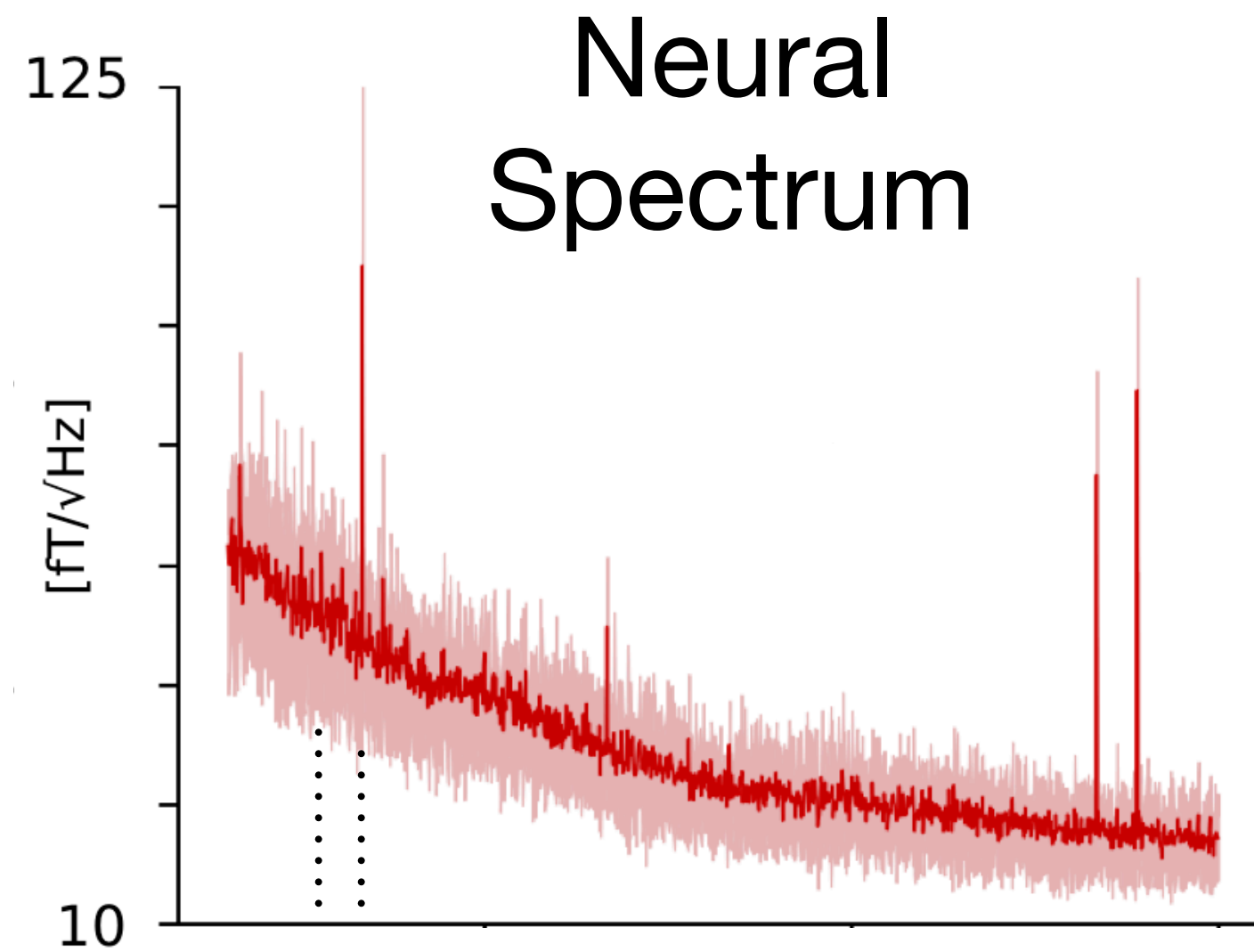
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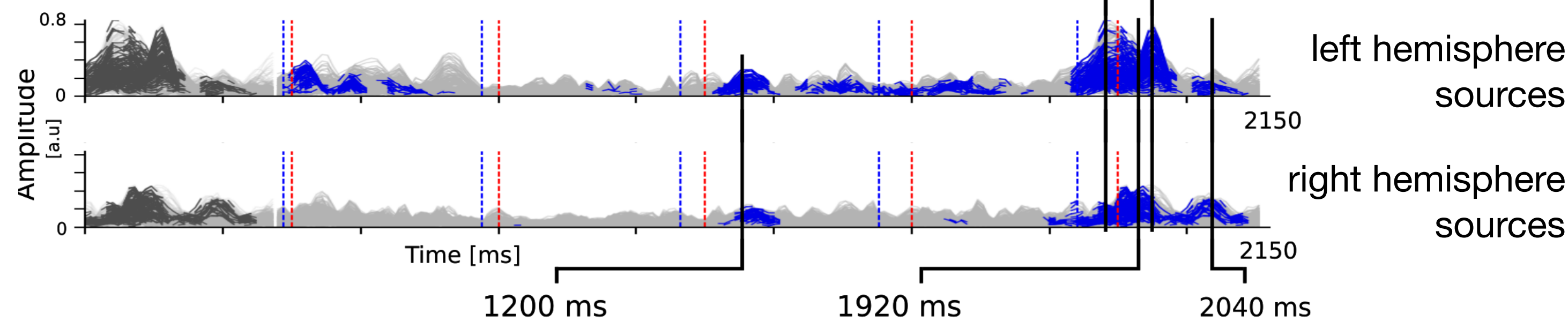
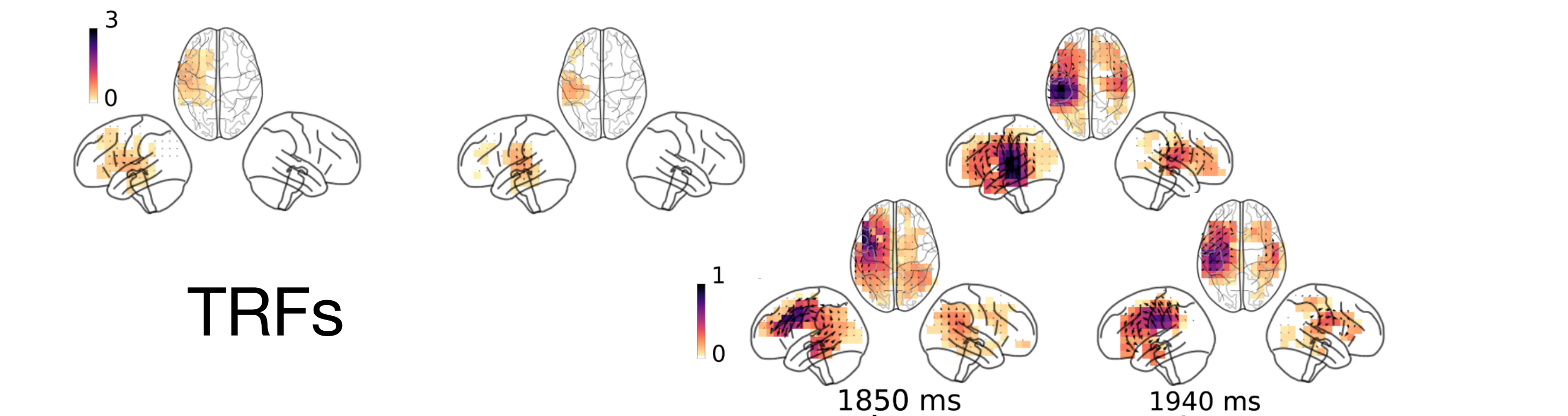
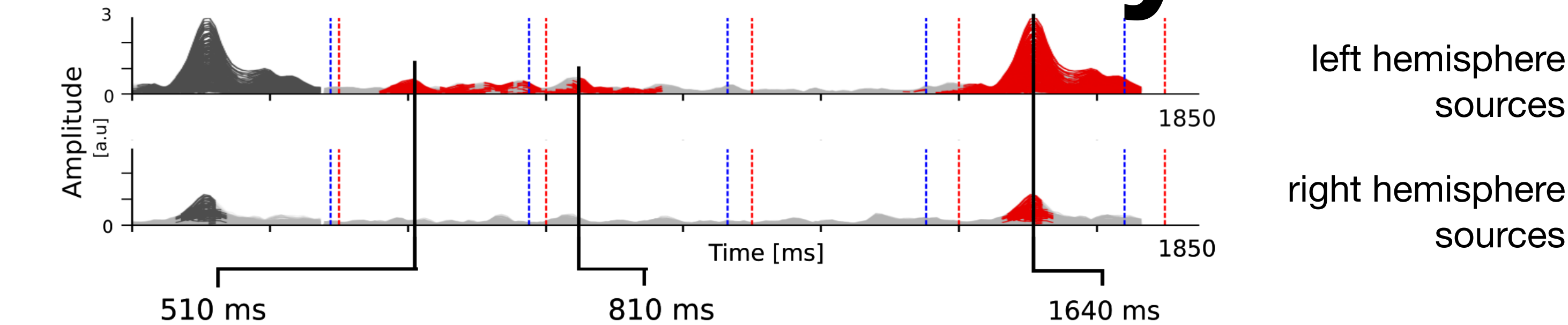
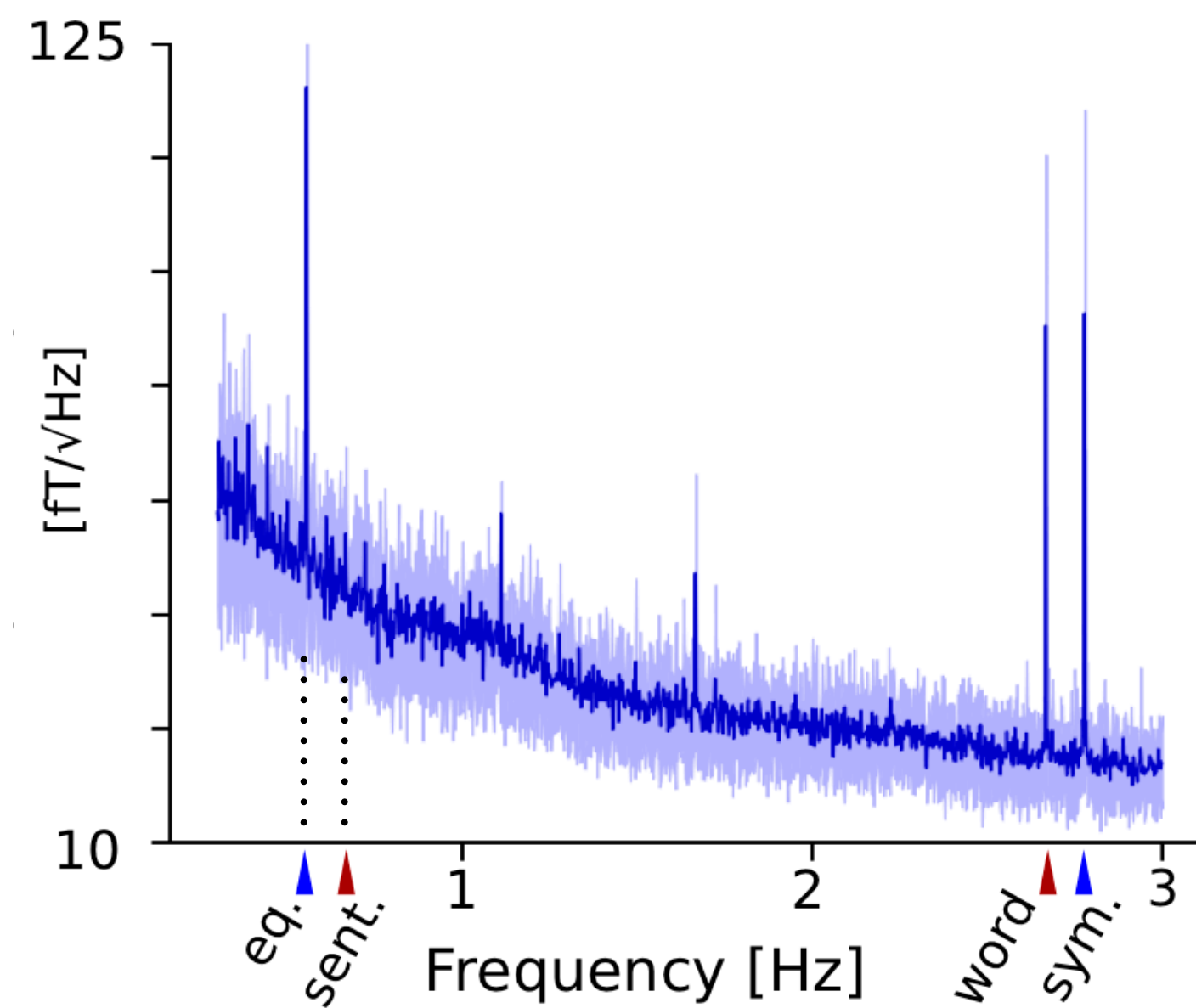
Attend to
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Isochronous Cocktail Party

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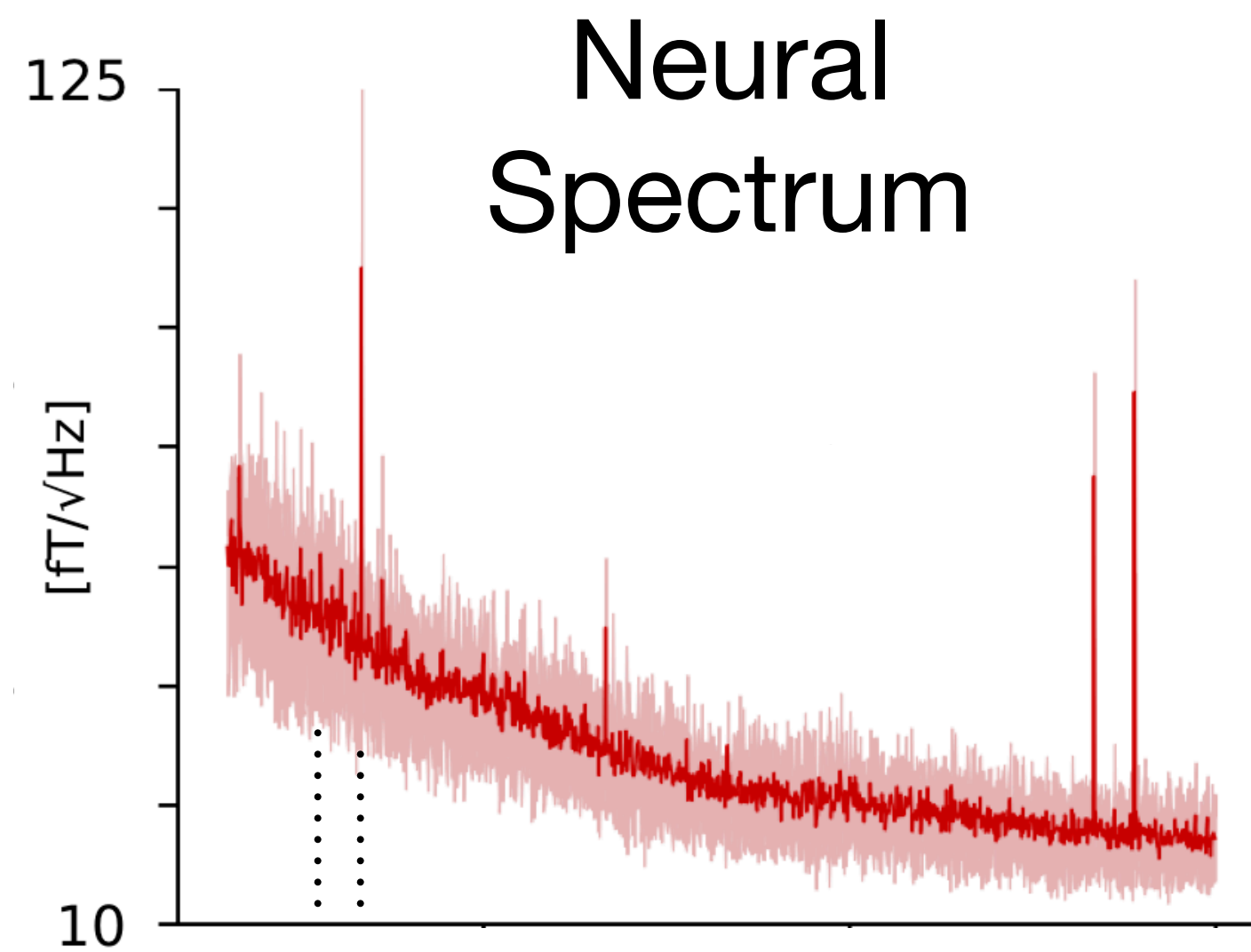


Attend to Equations

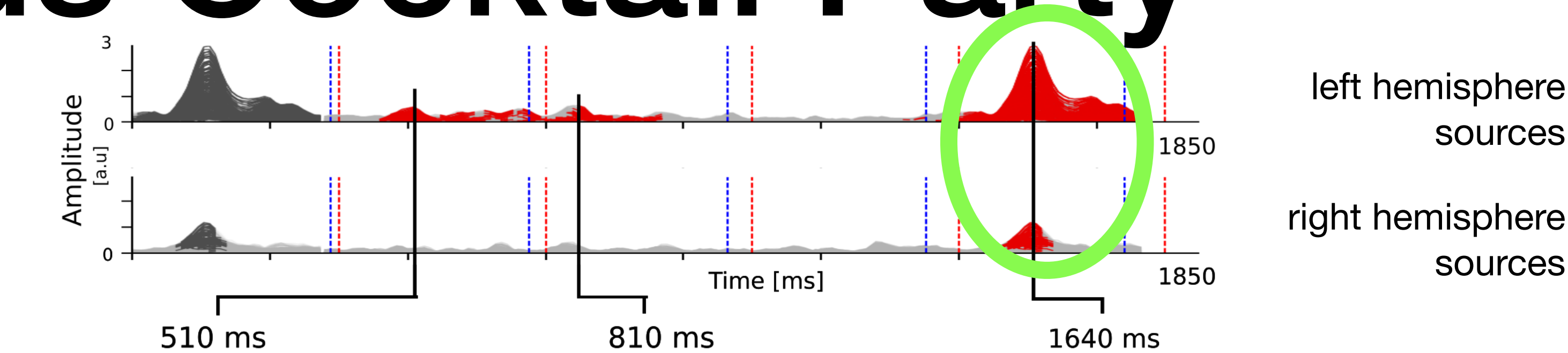
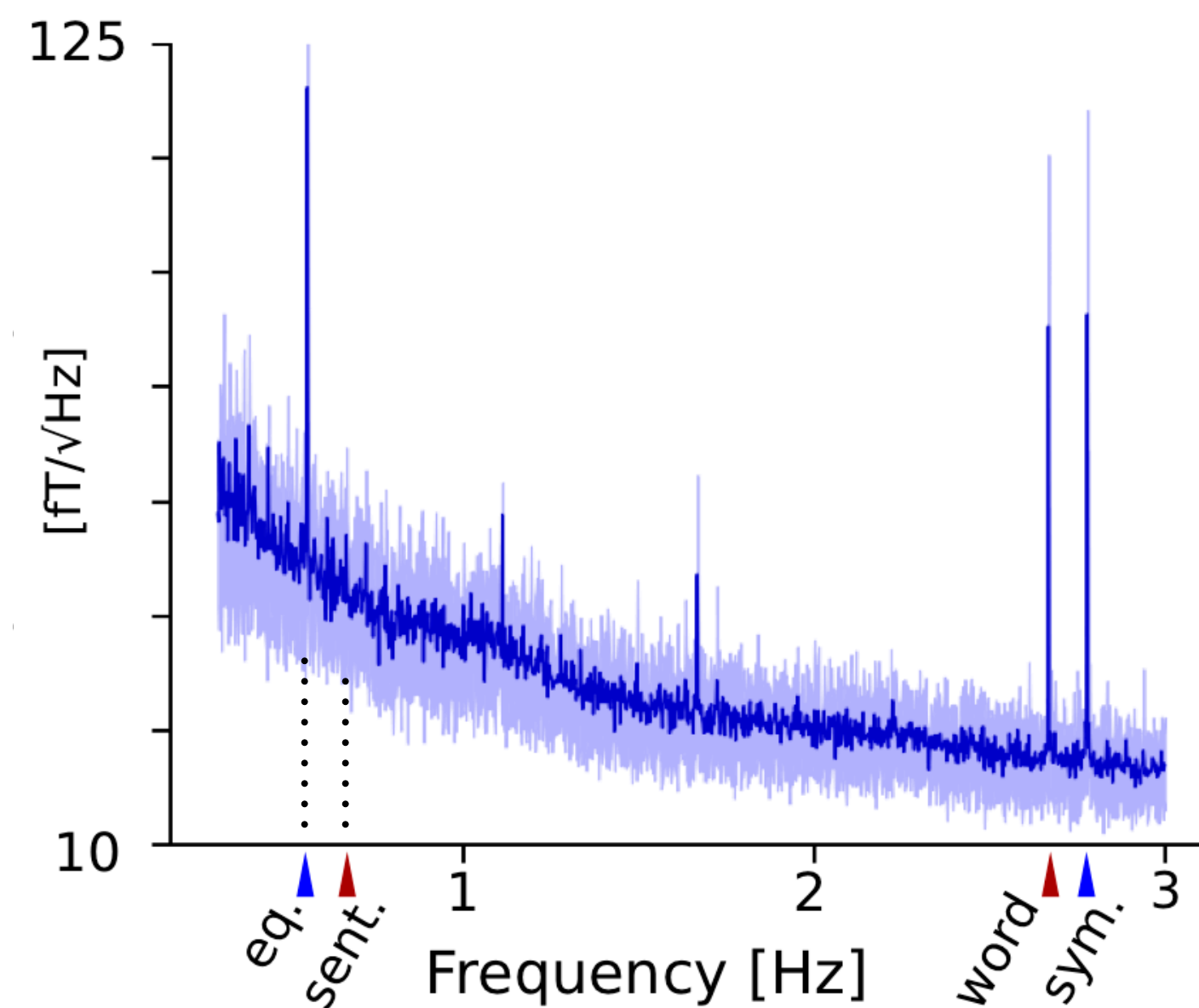


Isochronous Cocktail Party

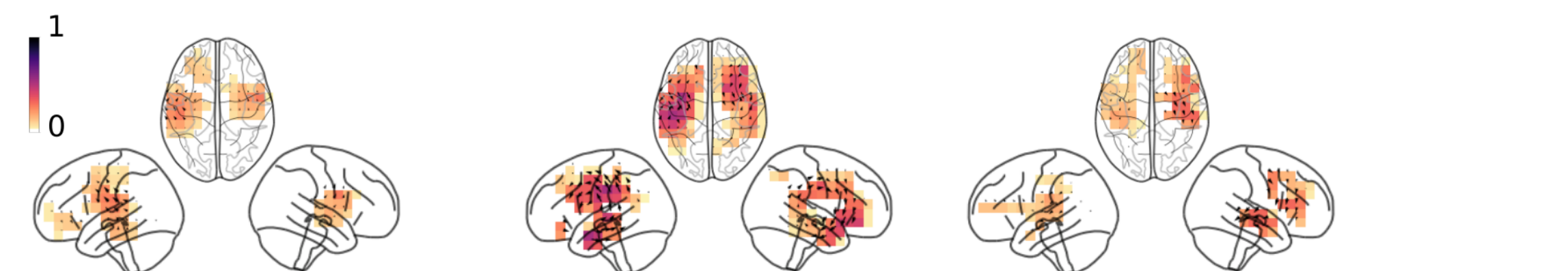
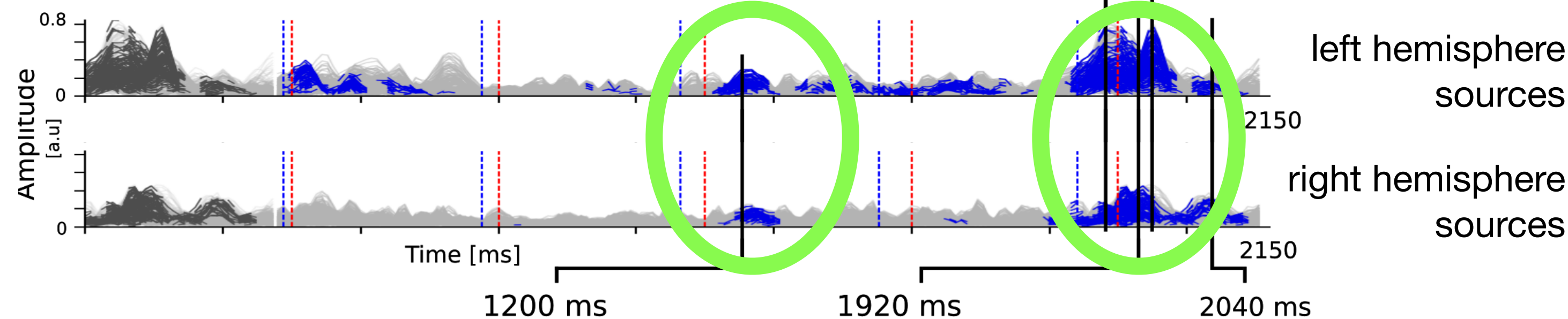
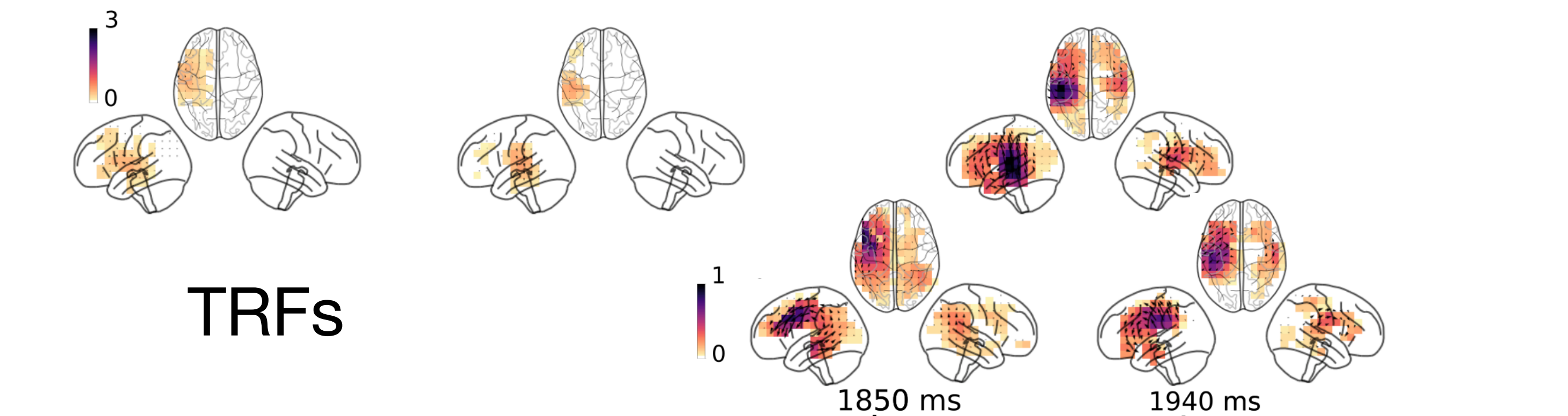
Attend to Sentences



Attend to Equations

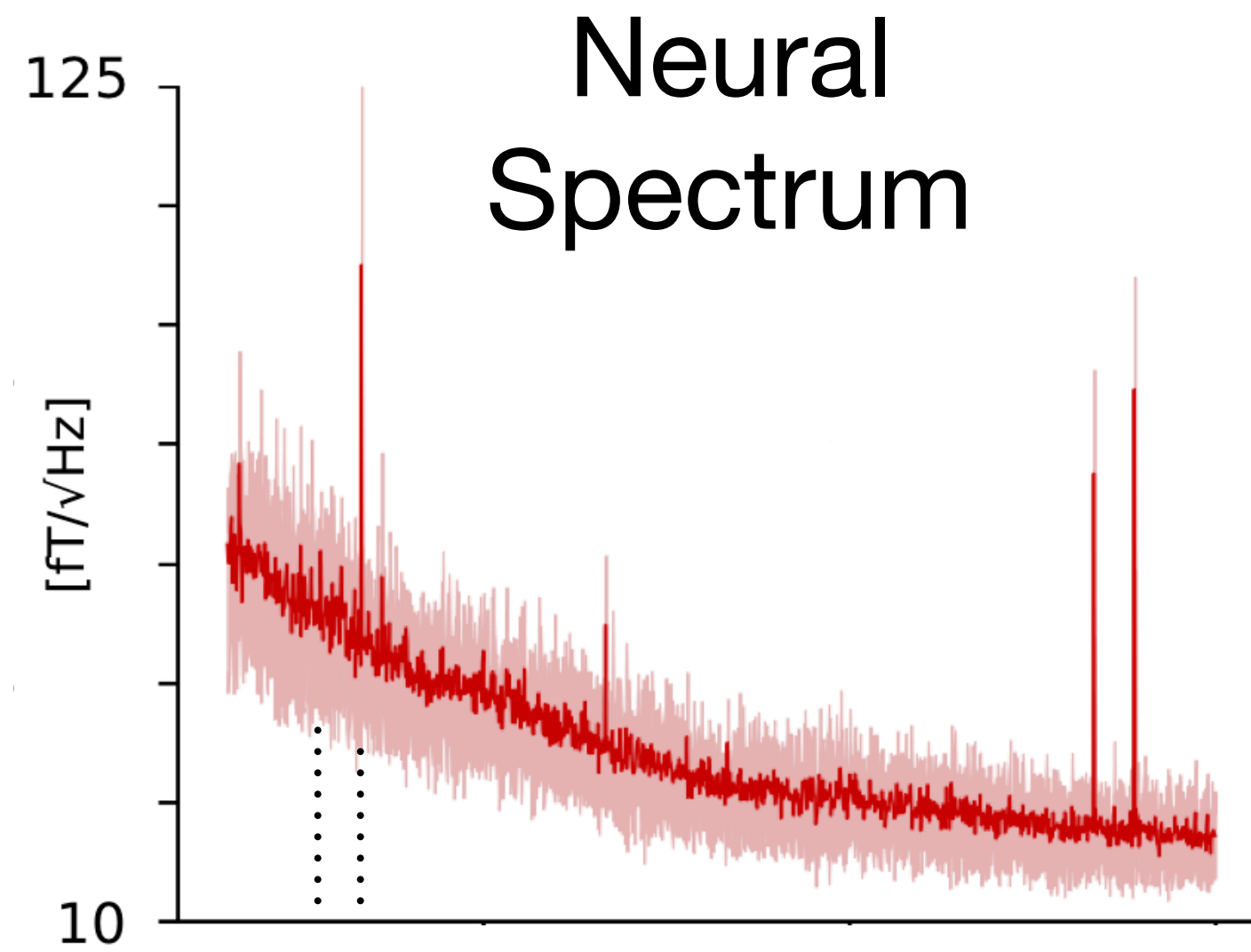


TRFs

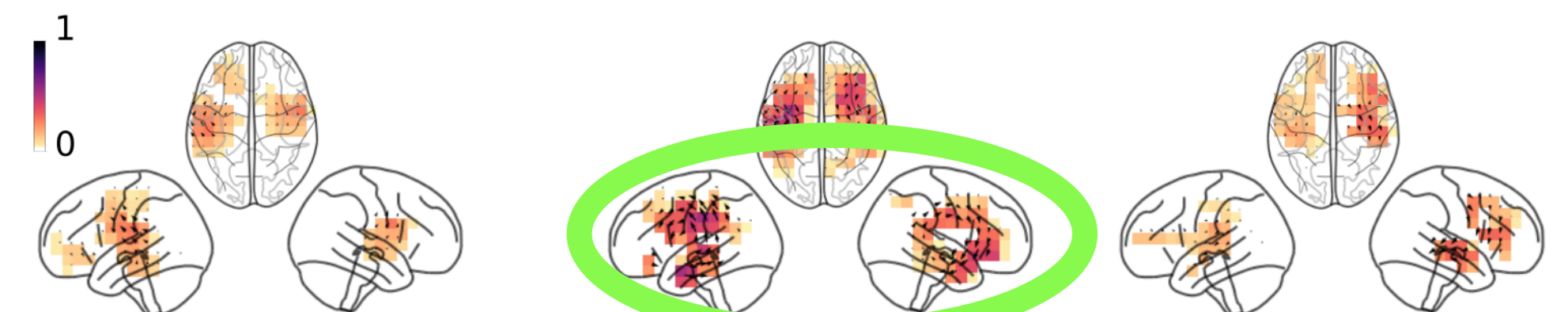
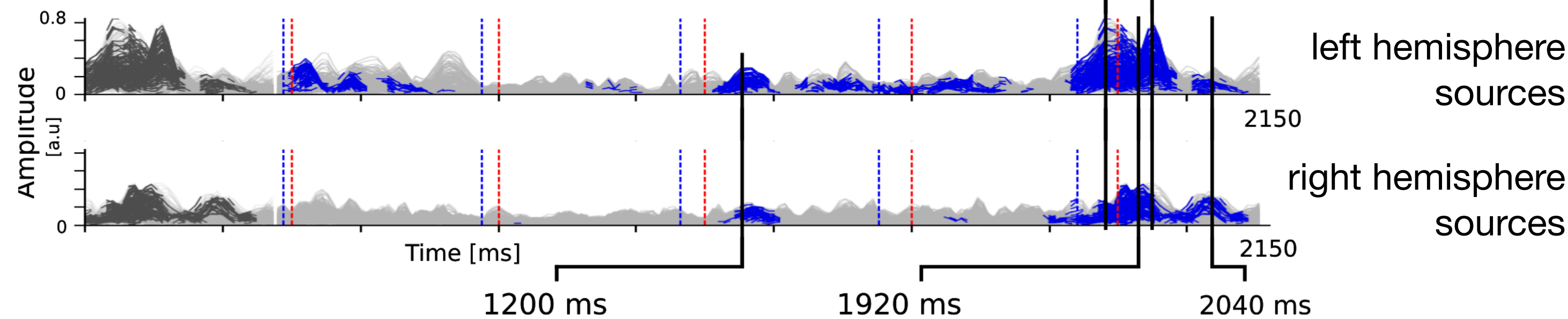
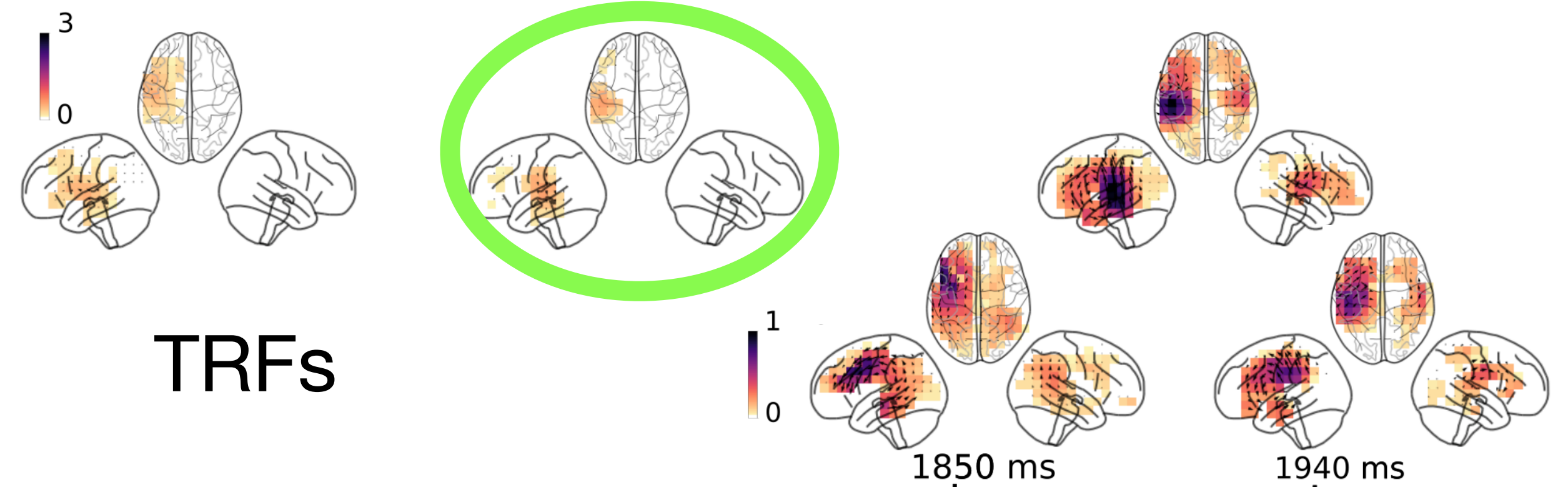
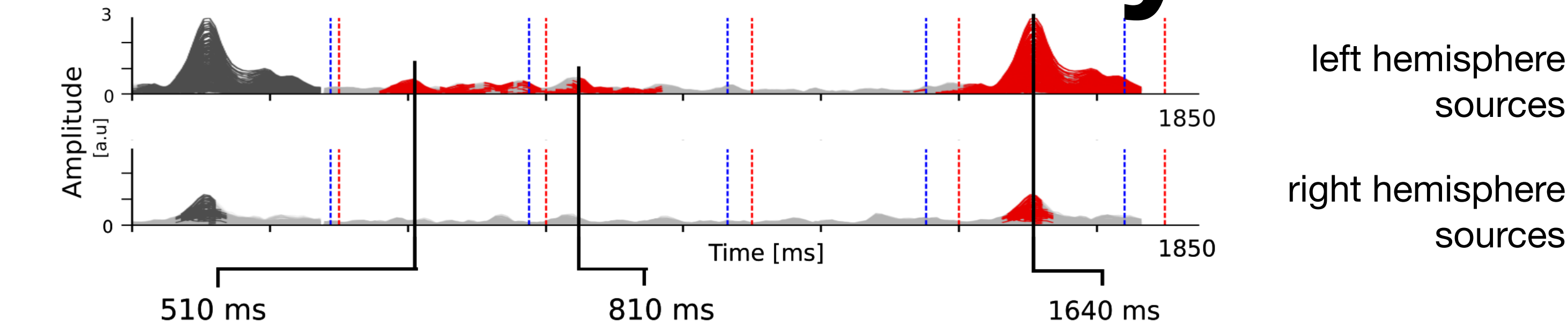
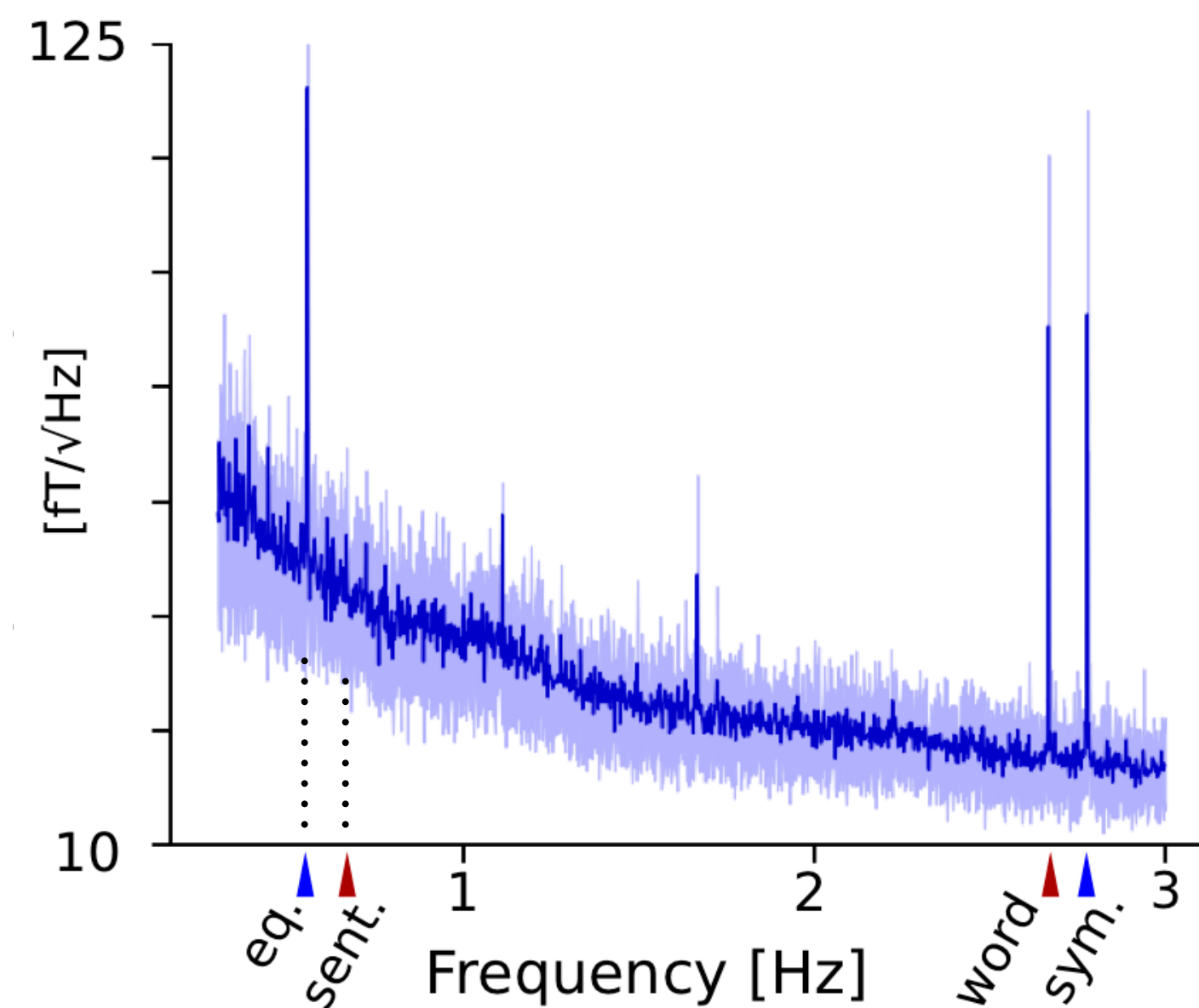


Isochronous Cocktail Party

Attend to Sentences

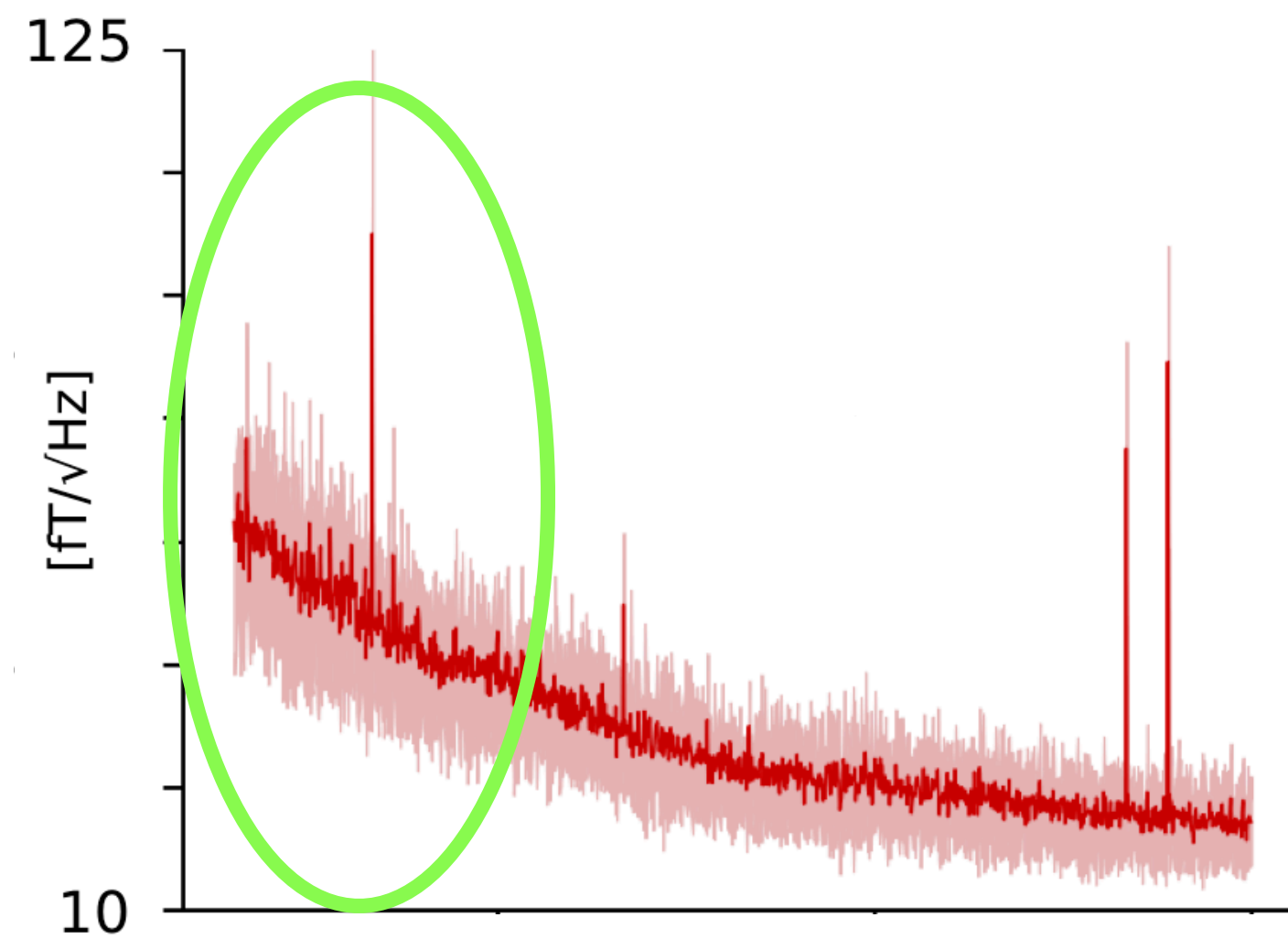


Attend to Equations

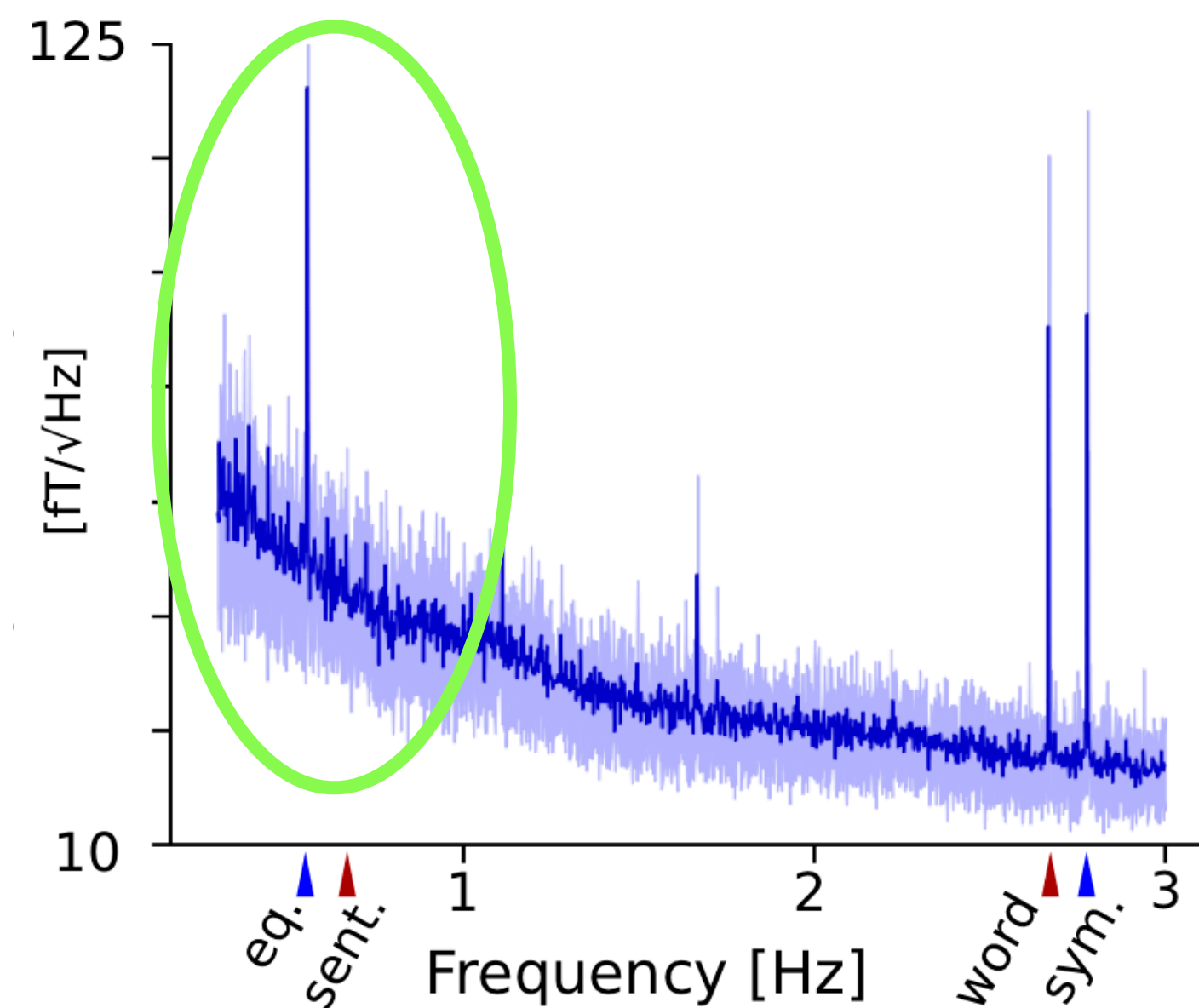


Representations of Understanding

Attend to
Sentences



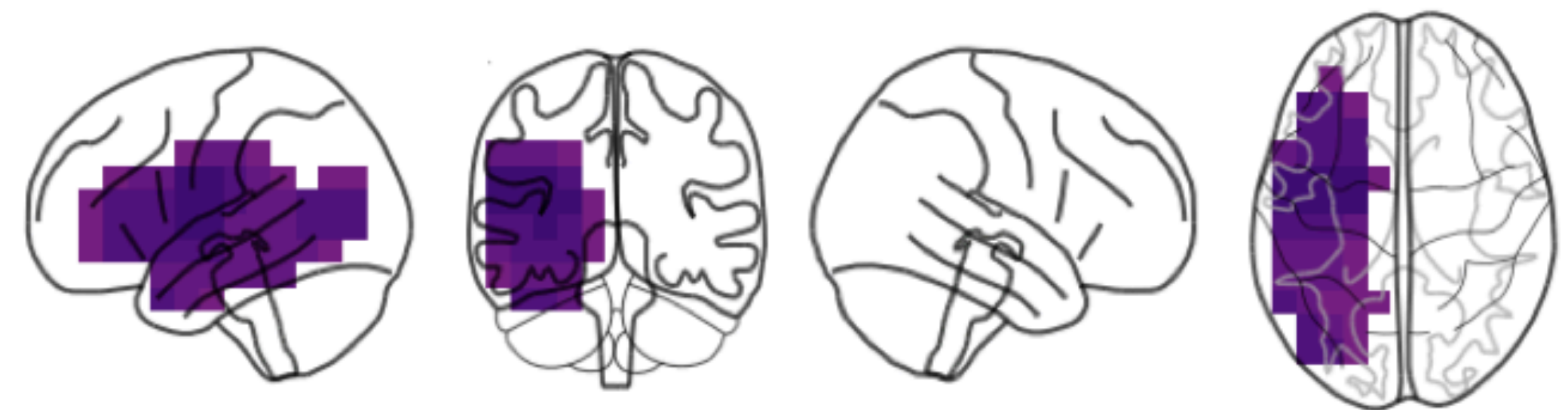
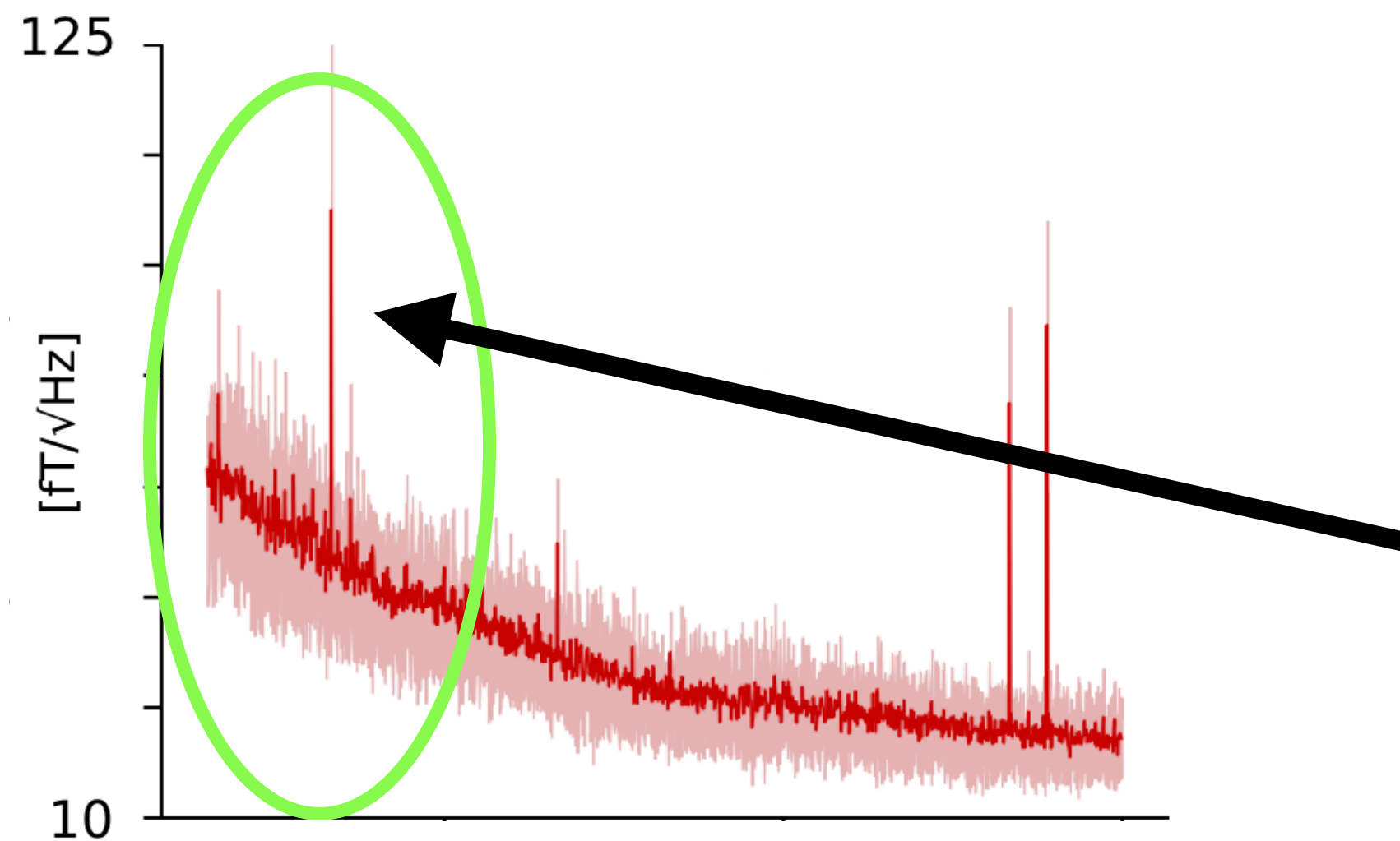
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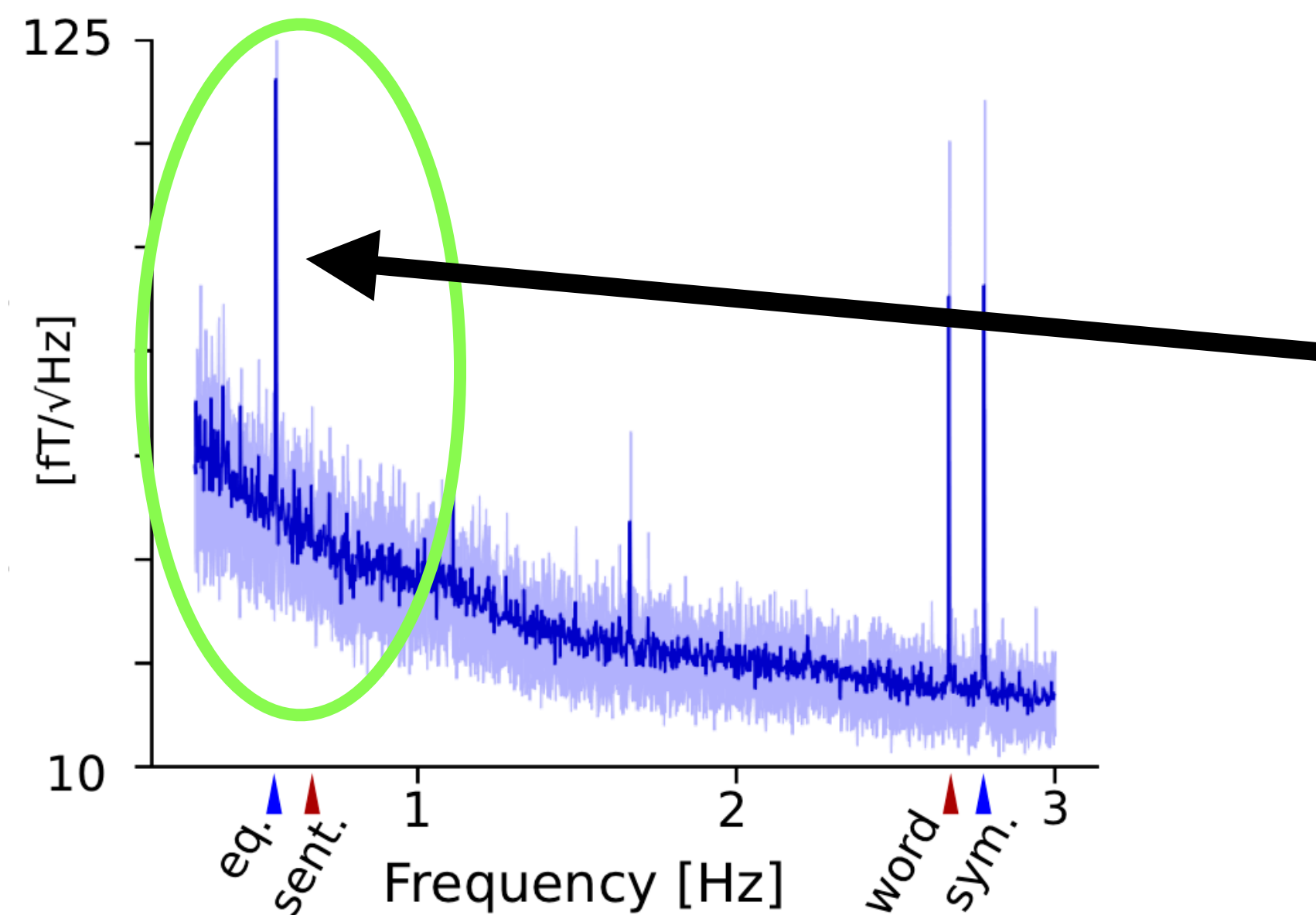
Representations of Understanding

Neural Correlation with Behavior

Attend to Sentences



Attend to Equations



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

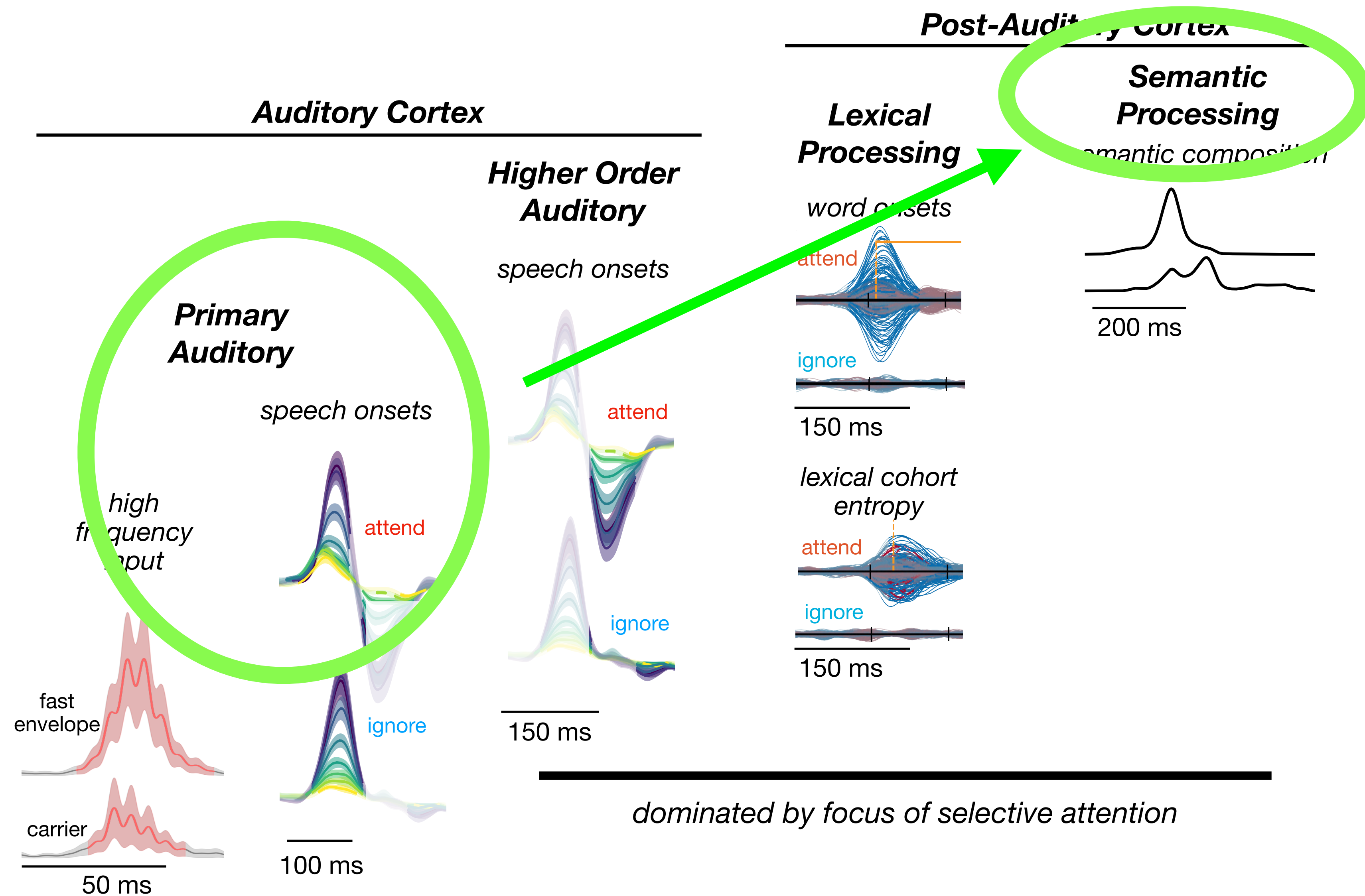
Outline

- 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

Outline

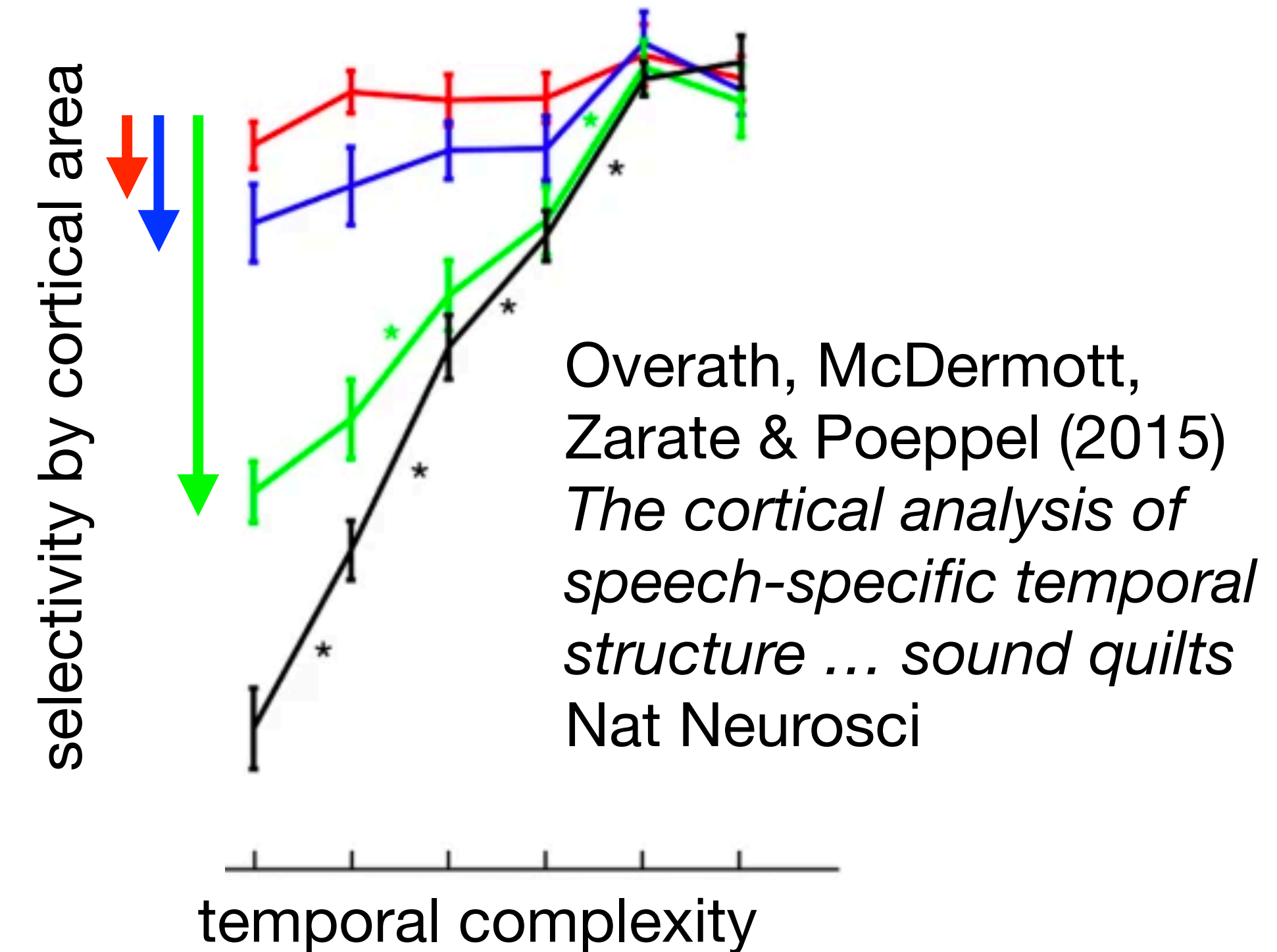
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Cortical Representations Across Cortex



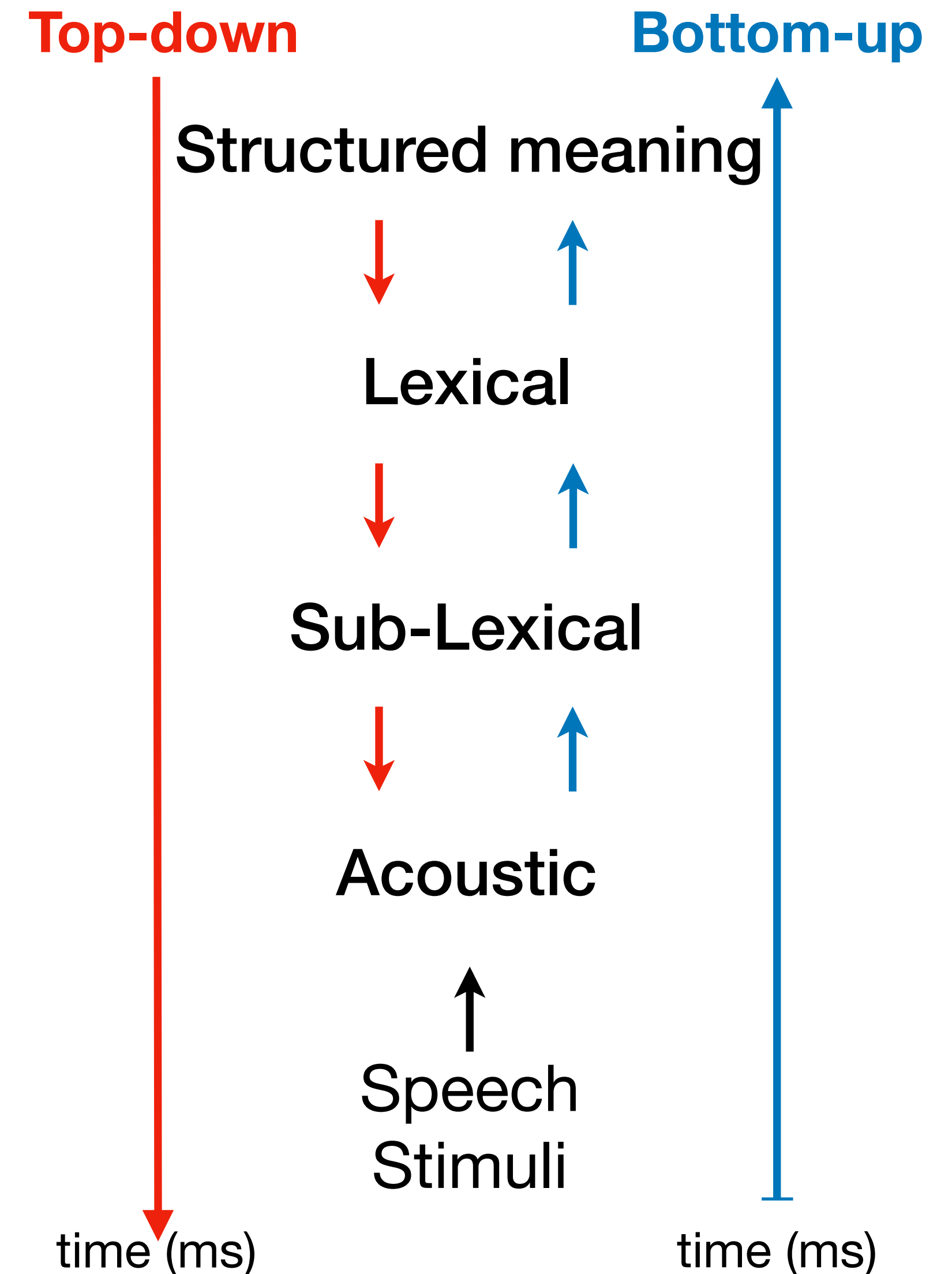
Progression of Speech Representations

- 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



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Experimental Design

Task

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

Stimuli

4 passage types

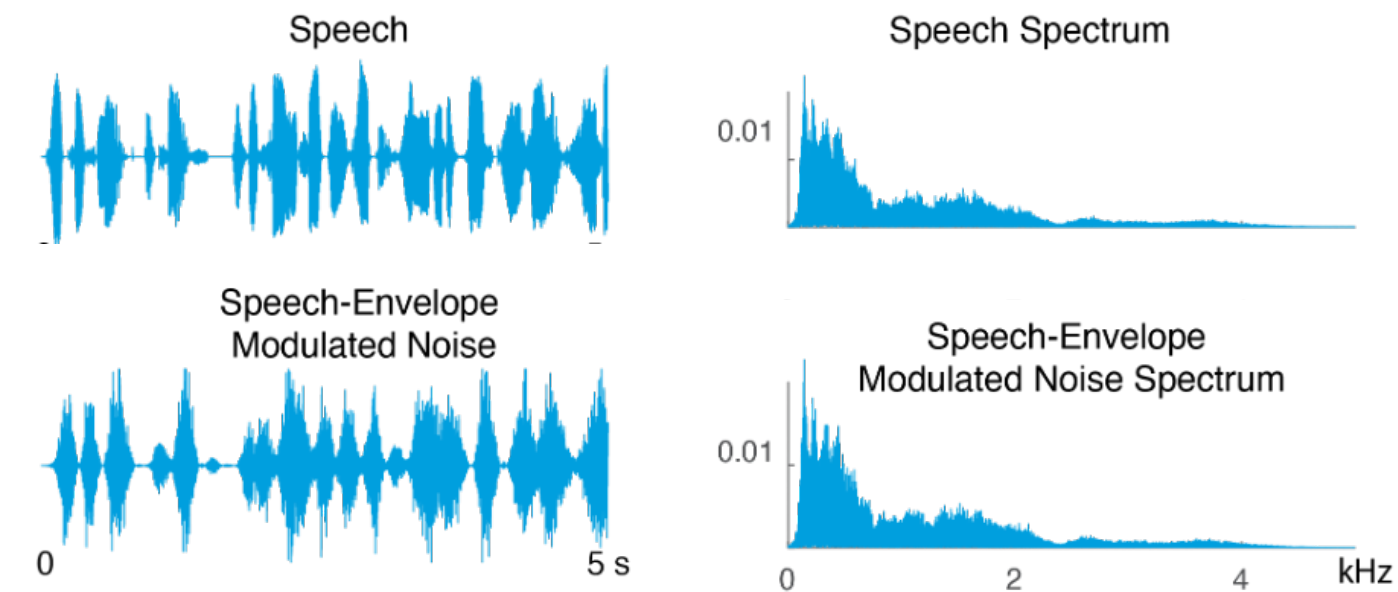
- Speech modulated noise
- Non-words
- Scrambled words
- Narrative

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



Experimental Design

Speech-envelope
Modulated Noise



Non-words

Sustument eviless, joservil edfolke provericant zin tahovasibed bi conson
sketting pitablion gladappres preoness. Feno unknoways, chasizer, giiz,
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hapem dahoperly pupleless....

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A liquid is only speak, second even for good reach the attack us. Living fact,
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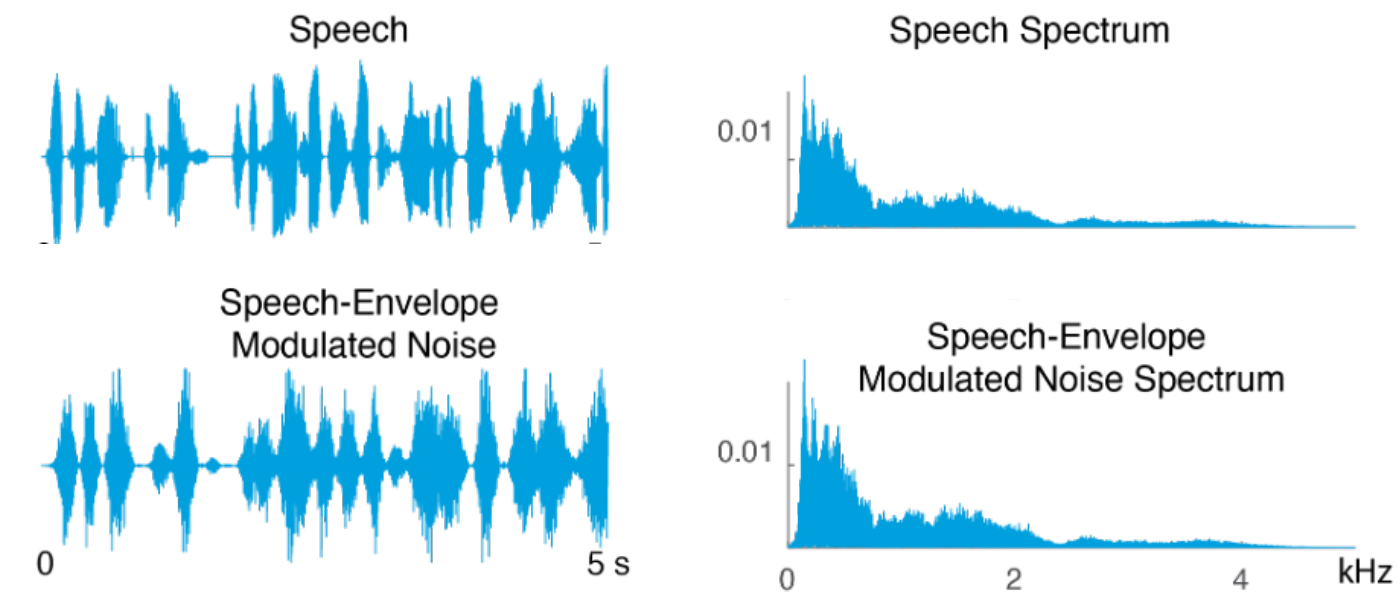
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continuous-
speech-like
prosody and
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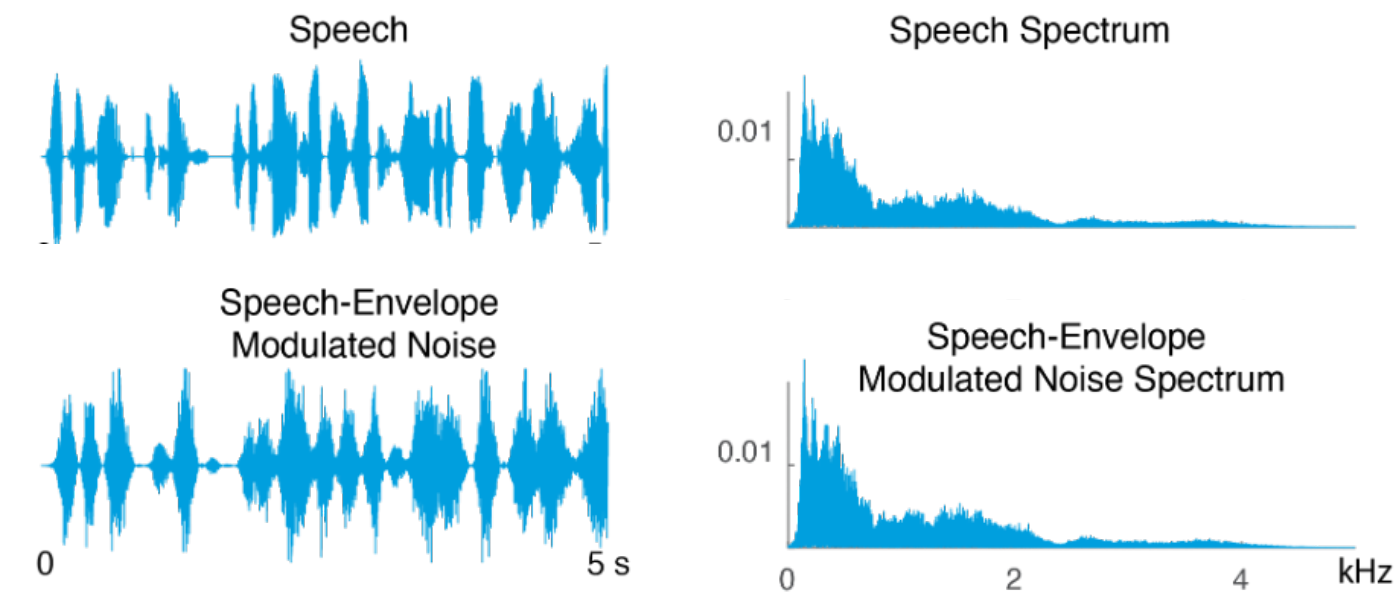
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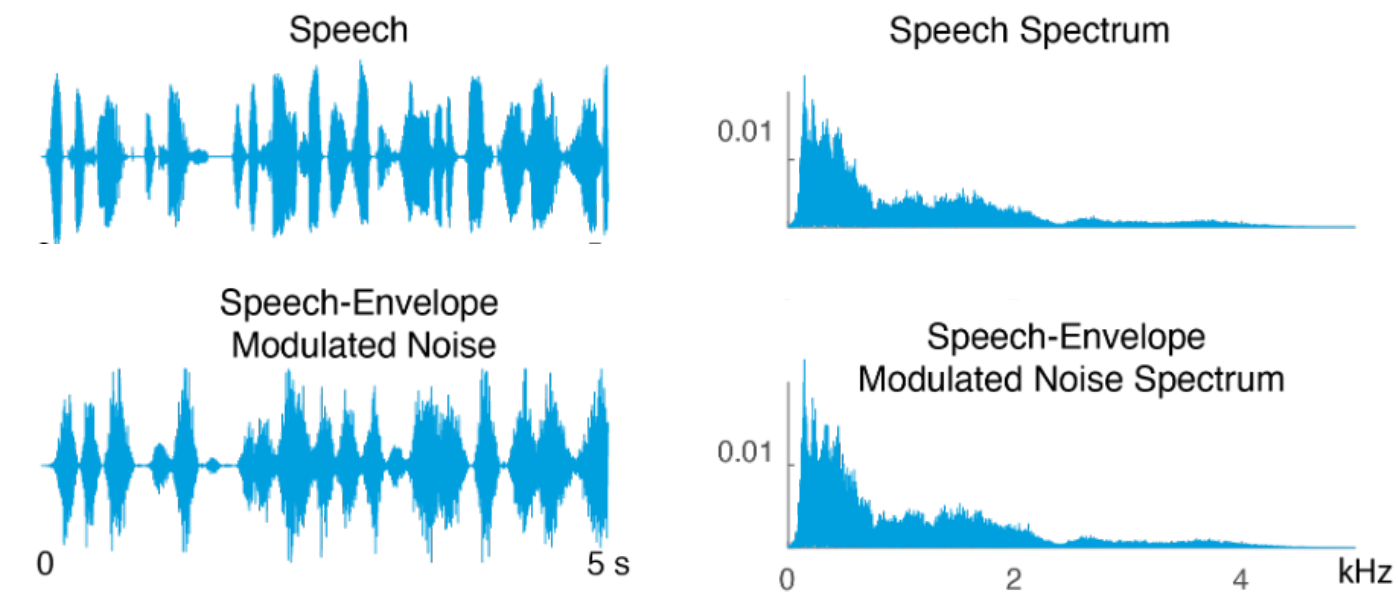
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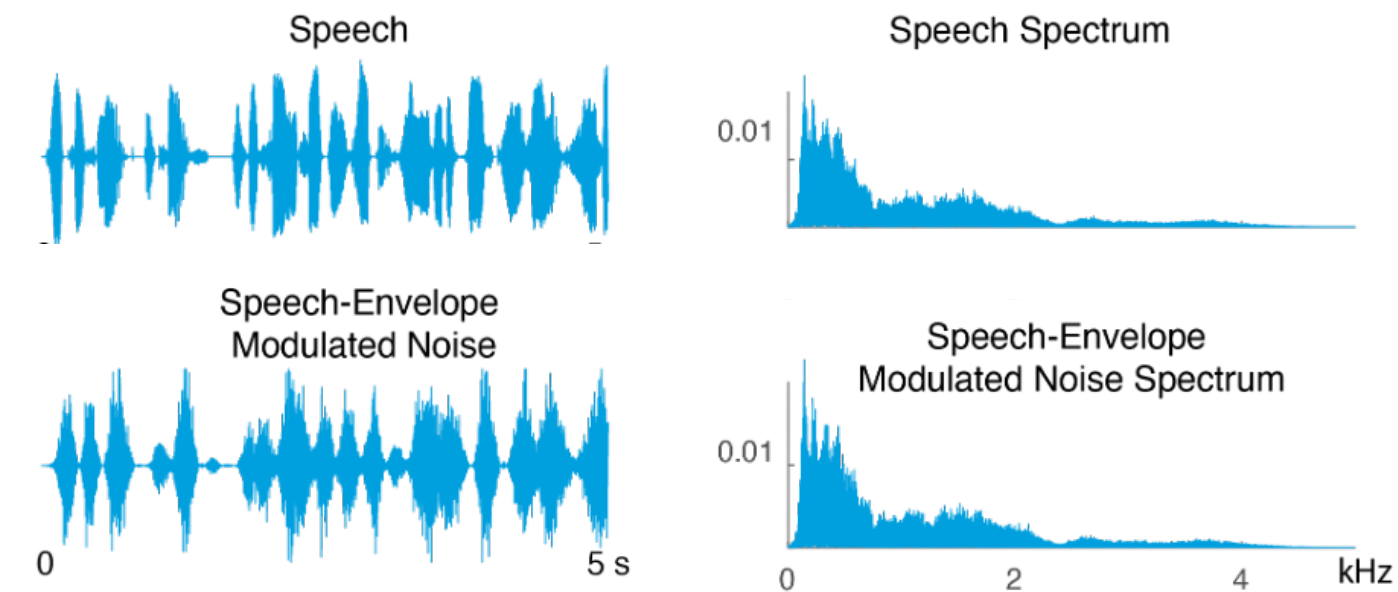
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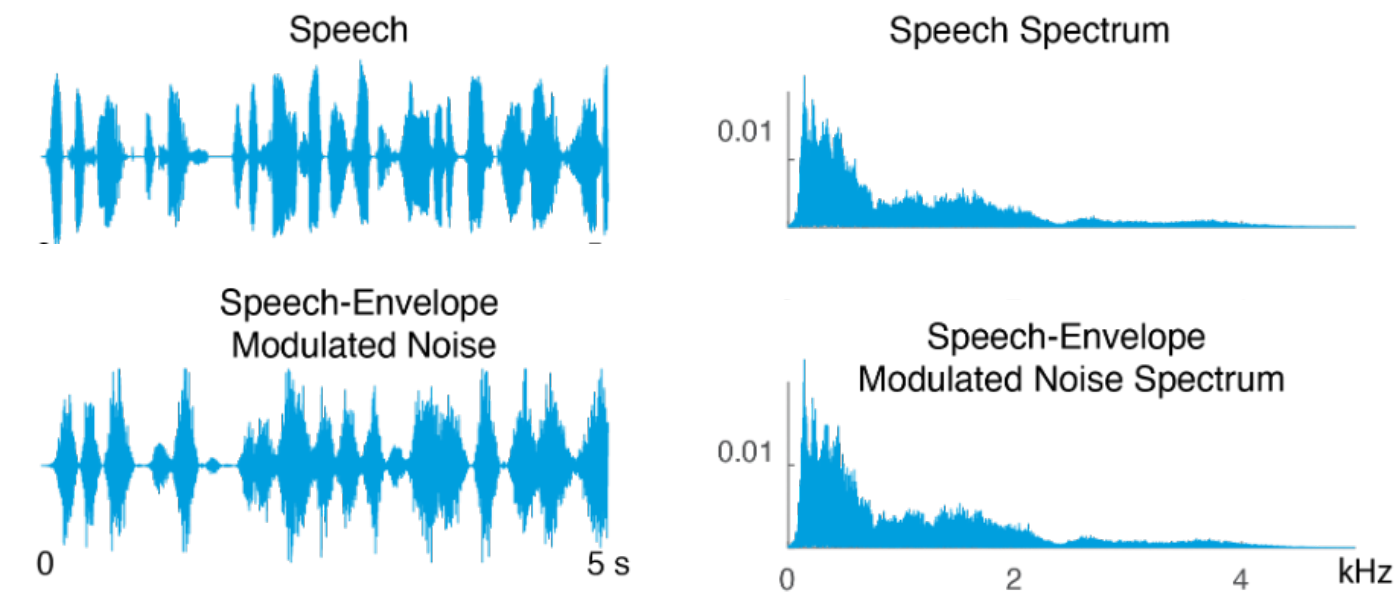
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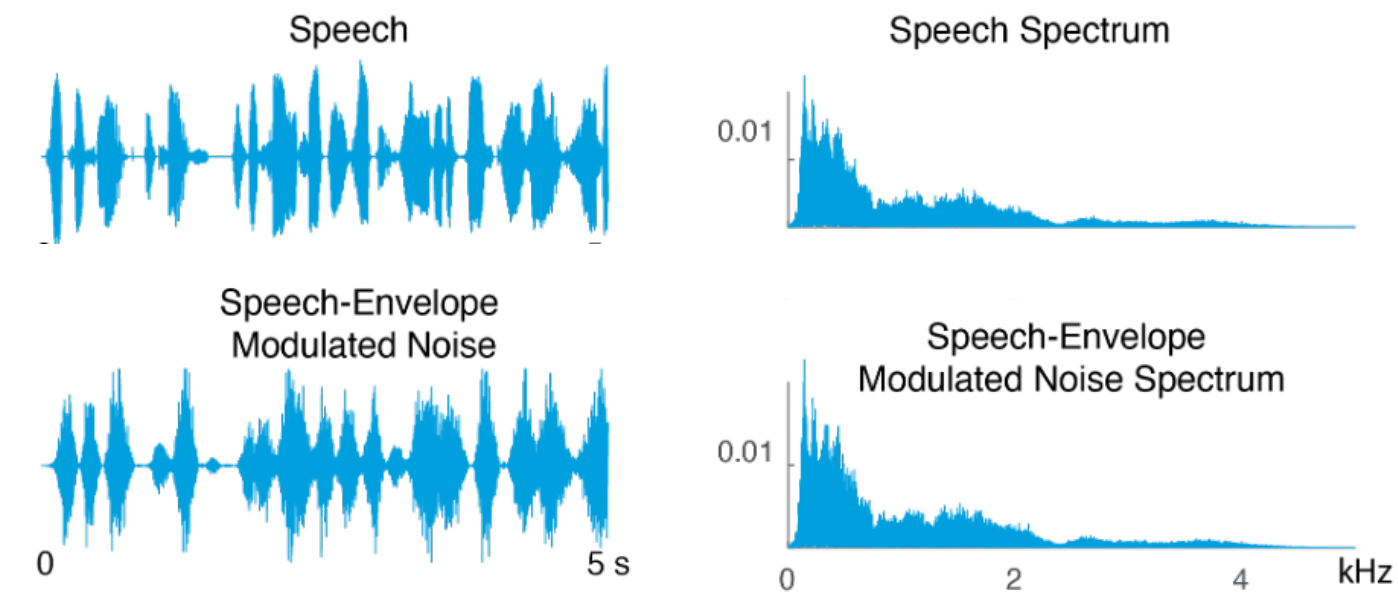
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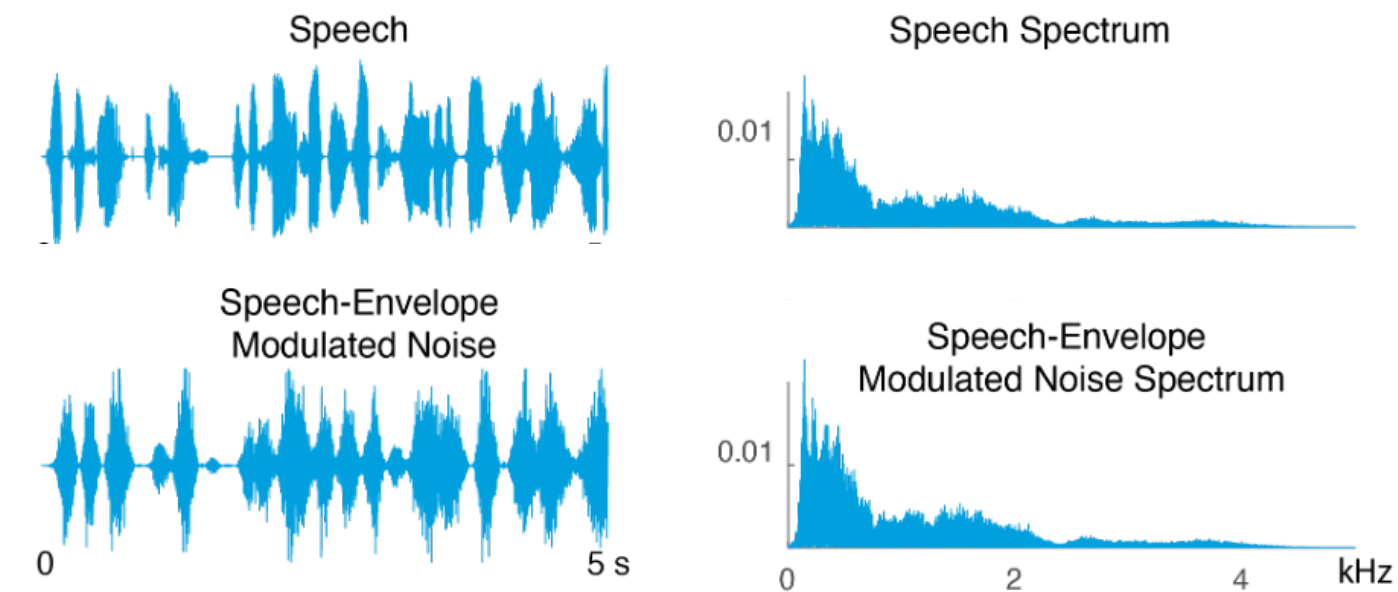
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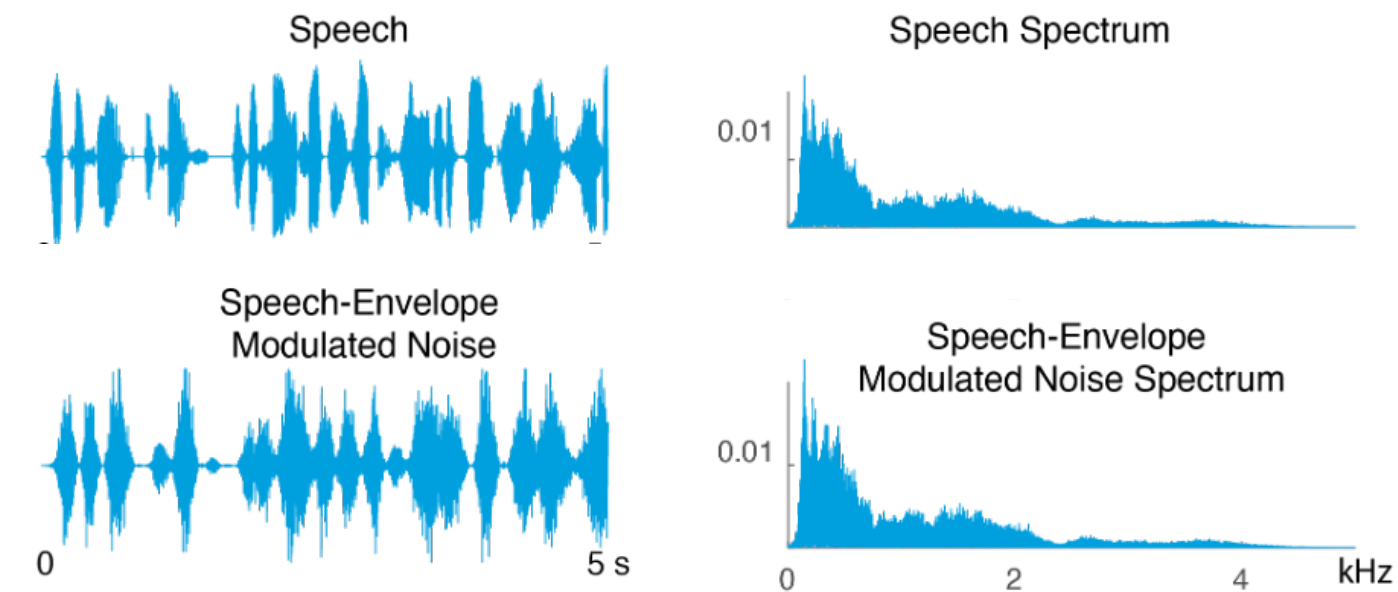
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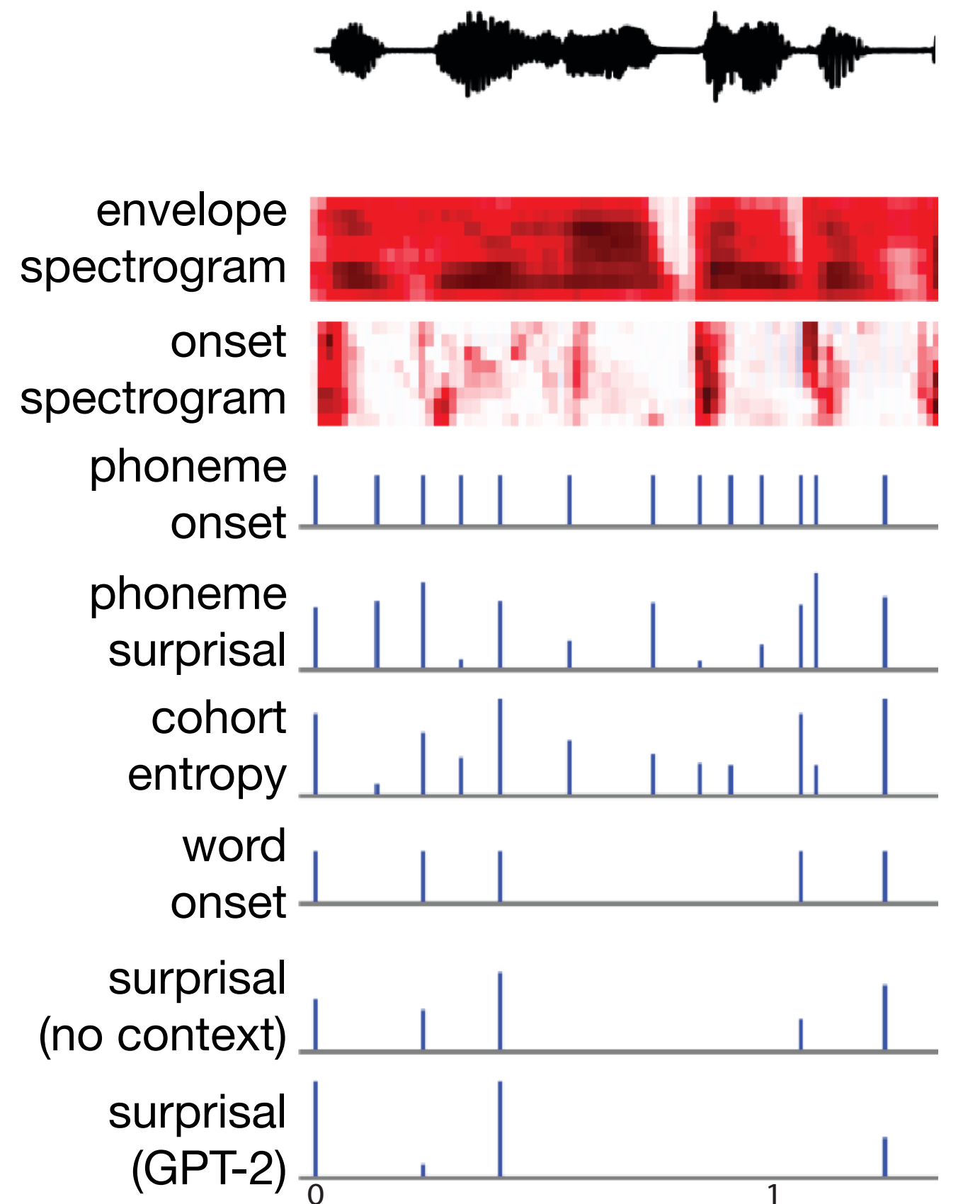
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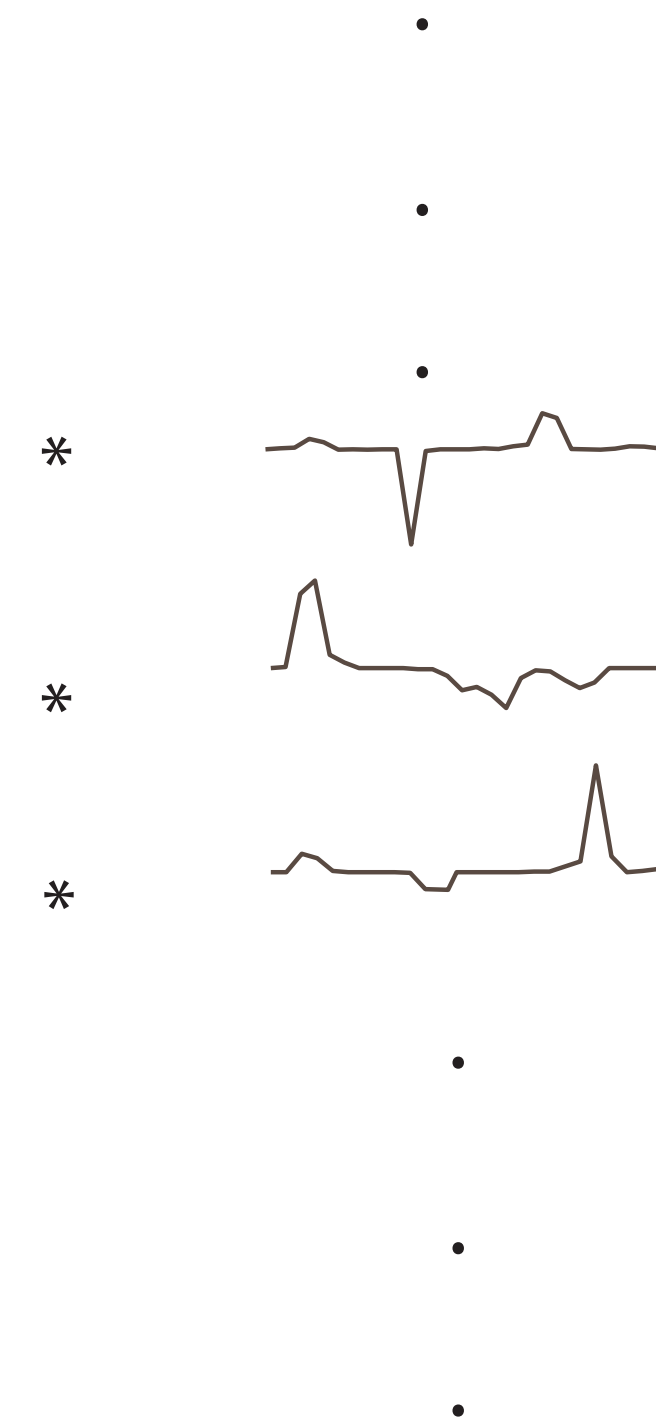


Simultaneous Temporal Response Functions

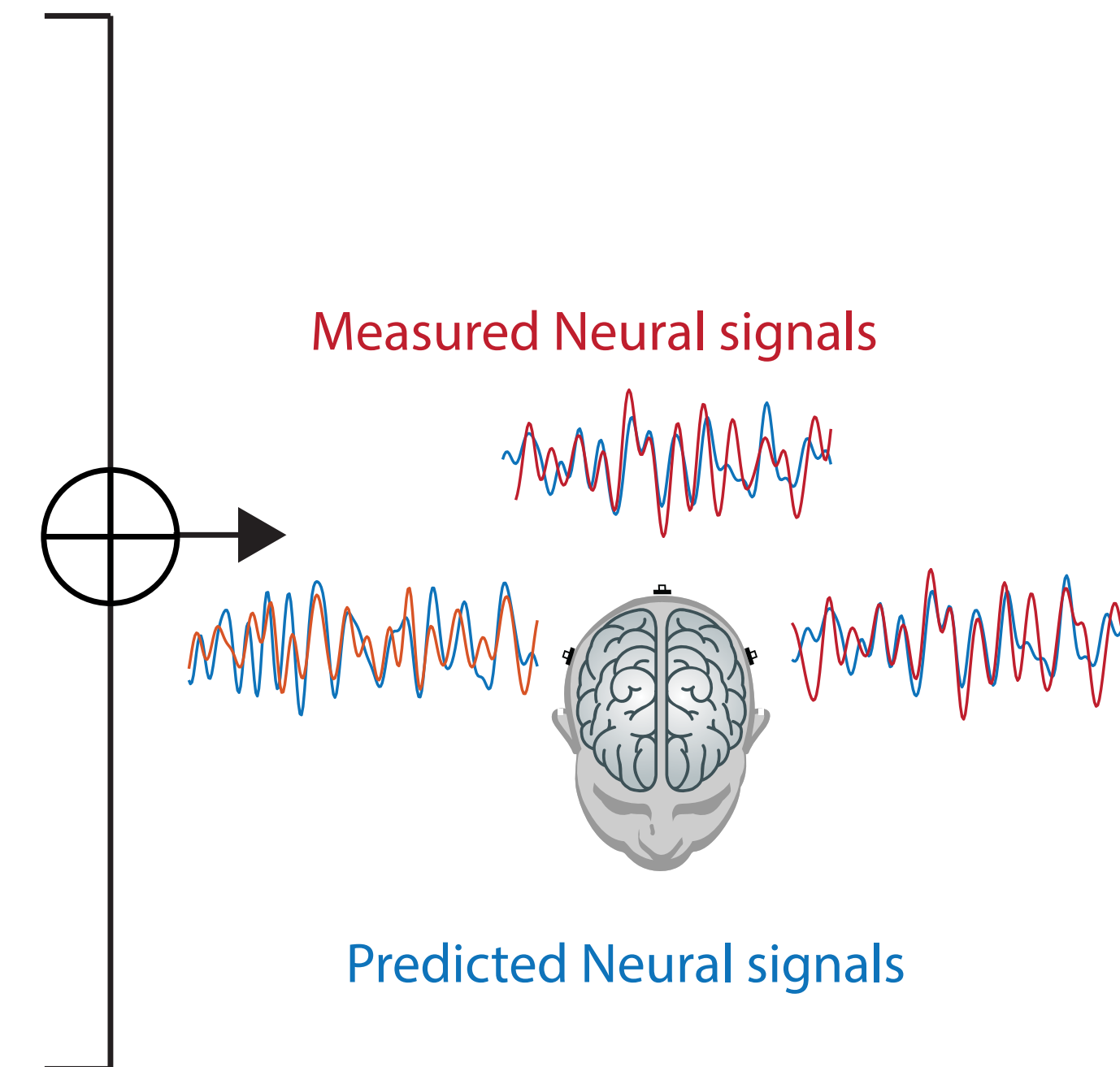
- TRFs predict neural response to speech
 - Analogous to evoked response
 - Peak amplitude \approx processing intensity
 - Peak Latency \approx source location
- Multiple TRFs estimated simultaneously
 - compete to explain variance (advantage over evoked response)



Speech Representations

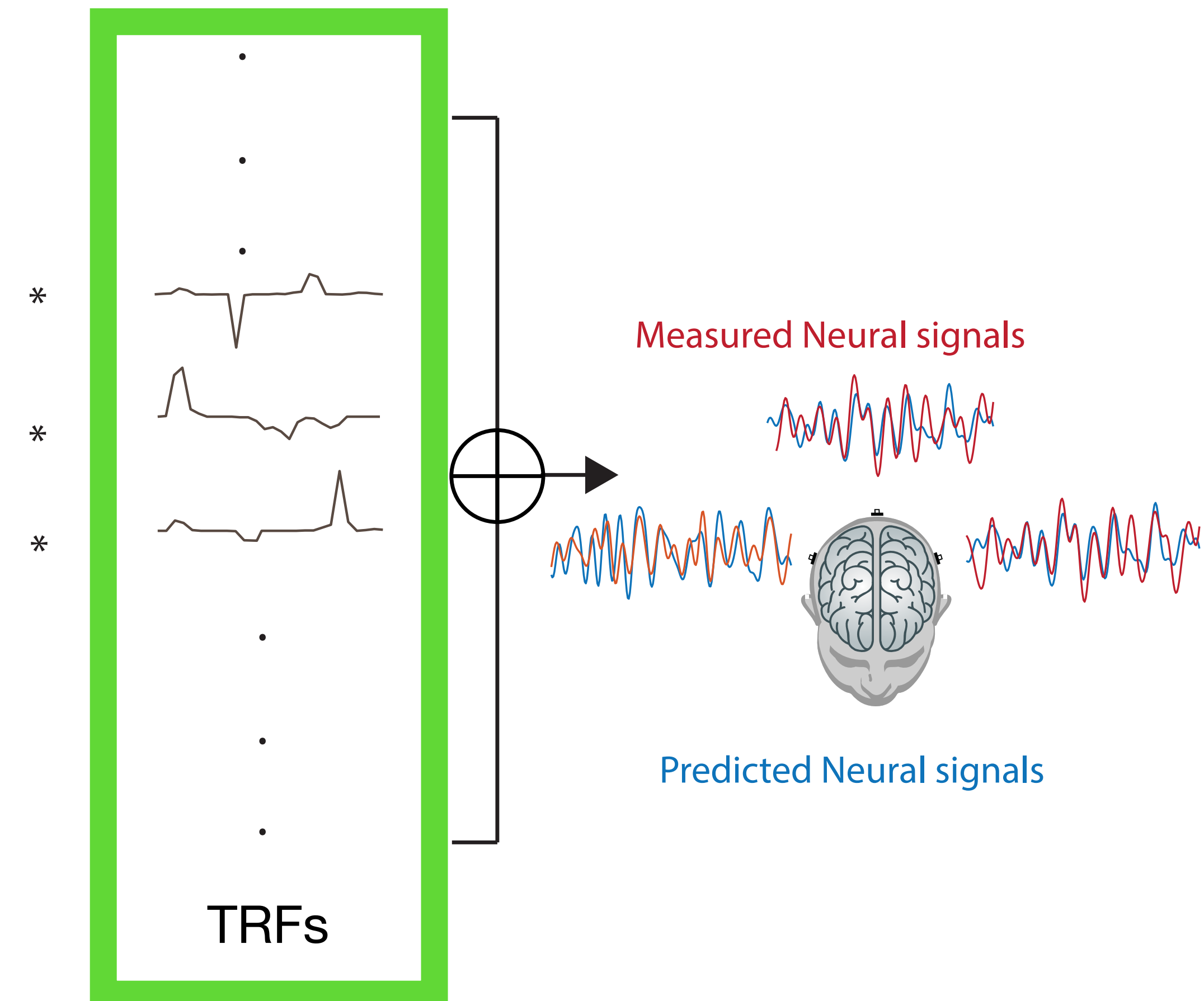
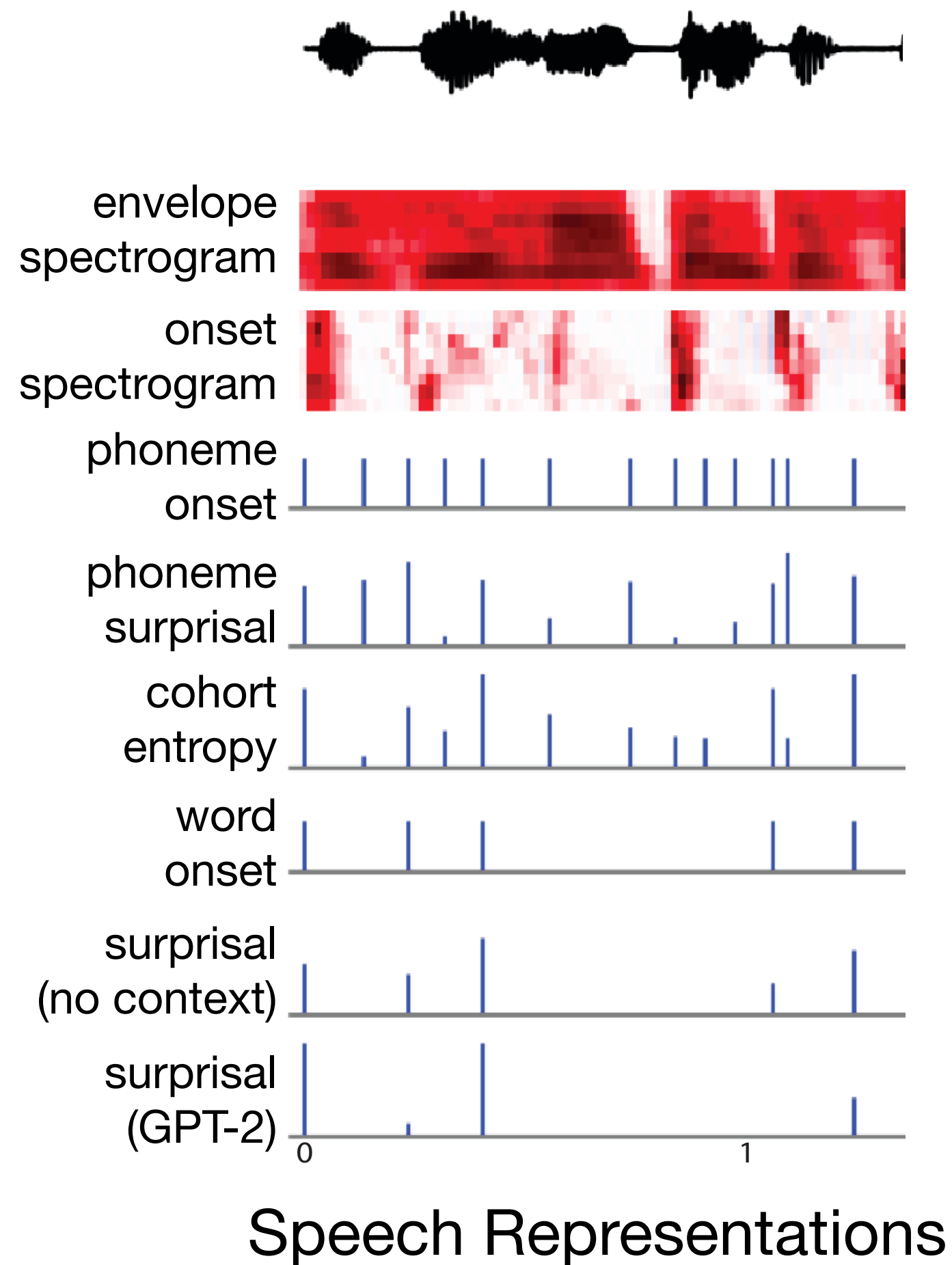


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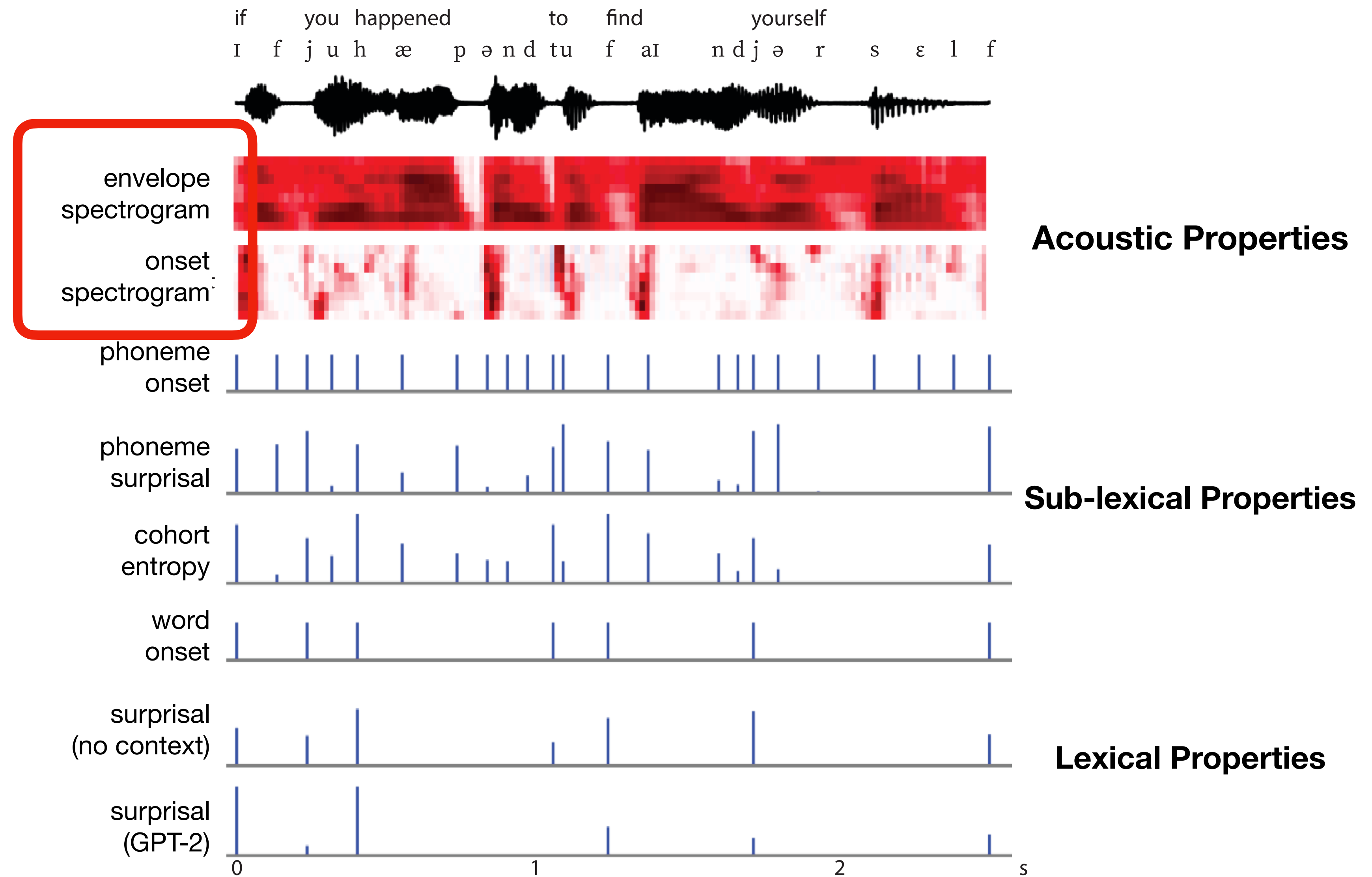


Simultaneous Temporal Response Functions

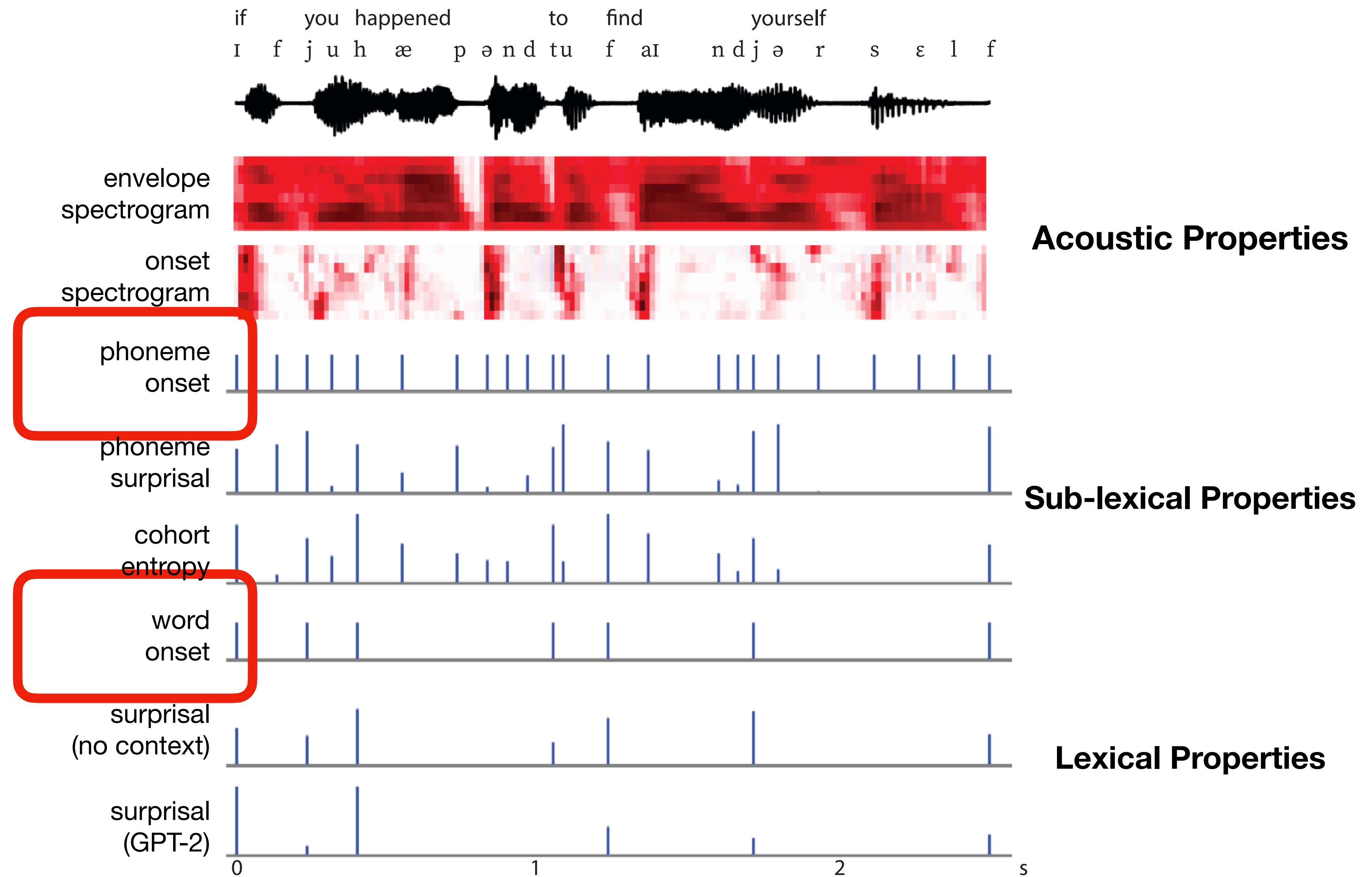
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Speech Representations



Speech Representations



Speech Representations

if you happened to find yourself
ɪ f j u h æ p ə n d t u f aɪ n d j ə r s ε l f



envelope
spectrogram



onset
spectrogram



Acoustic Properties

phoneme
onset



phoneme
surprisal



Sub-lexical Properties

cohort
entropy



word
onset



surprisal
(no context)



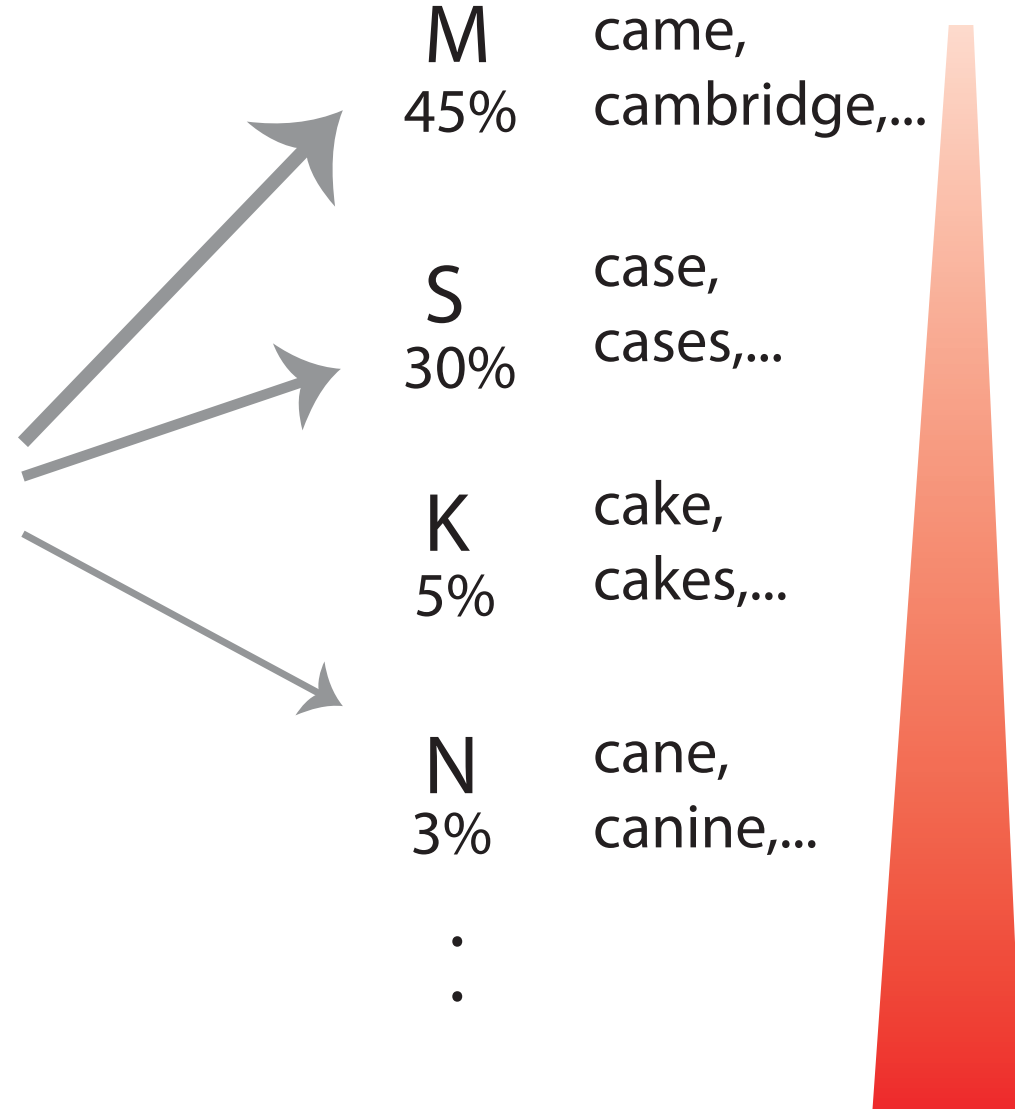
Lexical Properties

surprisal
(GPT-2)

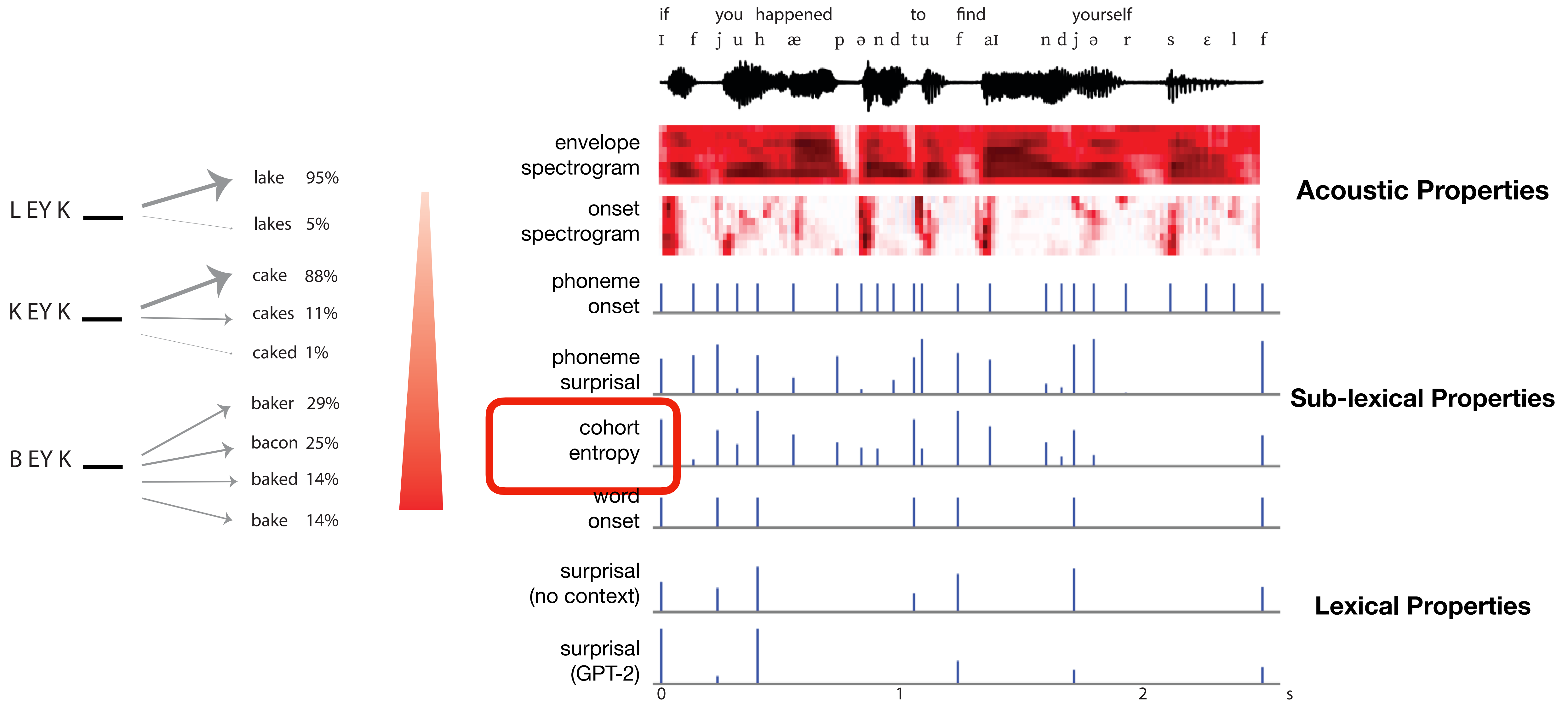


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KEY —



Speech Representations



Speech Representations

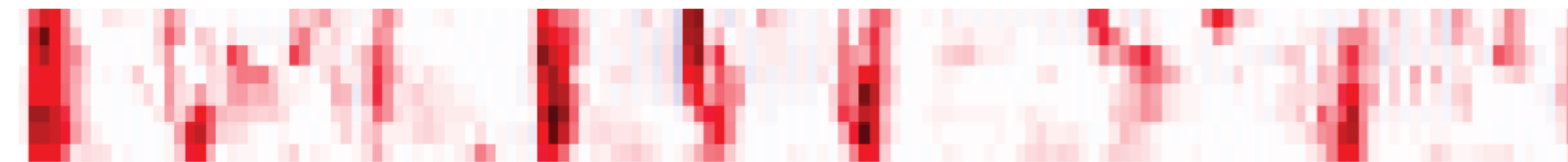
if you happened to find yourself
ɪ f j u h æ p ɒ n d t u f aɪ n d j ə r s ε l f



envelope
spectrogram

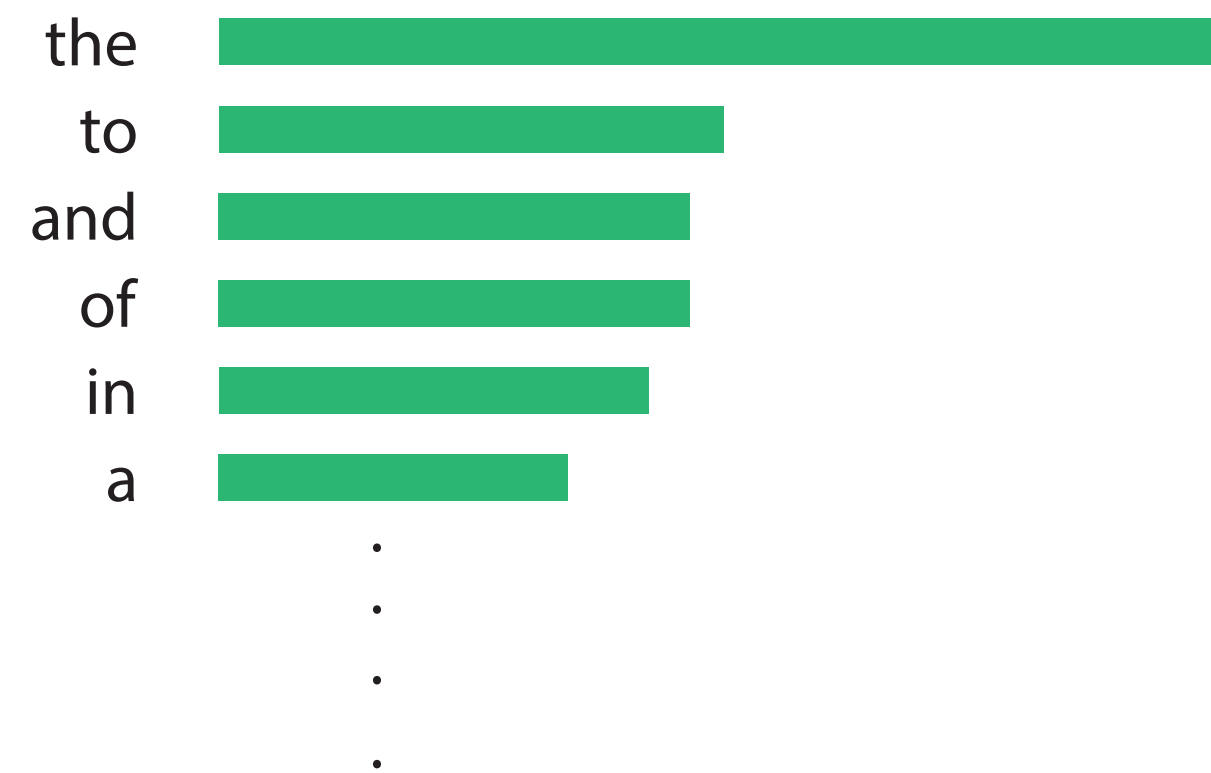


onset
spectrogram



Acoustic Properties

Frequency of words based on SUBTLEX



phoneme
onset



phoneme
surprisal



Sub-lexical Properties

cohort
entropy



word
onset



surprisal
(no context)



Lexical Properties

surprisal
(GPT-2)



0 1 2 s

Speech Representations

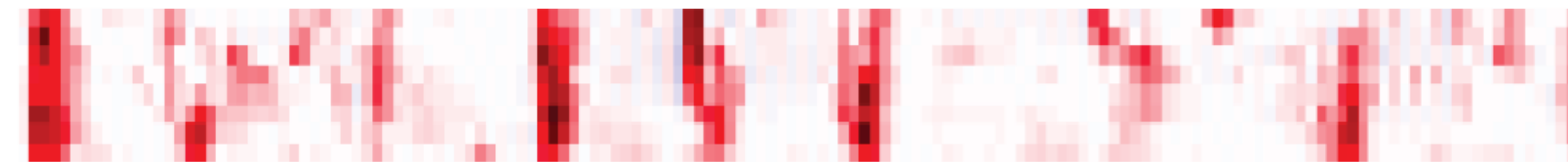
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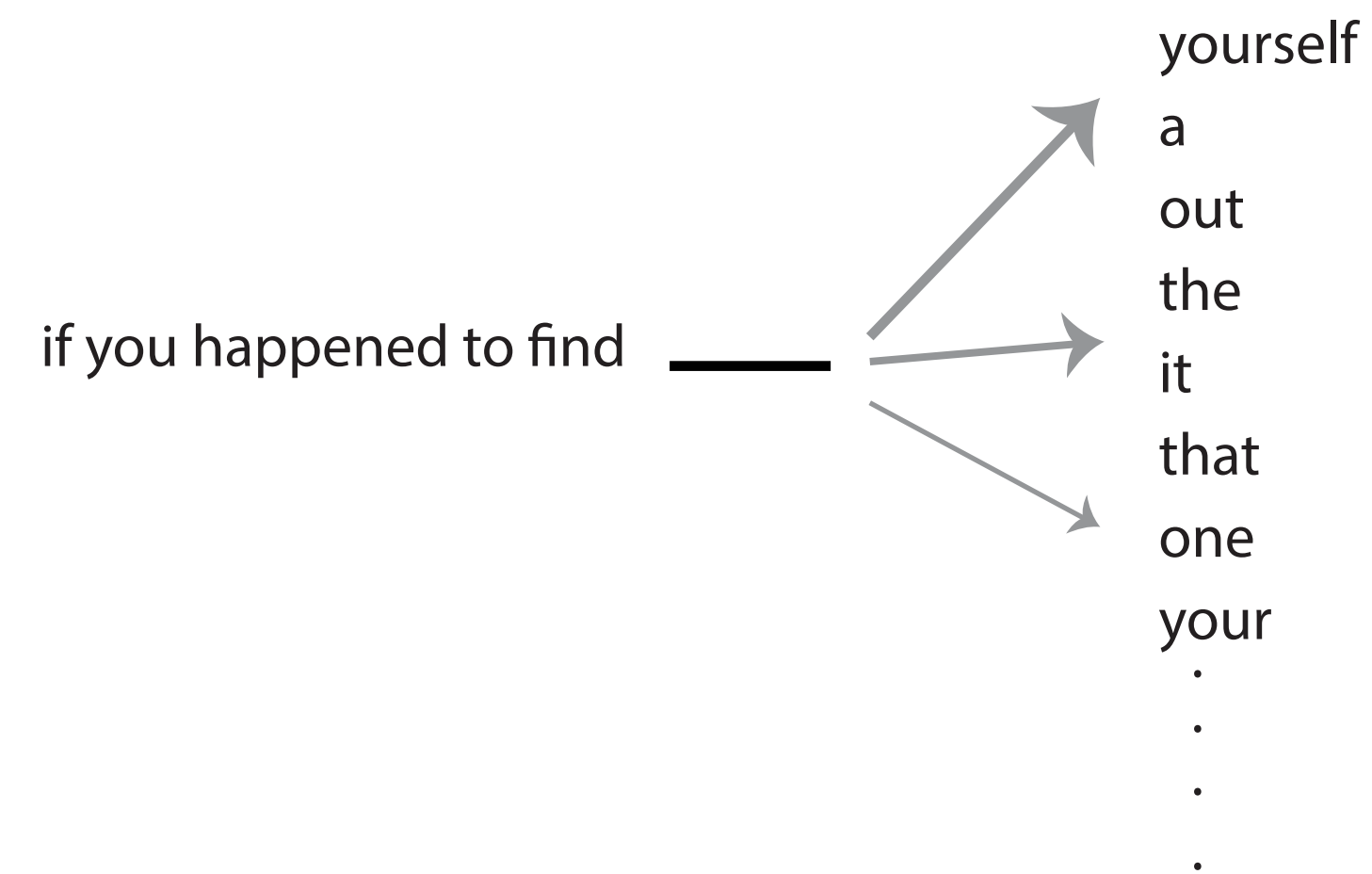


Lexical Properties

surprisal
(GPT-2)

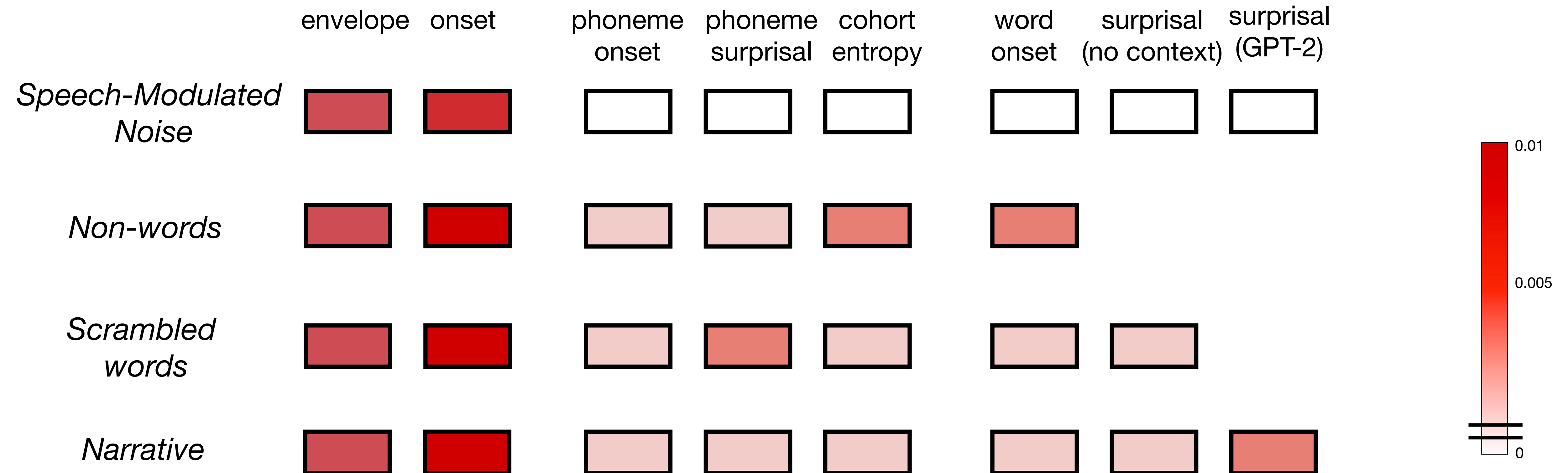


0 1 2 s



Neural Prediction Results

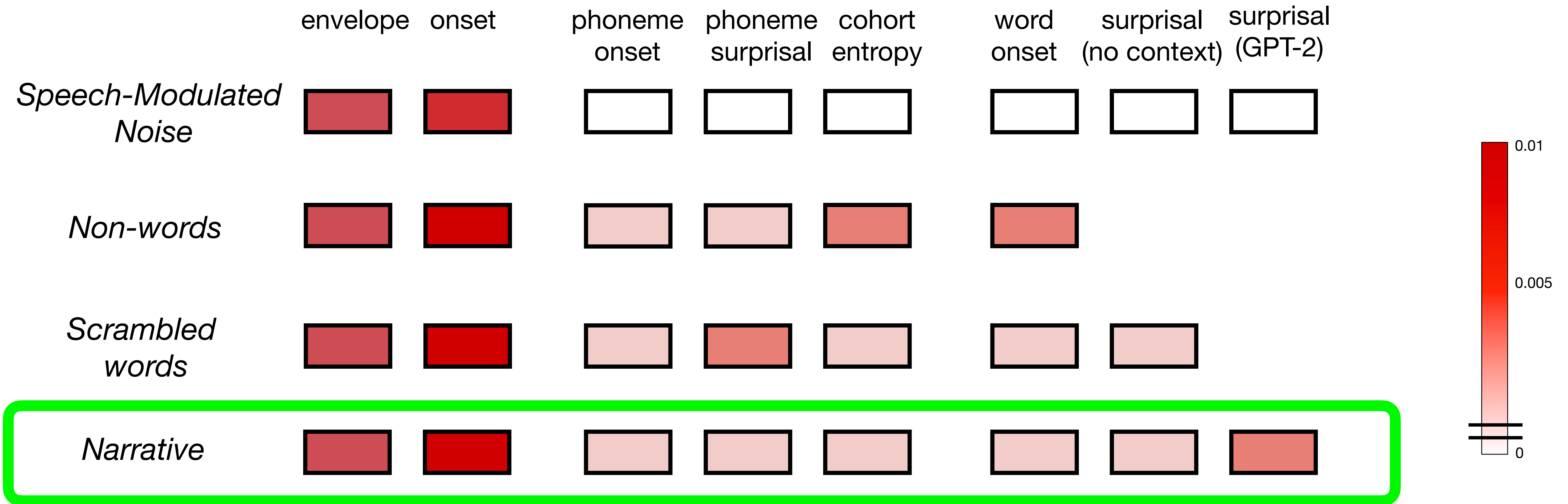
Emergence of neural features as the incremental processing occur



- 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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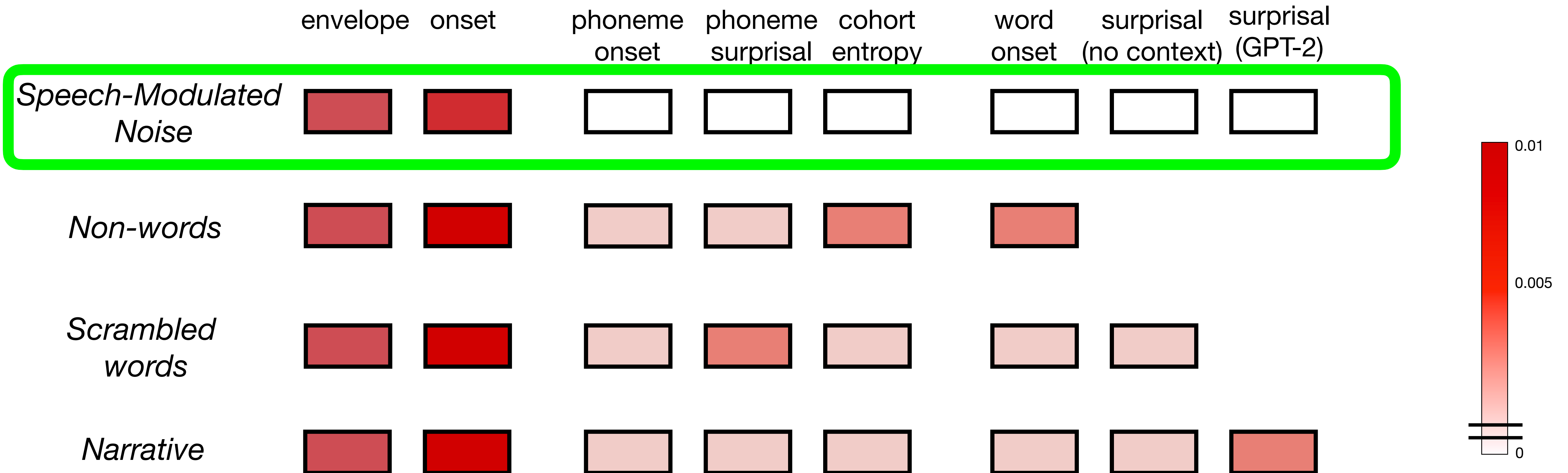
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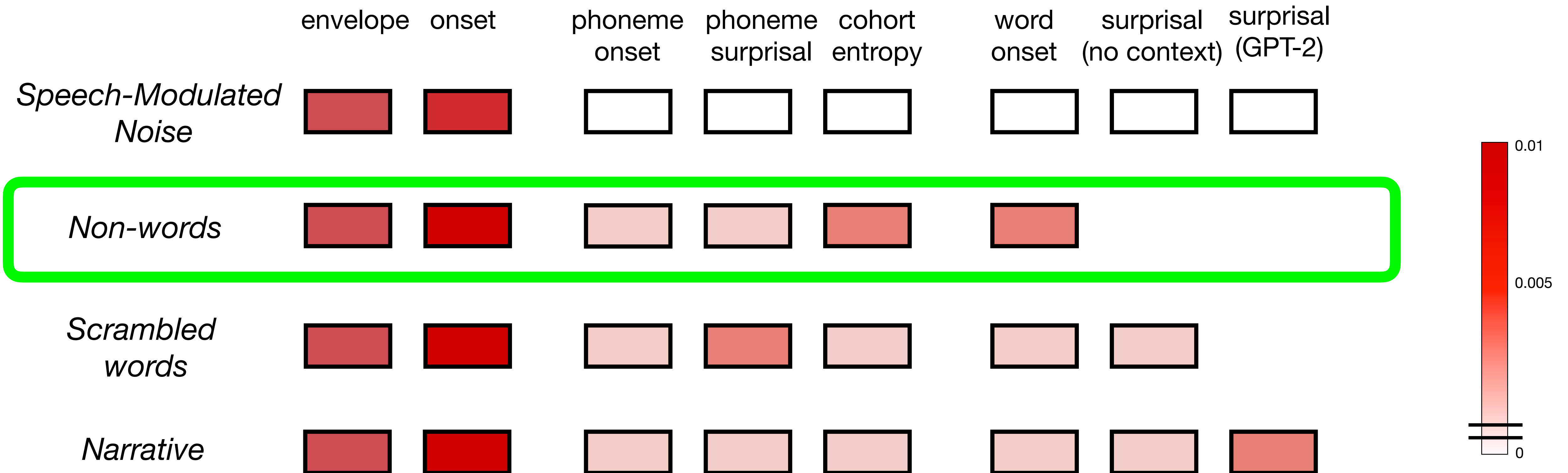
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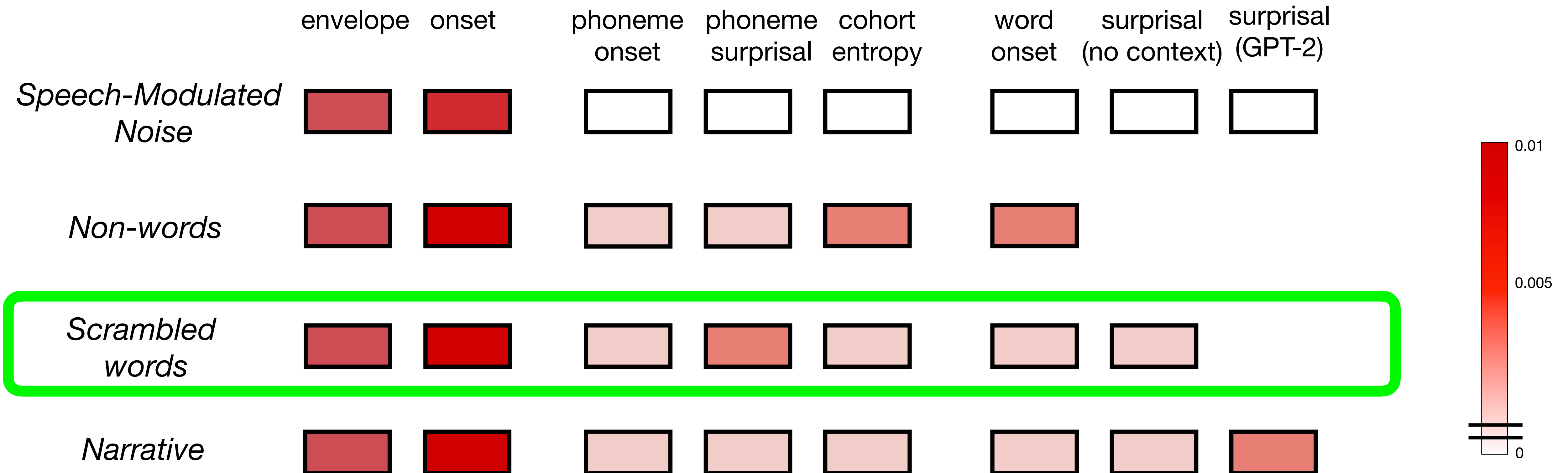
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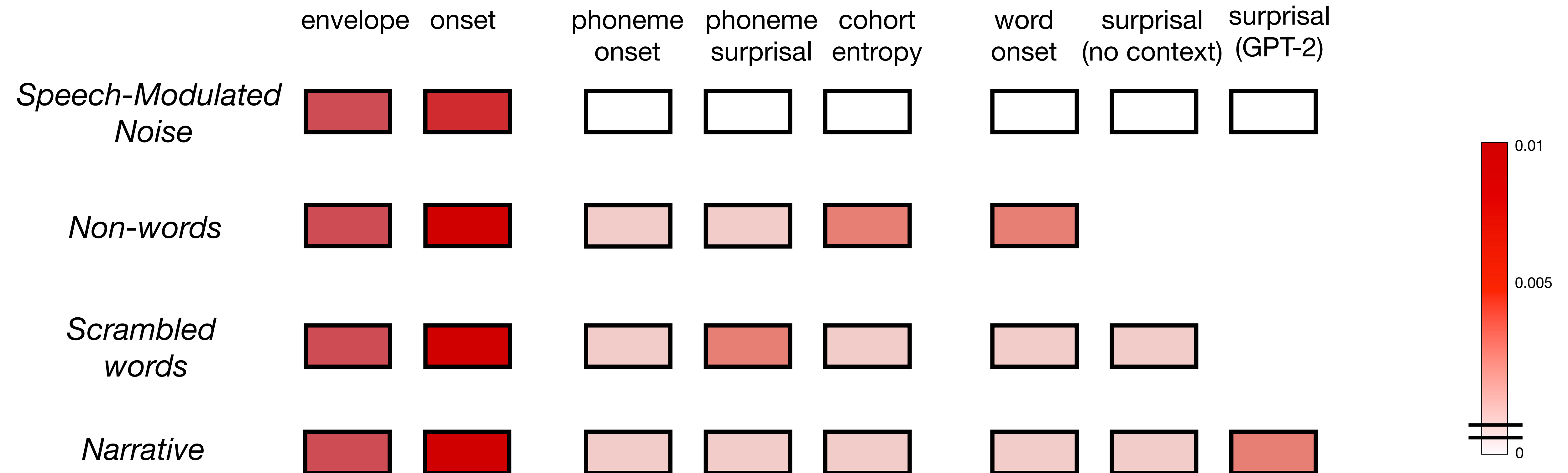
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Hemispheric Lateralization Results

Speech feature

Envelope Onset

Envelope

Phoneme Onset

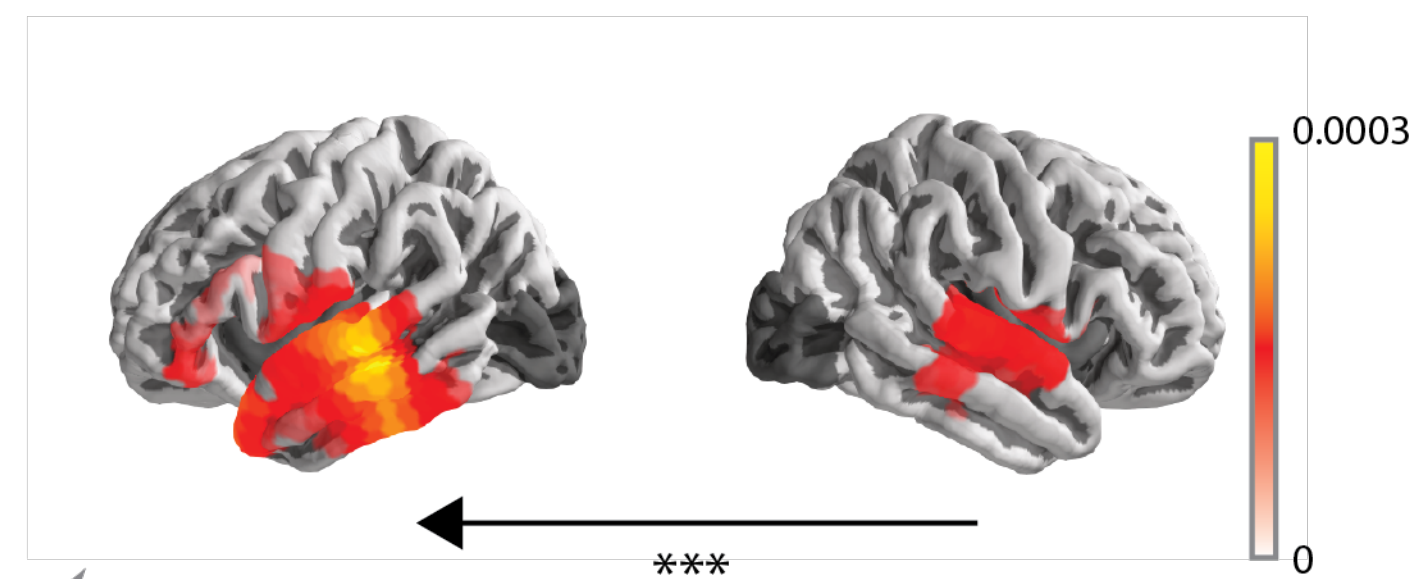
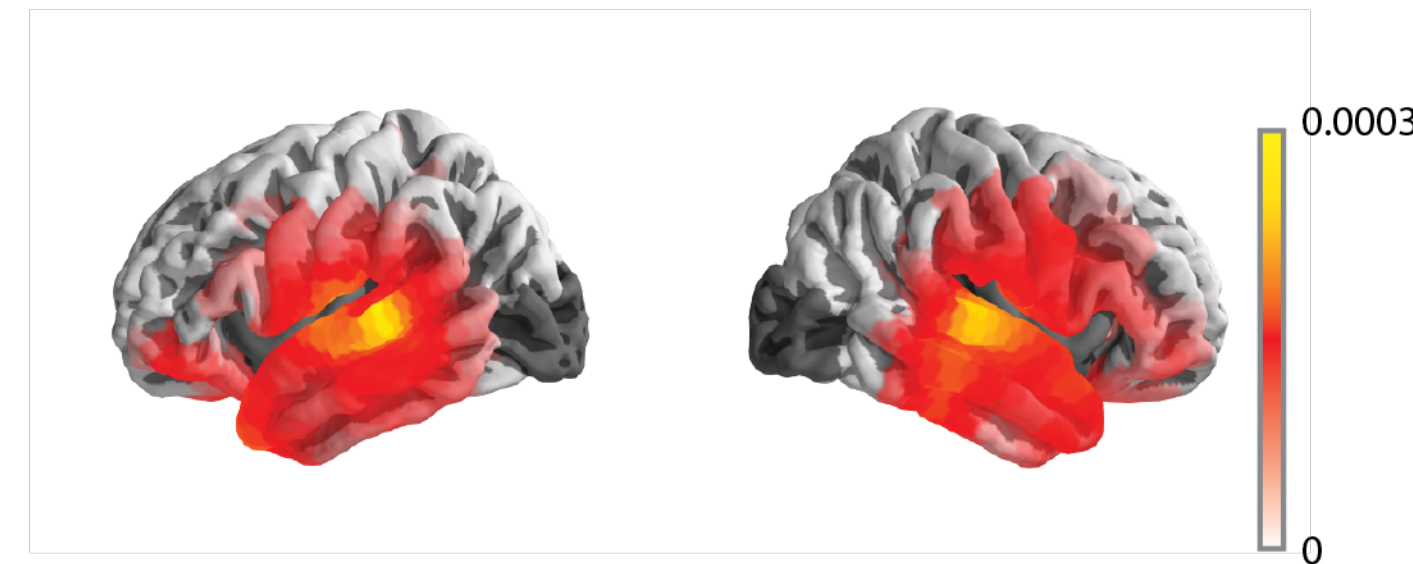
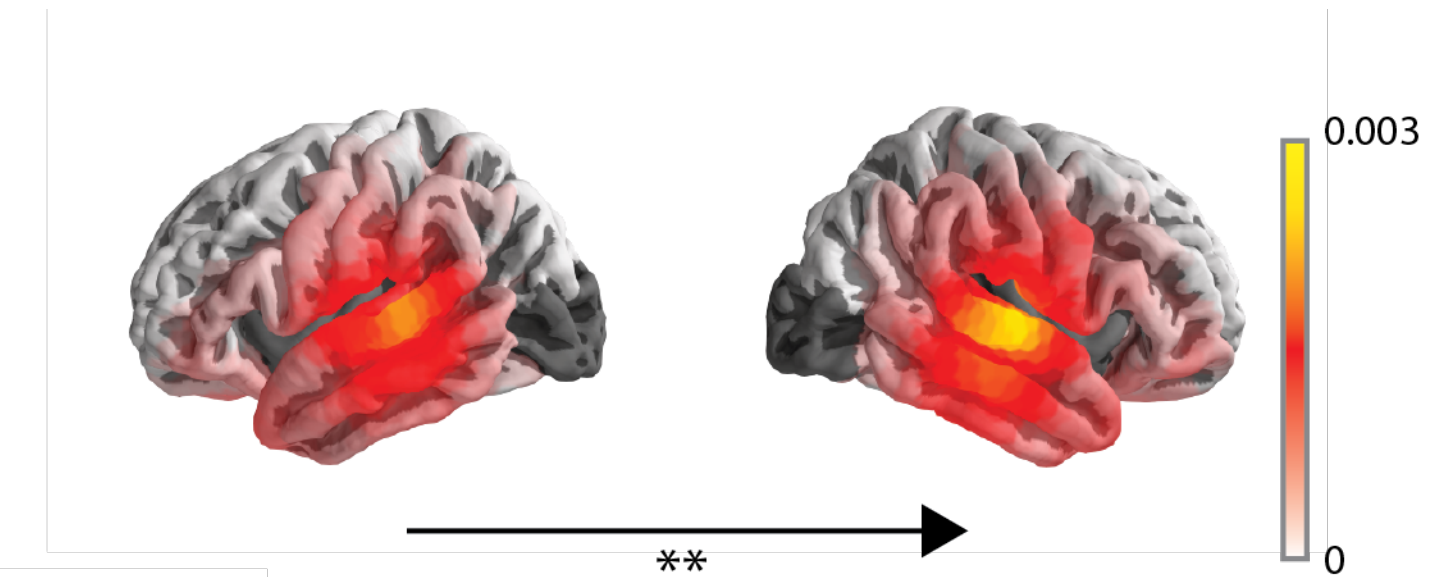
**Phoneme
Surprisal**

Cohort Entropy

Word Onset

Unigram
Surprisal

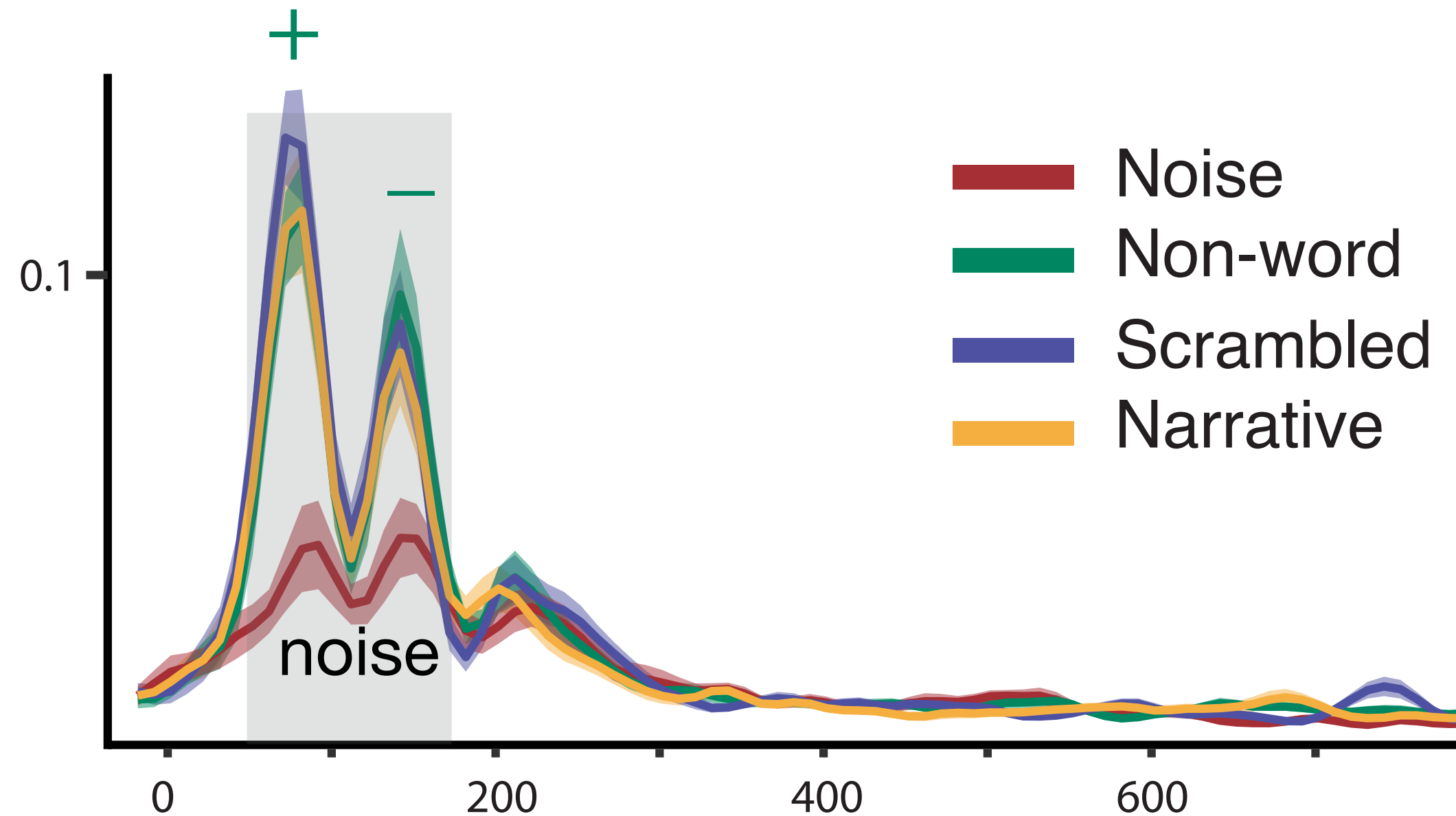
**GPT2
Surprisal**



Note: lateralization results can be task dependent

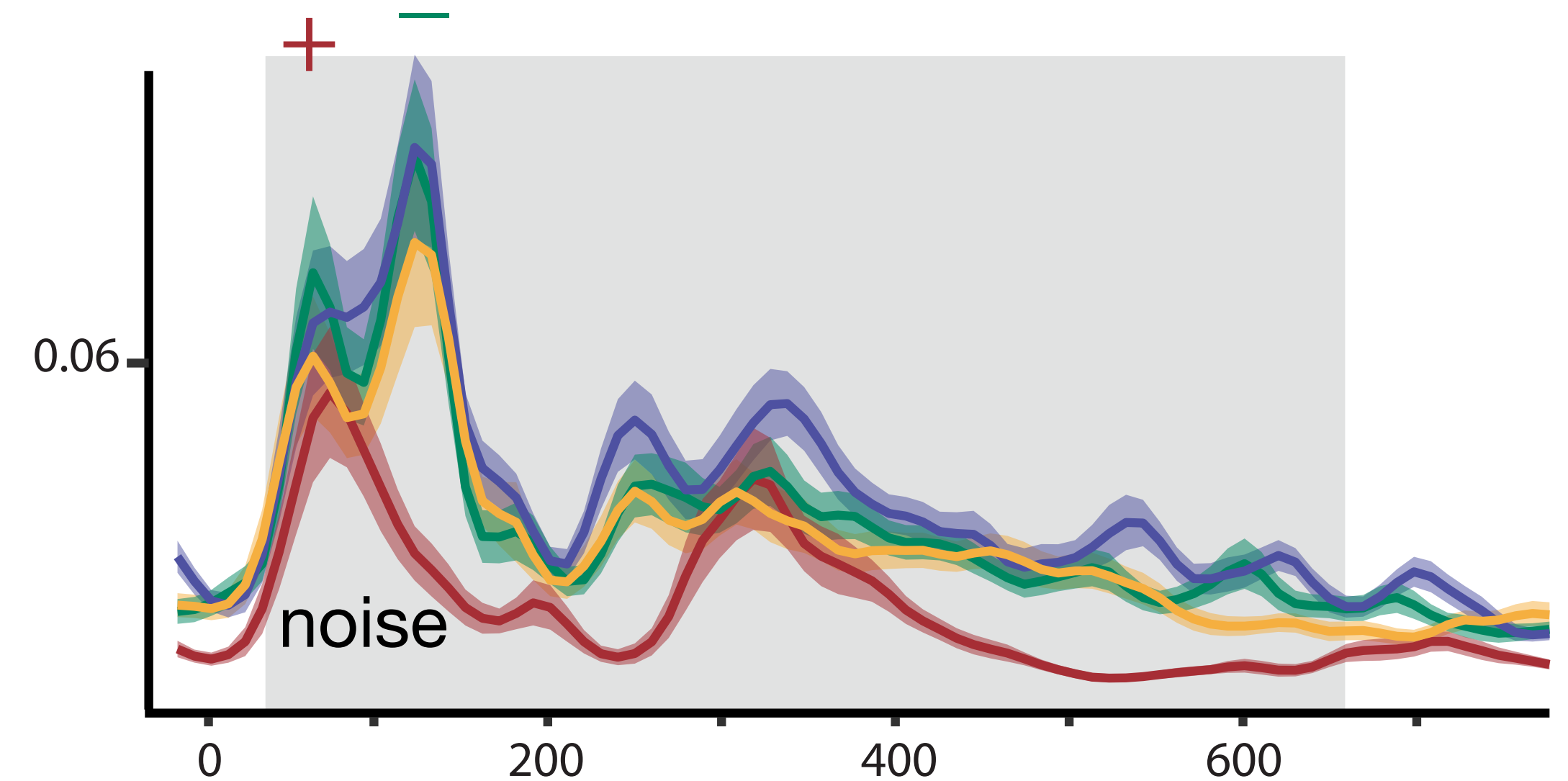
Acoustic TRF Results

acoustic onsets



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

acoustic envelope

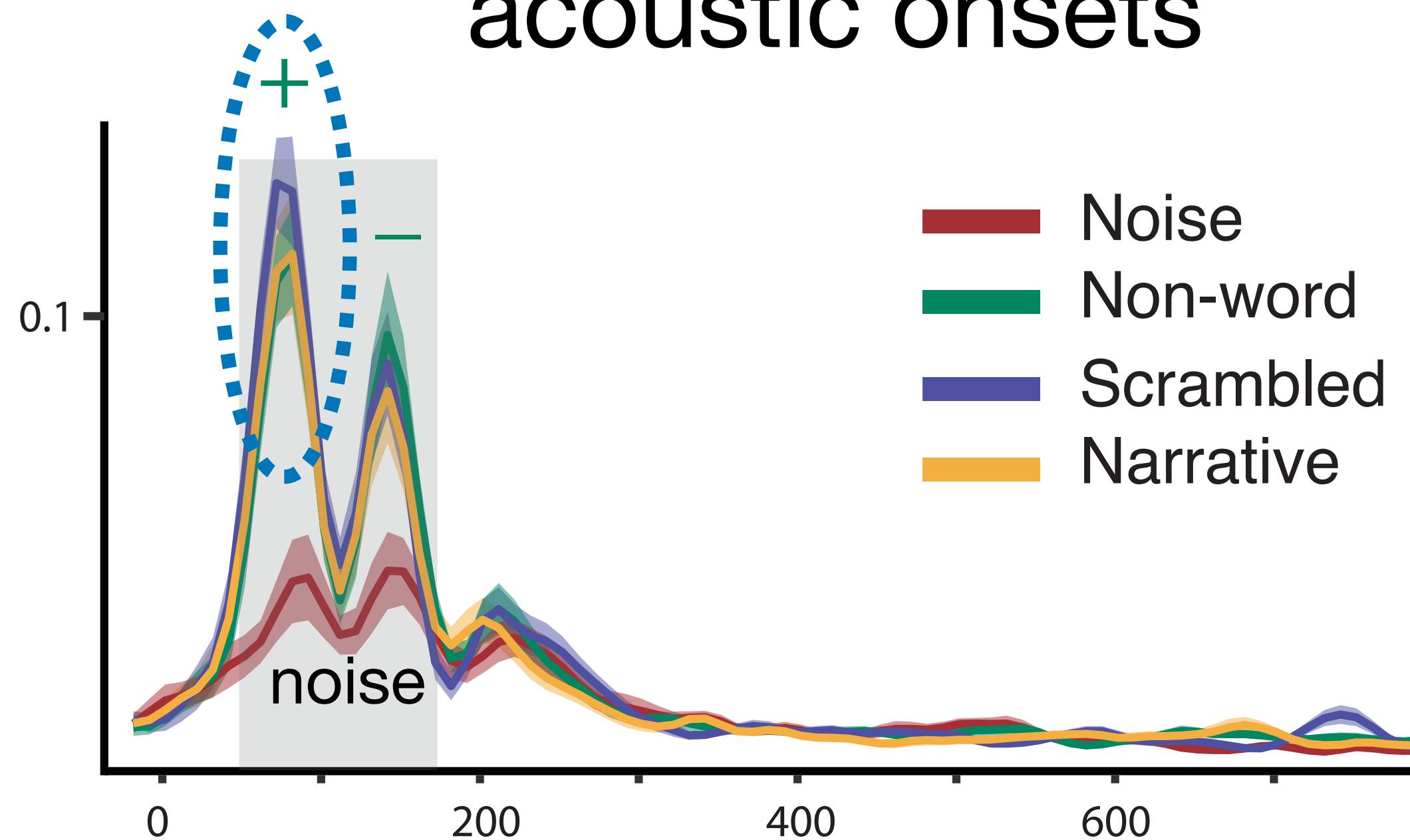


- Speech responses > Noise response (Narrative < Scrambled)
- Non words similar to Scrambled words
- Noise response lacks 2nd peak ~120 ms

right hemisphere shown
condition based differences similar in left

Acoustic TRF Results

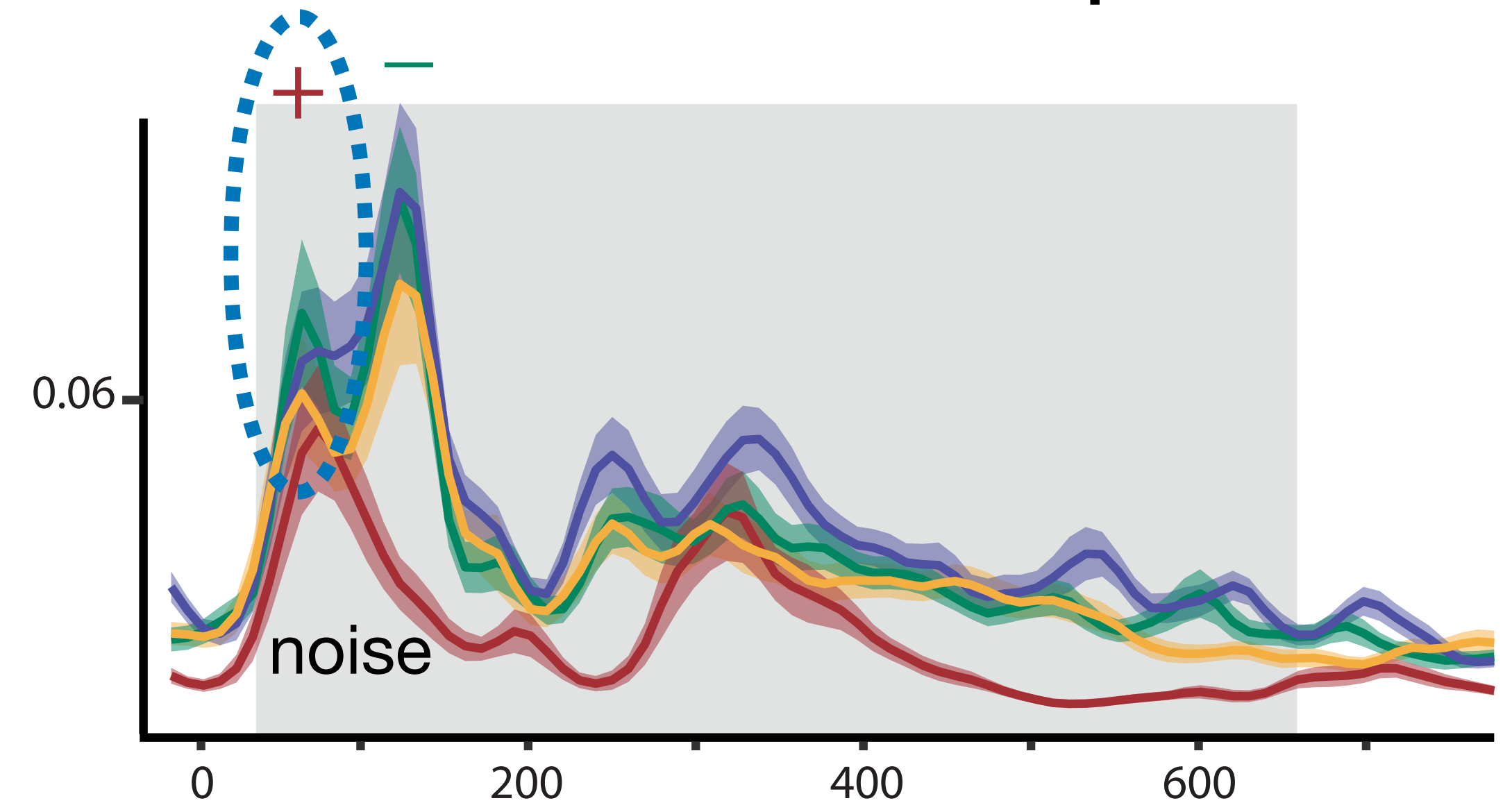
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60 ms: acoustic bottom-up processing

acoustic envelope

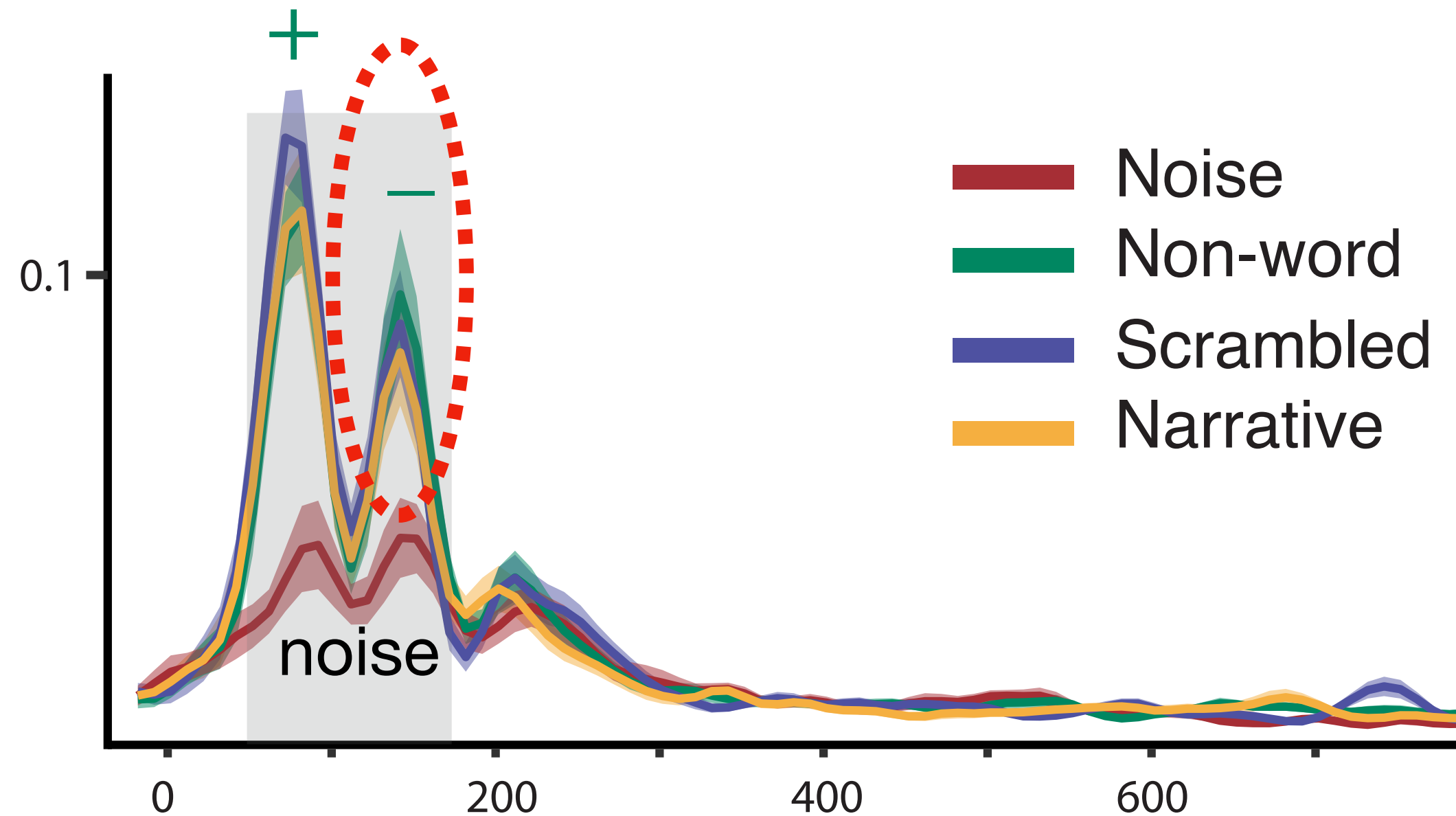


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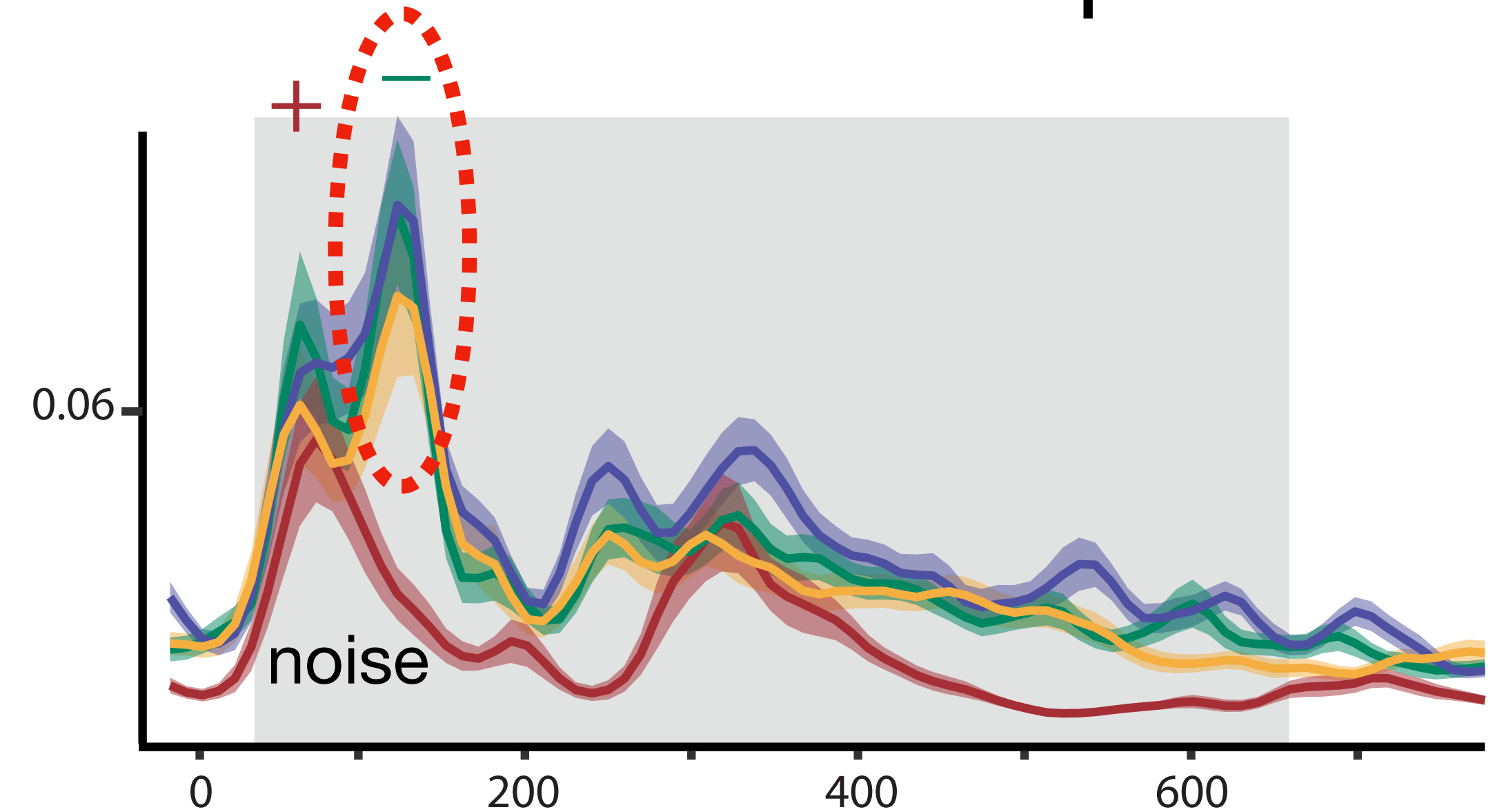
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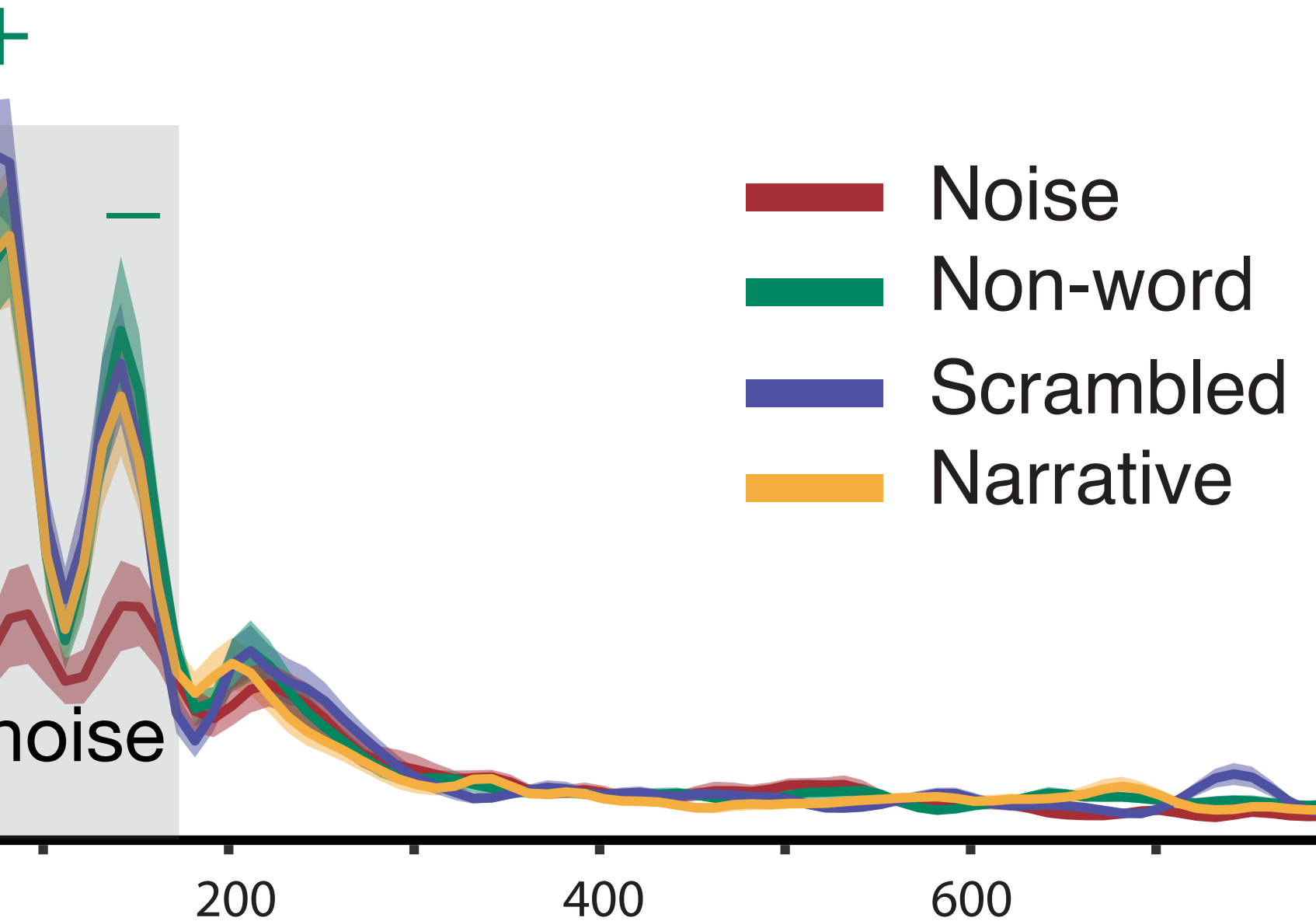
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120 ms: acoustic but attention-dependent

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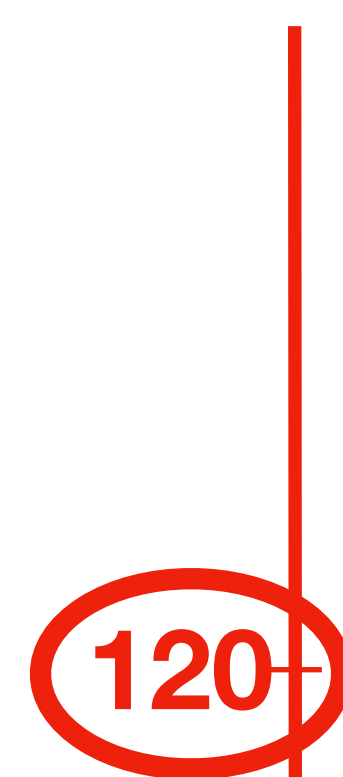
Acoustic TRF Results

acoustic onsets



h responses > Noise response
speech roughly equal)

Top-down



0

time (ms)

High level meaning

Acoustic

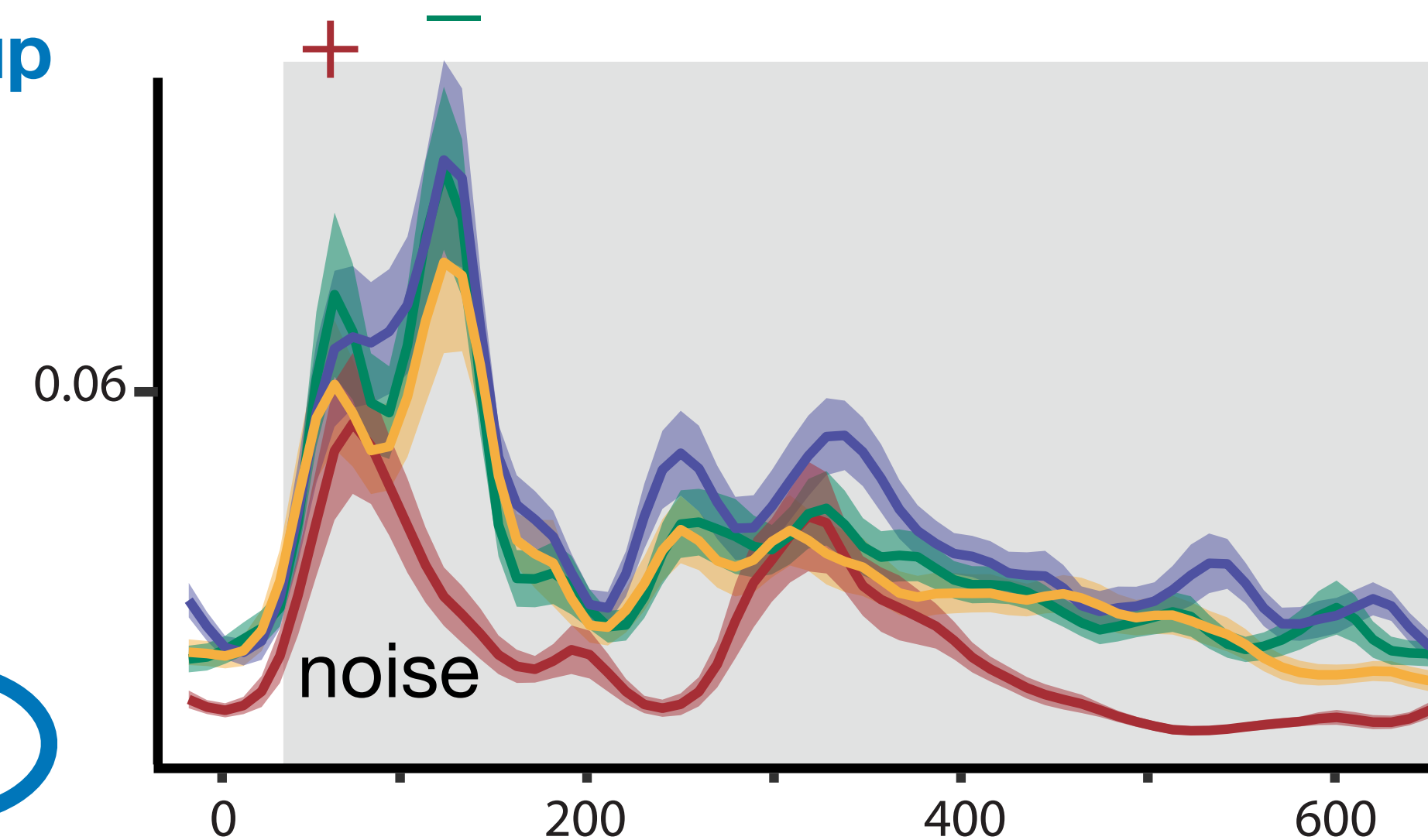
Speech
Stimuli

Bottom-up



0
time (ms)

acoustic envelope



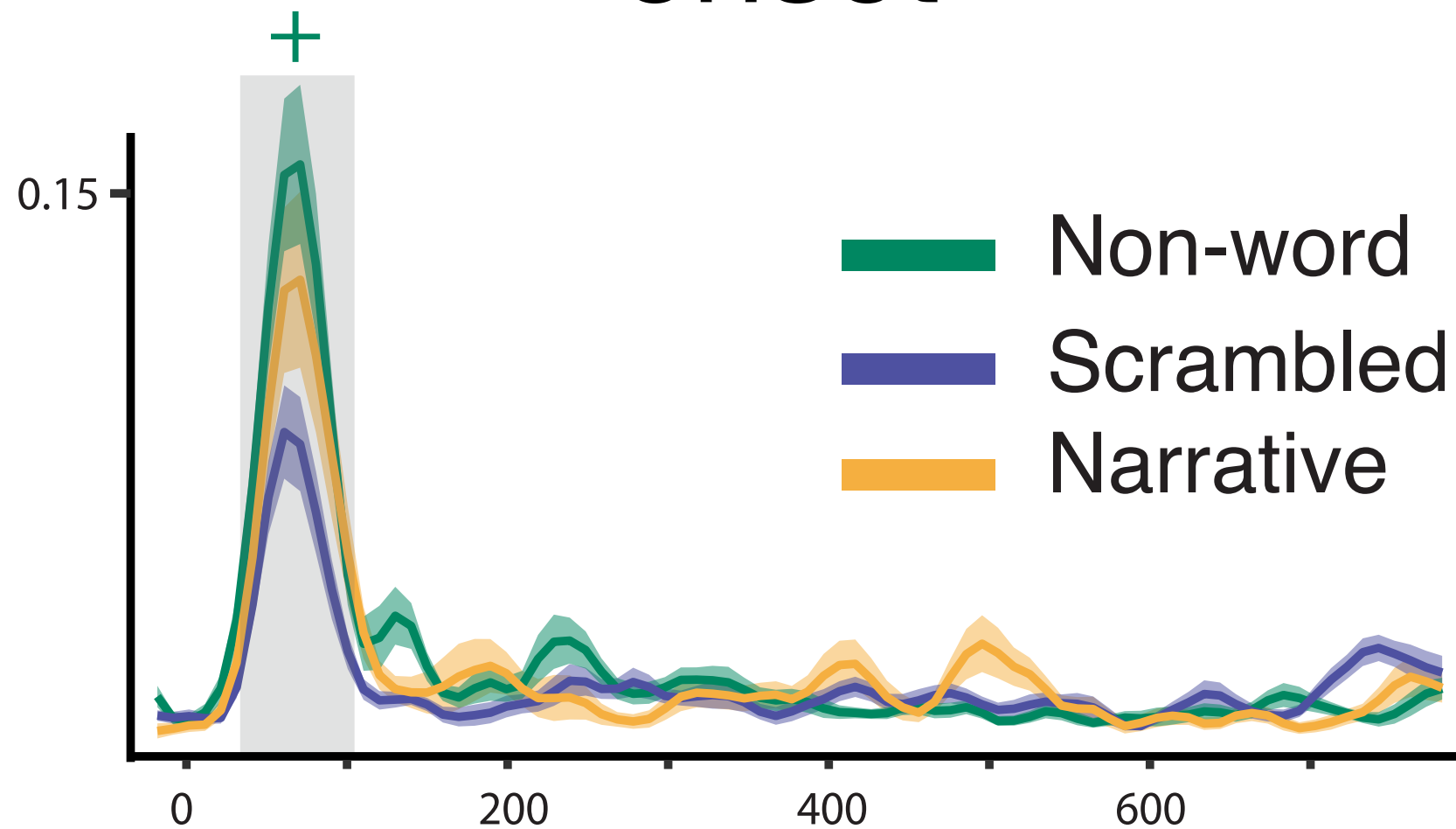
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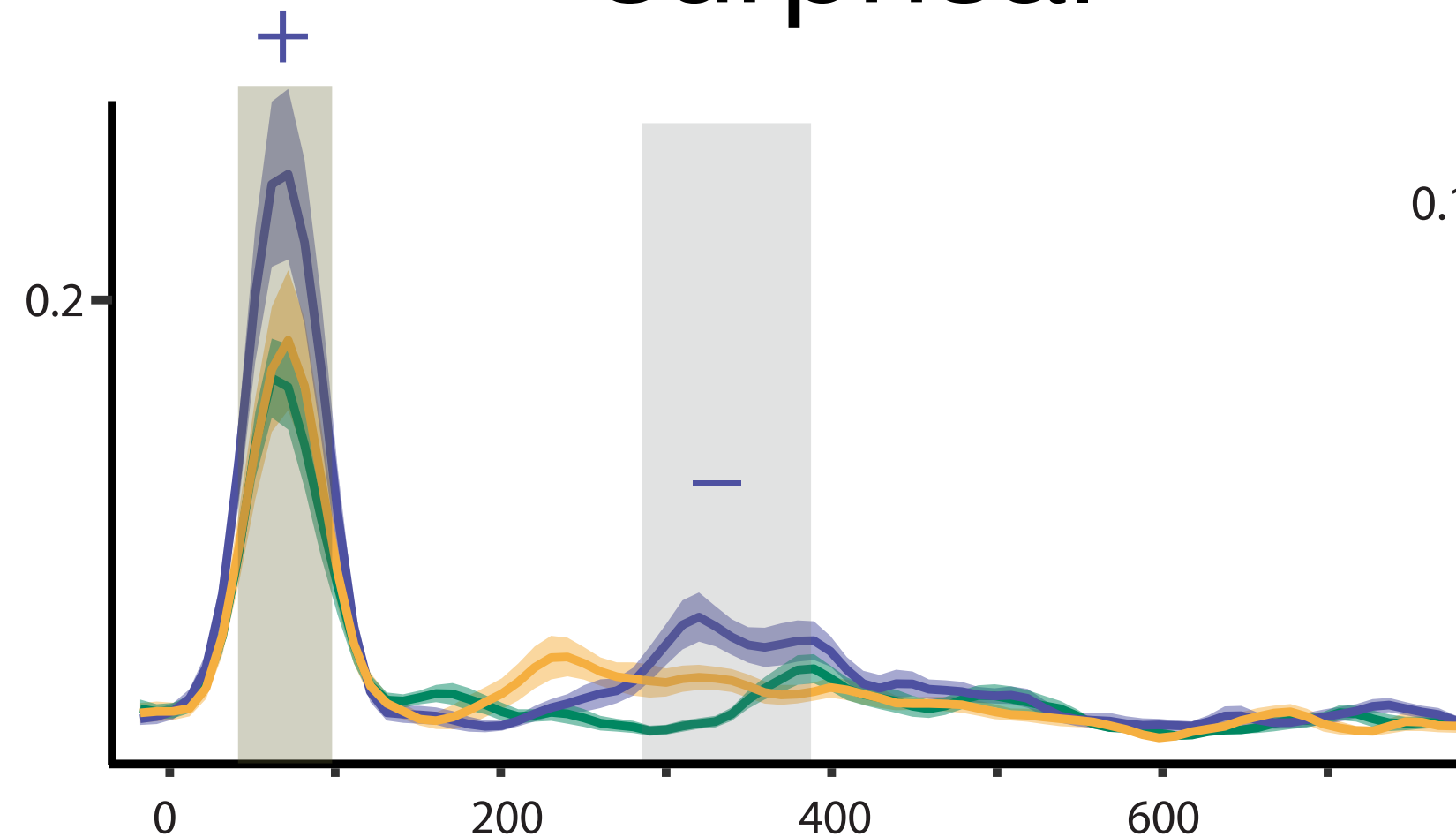
Phonemic TRF Results

phoneme
onset



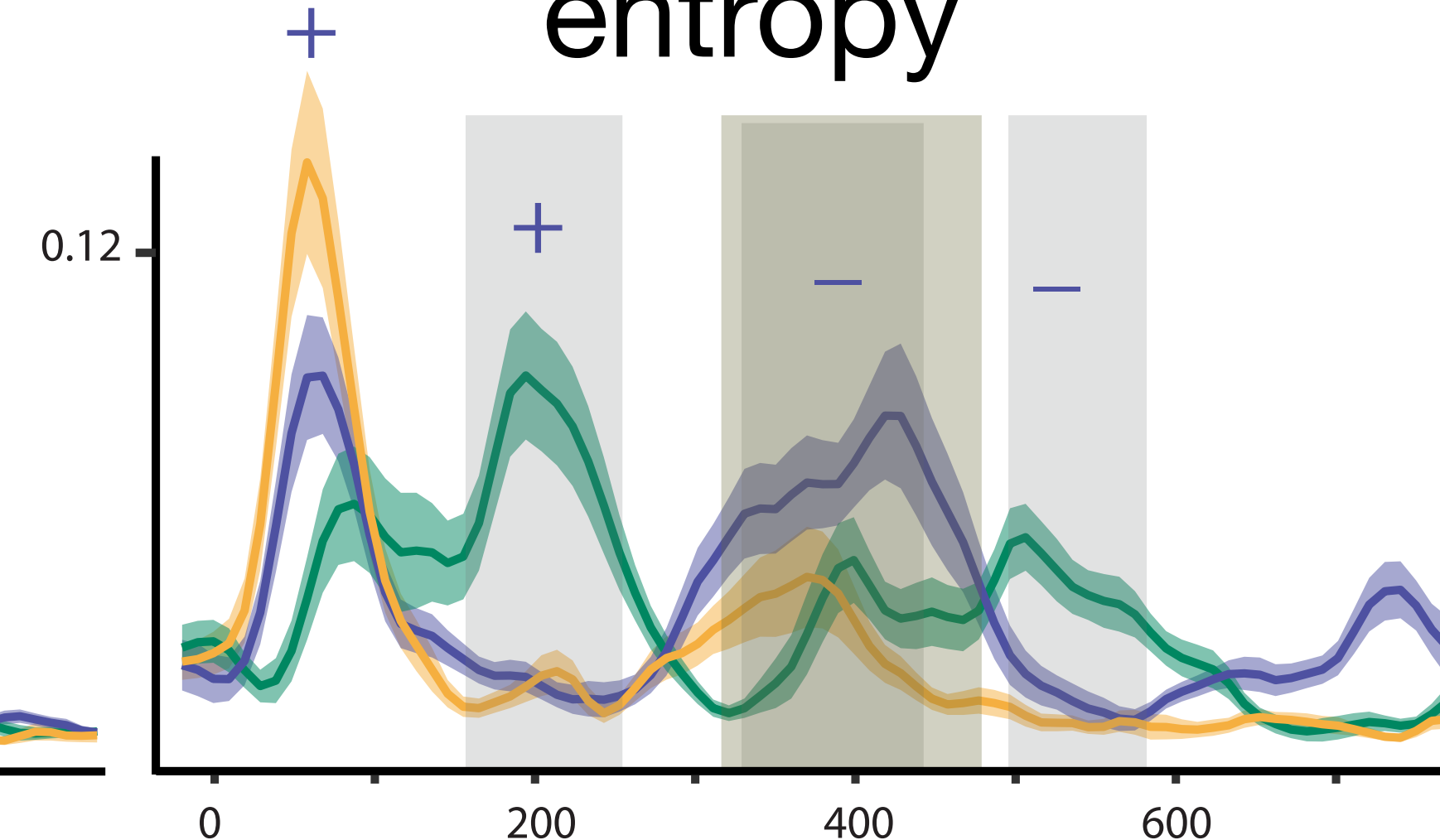
- Non-words largest
- No later processing

phoneme
surprisal



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

cohort
entropy

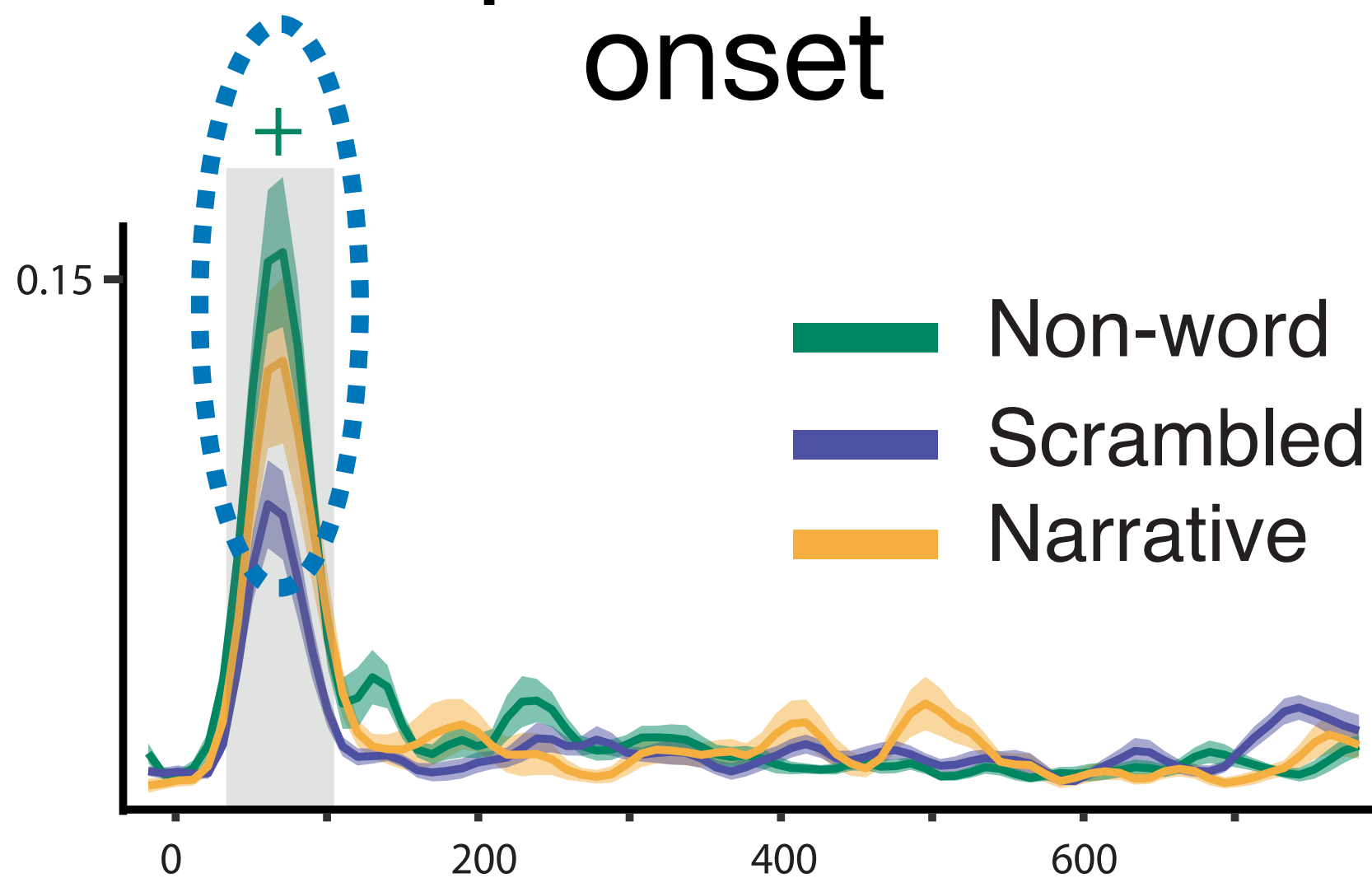


- Late context processing
- N400-like response (reduced for narrative)
- Additional/delayed peaks in non-words (difference in stimulus distributions)

left hemisphere shown (right similar)

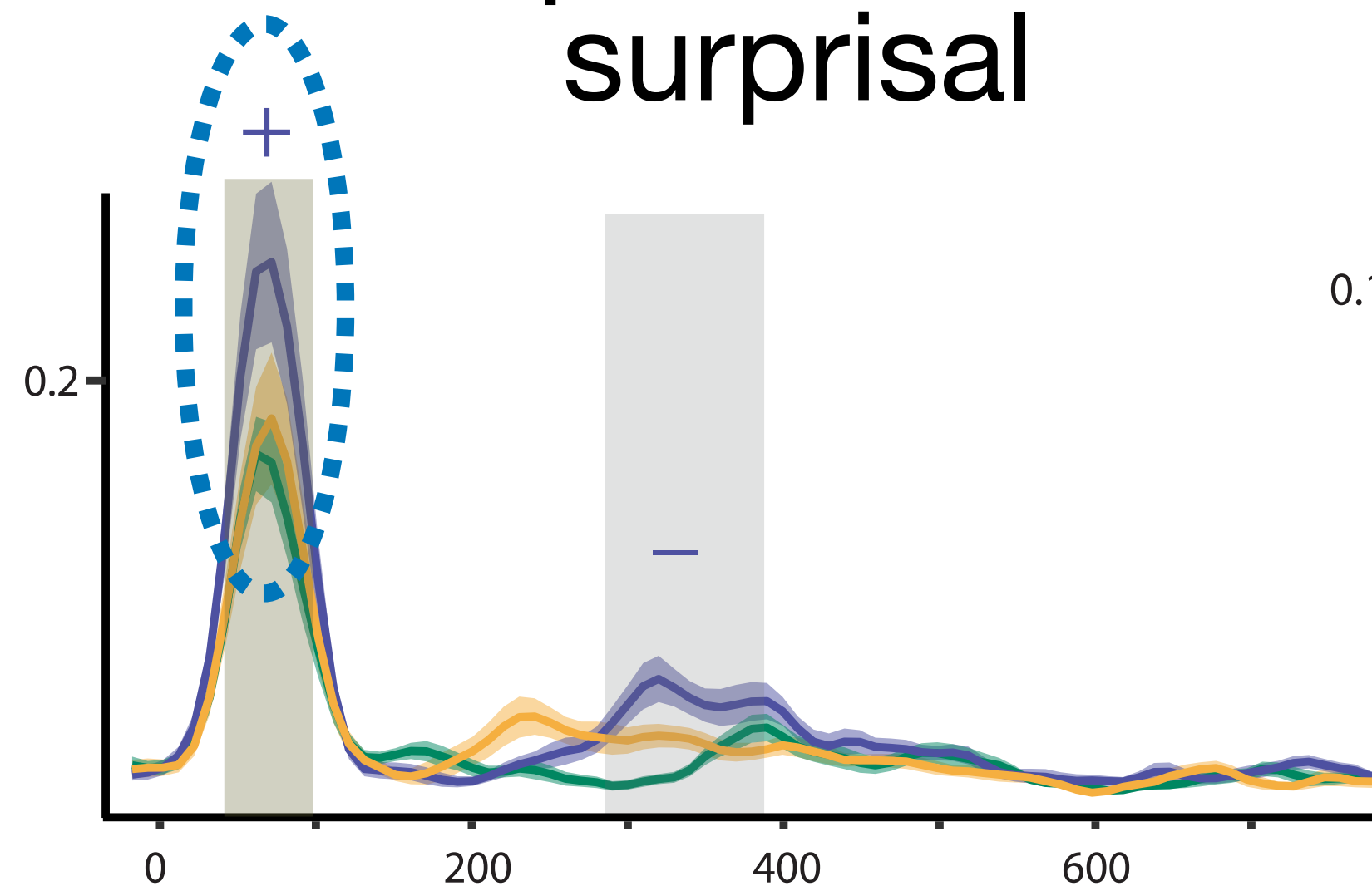
Phonemic TRF Results

phoneme
onset



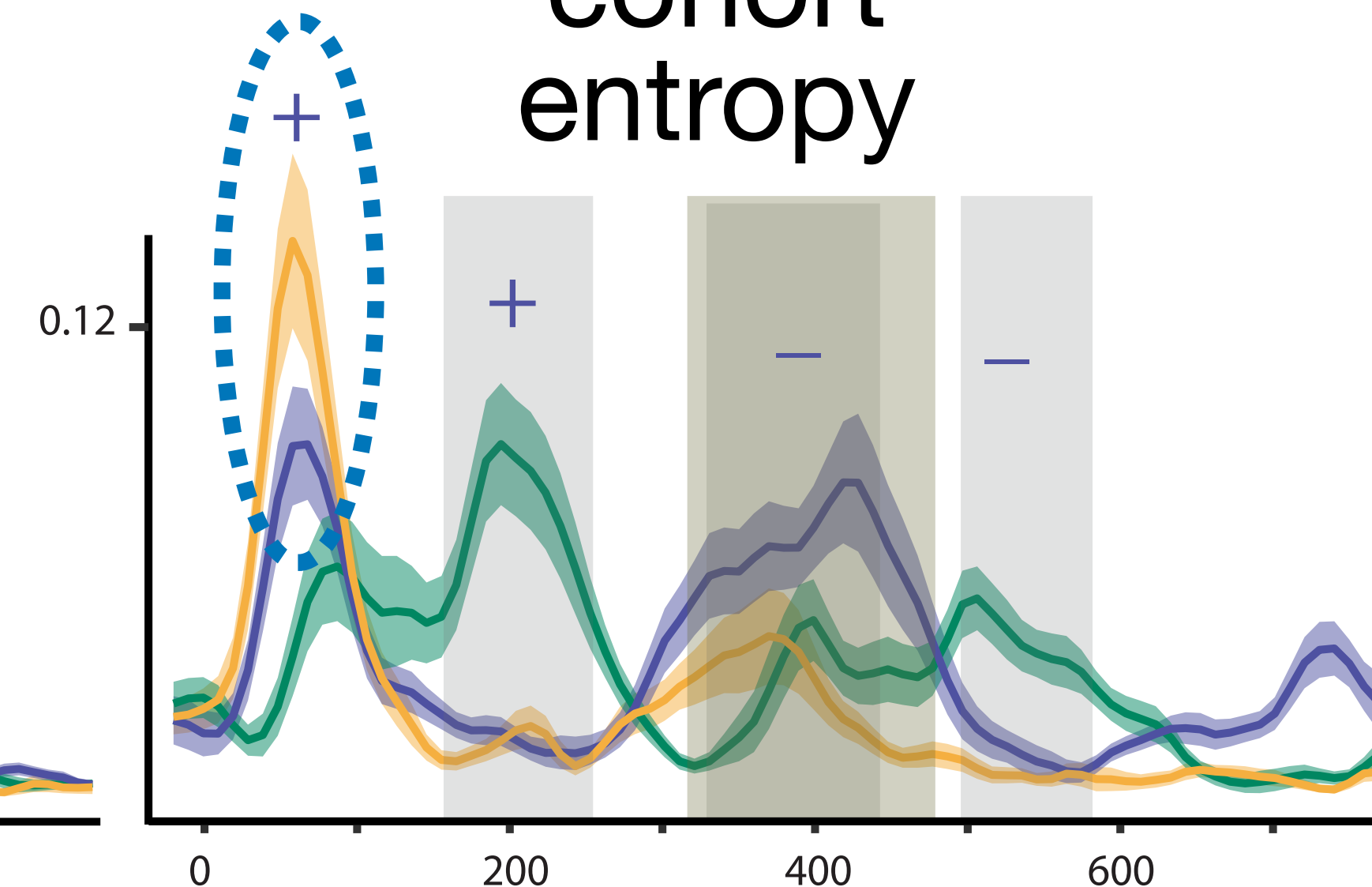
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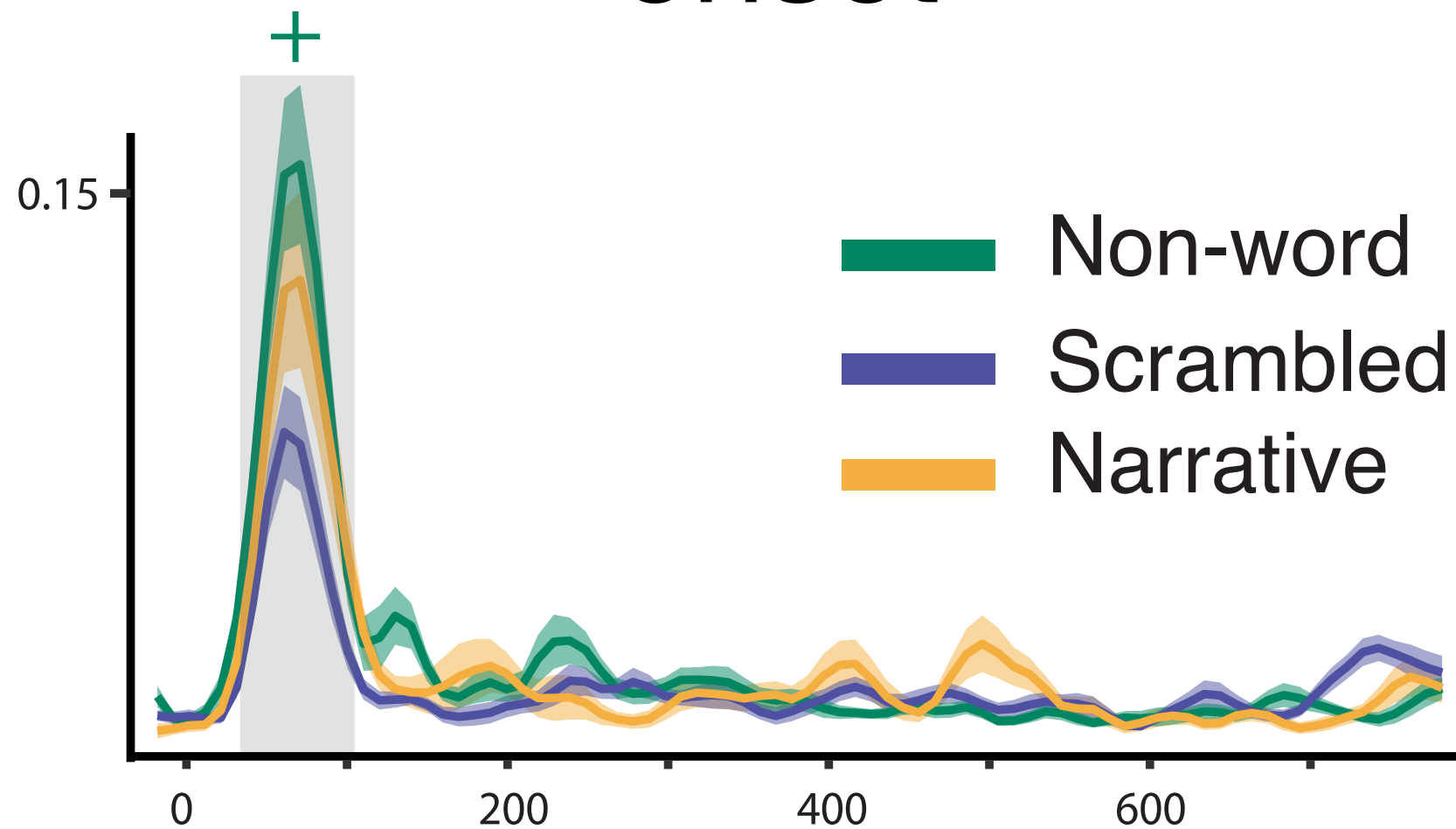
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85 ms: simple phoneme processing

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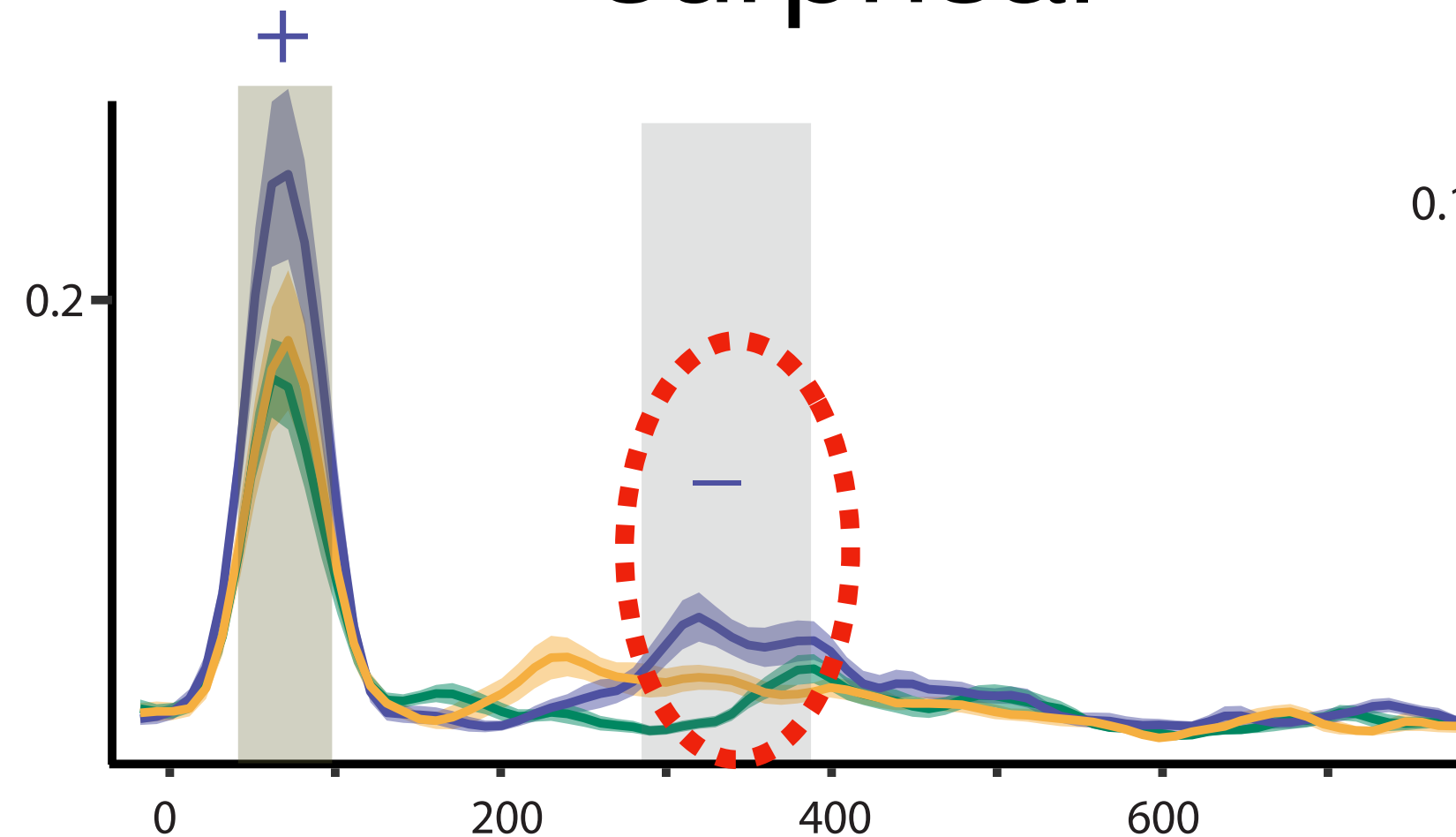
Phonemic TRF Results

phoneme
onset



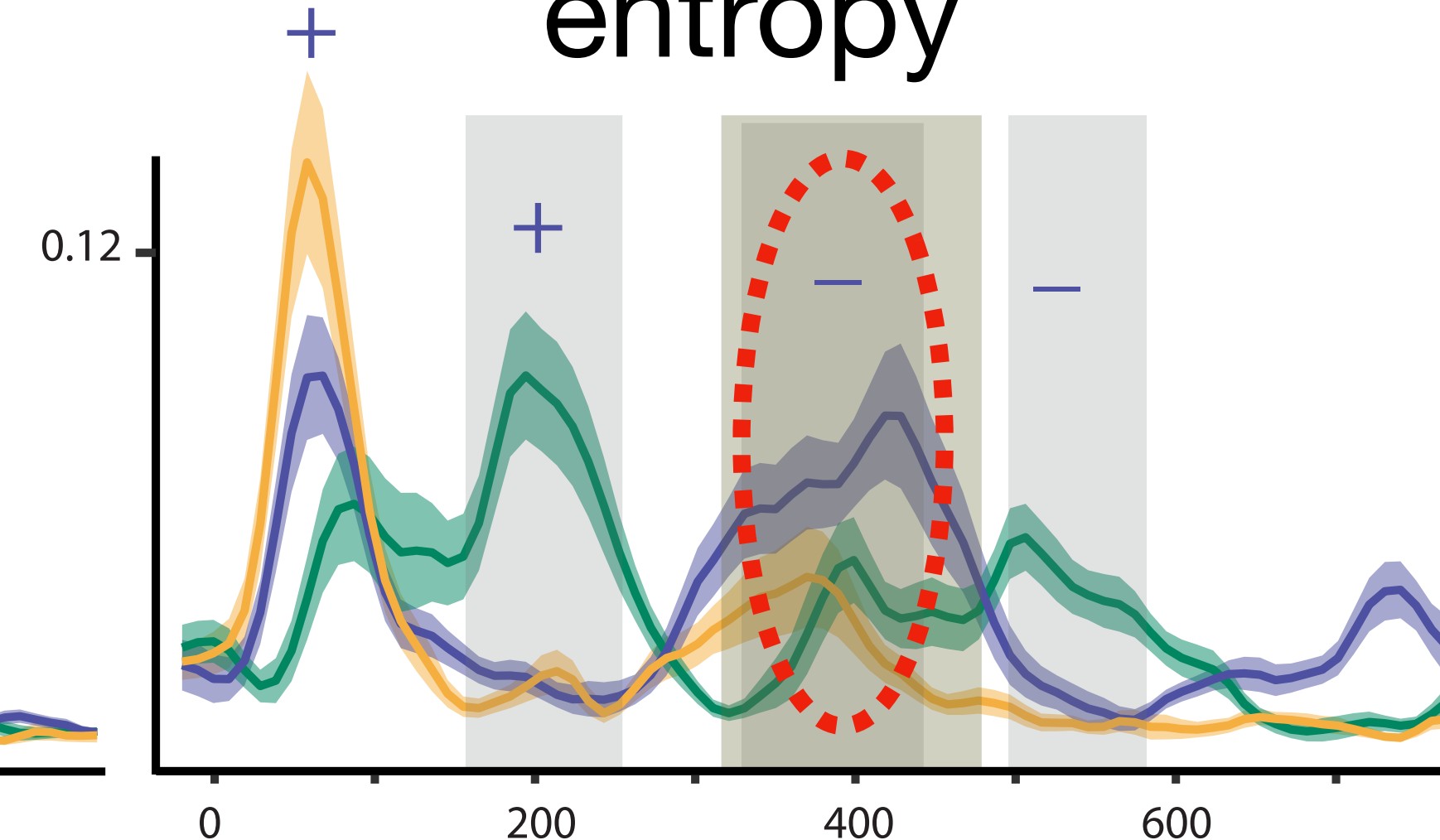
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phoneme
surprisal



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cohort
entropy

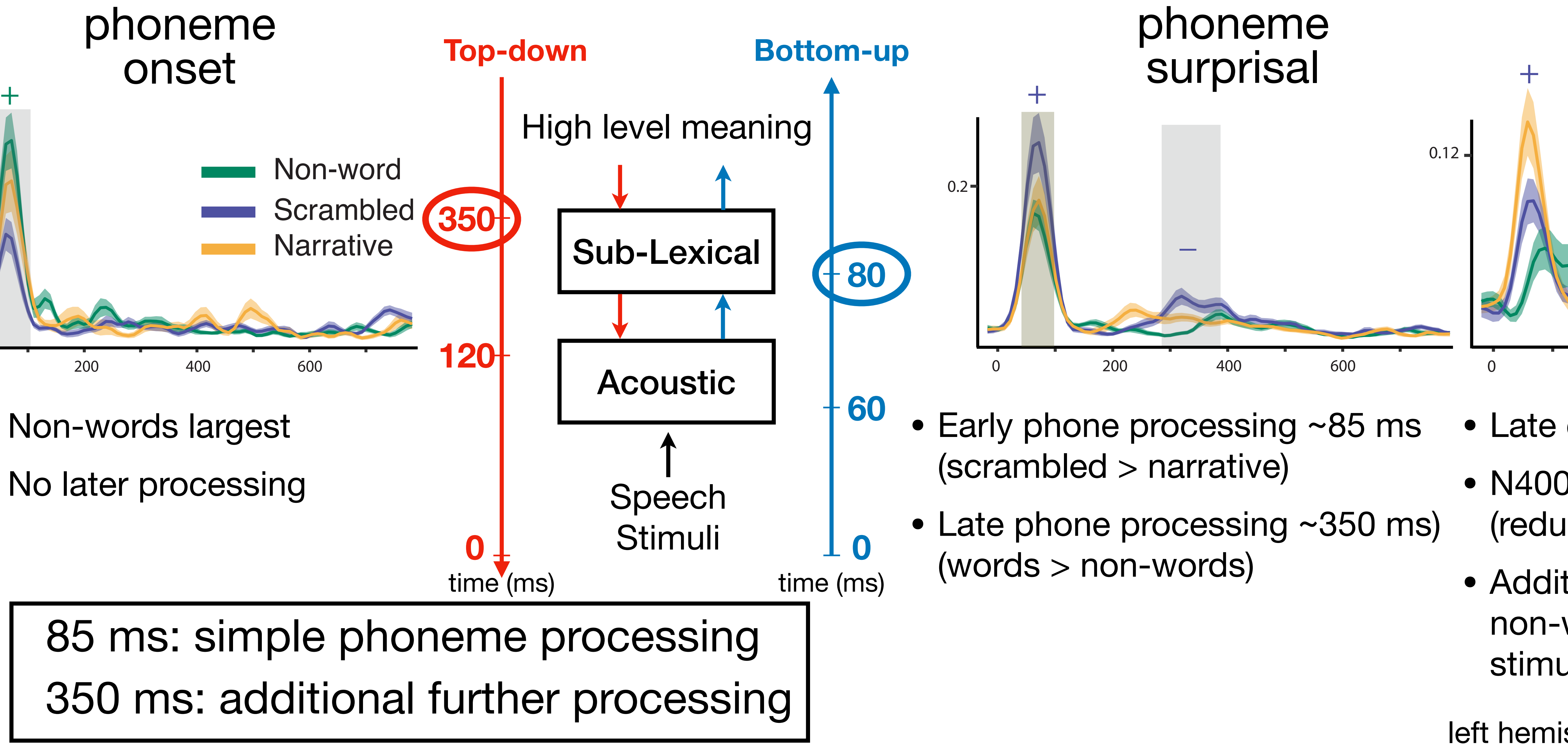


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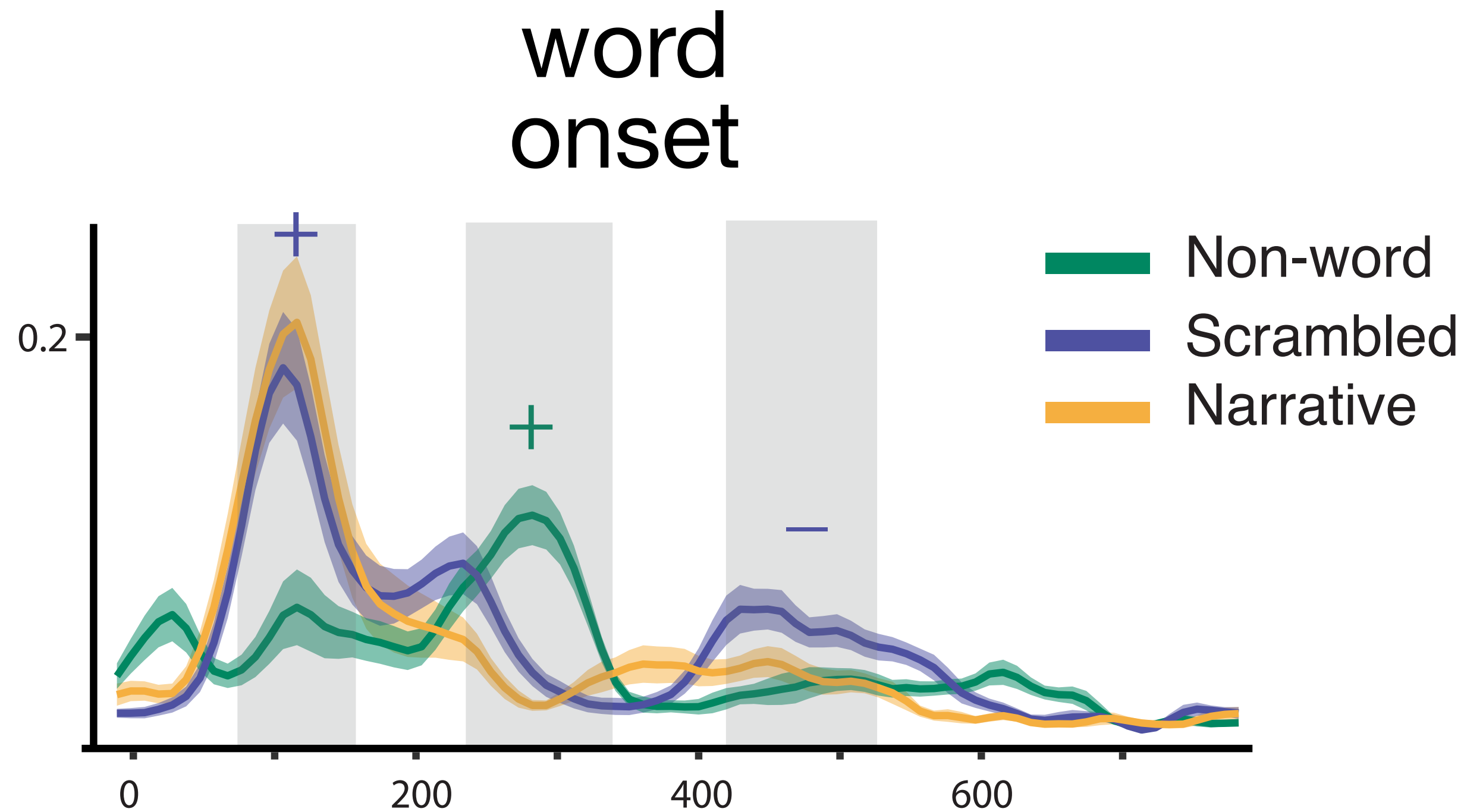
85 ms: simple phoneme processing
350 ms: additional further processing

left hemisphere shown (right similar)

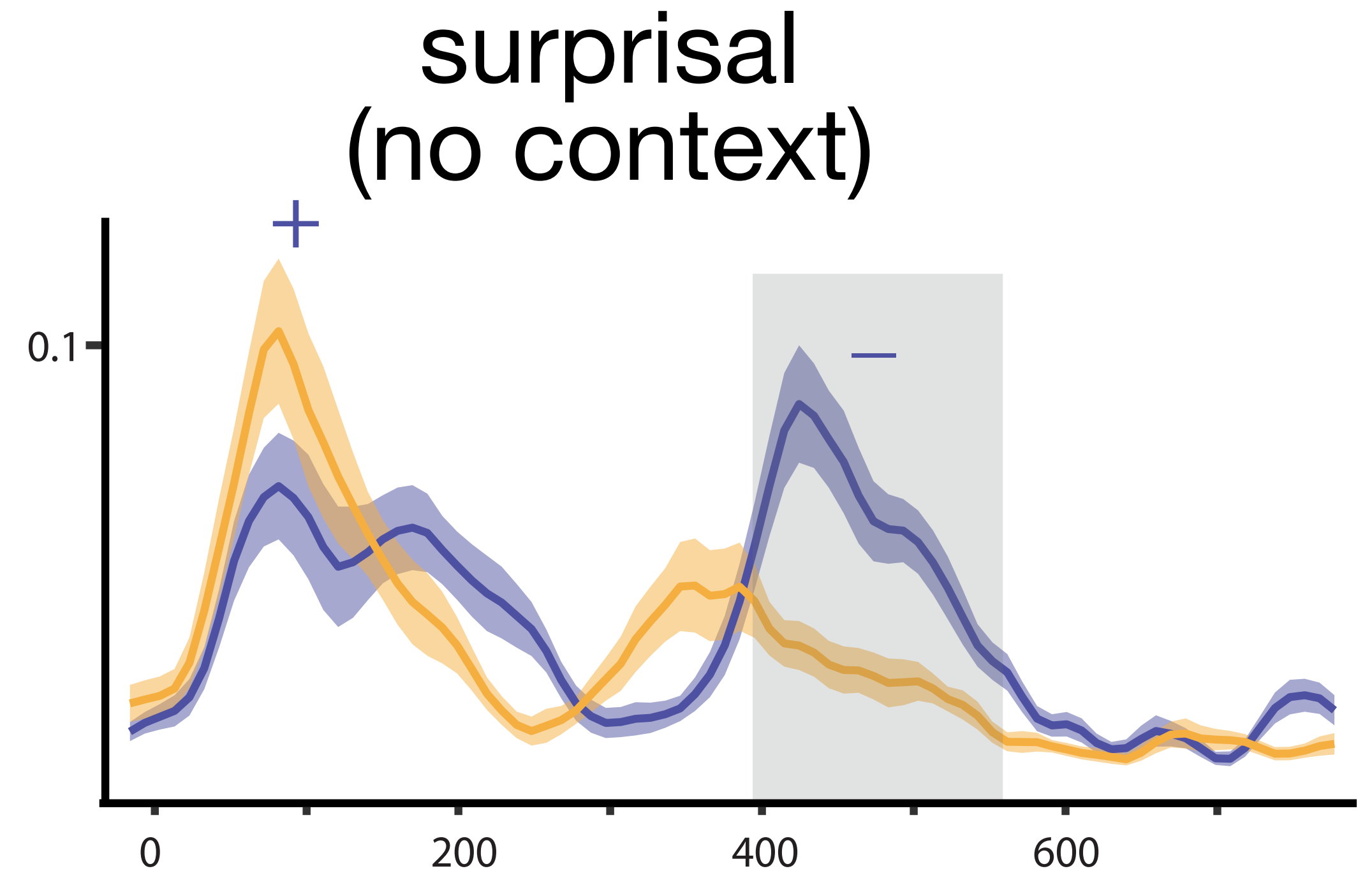
Phonemic TRF Results



Word-based TRF Results



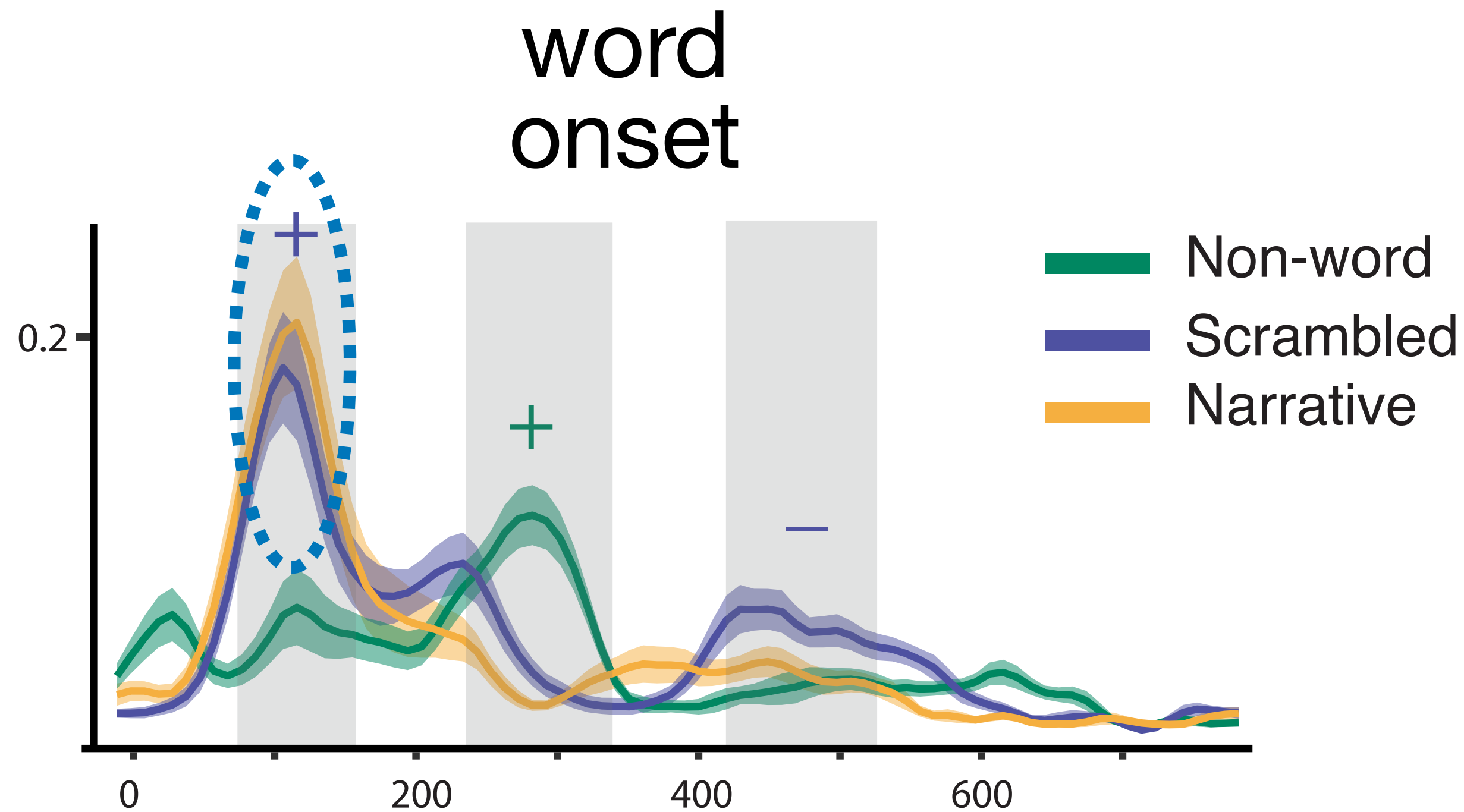
- Scrambled \approx narrative for rapid processing
- Scrambled words $>$ narrative at ~ 450 ms
- words: Left hemi $>$ Right (non-words: L \approx R)



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

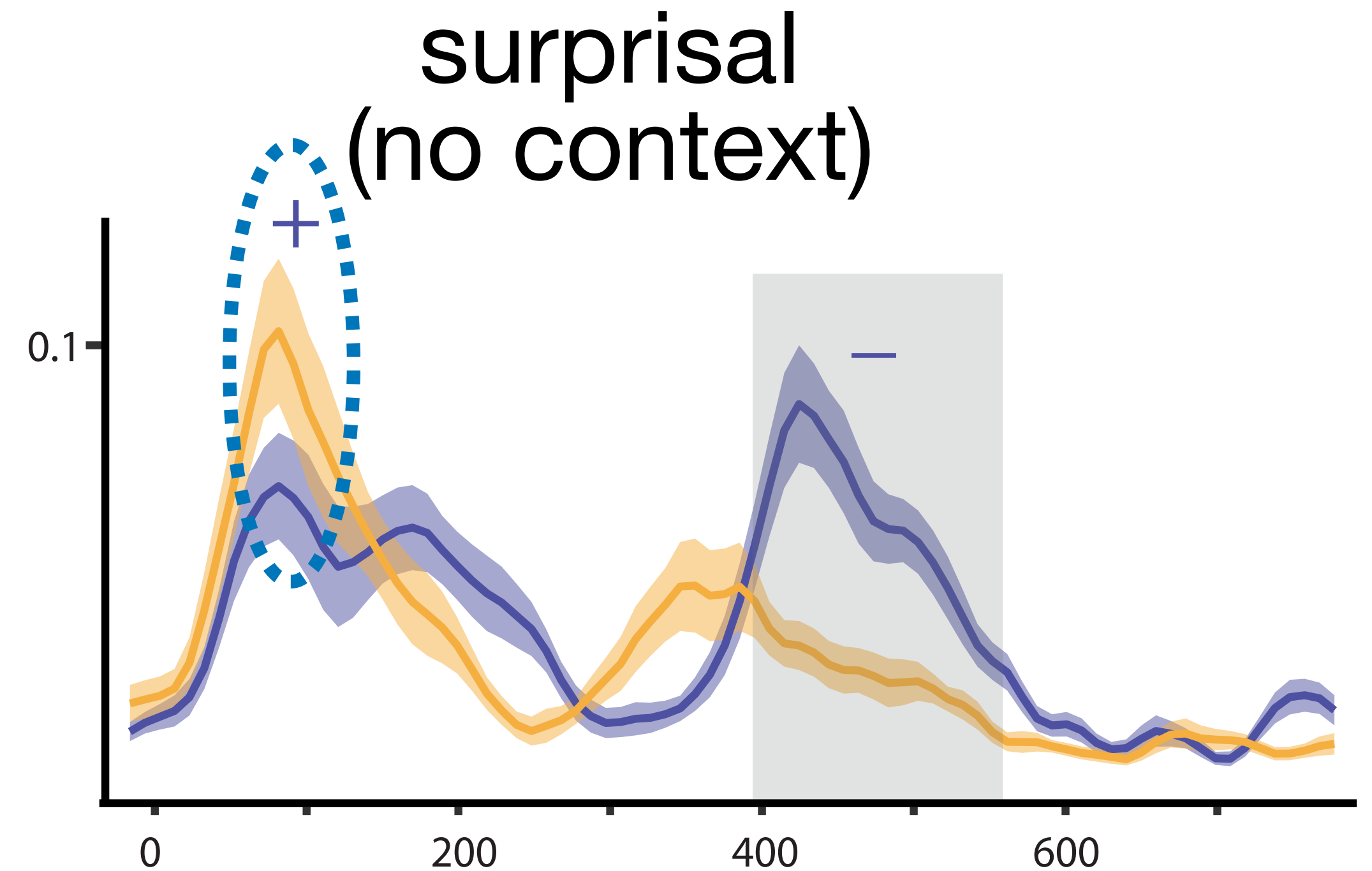
left hemisphere shown
(right much weaker except for non-word onset)

Word-based TRF Results



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100 ms: simple word processing

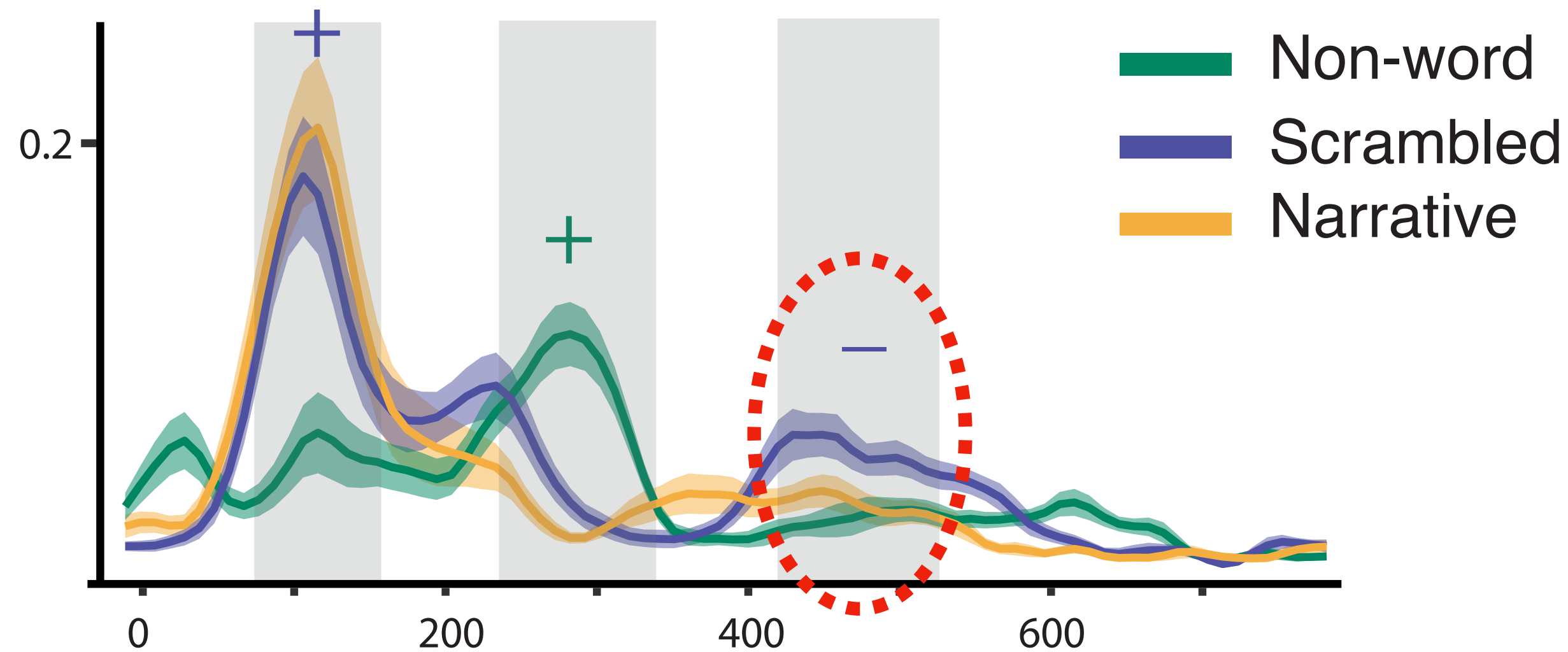


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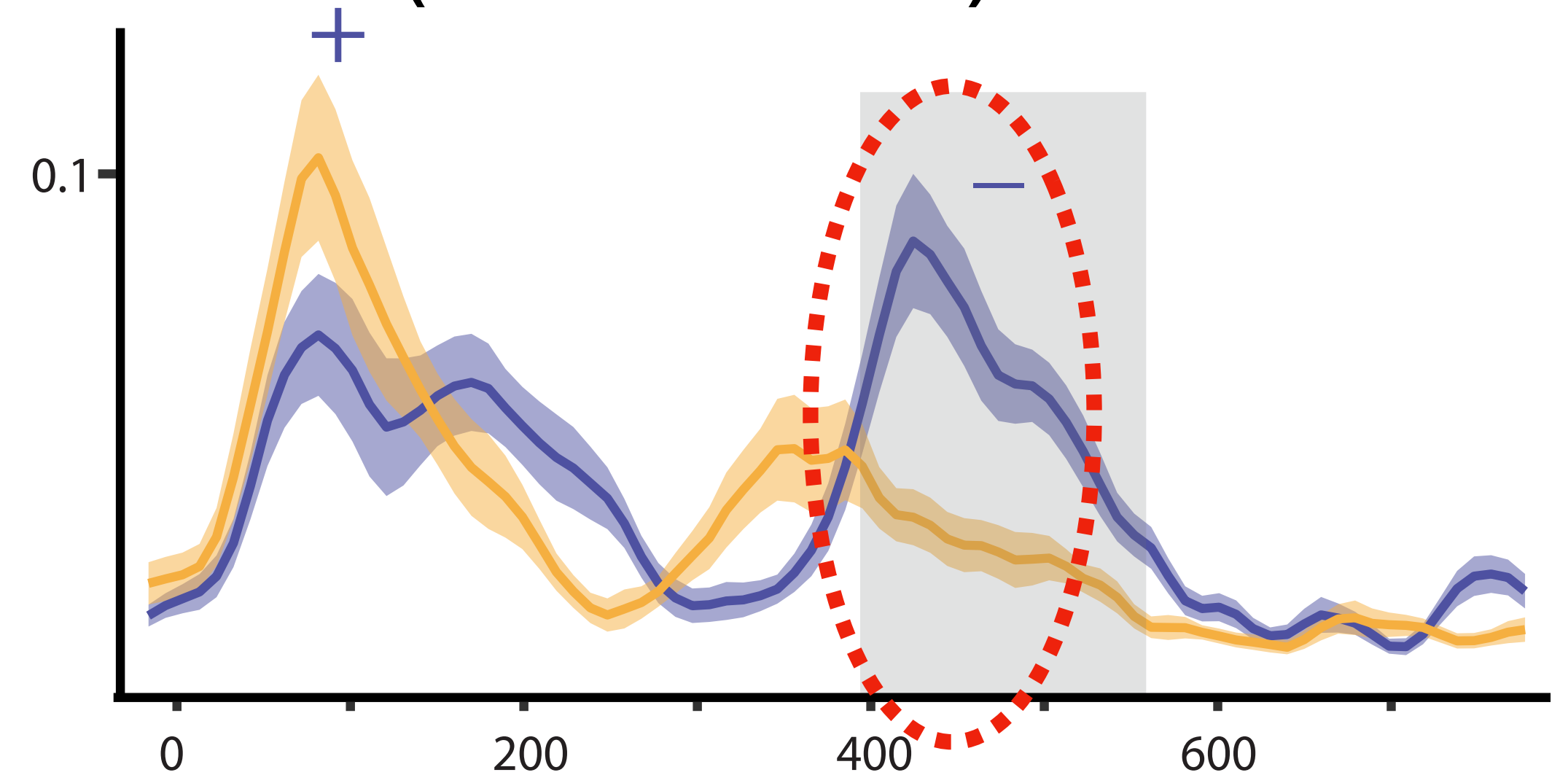
Word-based TRF Results

word
onset



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surprisal
(no context)



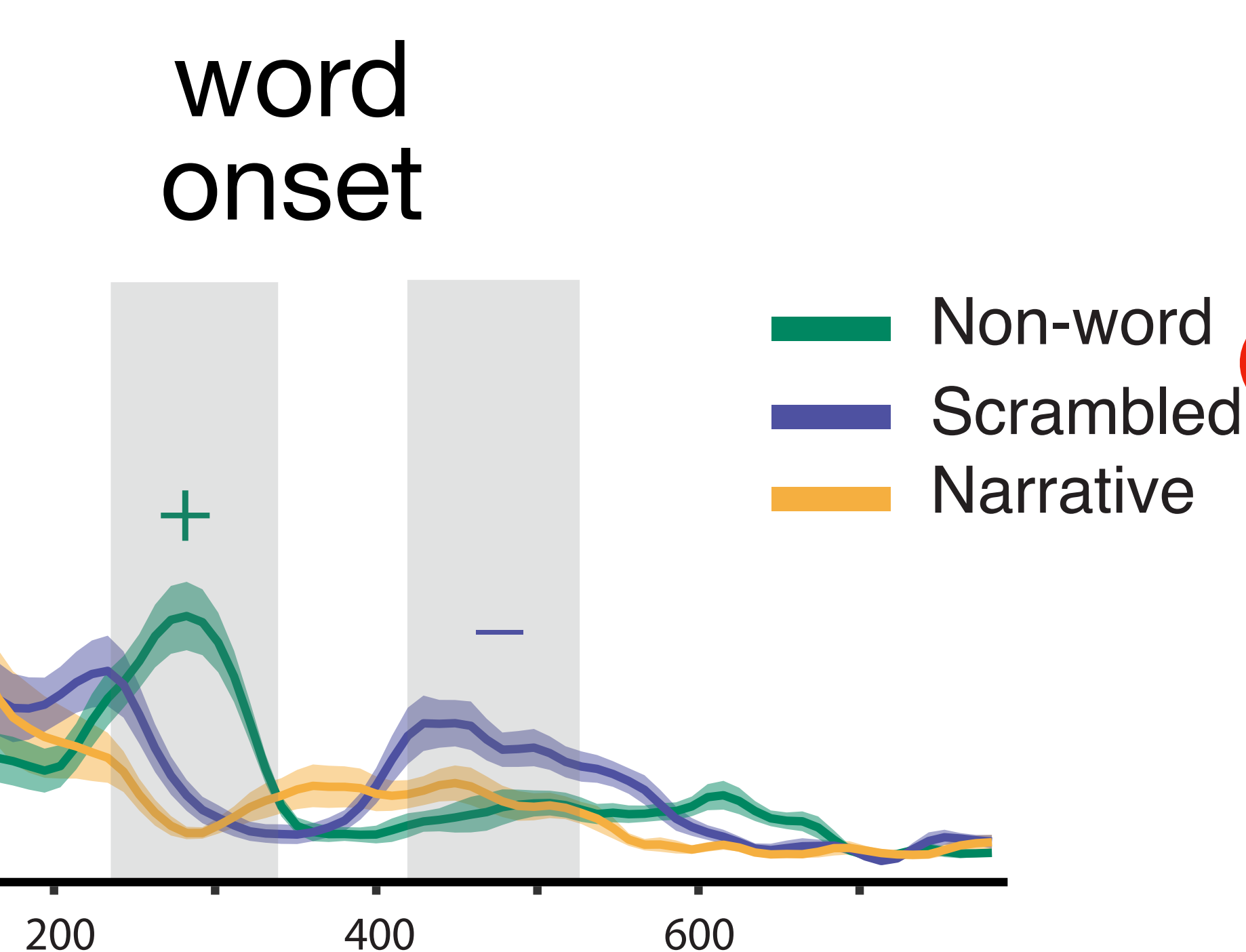
- N400 like response
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- Right hemisphere: Scrambled \approx Narrative

100 ms: simple word processing

450 ms: “error” correction processing

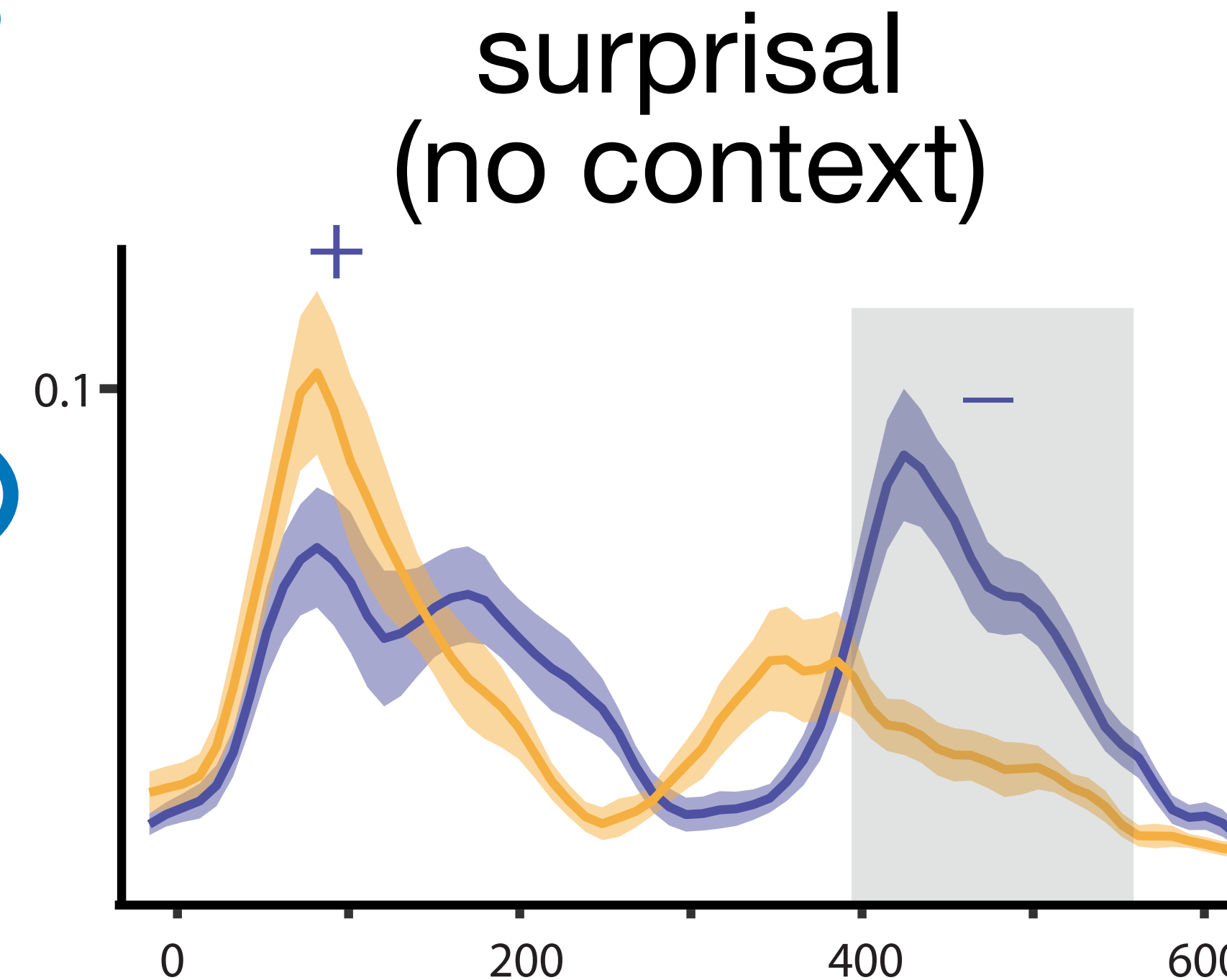
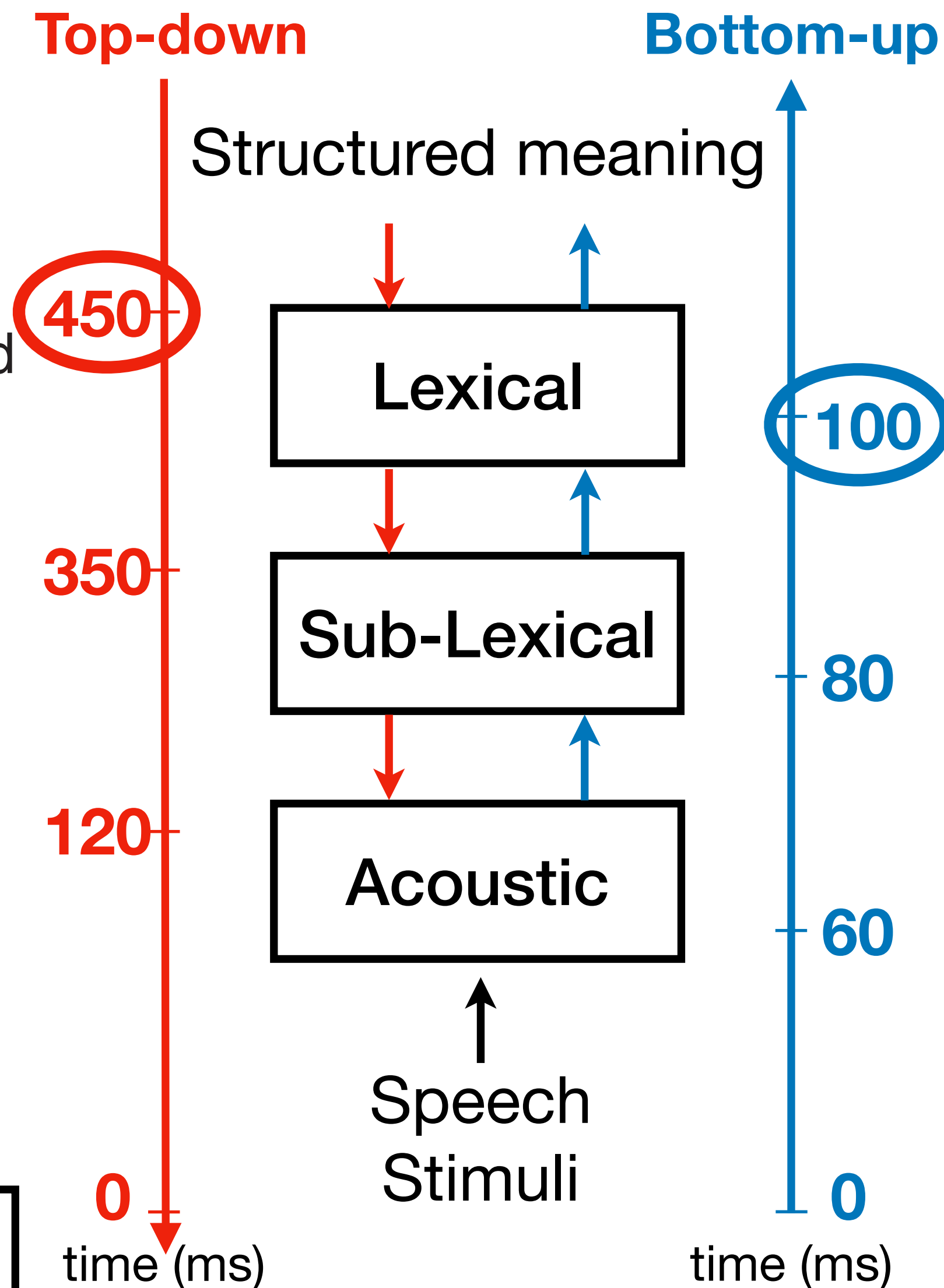
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Word-based TRF Results



ed \approx narrative for rapid processing
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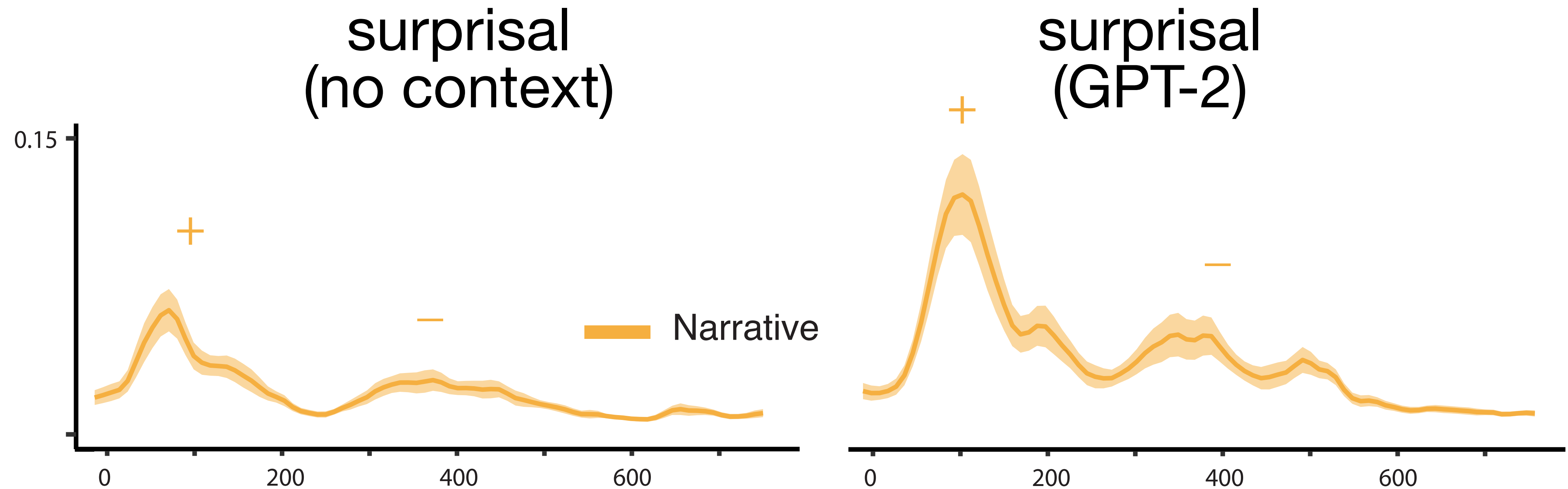
simple word processing
 or" correction processing



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

left hemisphere shown
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Contextual Word Surprisal Results

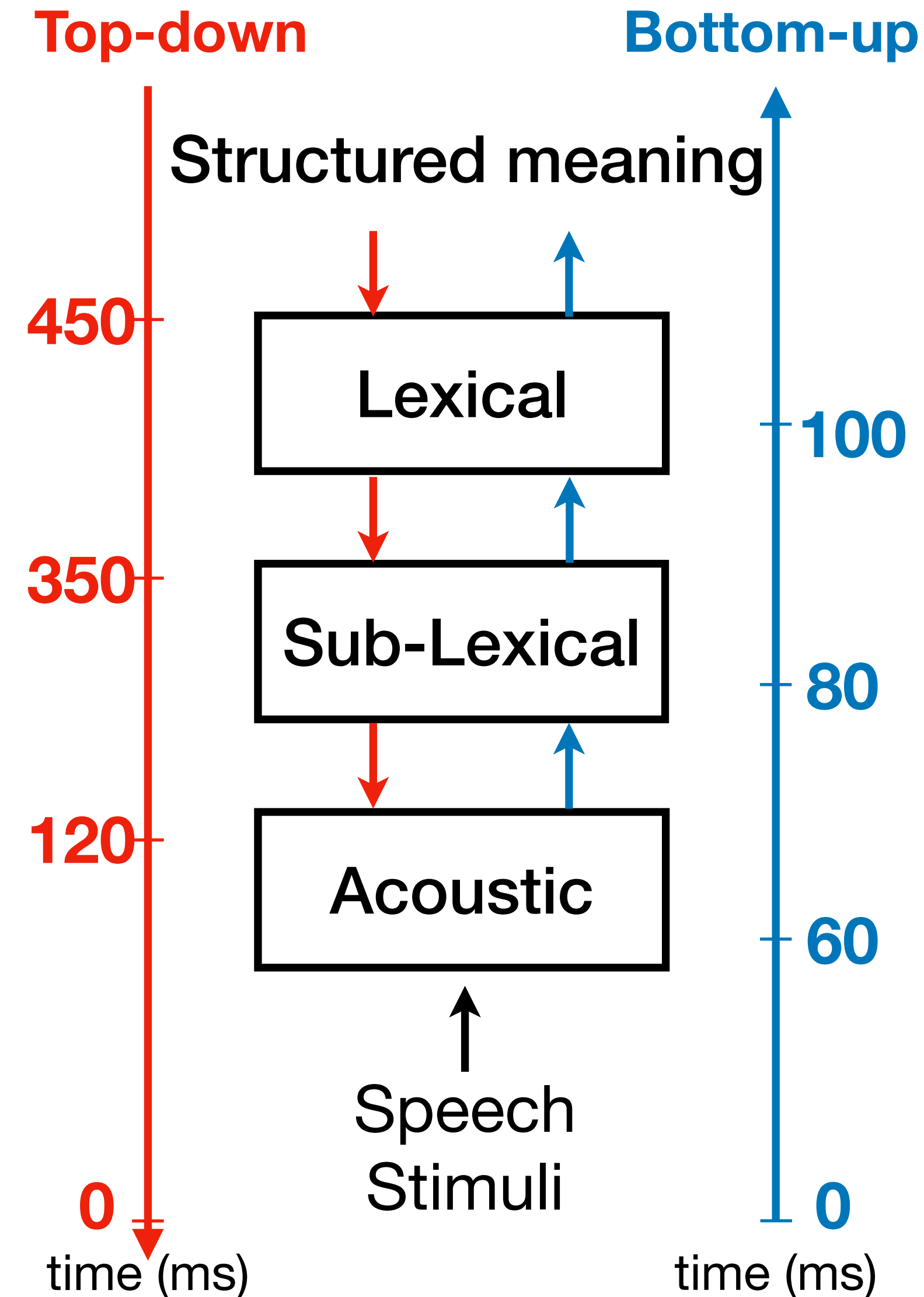


- When context helps, context-based surprisal is better tracked than raw surprisal
- N400 like response in both predictors

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



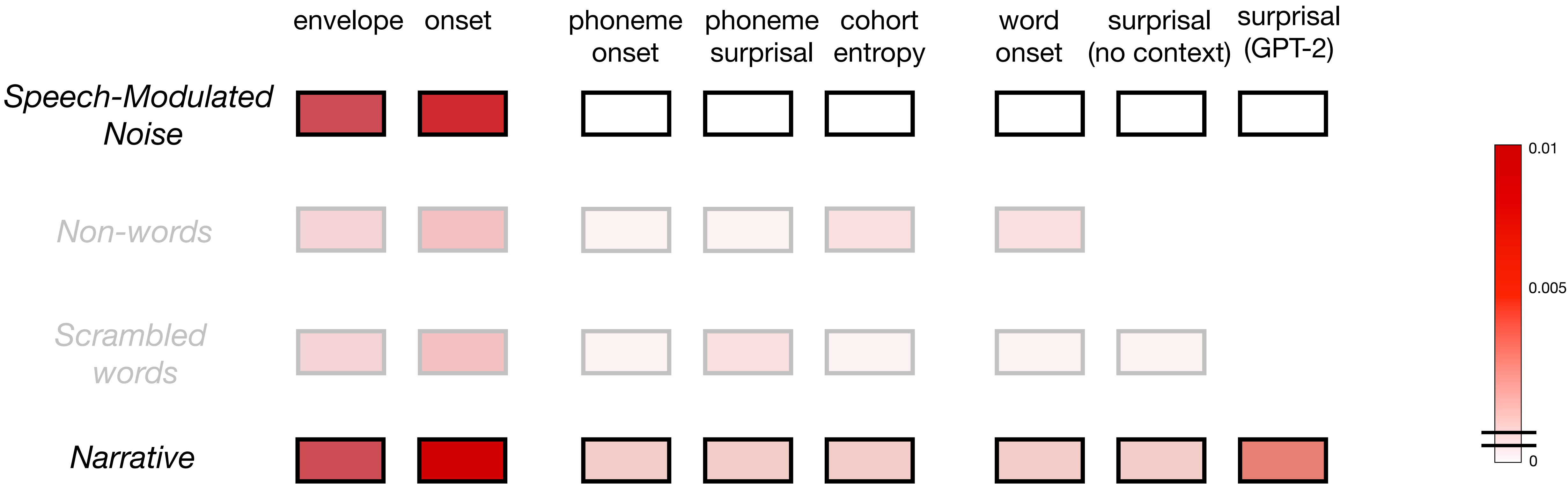
Outline

- 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

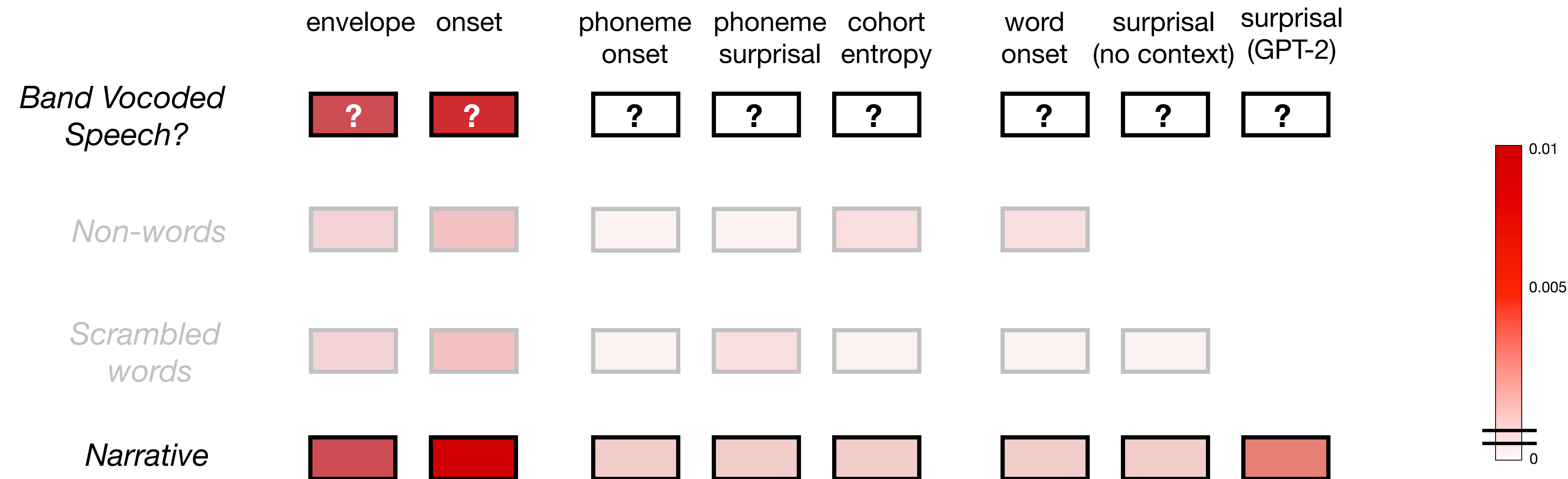
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Previous Neural Prediction Results

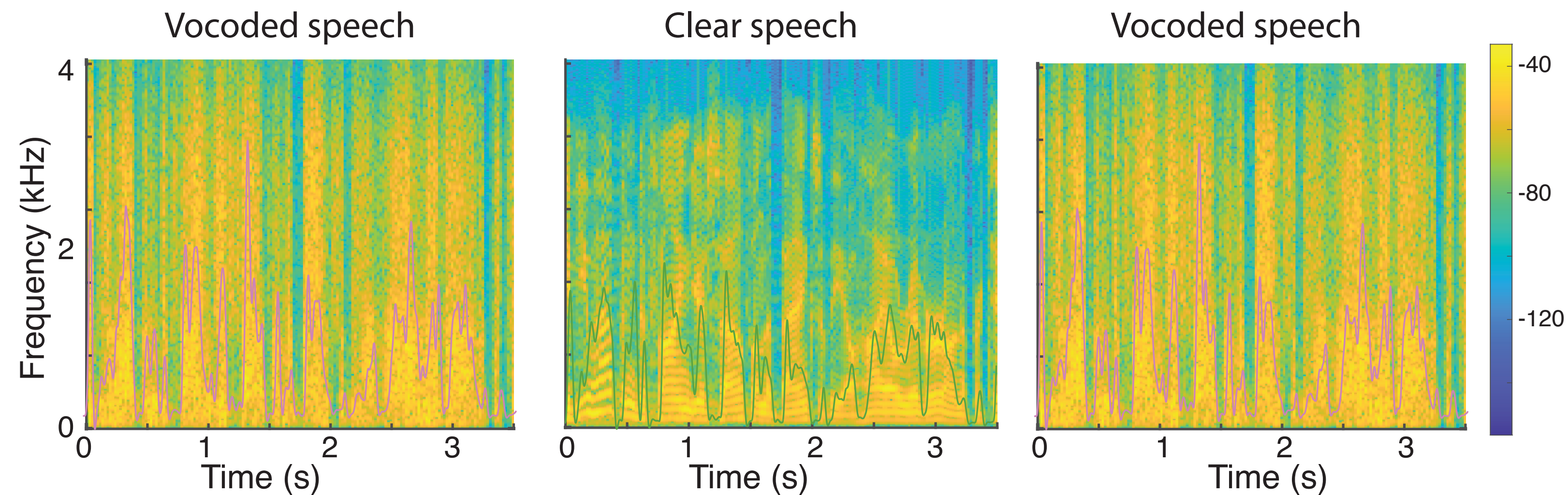
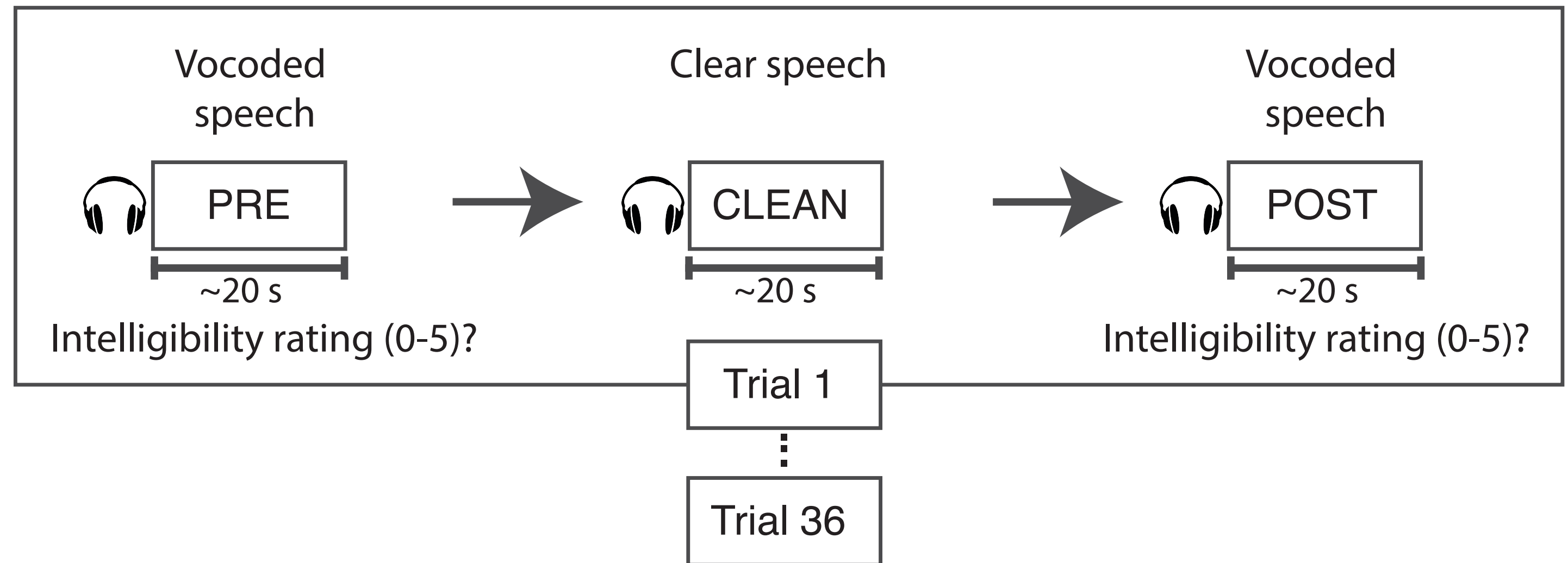


Possible Neural Prediction Results



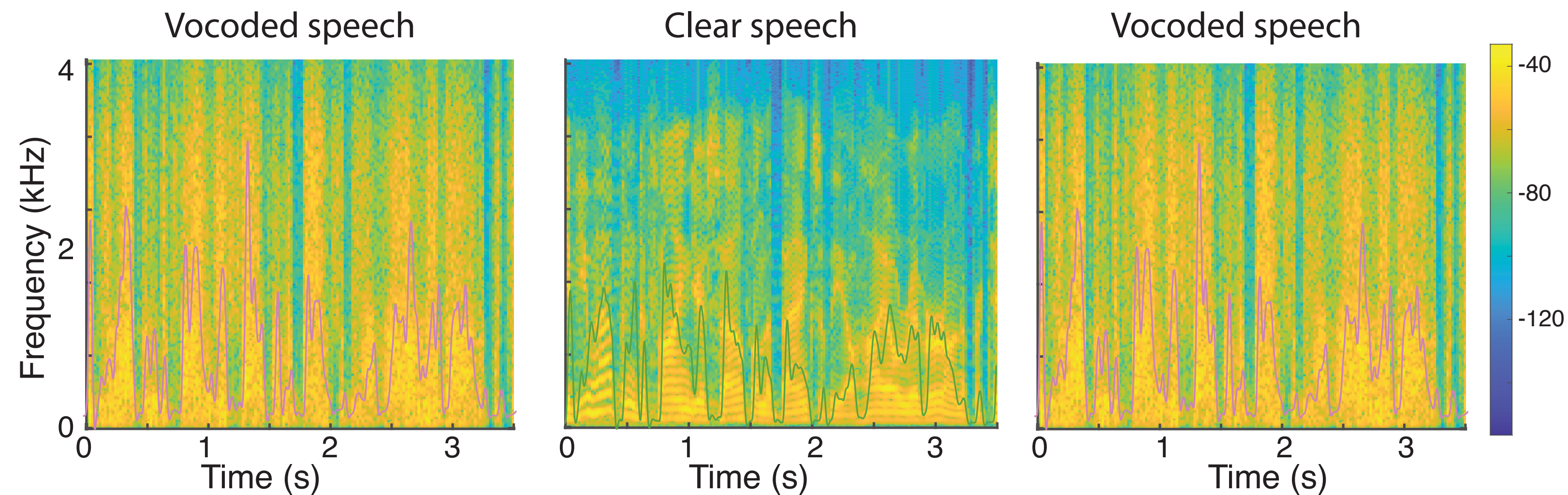
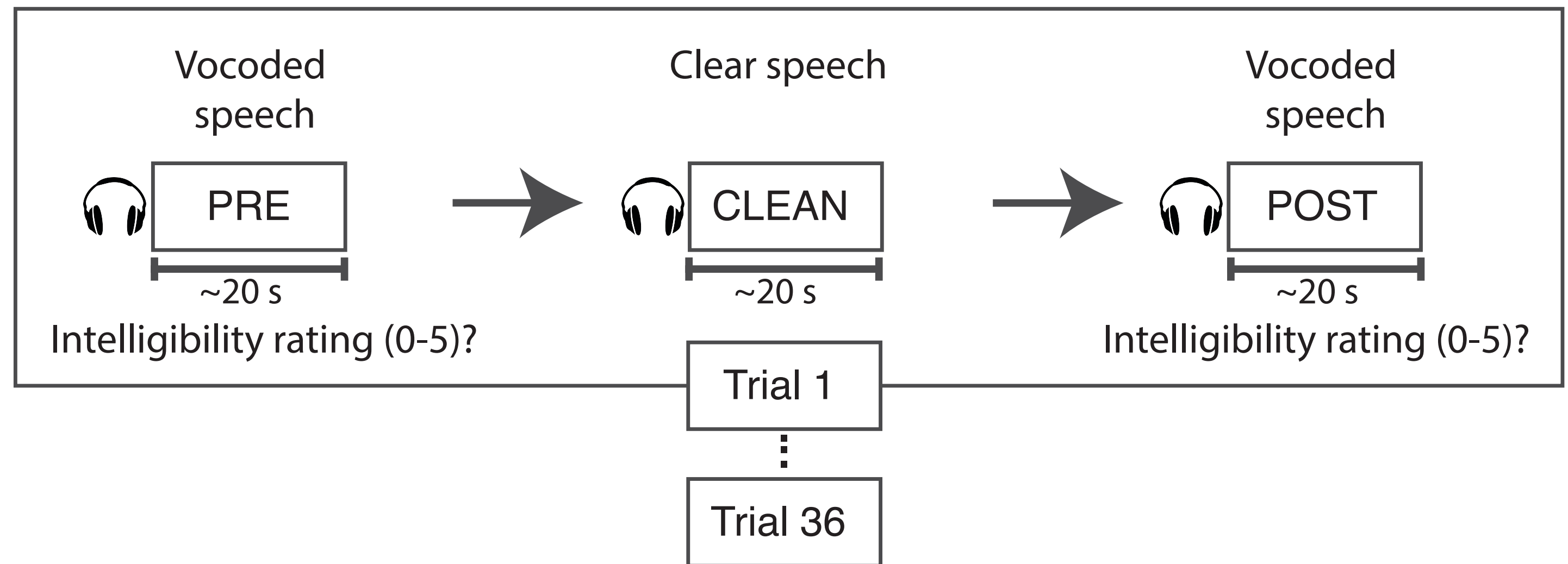
Intelligibility Experimental Design

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



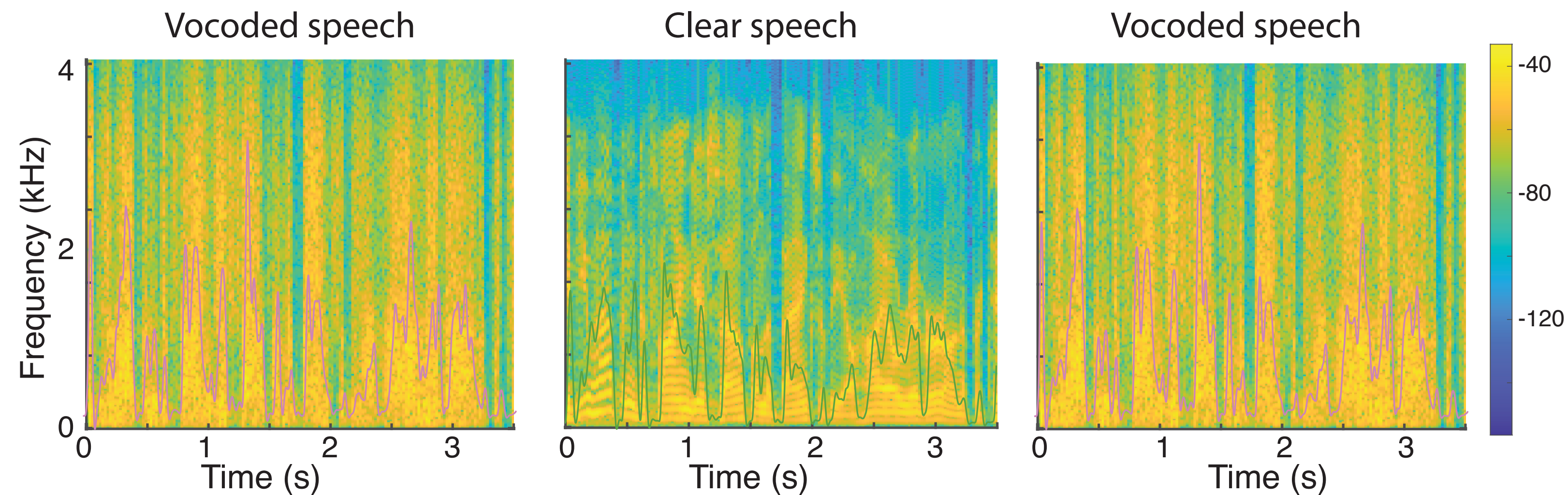
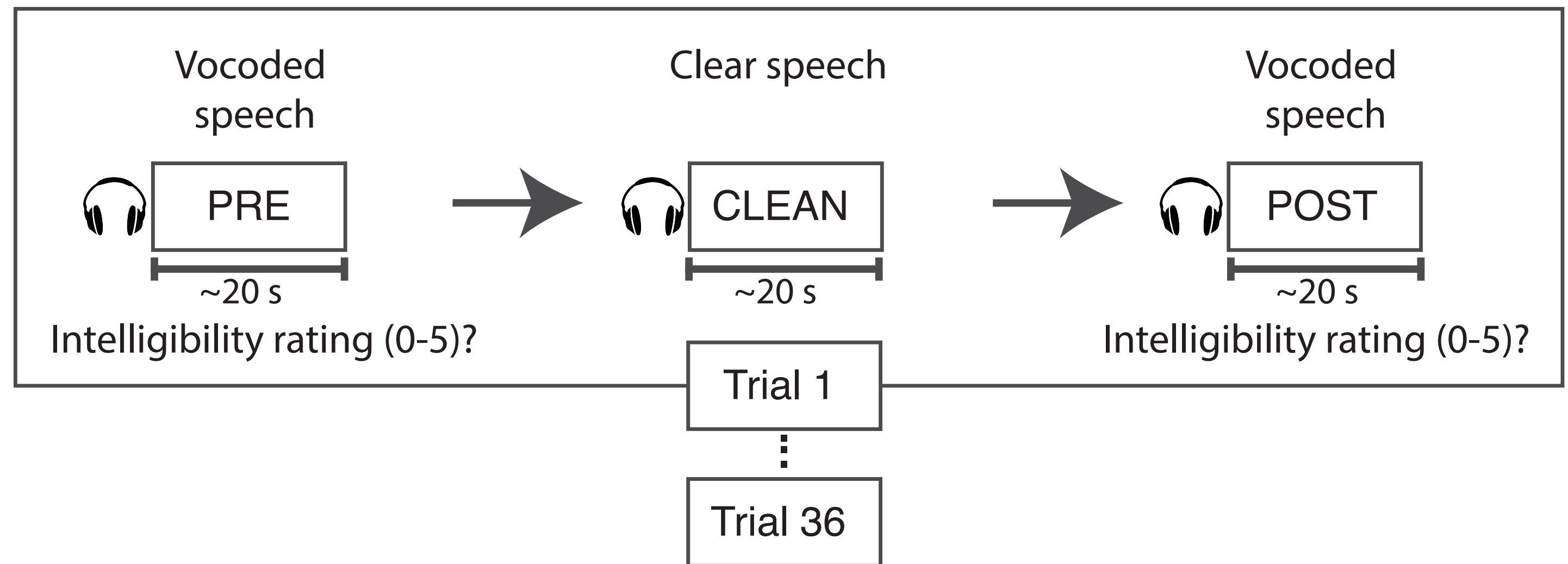
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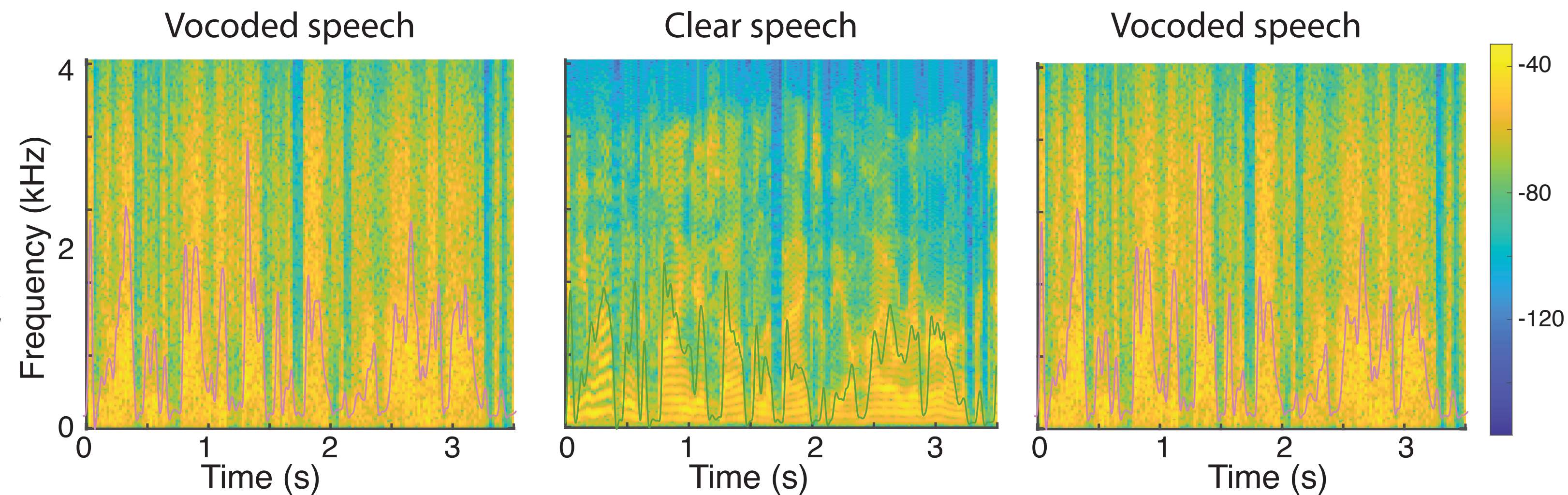
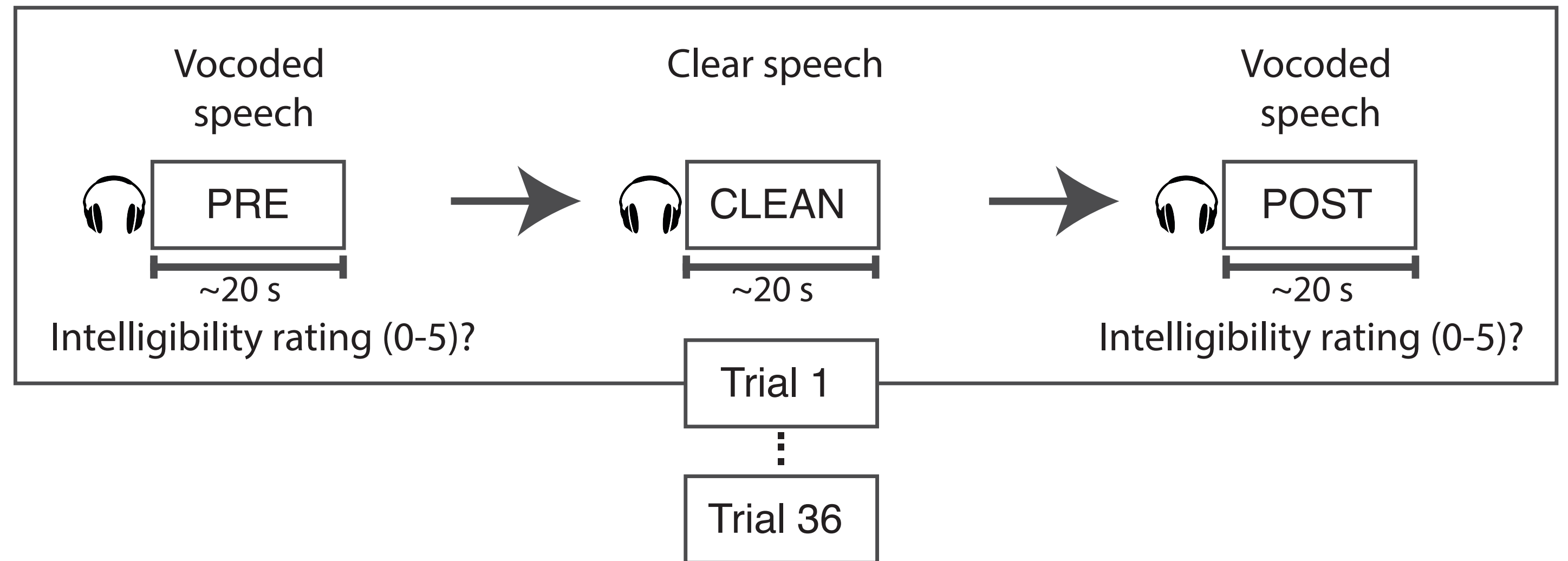
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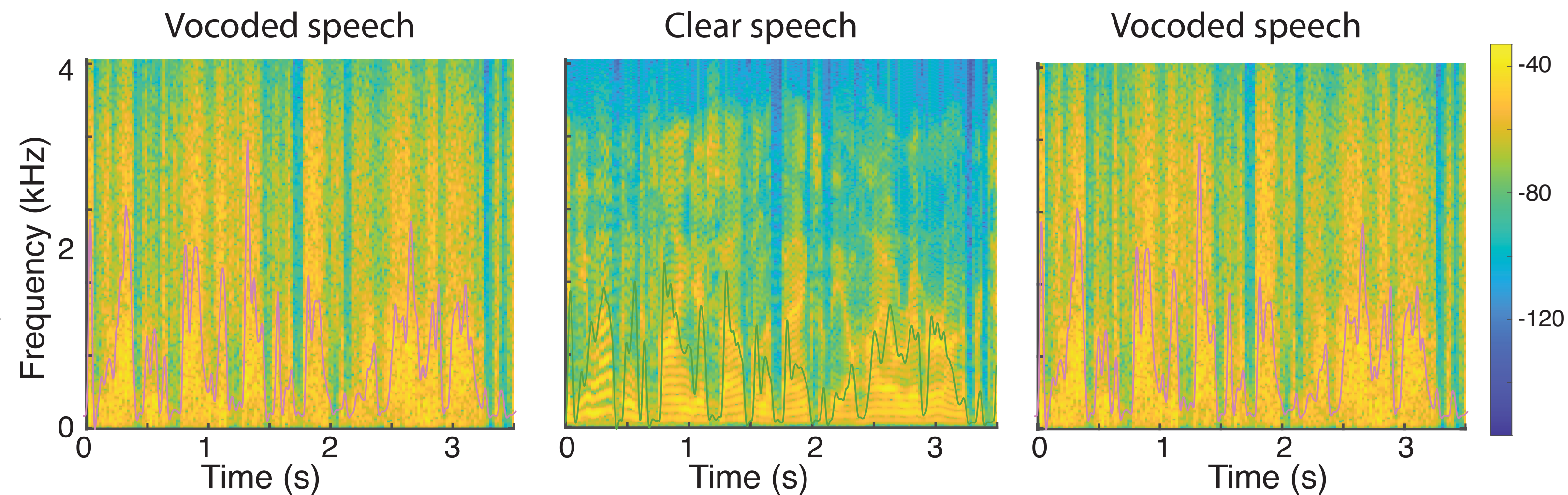
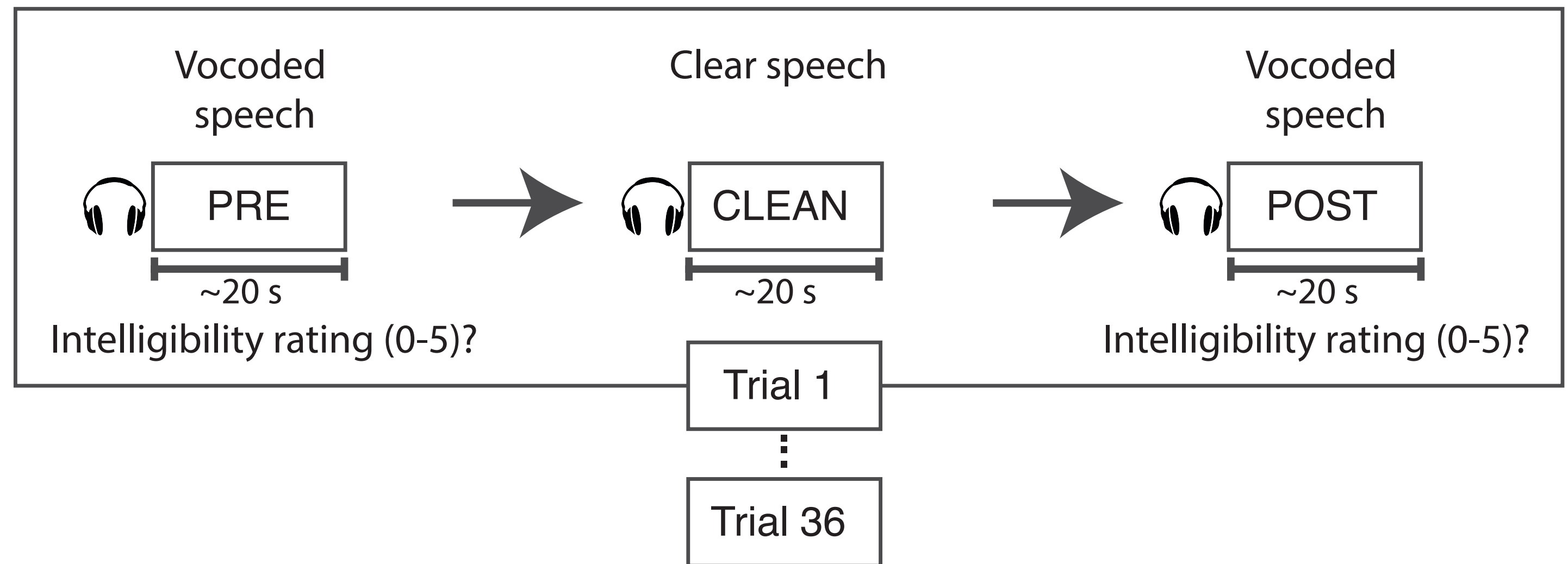


“Slice an apple through at its equator, and you will find five small chambers arrayed in a perfectly symmetrical starburst—a pentagram.”

Karunathilake et al. *in preparation*

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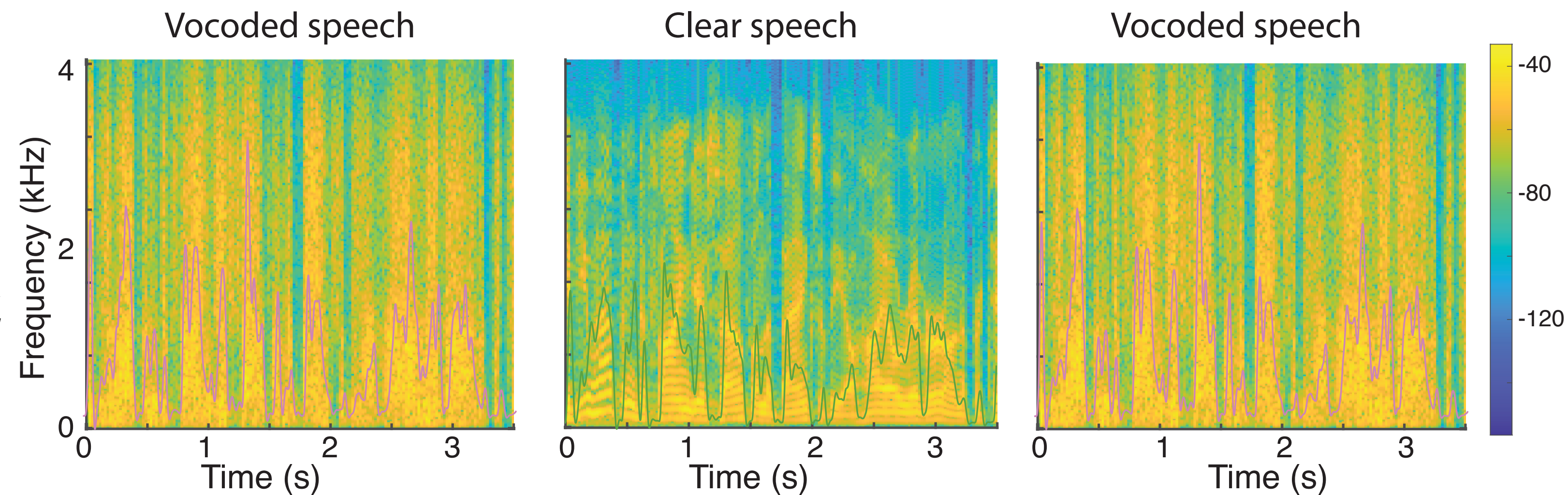
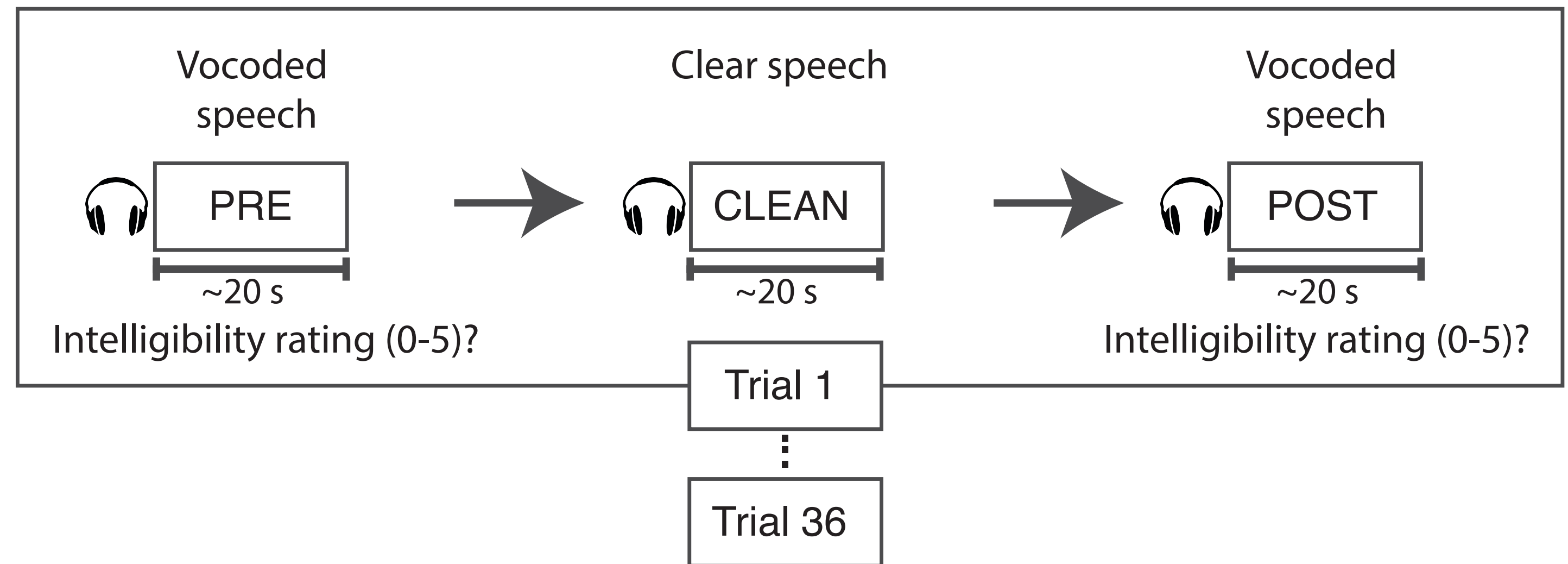


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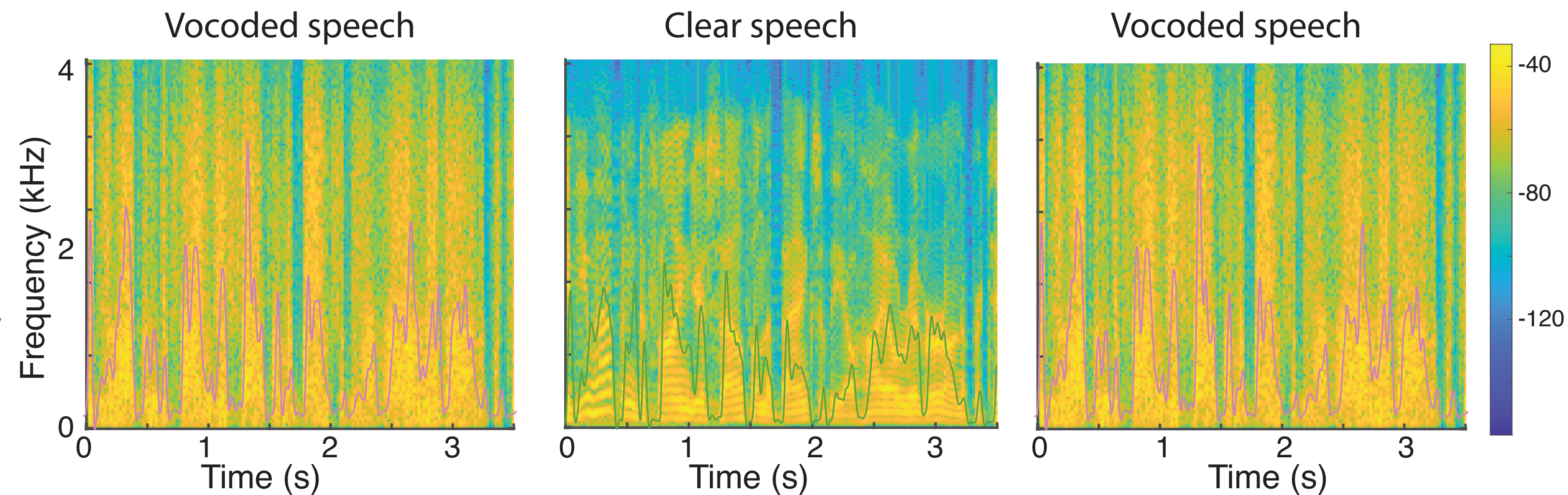
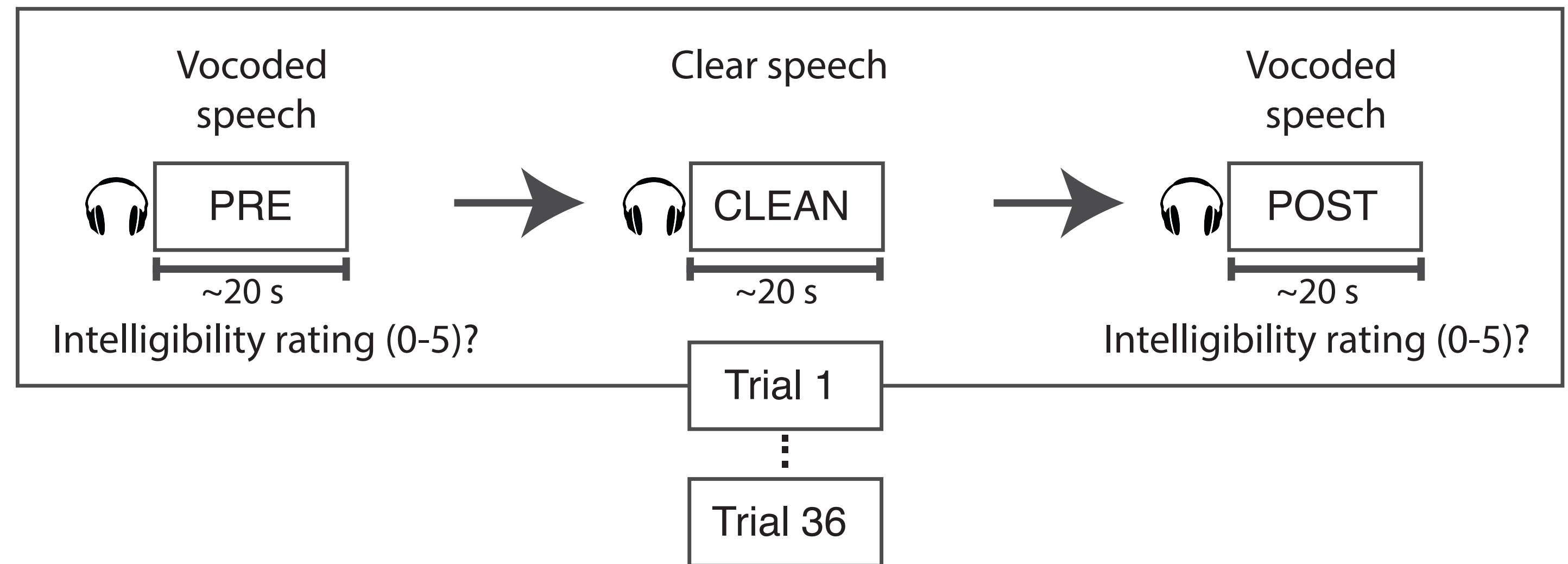


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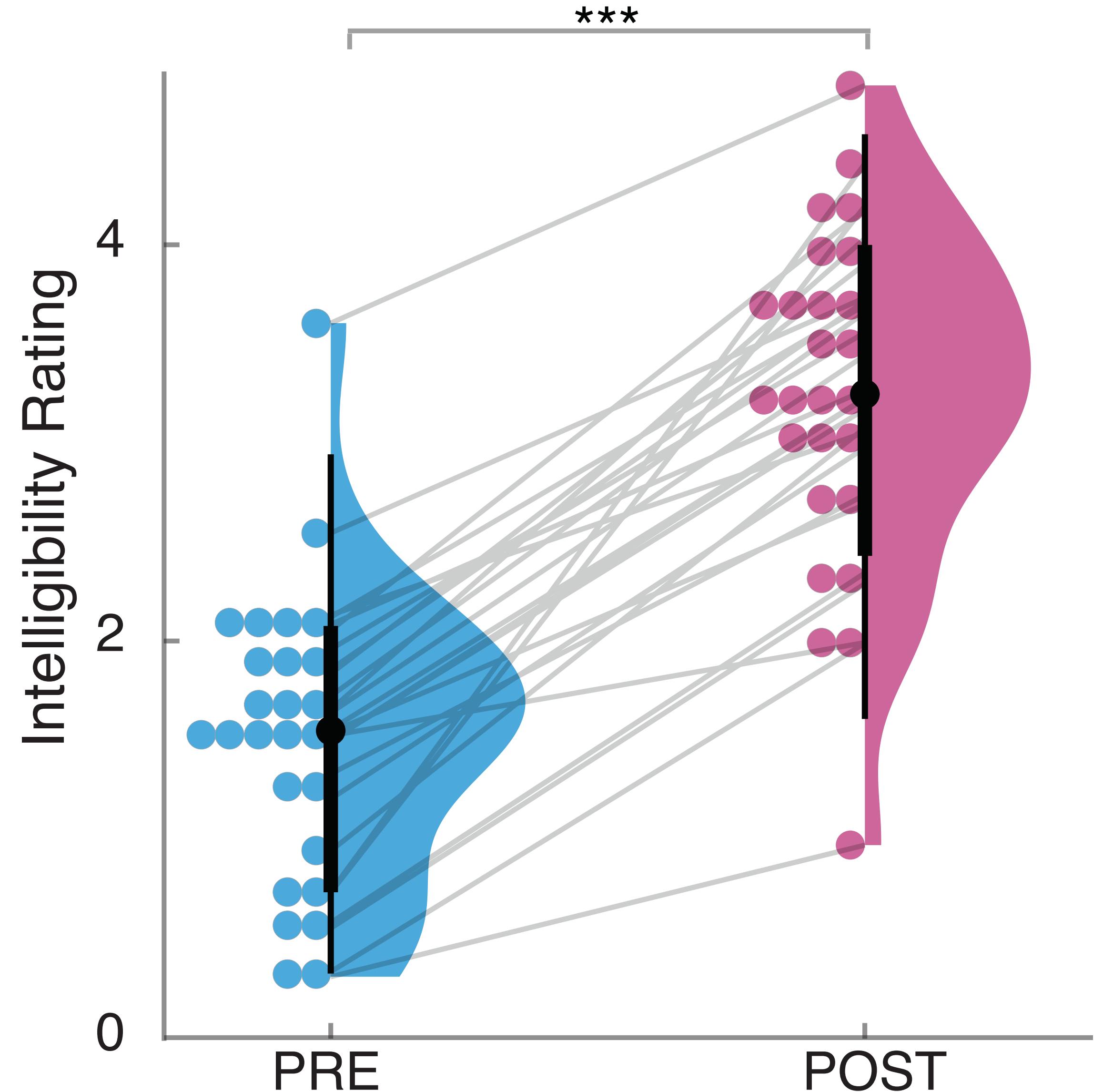


“Slice an apple through at its equator, and you will find five small chambers arrayed in a perfectly symmetrical starburst—a pentagram.”

Karunathilake et al. *in preparation*

Intelligibility Behavioral Results

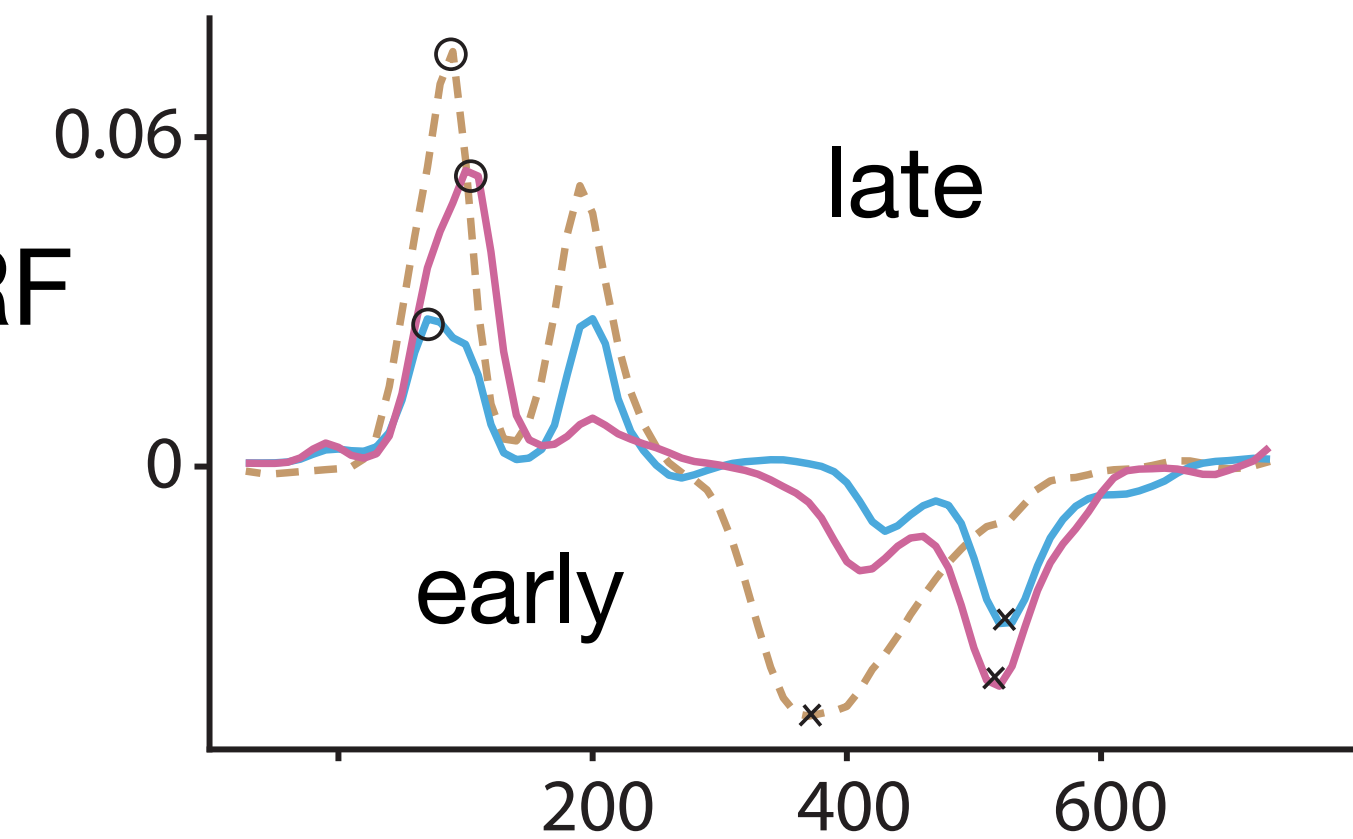
Intelligibility rating **increases**
from PRE condition
to POST condition



Intelligibility Neural Results

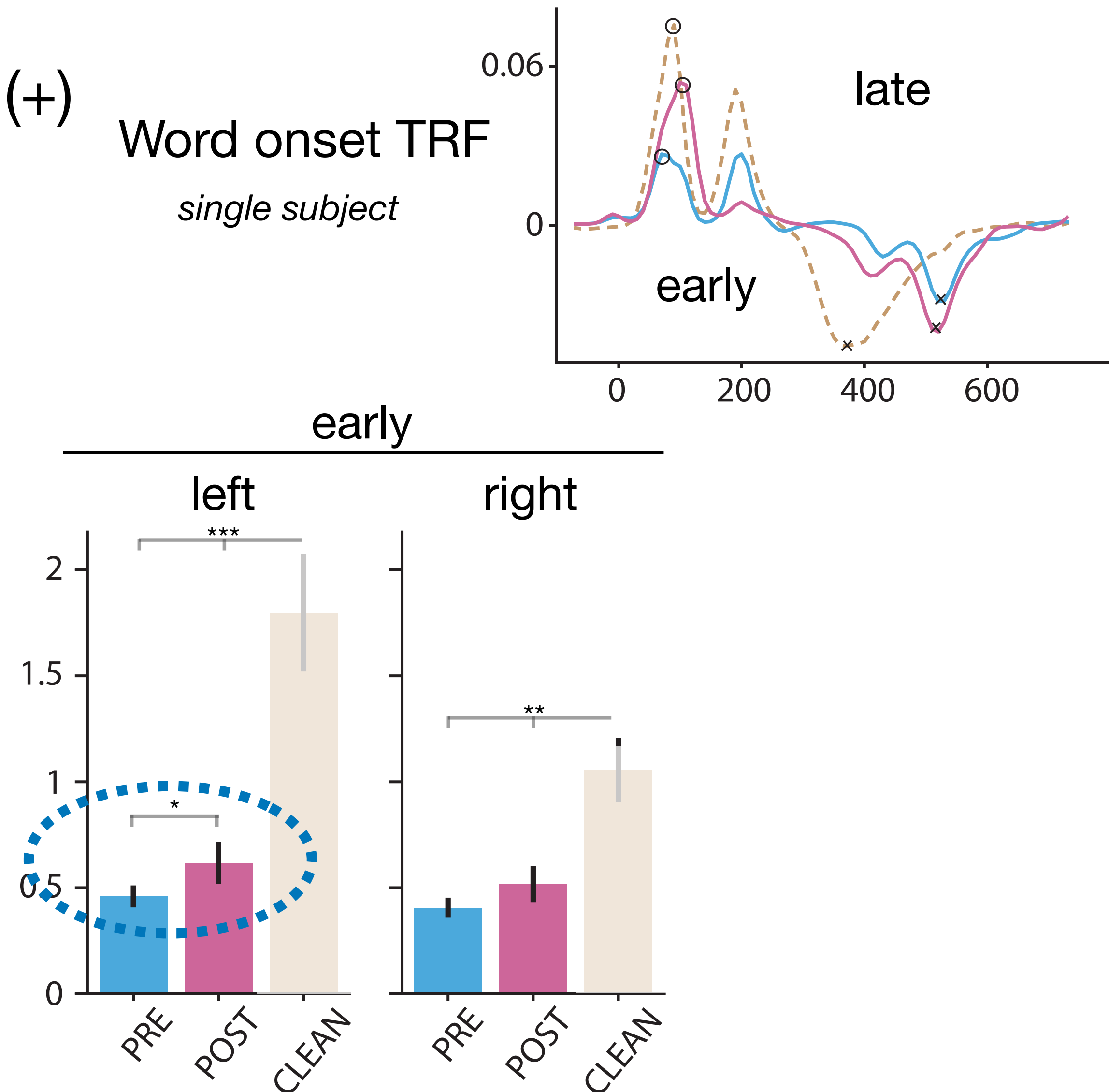
- Word onset TRF shows both early (+) and late (-) processing stages

Word onset TRF
single subject



Intelligibility Neural Results

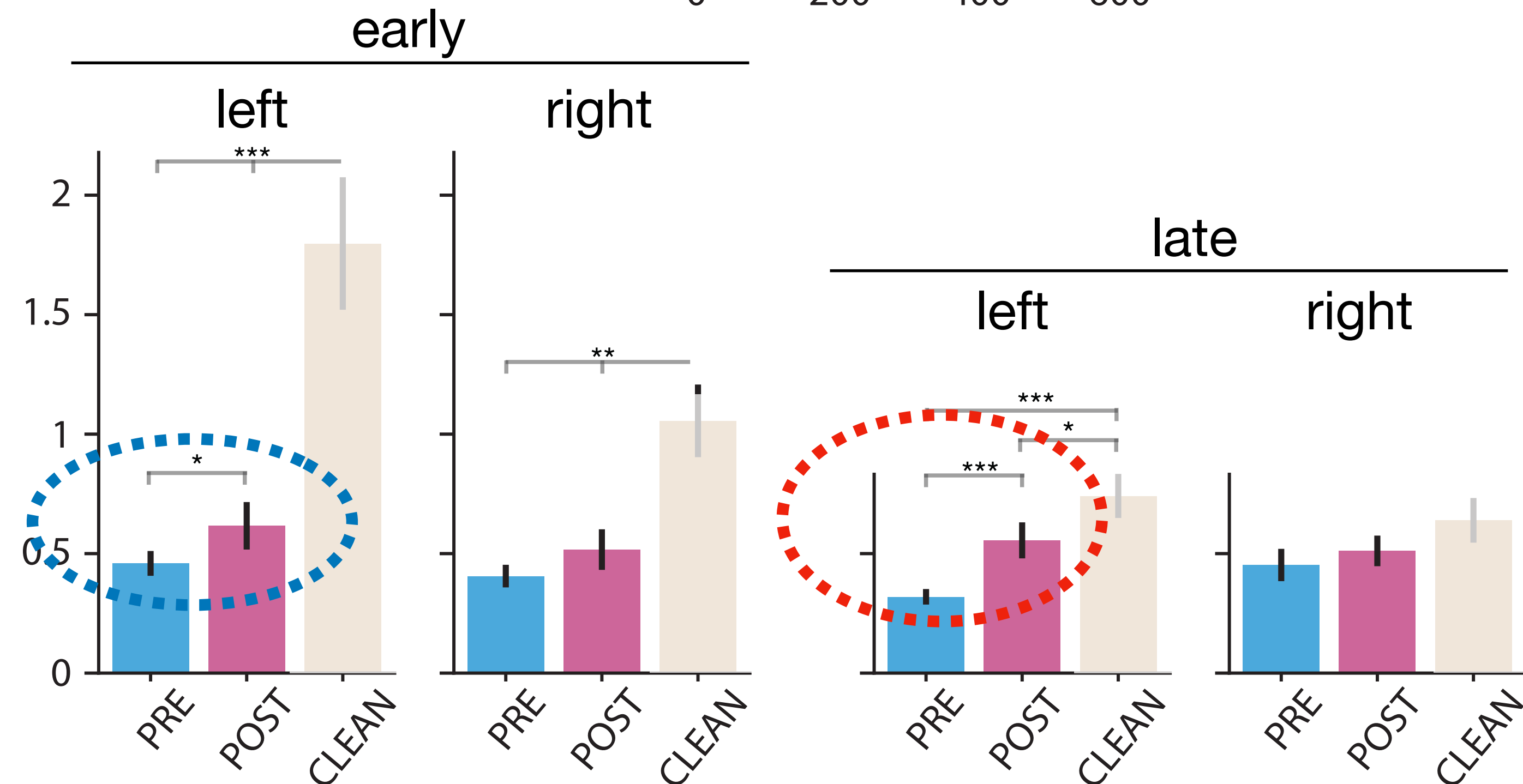
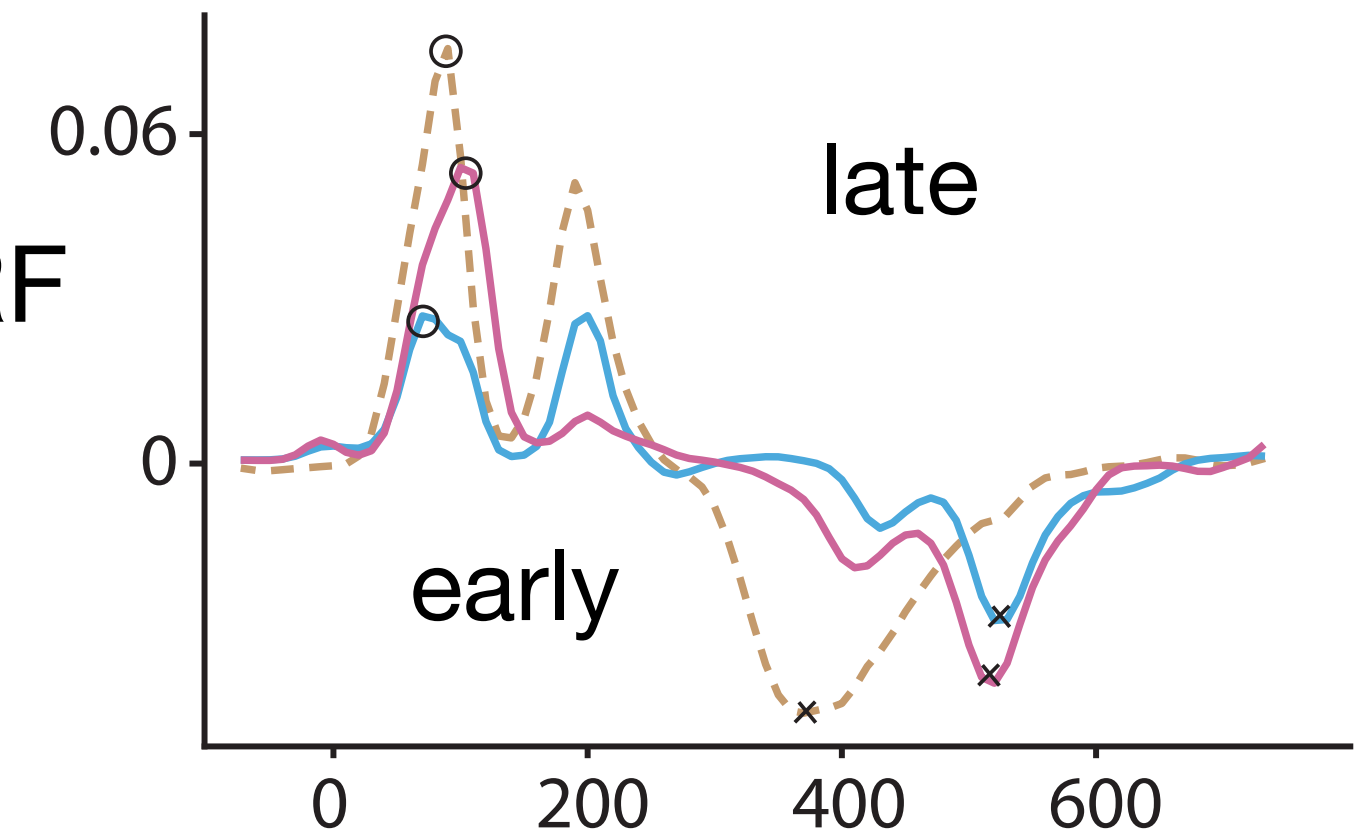
- Word onset TRF shows both early (+) and late (-) processing stages
- Response increases Pre→Post
 - Only in left hemisphere



Intelligibility Neural Results

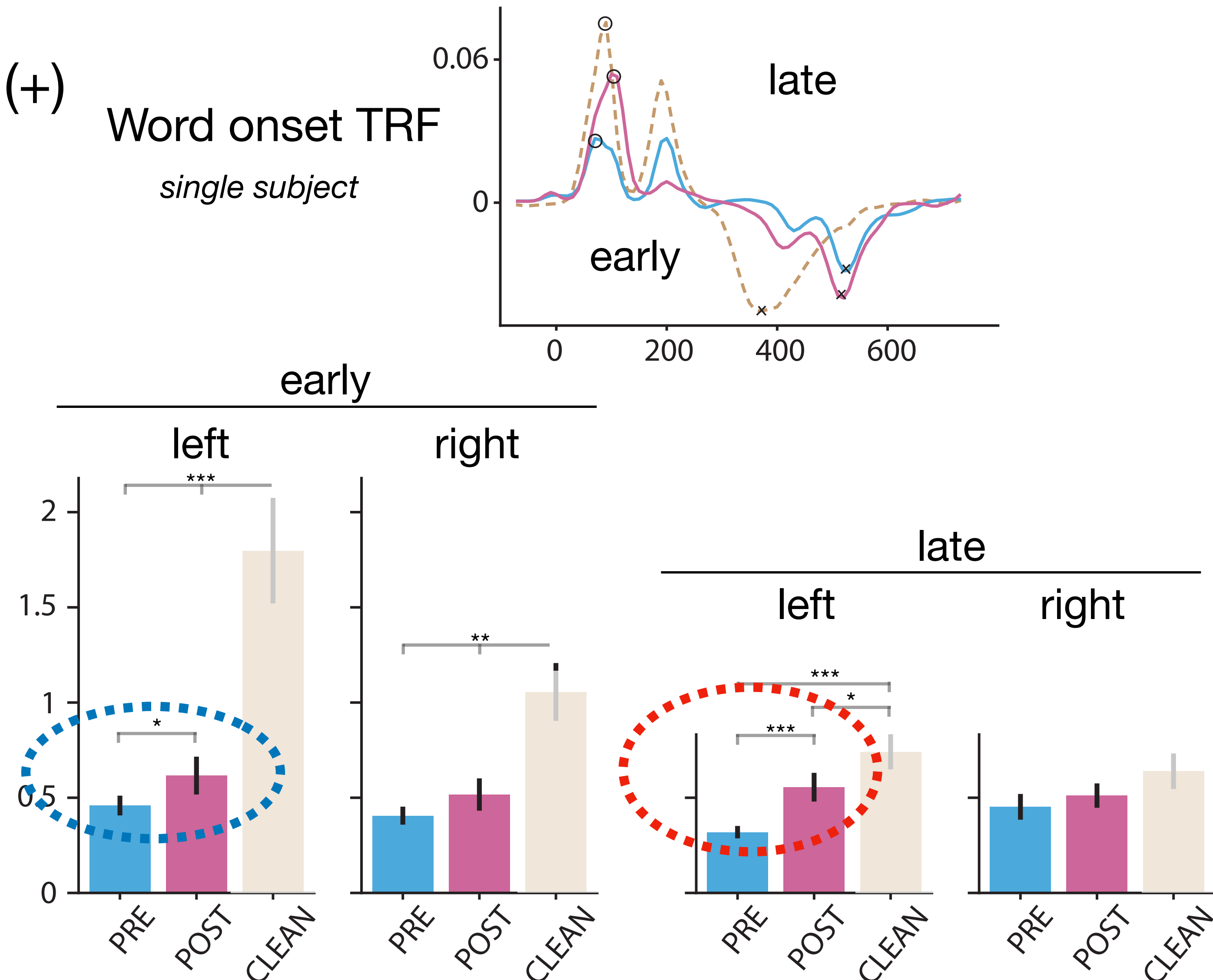
- Word onset TRF shows both early (+) and late (-) processing stages
- Response increases Pre→Post
 - Only in left hemisphere
 - Late processing stage shows larger change than early

Word onset TRF
single subject



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



Outline

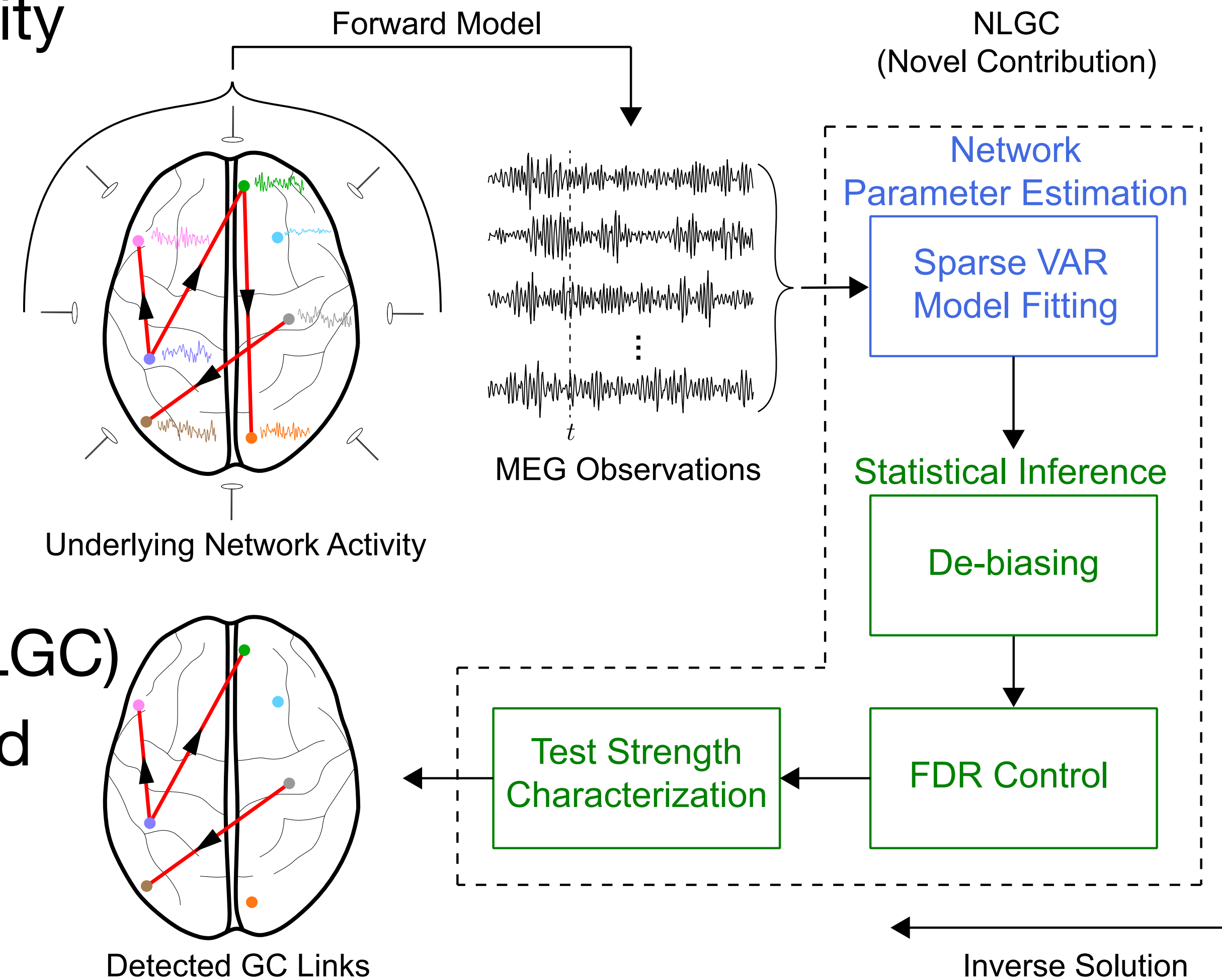
- Introduction—Cortical representations of continuous speech
- *Early & fast* cortical representation of continuous speech
- Cortical representations of speech *meaning*
- *Progression* of representations of continuous speech through cortex (bottom-up and top-down)
- **Objective measures of speech *intelligibility***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

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

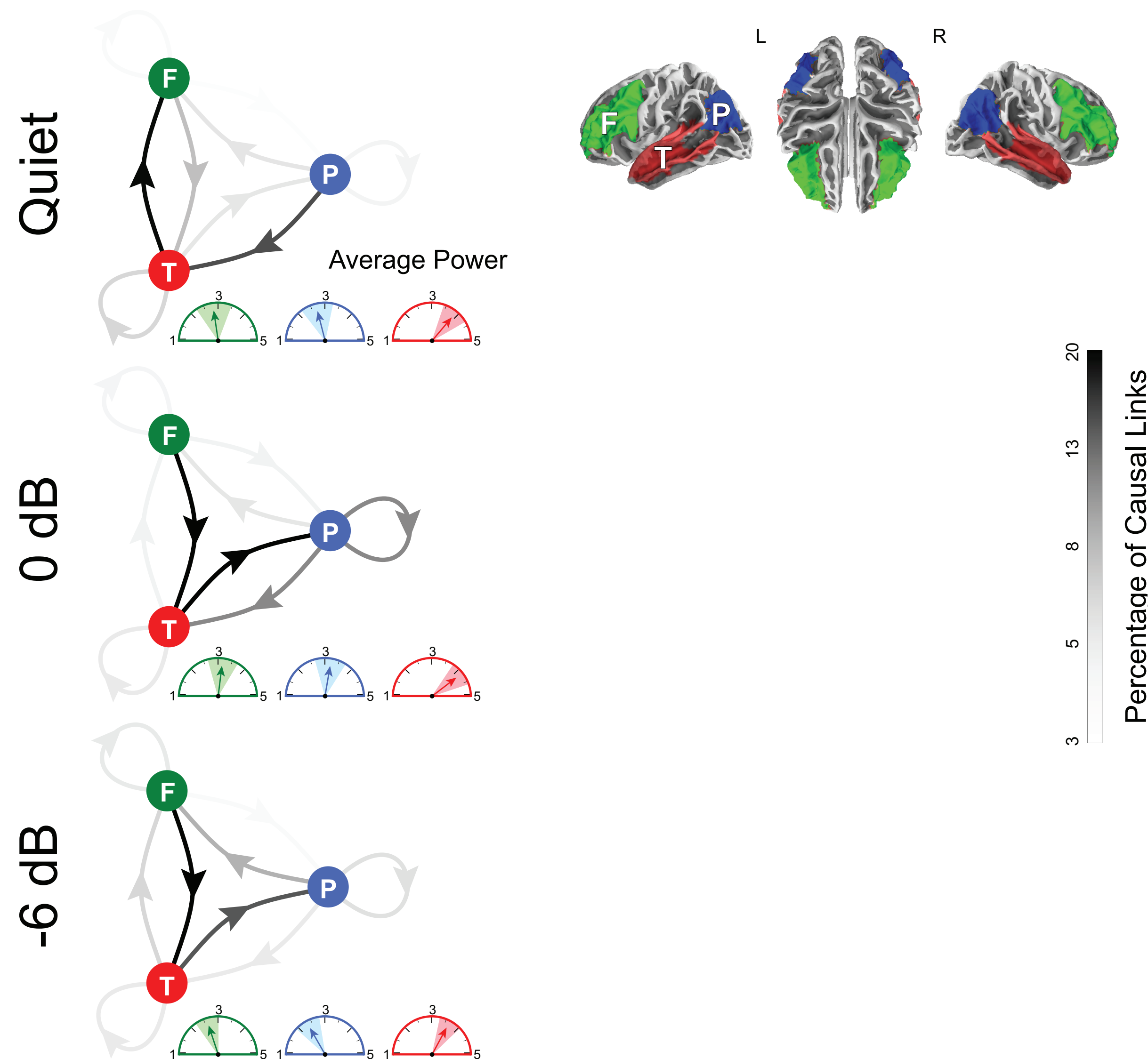
- Novel method, based on Granger Causality (if source A can predict source B)
 - Directional (bi-directional allowed)
 - Localizes neural sources & GC link strengths simultaneously
 - source currents: latent sparse vector autoregressive (VAR) processes
- Network Localized Granger Causality (NLGC)
 -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



Cocktail Party Speech Results

Theta band example

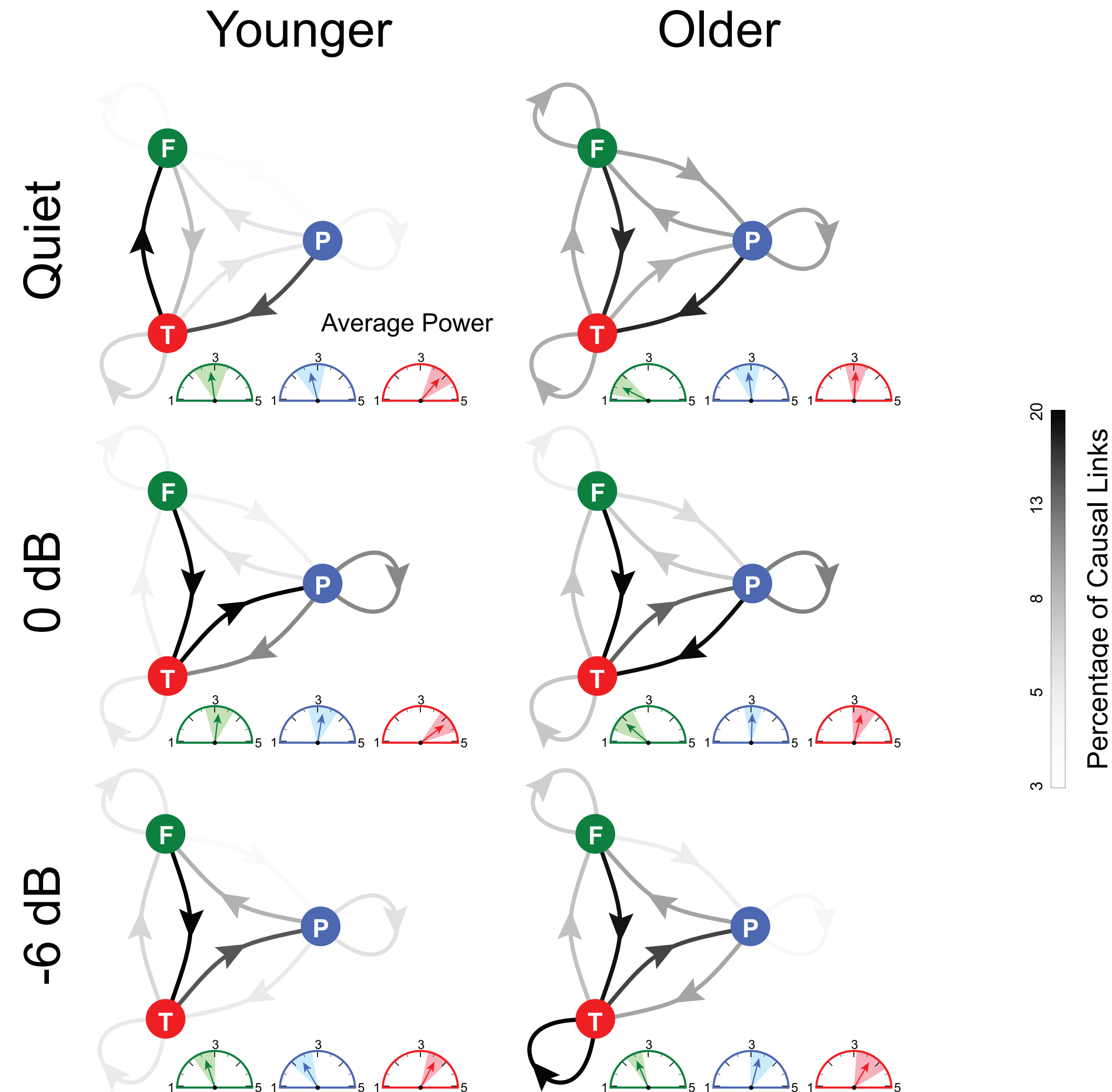
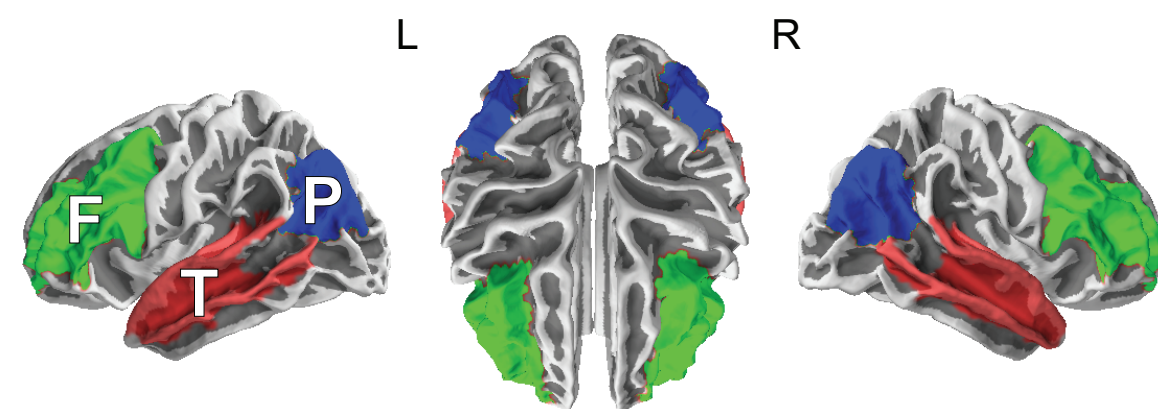
- Speech in quiet connectivity: dominantly Temporal→Frontal and Parietal→Temporal
- Cocktail Party listening (moderate SNR): Temporal-Frontal switches direction; Parietal-Temporal now bi-directional
- Cocktail Party listening (poor SNR): Temporal←Frontal remains; Parietal→Temporal dominant



Cocktail Party Speech Results

Older Listeners exhibit strongly different connectivity

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



Cocktail Party Speech Results

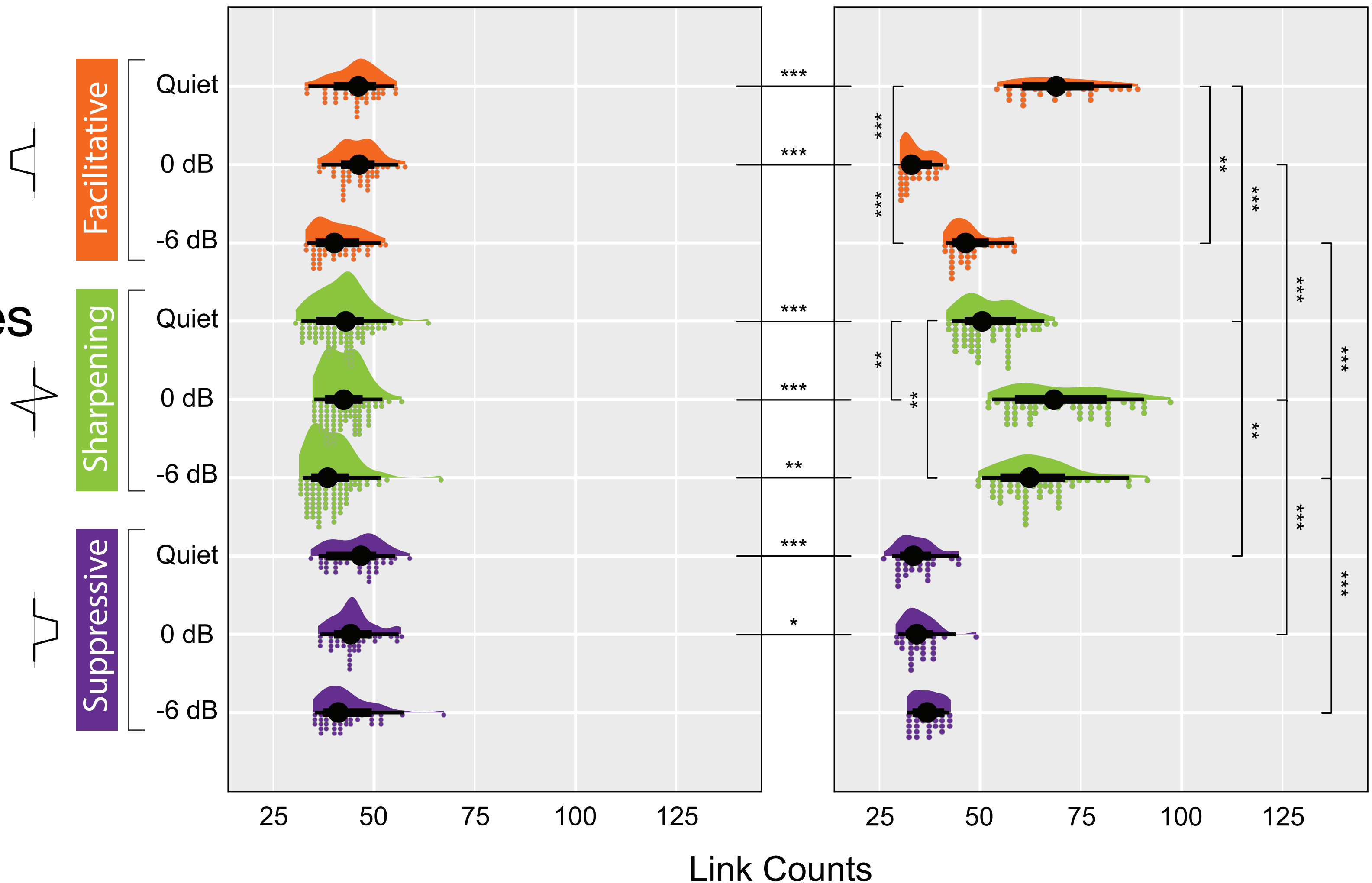
“Excitatory/Inhibitory”
balance changes with task
difficulty for Older Listeners
only

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

Nature of the Links in Theta Band

Younger

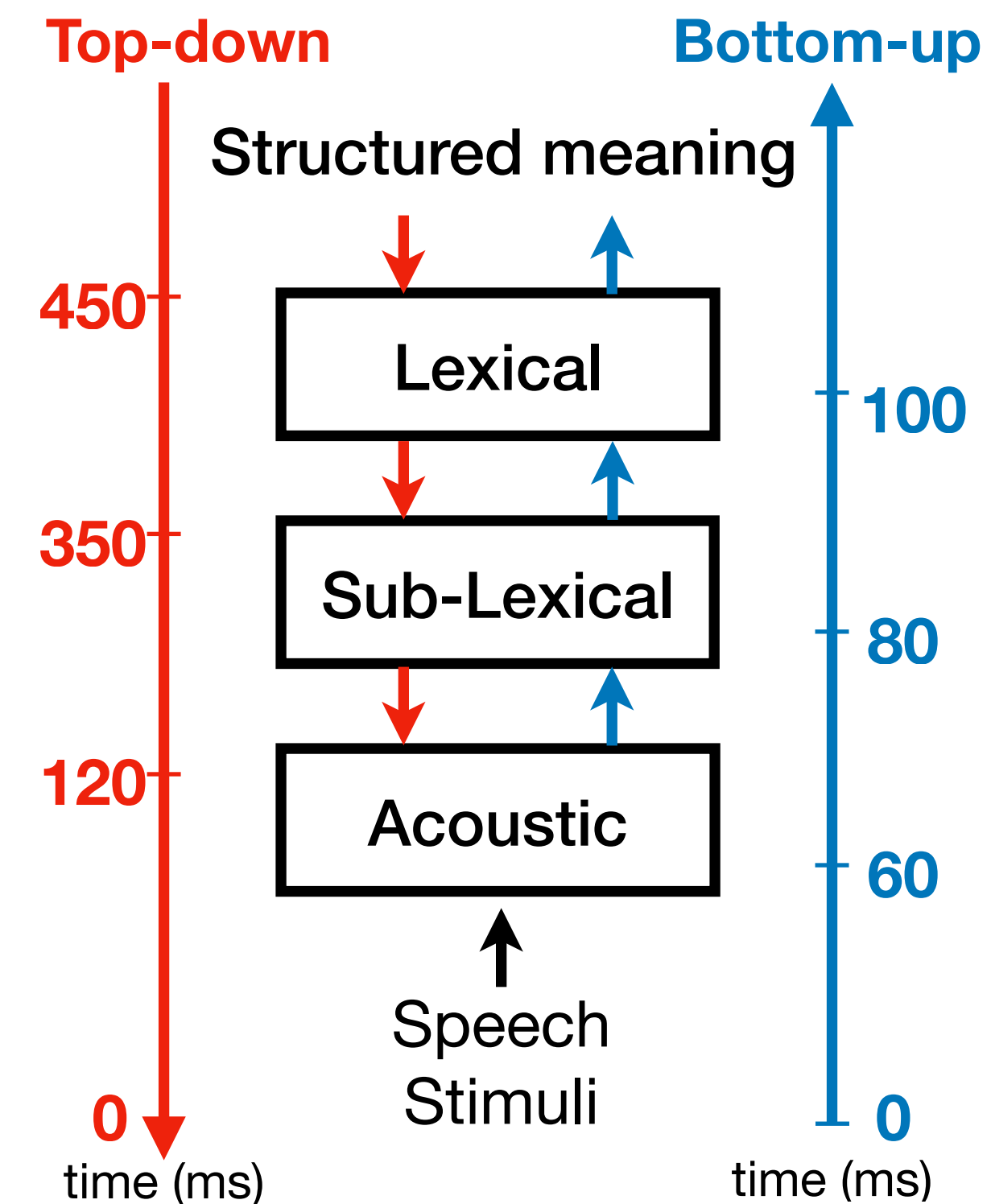
Older



Final Summary

*temporal patterns in **speech acoustics***
*temporal **neural** patterns \rightleftharpoons 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

These slides
available at:
ter.ps/simonpubs



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