Organization of Human Brain Mapping, Geneva 2016

New Directions in the Neurobiology of Language

David Poeppel
Max-Planck-Institute, Frankfurt
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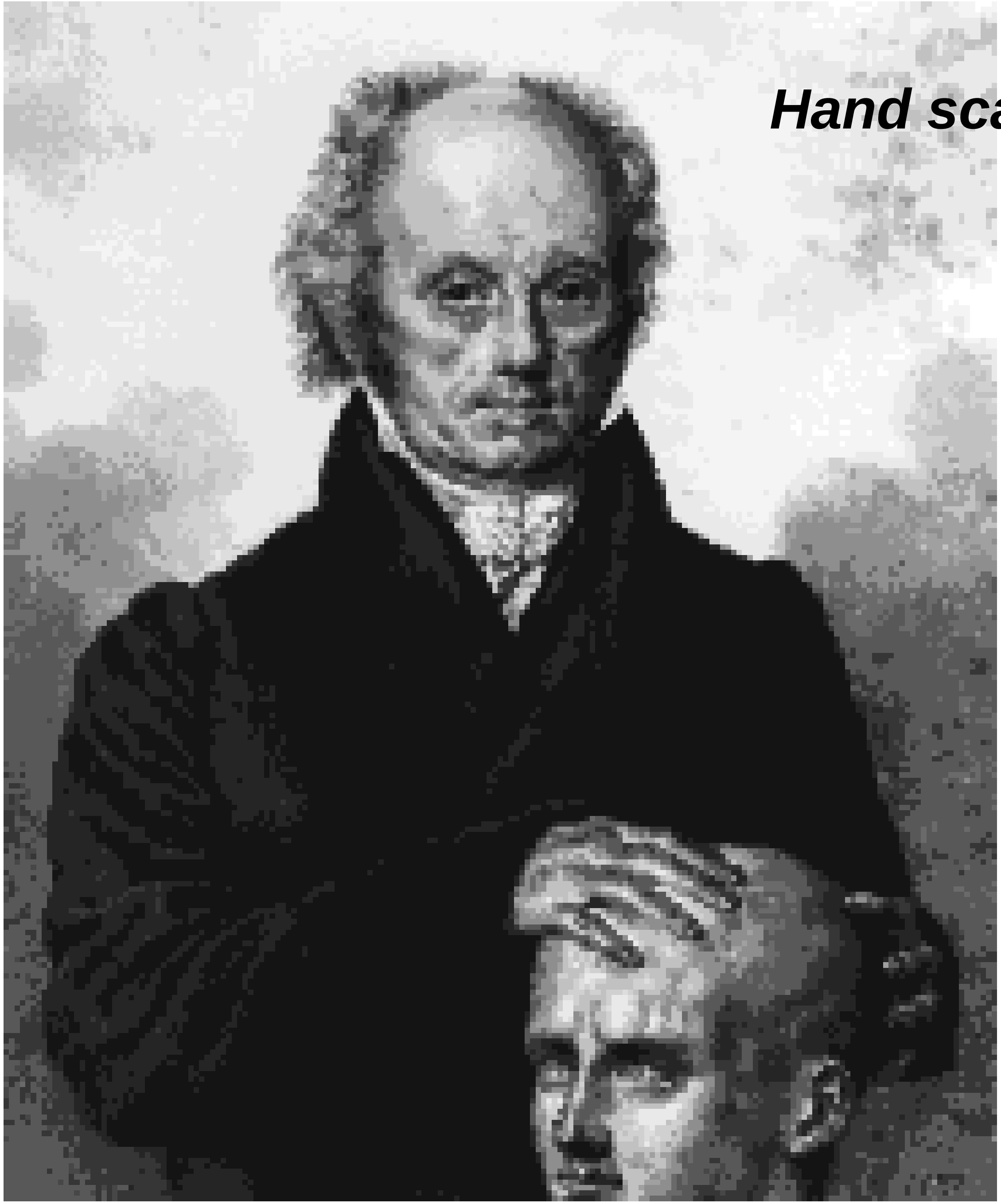
Le Medecin guarissant Phantasie
Purgeant aussi Par drogues la folie.

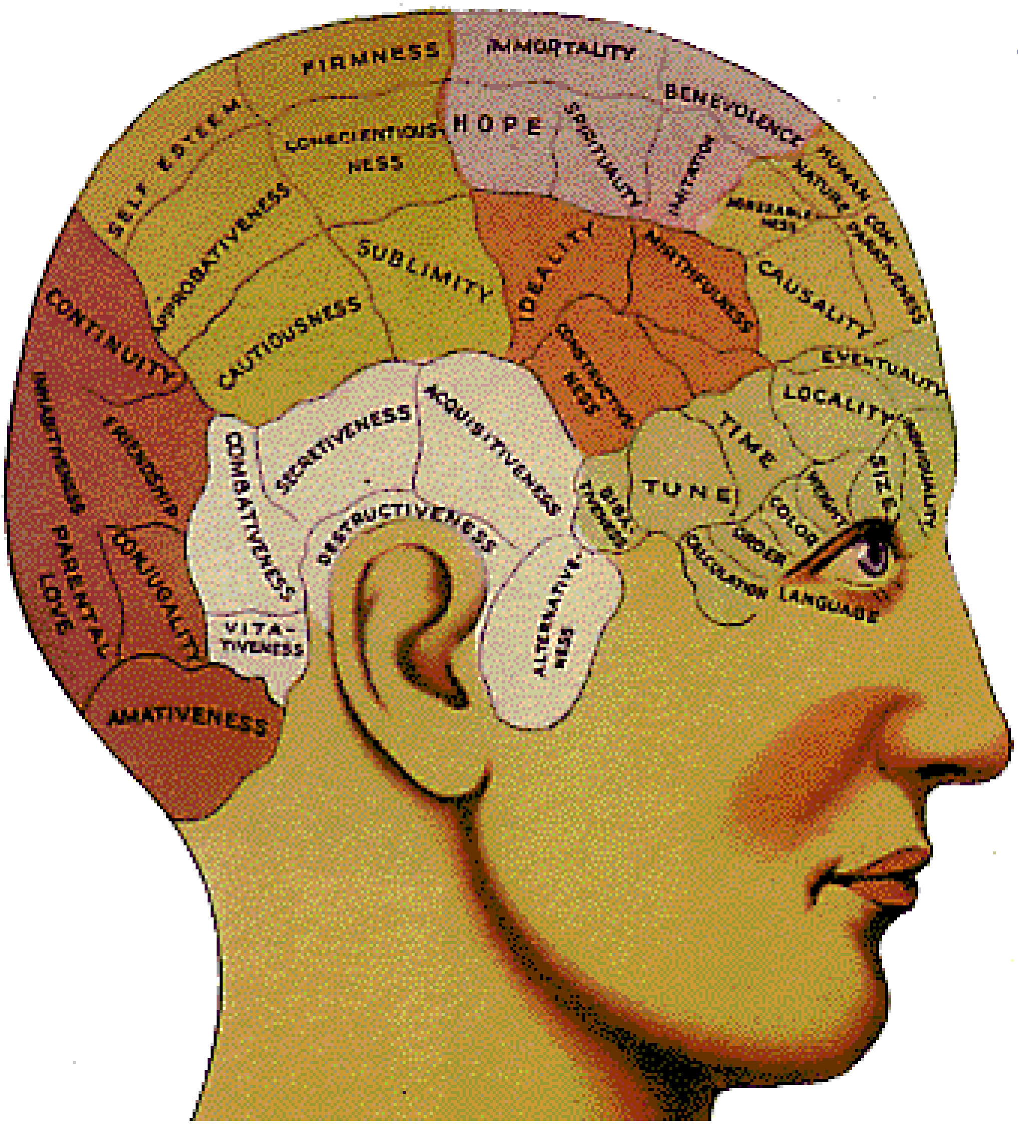


Hand scanner

Phrenology (bad idea)

Organology (good idea)

Franz Josef Gall
1758-1828



Two enduring ideas deriving from Gall

- ***Faculty psychology***
  The mind has a 'parts list.'

- ***Experience-dependent plasticity***
  Using the parts changes their neuronal realization.

Outline

- The maps problem

Localizing what?

- The mapping problem

What are appropriate linking hypotheses between domains?

- The experimental granularity problem

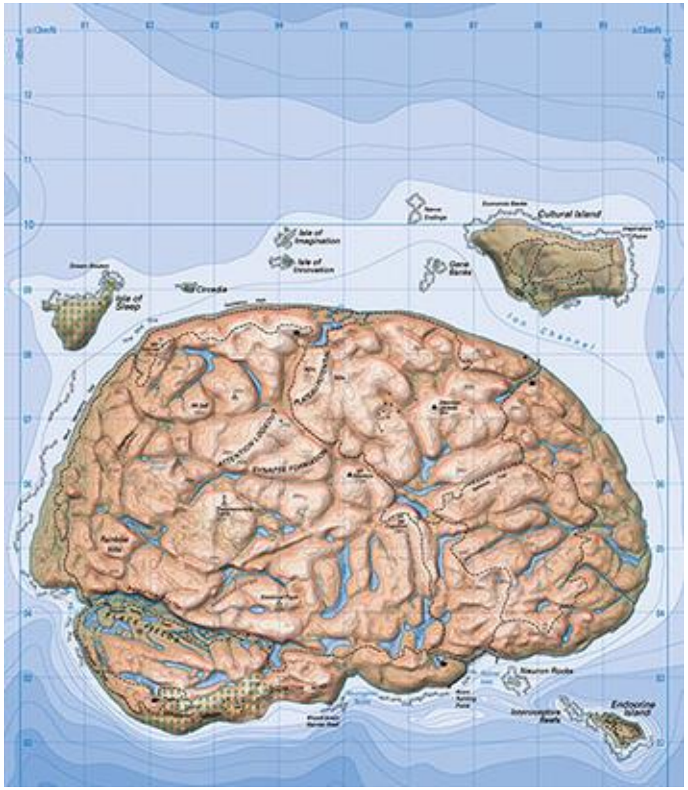
More naturalism versus more hypothesis testing?

1. The map(s) problem

In the last 25 years, the dominant research program has become to map out the “localization of function.”

The principal question has been “where are different functions localized”?

The cartographic imperative approach: lots about ‘where’ - but relatively little about ‘how’ things work.



Language is not monolithic

language-o-topy

Phonetics/phonology
sound structure

Morphology
word structure

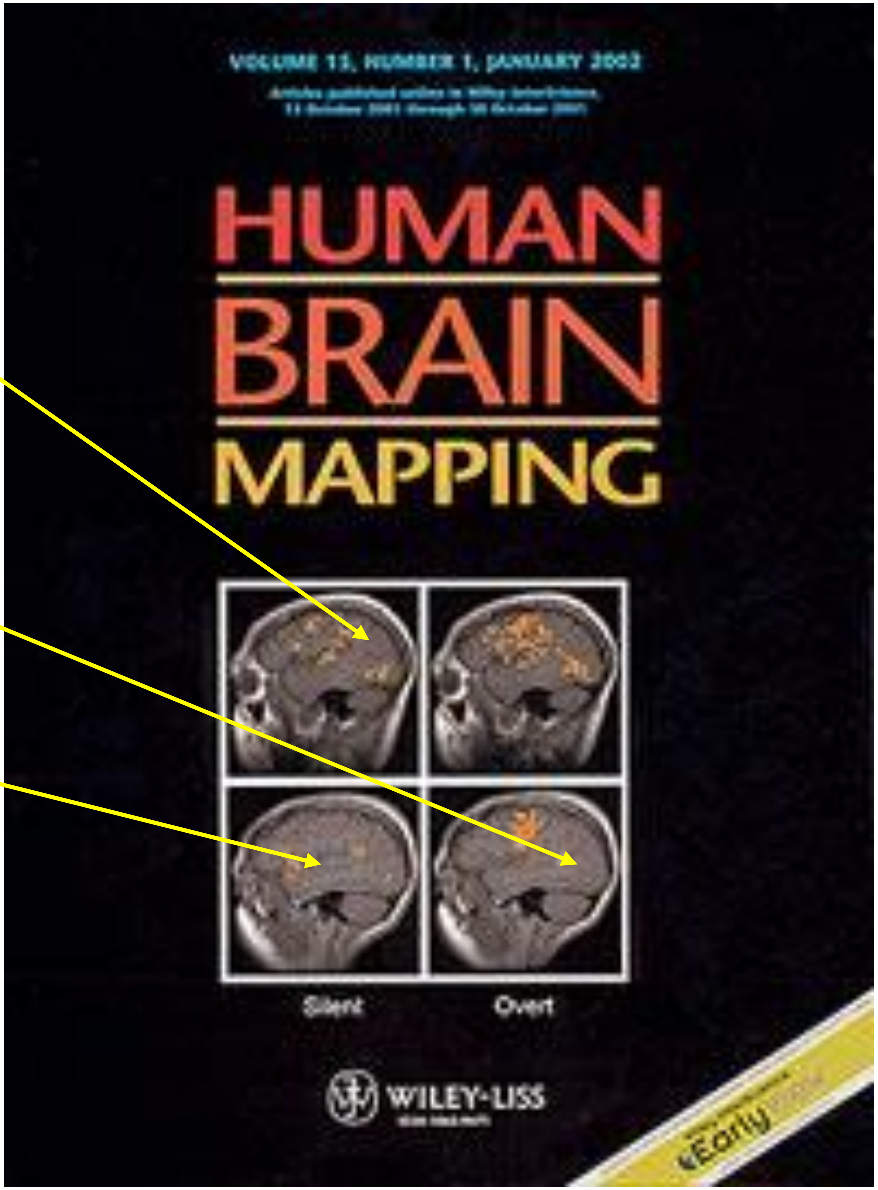
Lexical semantics
word meaning

Syntax
sentence structure

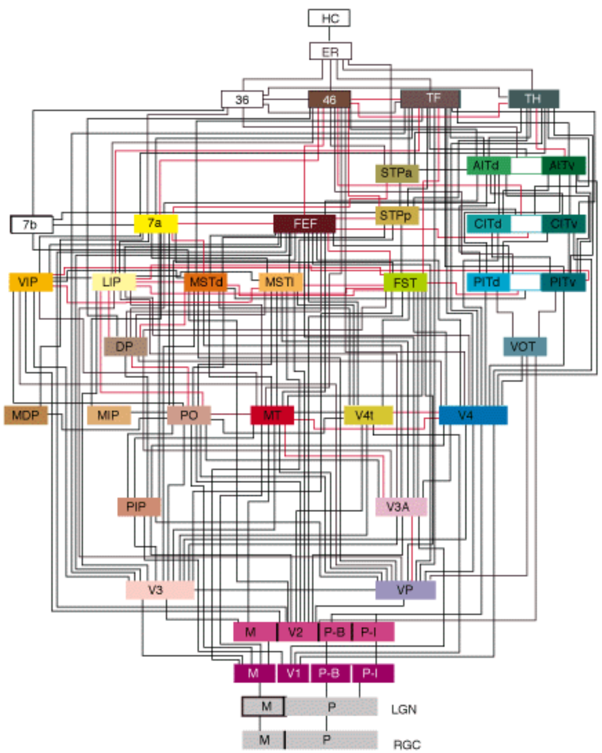
Prosody
sentence melody

Compositional semantics
sentence meaning

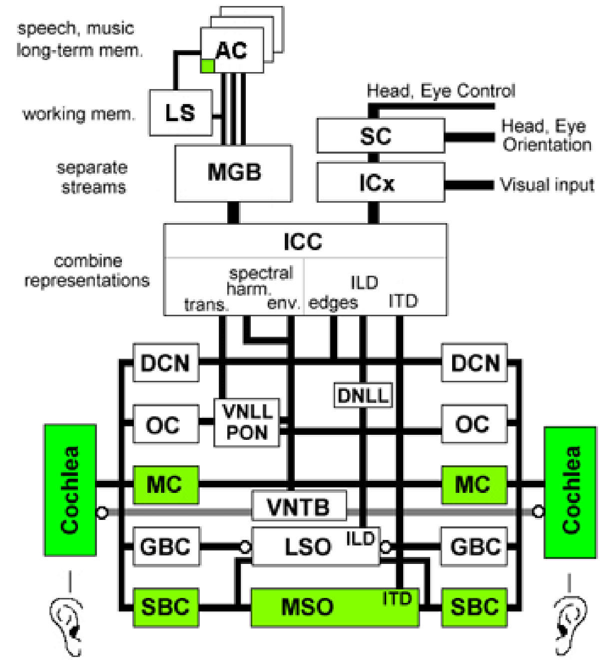
Discourse
larger meaning scale



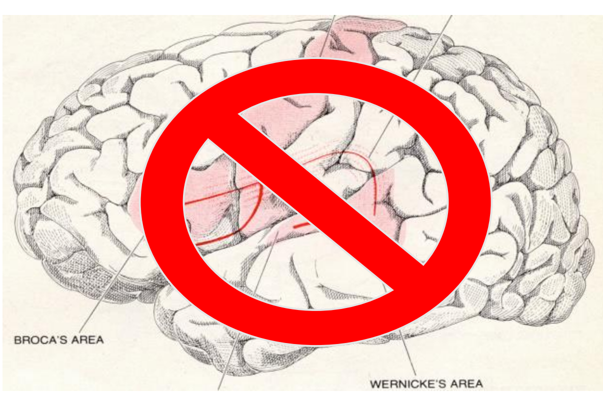
How naïve are we willing to be?



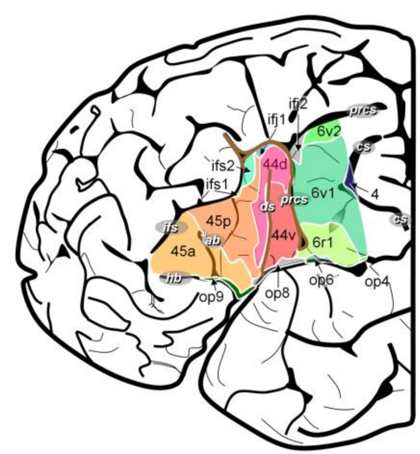
Visual system



Auditory system

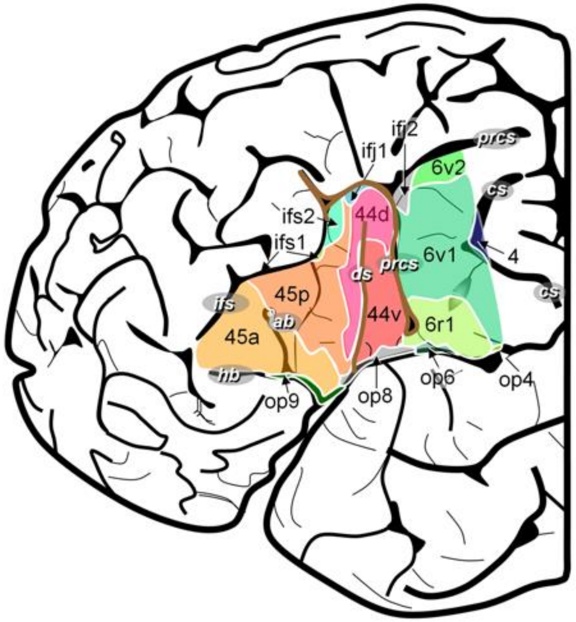


Language system



For example … "Broca's area" is, if anything, "Broca's region", with many subdivisions (not even counting laminar specialization).

=> Monolithic generalizations about function are not even wrong.



Amunts et al., 2010, PLoS Biology

frontiers in
NEUROSCIENCE

ORIGINAL RESEARCH ARTICLE
published: 11 September 2014
doi: 10.3389/fnins.2014.00289

The functional organization of the left STS: a large scale meta-analysis of PET and fMRI studies of healthy adults

Einat Liebenthal[1,2]*, Rutvik H. Desai[3], Colin Humphries[1], Merav Sabri[1] and Anjali Desai[1]

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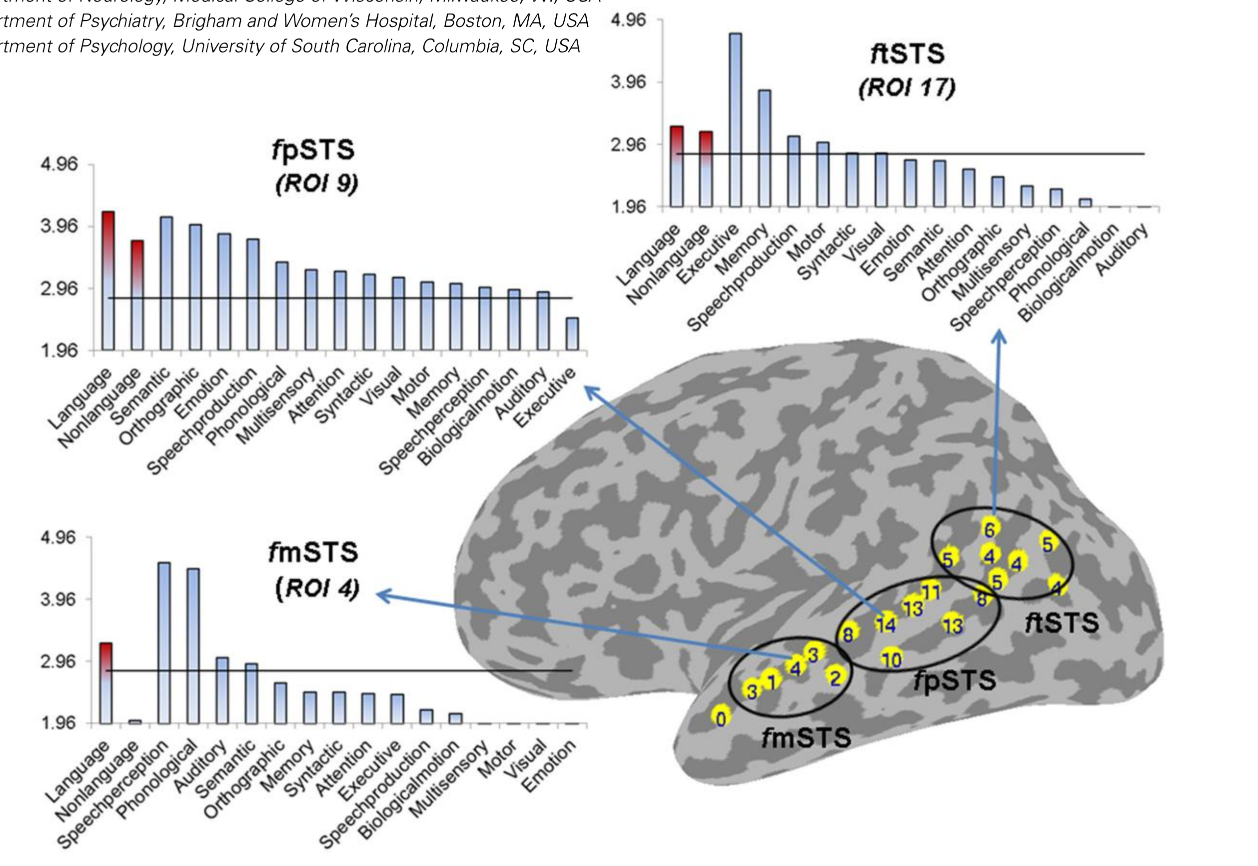


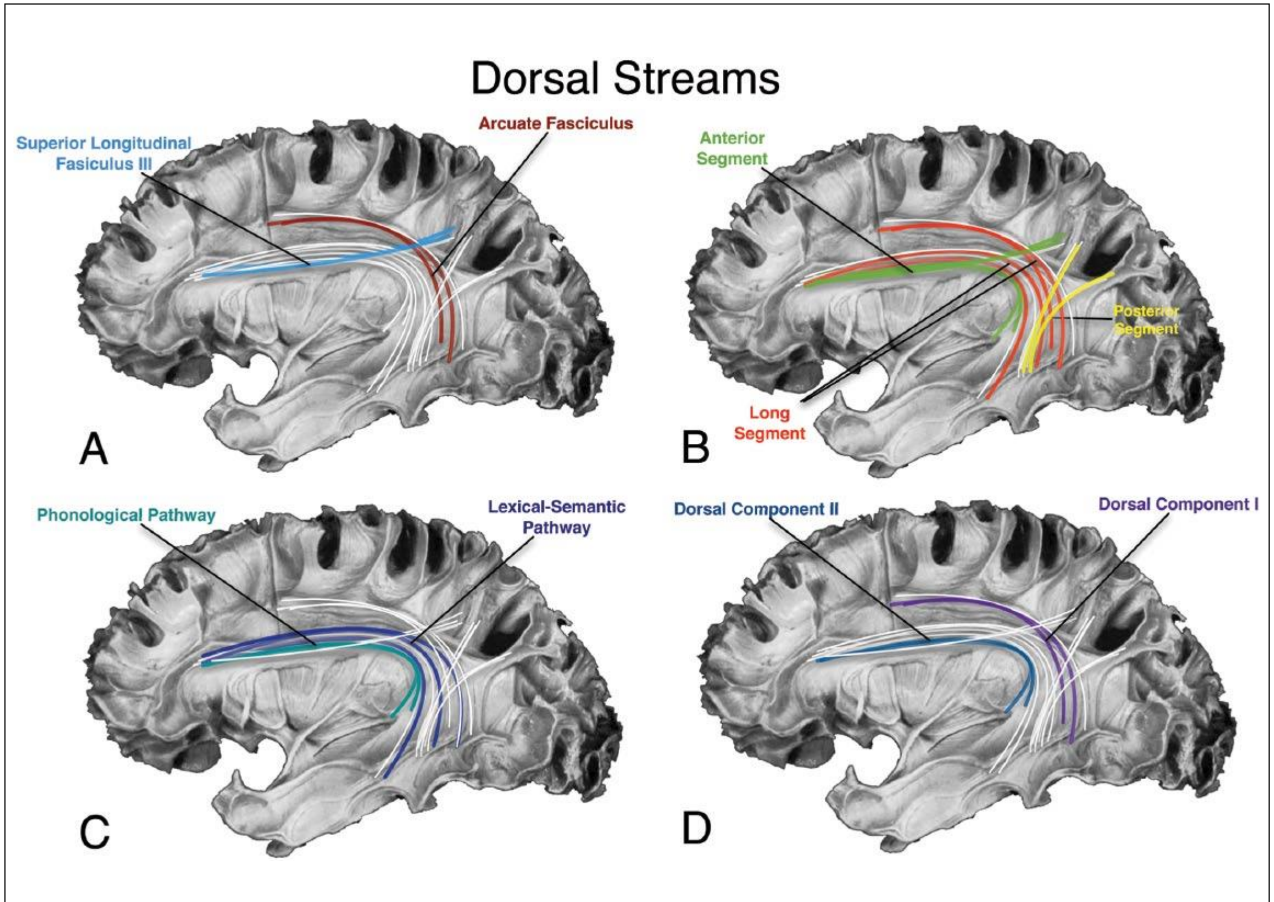
FIGURE 5 | Partition of left STS into three subdivisions based on functional specificity. The number label within each ROI represents its functional specificity, expressed as the number of functional categories with a significant mean ALE measure in this region ($p < 0.005$). The functional mSTS (*f*mSTS) subdivision was defined as a region activated by a small number of functional categories (range 1–4, mean 2.6), the functional pSTS (*f*pSTS) subdivision was defined as a region activated by the largest number of functional categories (range 8–14, mean 11), and the functional tSTS (*f*tSTS) subdivision was defined as a region activated by an intermediate number of functional categories (range 4–6, mean 4.7). The three graphs show the mean ALE measure (expressed in Z-scores) for each stimulus (in red) and functional (in blue) category in descending order of magnitude, in the ROIs that were activated by the largest number of functional categories in each subdivision (ROIs number 4, 9, and 17 in the left *f*mSTS, *f*pSTS, and *f*tSTS, respectively). The horizontal line corresponds to $z = 2.807$ ($p < 0.005$).

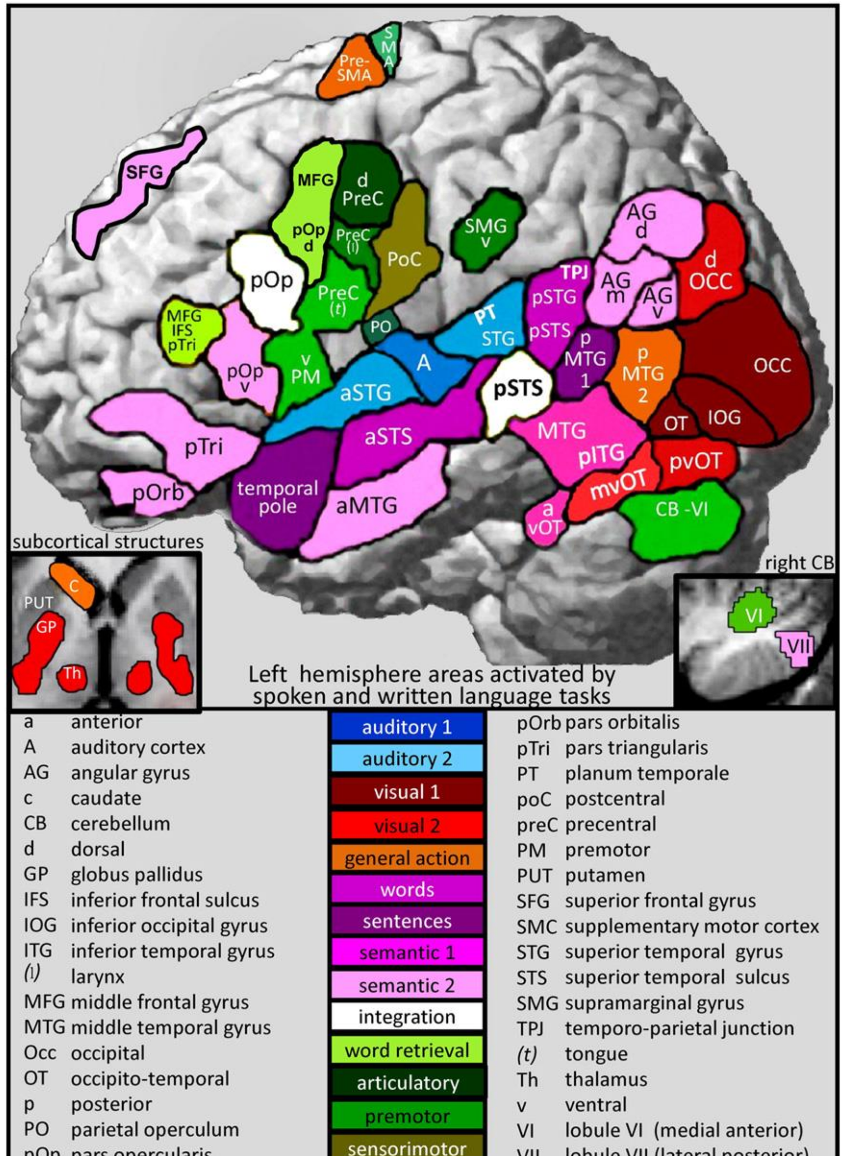
The Language Connectome: New Pathways, New Concepts

The Neuroscientist
2014, Vol. 20(5) 453–467

DOI: 10.1177/1073858413513502
nro.sagepub.com

Anthony Steven Dick[1], Byron Bernal[2], and Pascale Tremblay[3]





Price 2012, *NeuroImage*

OPINION

The cortical organization of speech processing

Gregory Hickok and David Poeppel

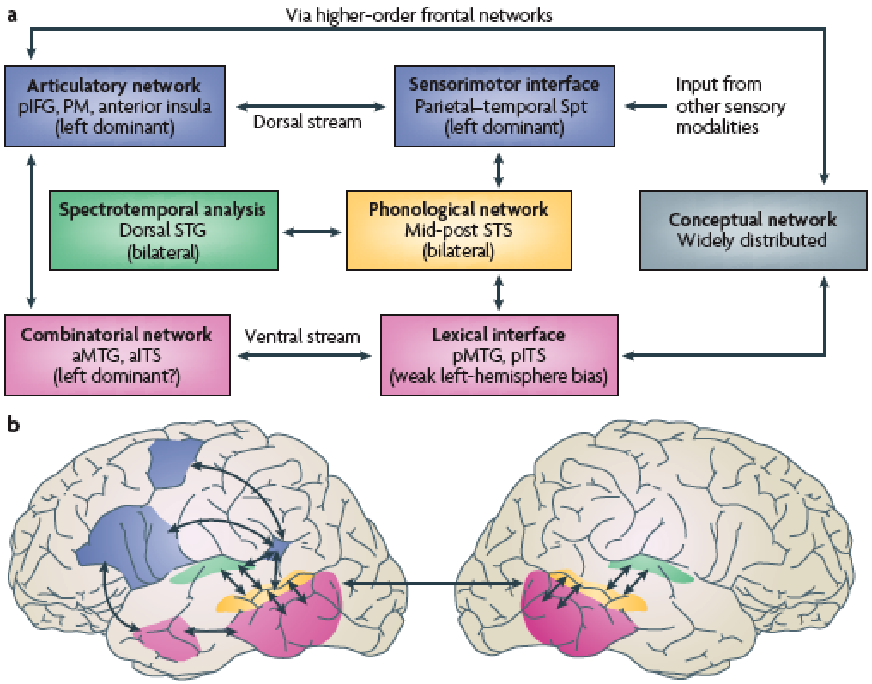


Figure 1 | **The dual-stream model of the functional anatomy of language. a** | Schematic diagram

Nature Reviews Neuroscience 2007

A cortical network for semantics: (de)constructing the N400

Ellen F. Lau, Colin Phillips*‡ and David Poeppel*‡§||*

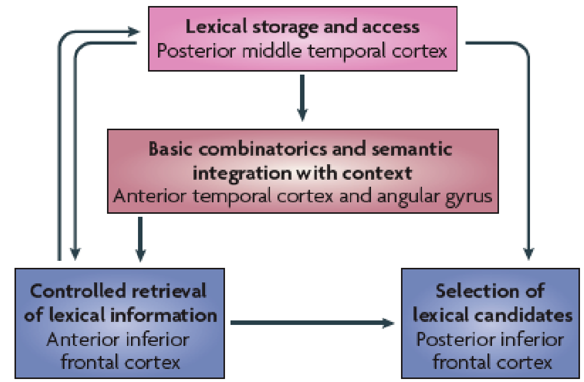


Figure 2 | **Schematic model for semantic processing.**

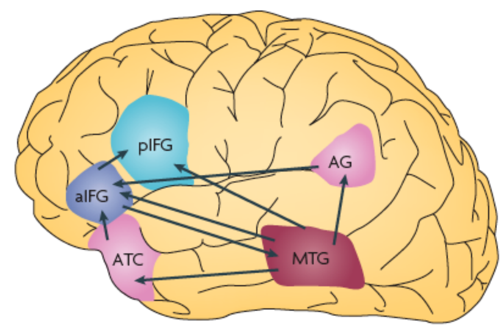
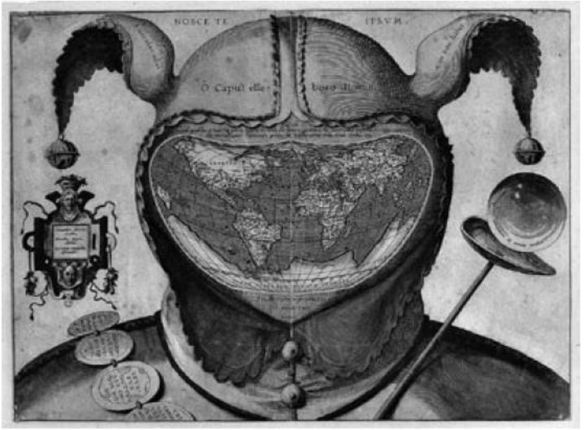


Figure 5 | **A functional neuroanatomic model for semantic processing of words in context.** Lexical

Nature Reviews Neuroscience 2008

Productive engagement with the maps problem is an important part of our ‘homework’ in the neuroscience of language – a critical intermediate step on the path towards developing a more comprehensive understanding. But ….

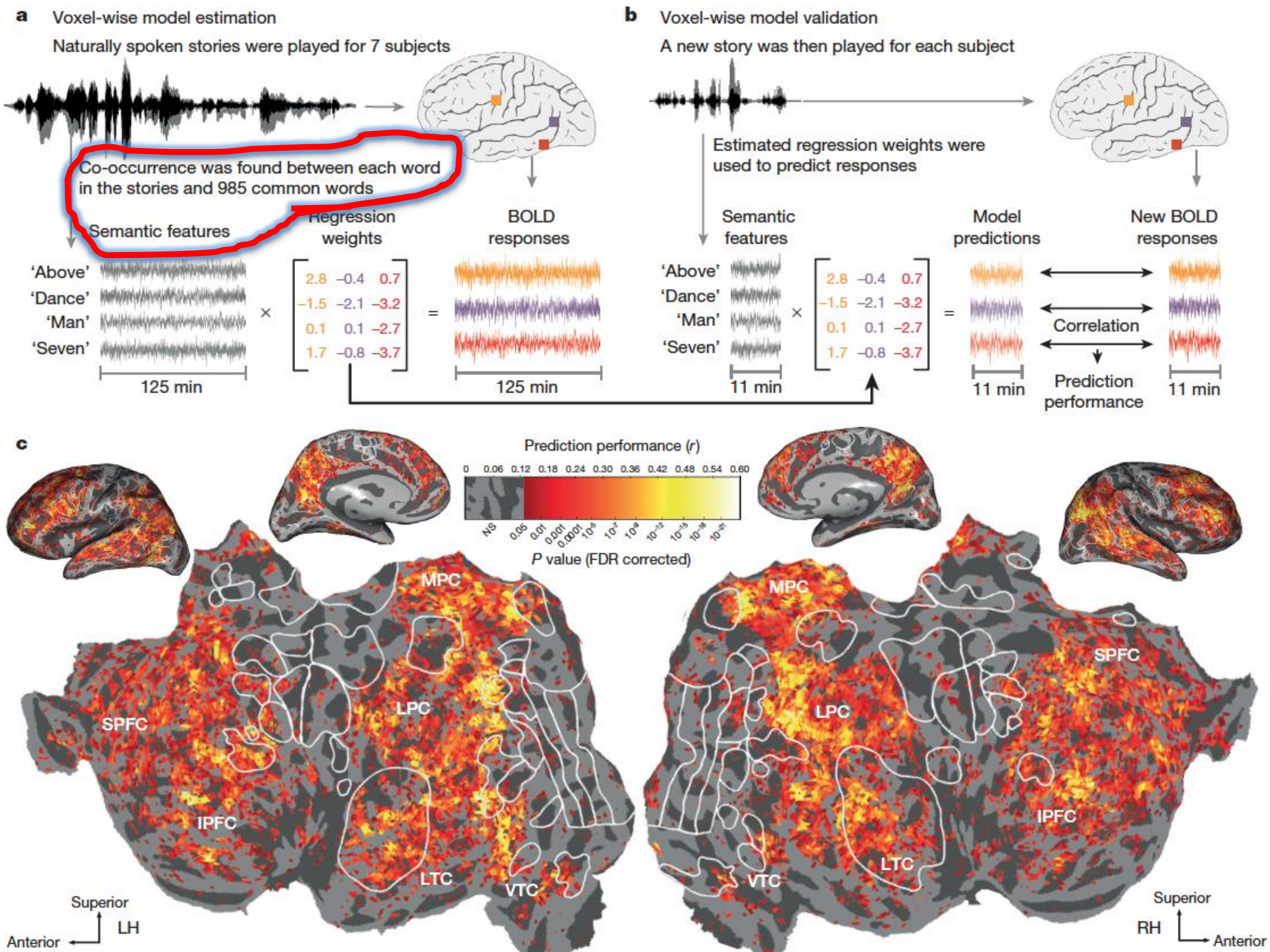
We must not confuse localization with explanation! The cartographic imperative should be followed, but it is not sufficient.



David Poeppel

The Cartographic Imperative: Confusing Localization and Explanation in Human Brain Mapping

Making maps has a long and respectable history in (obvious) disciplines such as geography and politics as well as in (less obvious) disciplines ranging from anthropology to zoology. Maps tell us where things are – whether in the cosmos, on the Earth, in the body, on strands of DNA, on an electronic circuit, and so on – and identifying the local position of something is, arguably, the principal func-

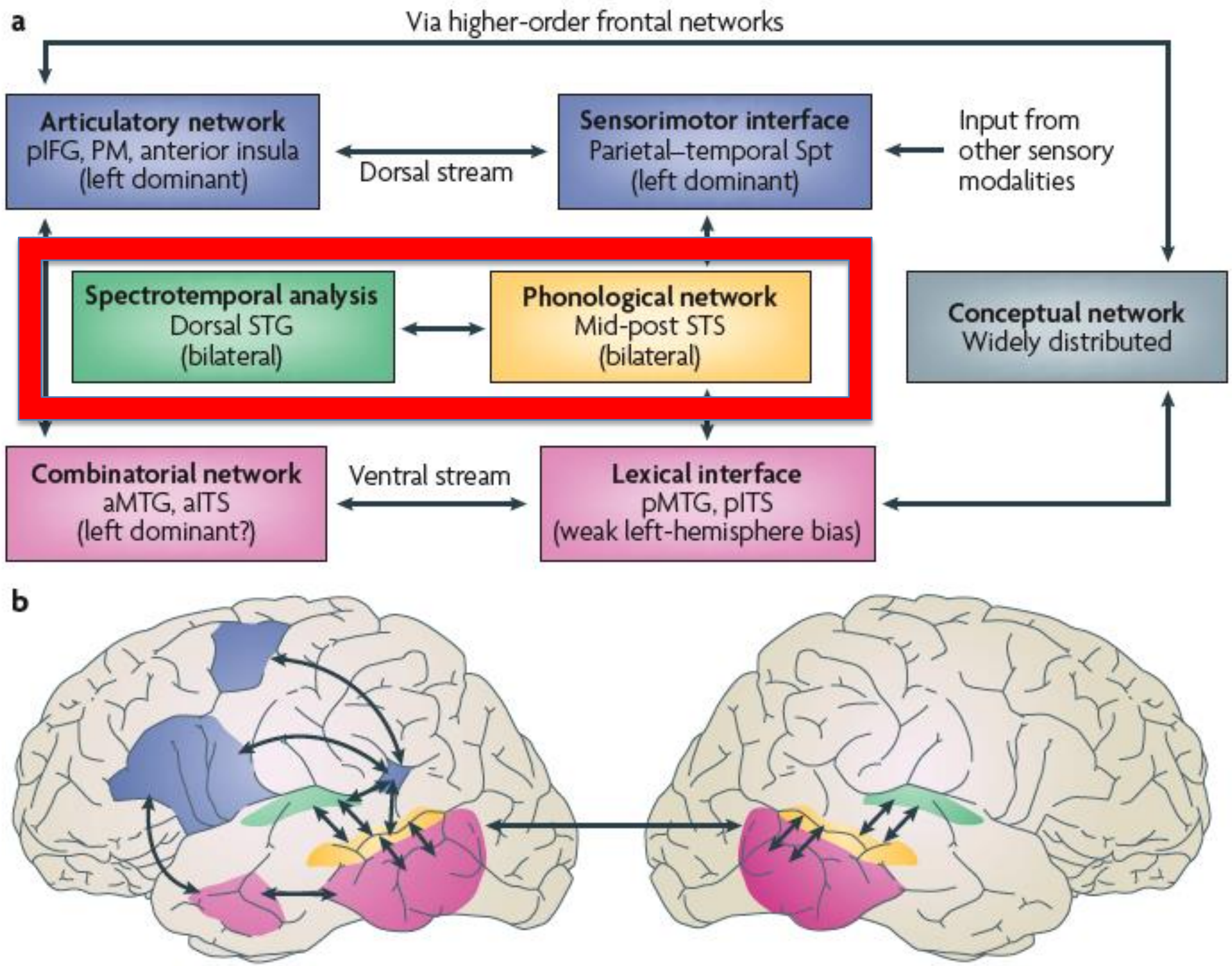


Huth et al. 2016, *Nature*

Huth et al. 2016, *Nature*

unflushable

Functional anatomy of speech sound processing



Hickok & Poeppel, 2007, Nat Rev Neurosci

The cortical analysis of speech-specific temporal structure revealed by responses to sound quilts

Tobias Overath, Josh H. McDermott, Jean Mary Zarate, David Poeppel

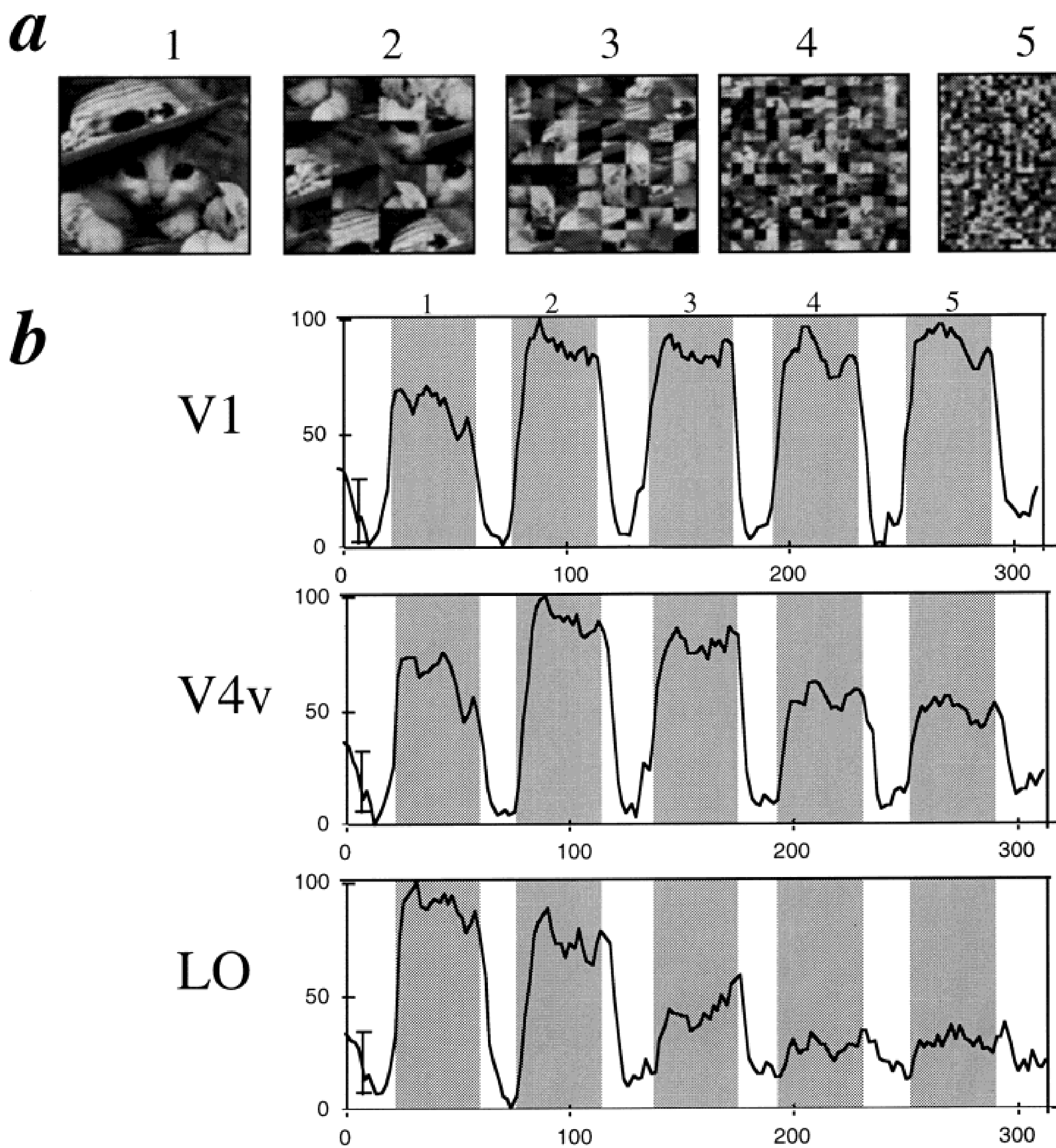
Nature Neuroscience, 2015

Duke

MIT

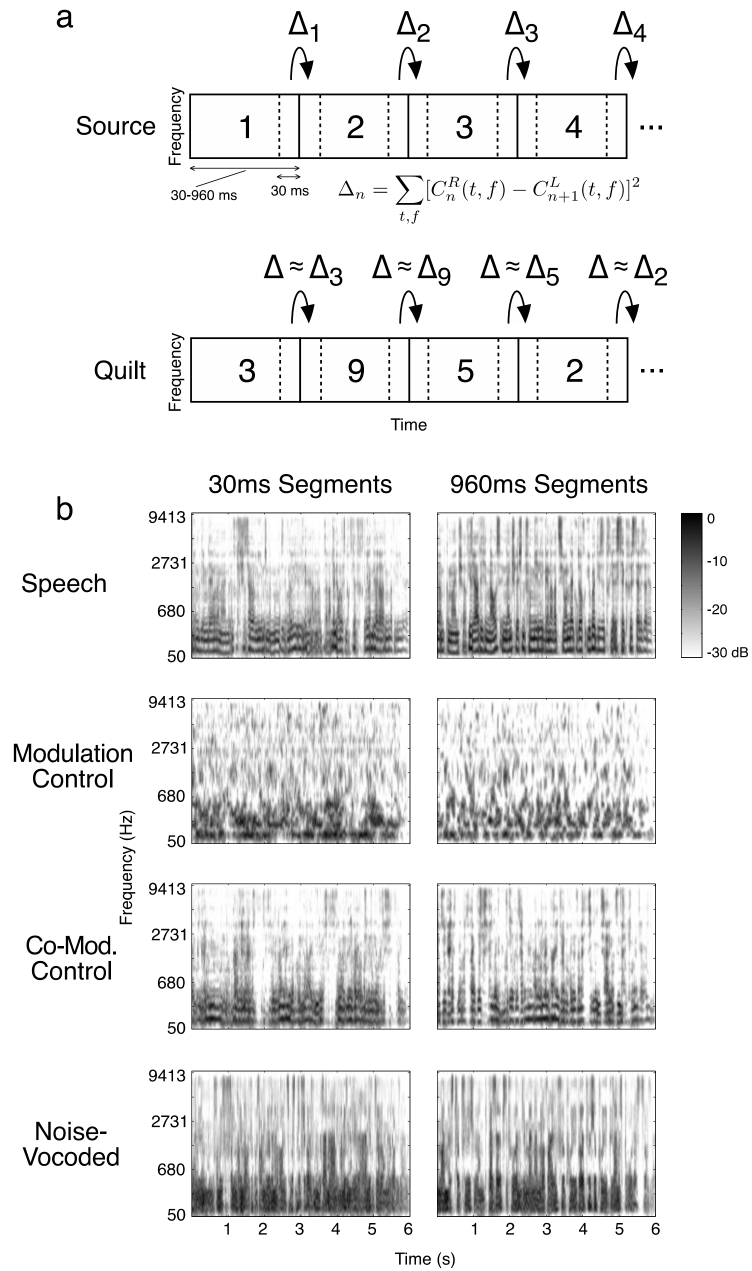
NPG

A Sequence of Object-Processing Stages Revealed by fMRI in the Human Occipital Lobe
Grill-Spector et al. (1998), *Human Brain Mapping*



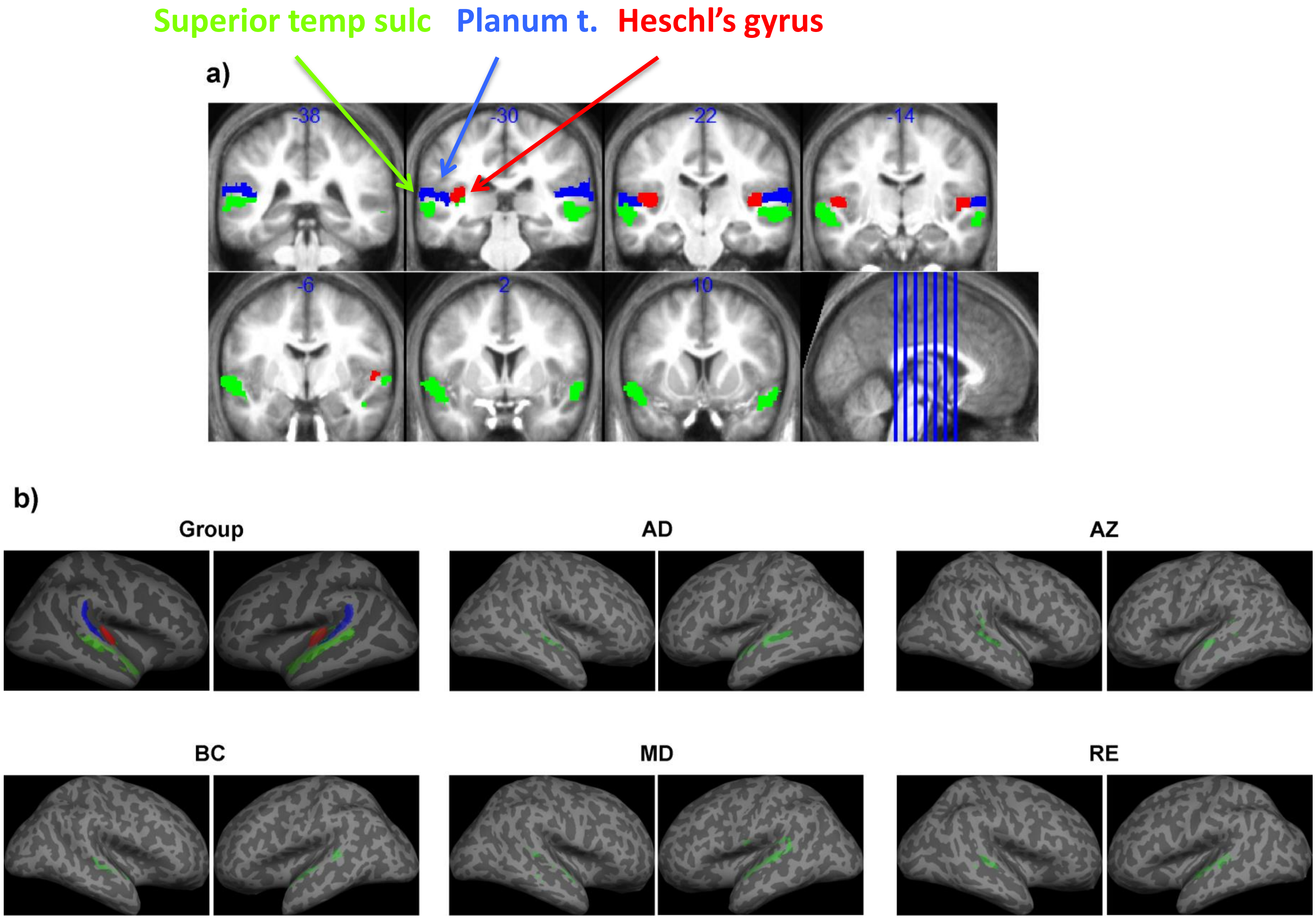
Regions subserving speech-specific analysis should exhibit an increasing response to speech quilts as the segment length increases,

because this manipulation increases the temporal extent over which the signal contains naturalistic speech structure.

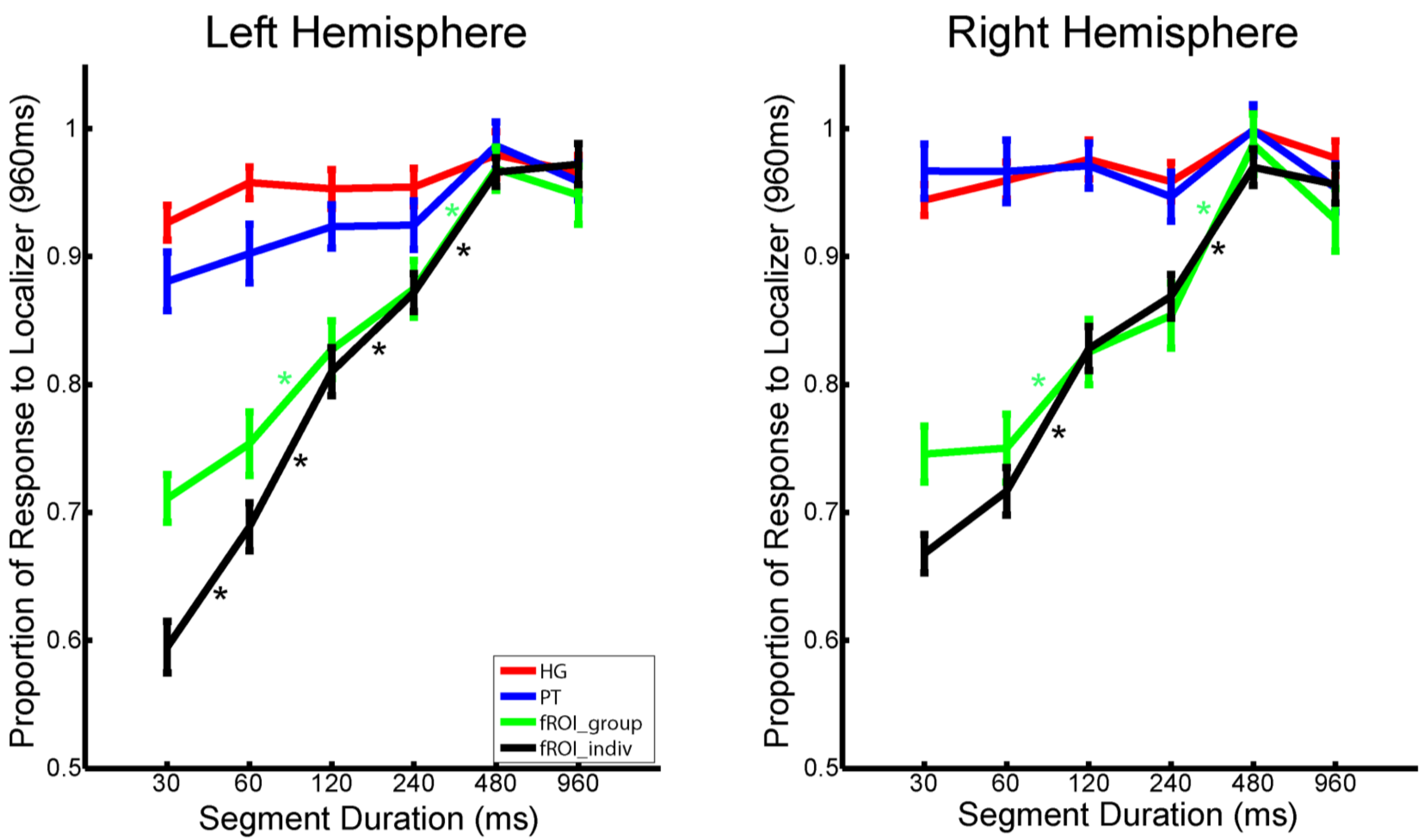


The structure of a quilted signal is similar to that of the source signal within a segment and across a segment's border,

but differs from the source at larger scales for source signals that contain large-scale dependencies.

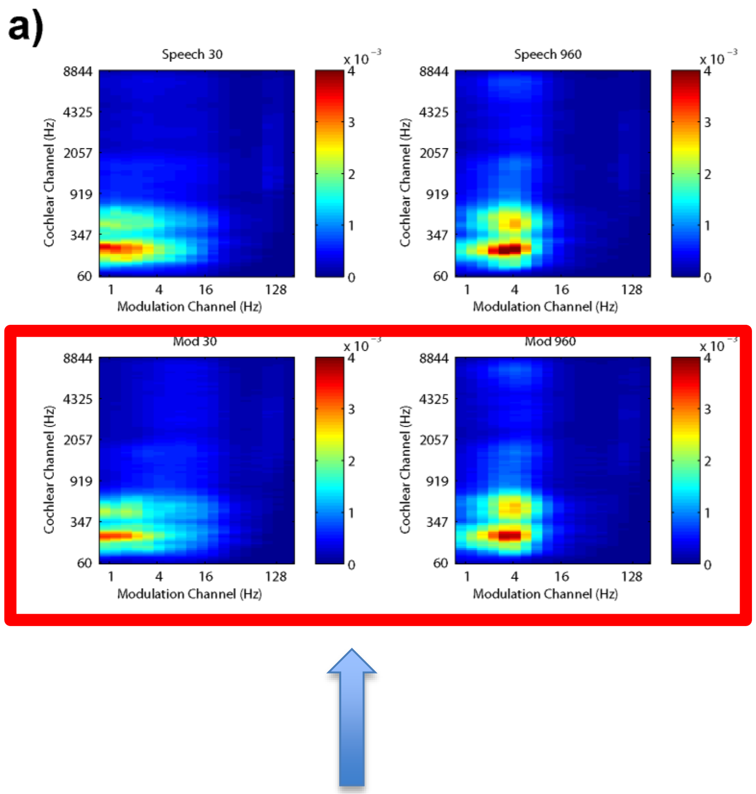


Superior temp sulc
Planum t.
Heschl's gyrus
a)
-38
-30
-22
-14
-6
2
10
b)
Group
AD
AZ
BC
MD
RE



Left Hemisphere
Right Hemisphere
Proportion of Response to Localizer (960ms)
1
0.9
0.8
0.7
0.6
0.5
30
60
120
240
480
960
Segment Duration (ms)
HG
PT
fROI_group
fROI_indiv
*

… but the modulation spectra are a bit different, especially in the syllable range.



Simoncelli & McDermott texture synthesis

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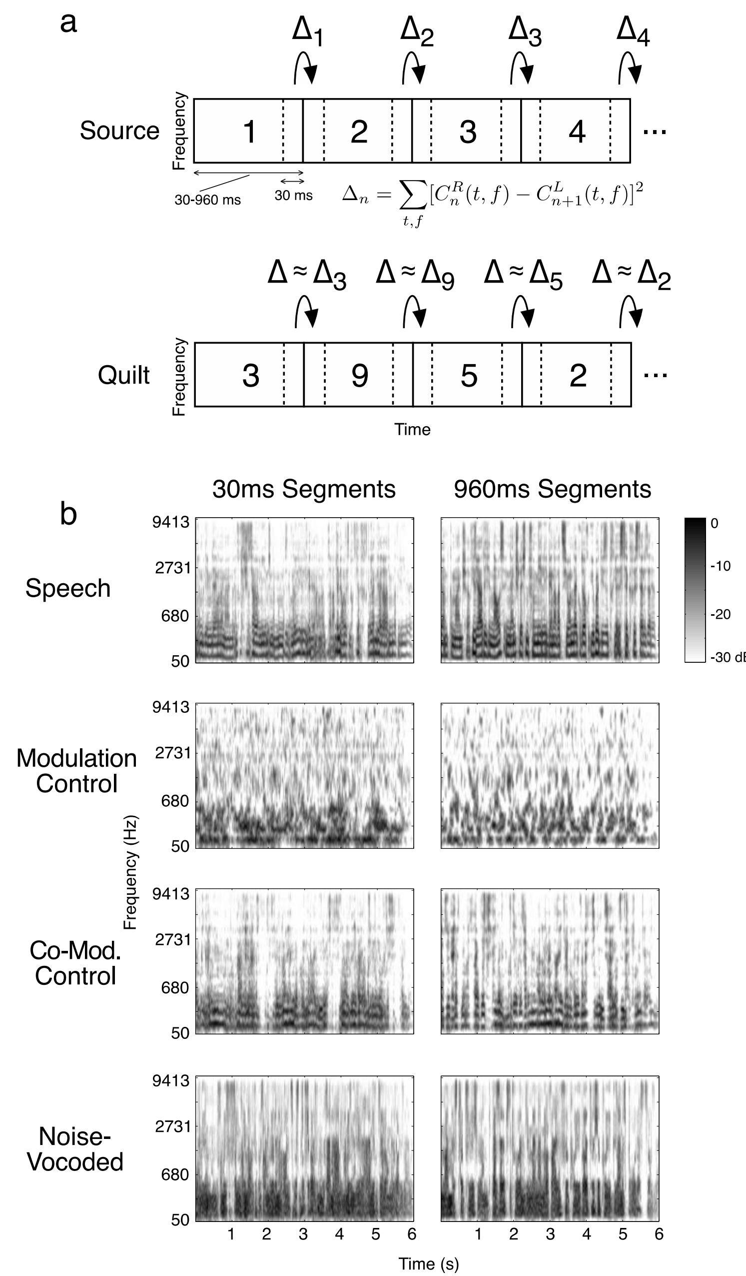

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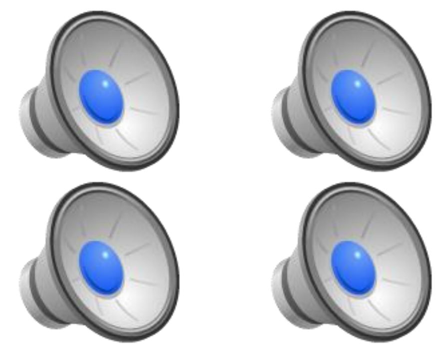
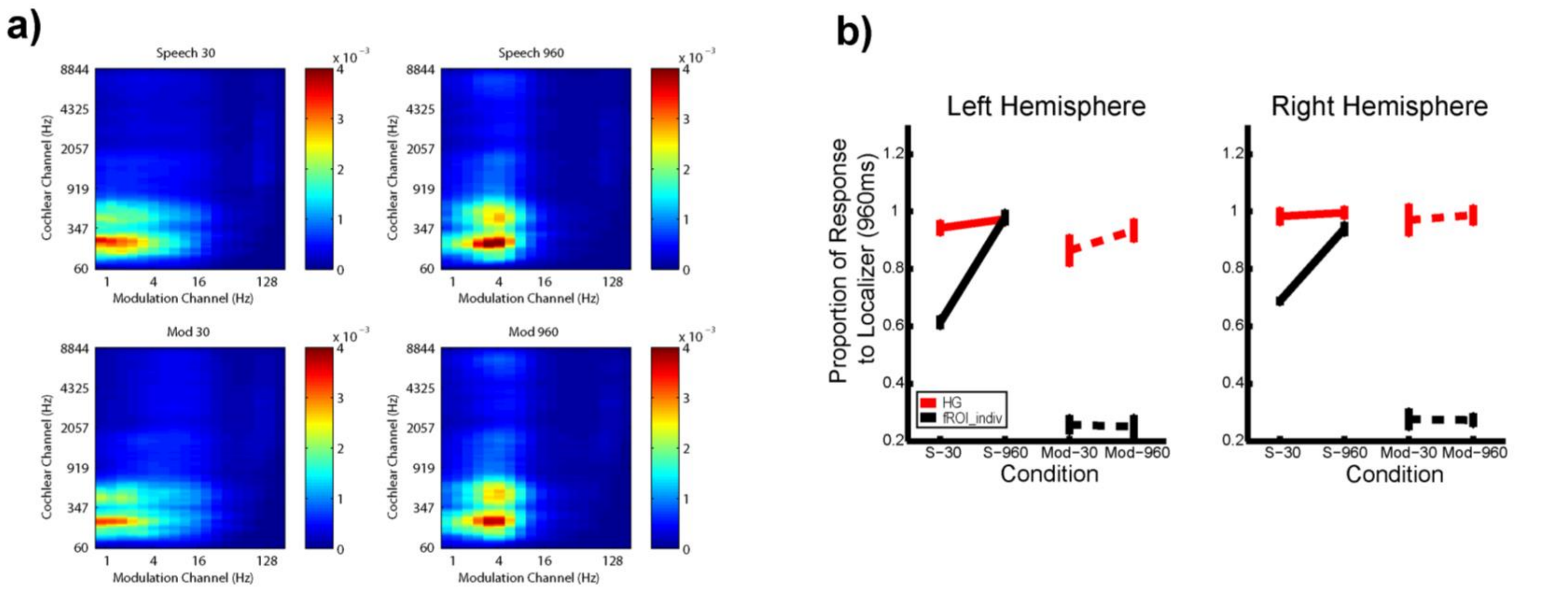
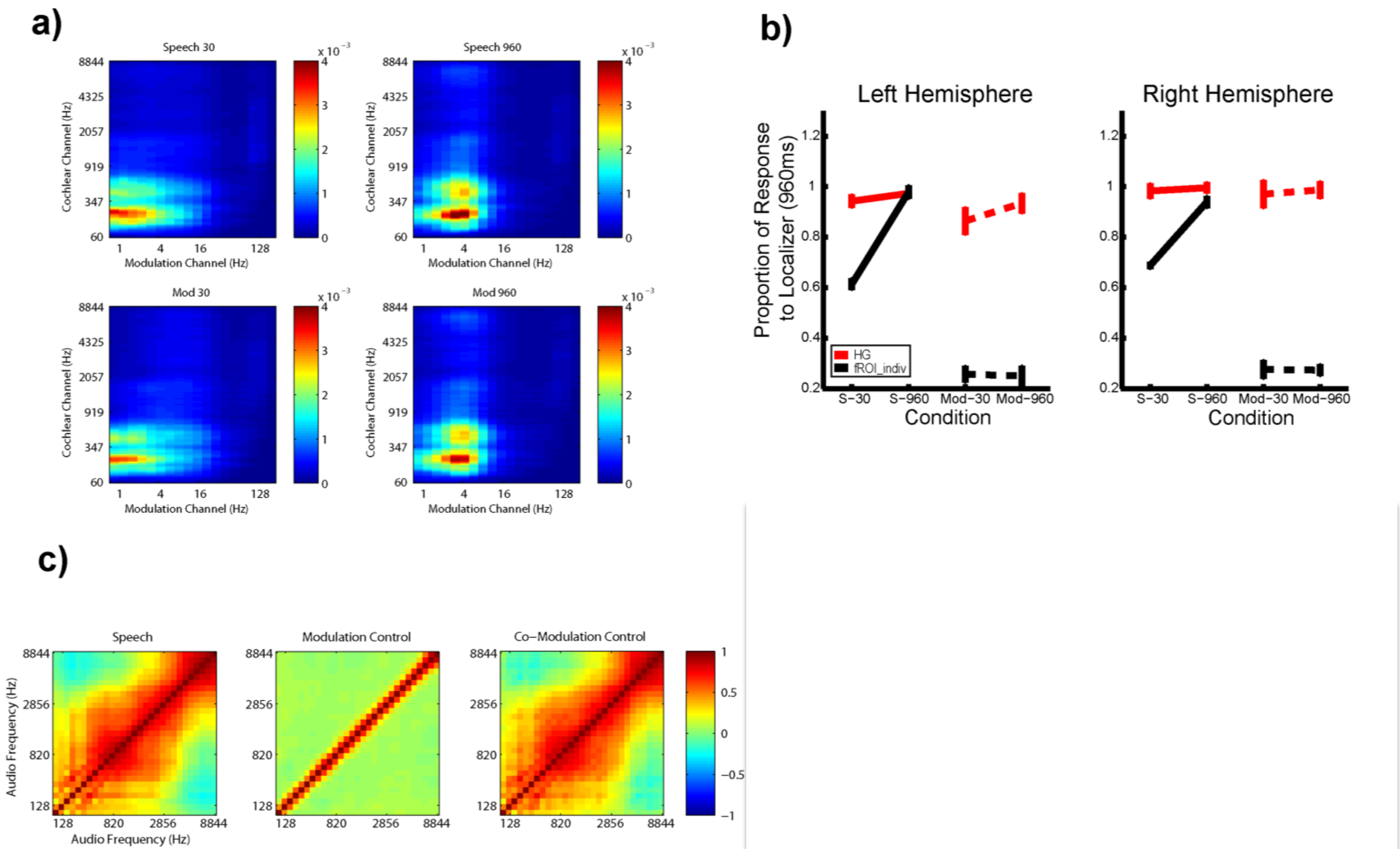




Synthetic signals (20s in length) were generated that matched either 1) the envelope marginal statistics and modulation power or 2) the envelope marginal statistics, modulation power, and cochlear correlations of each of the 20s speech source signals used for speech quilts.



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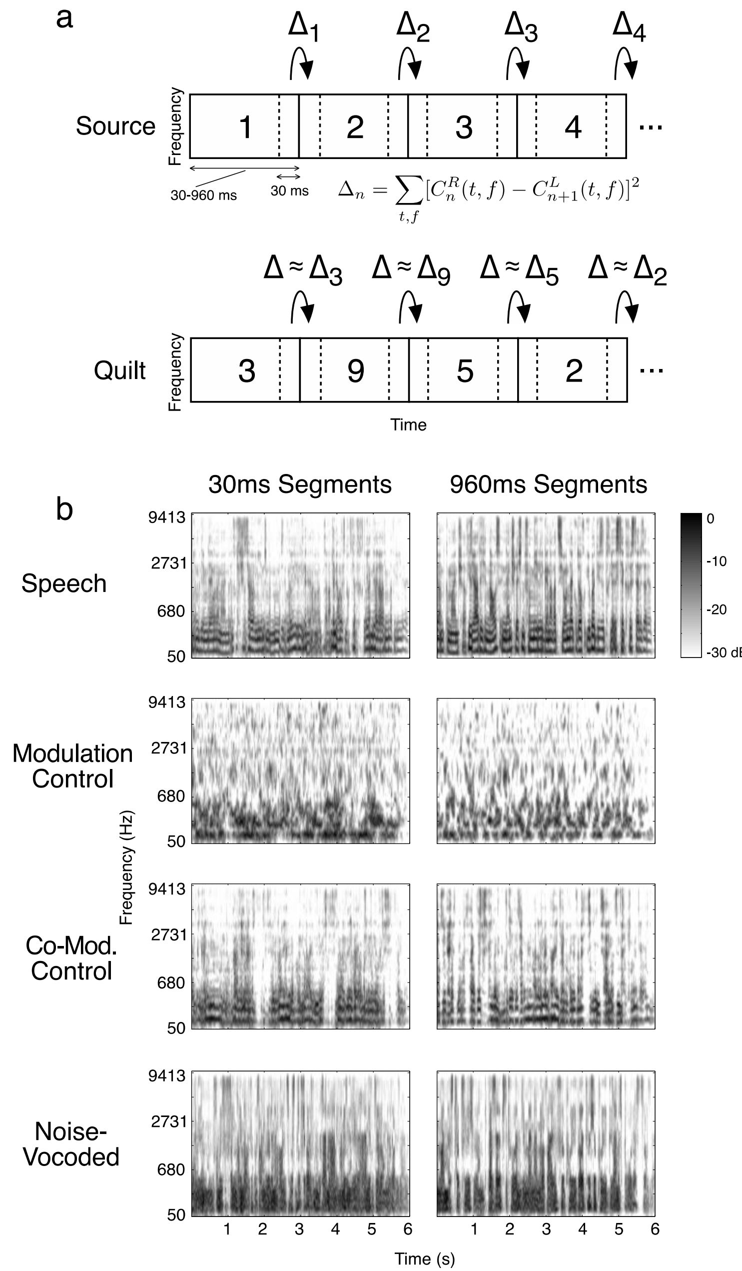

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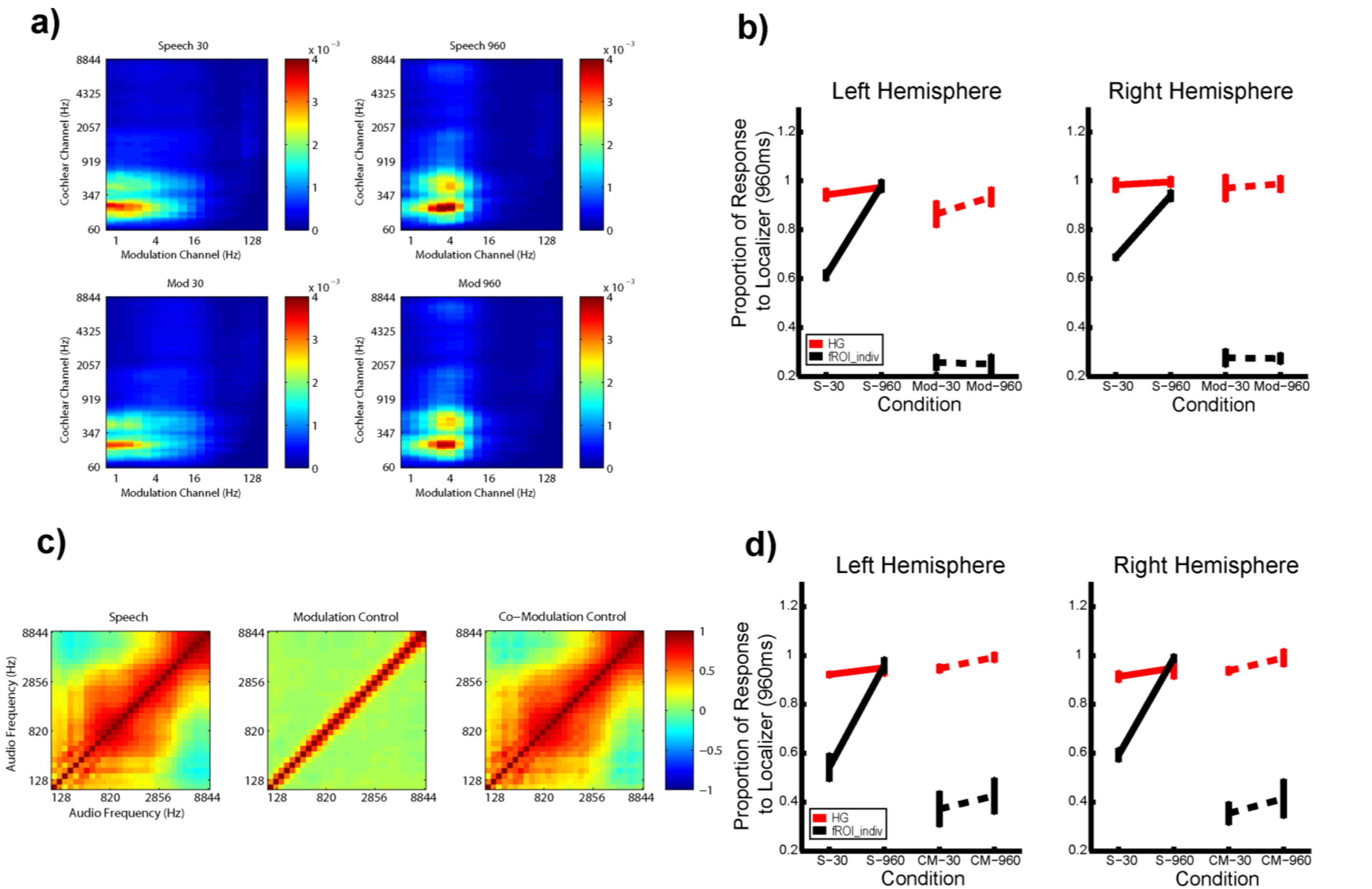

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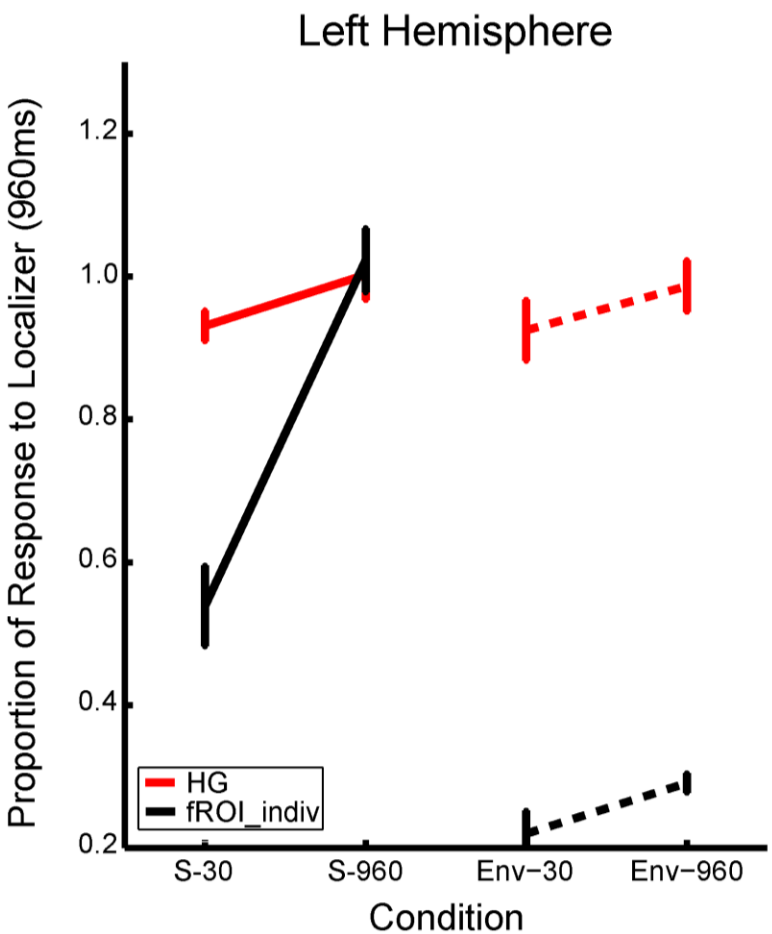
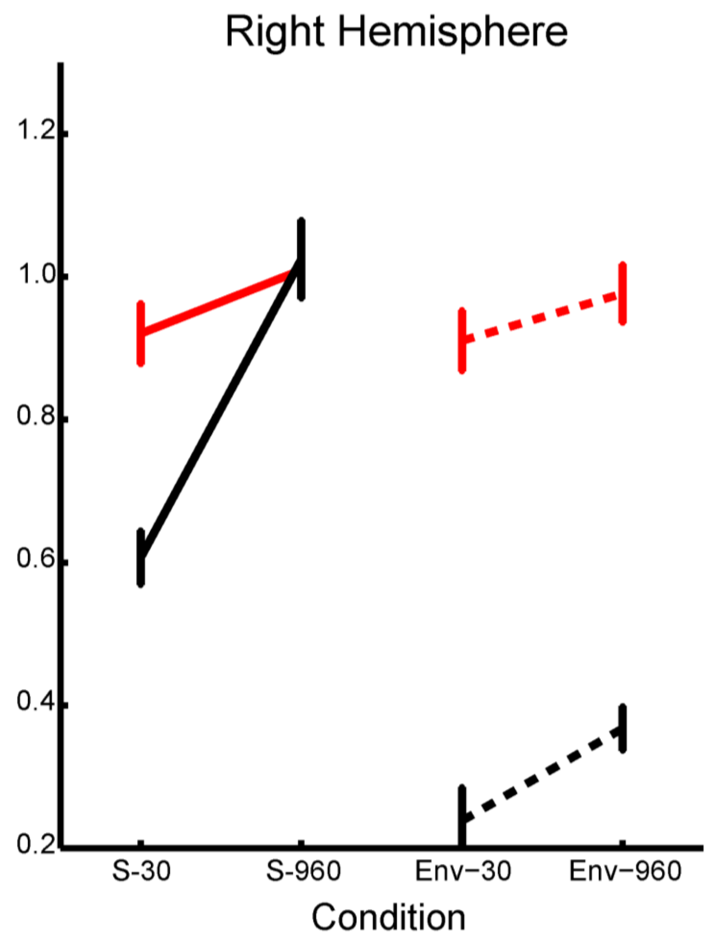
ENV30 

ENV960 





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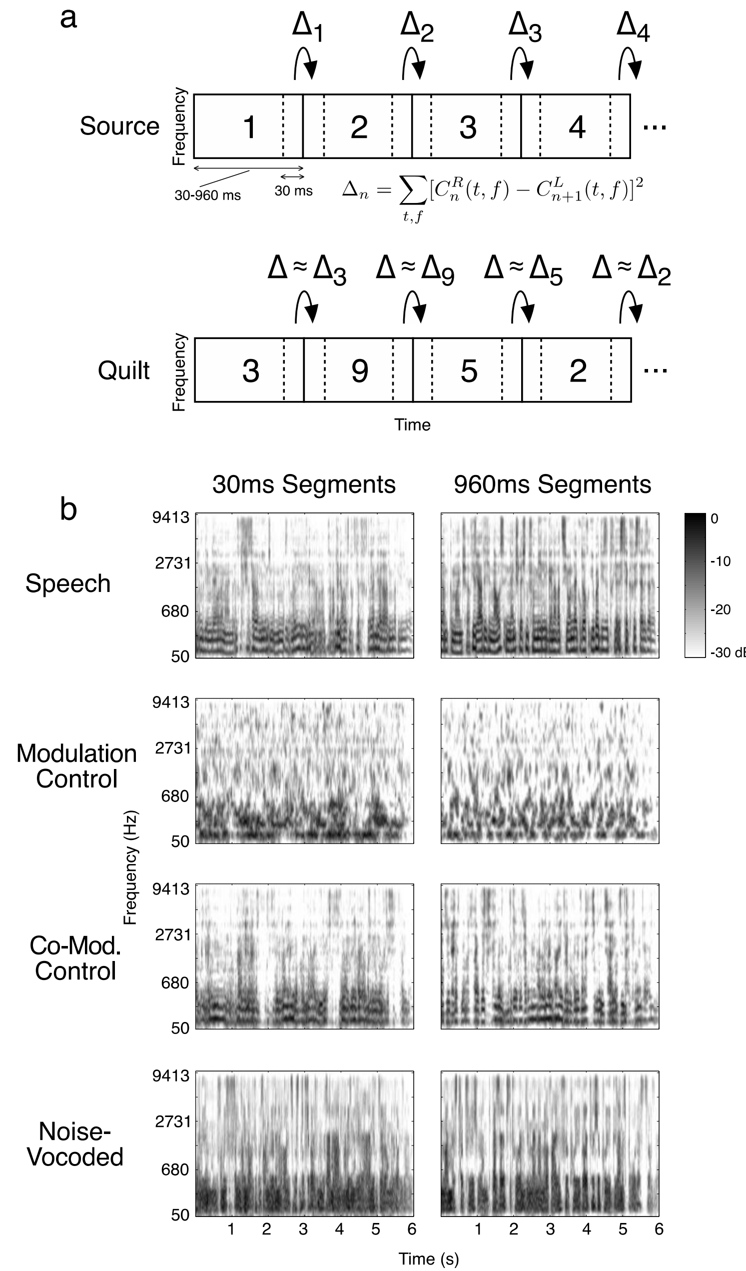

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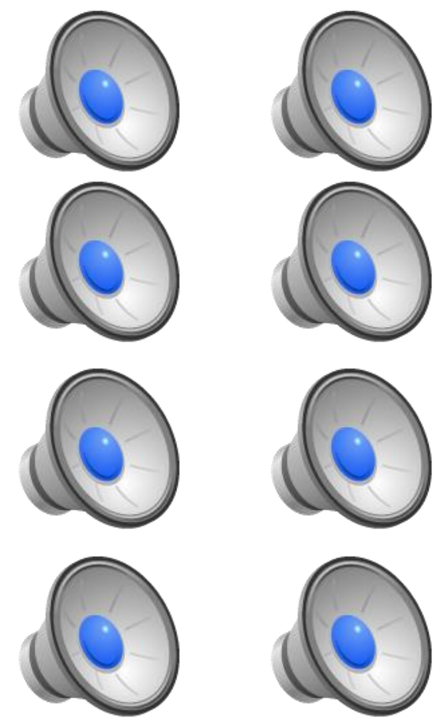
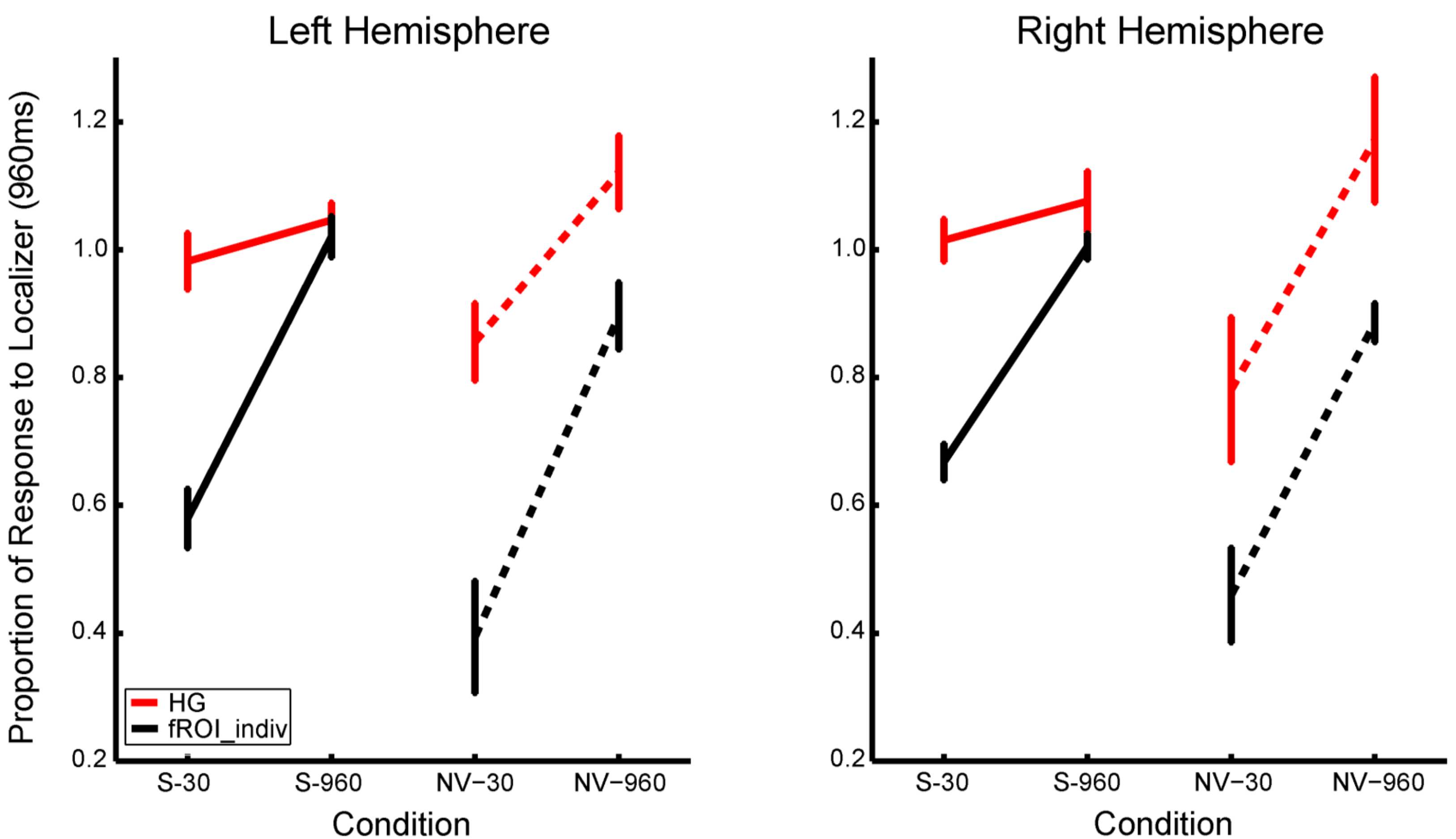
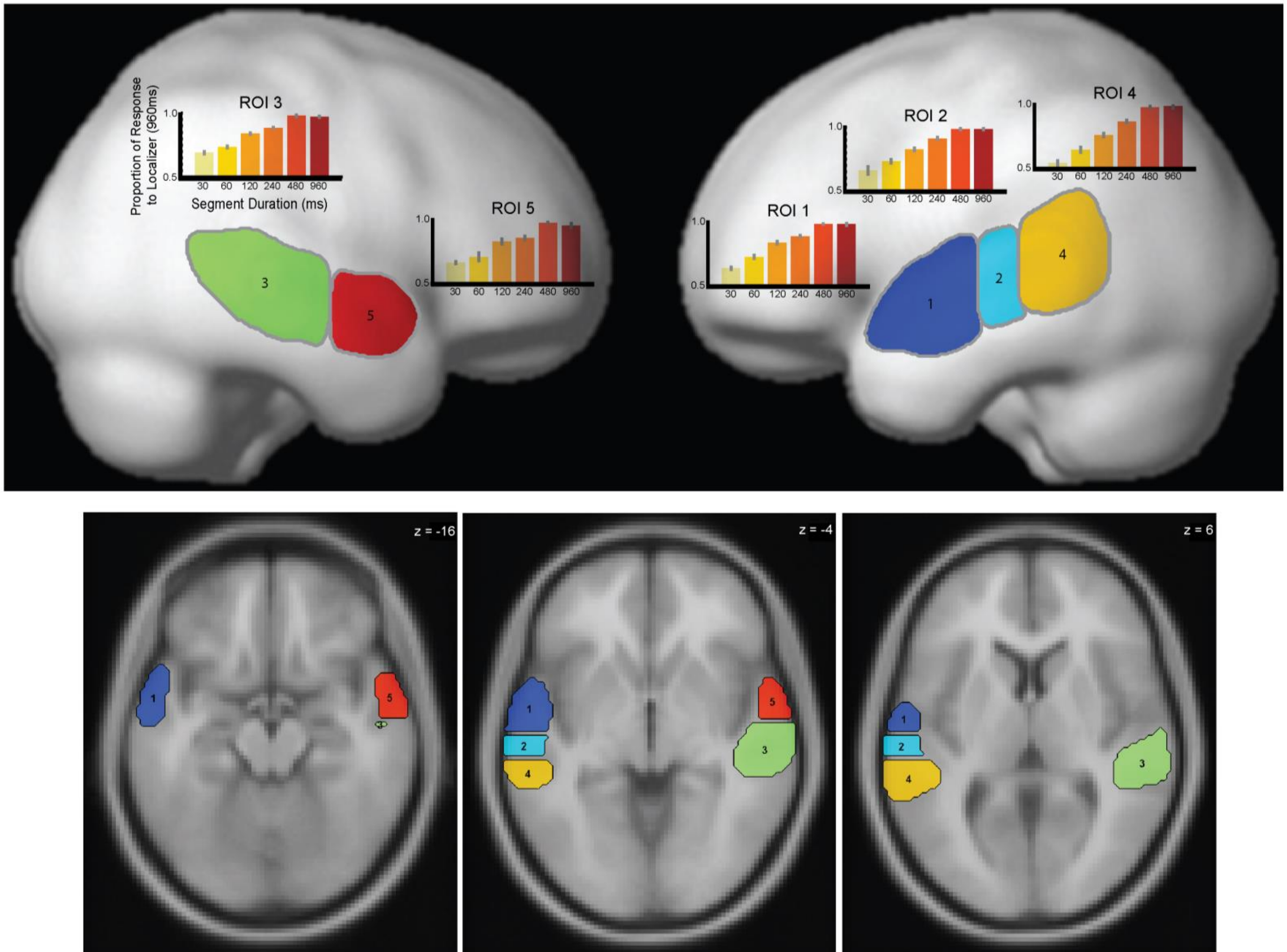


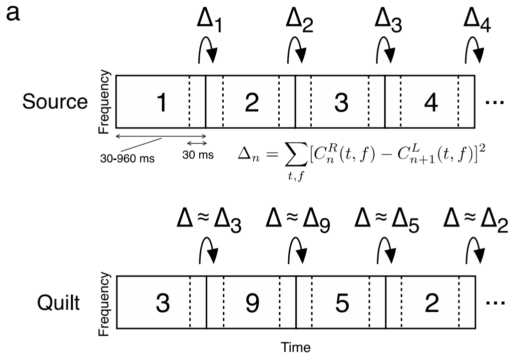
One possible account: responses are driven by prosody, and in particular the **prosodic pitch variation** that occurs in natural speech.
Such patterns are largely preserved in quilts made from long segments of speech, but are severely disrupted in quilts made from short segments.

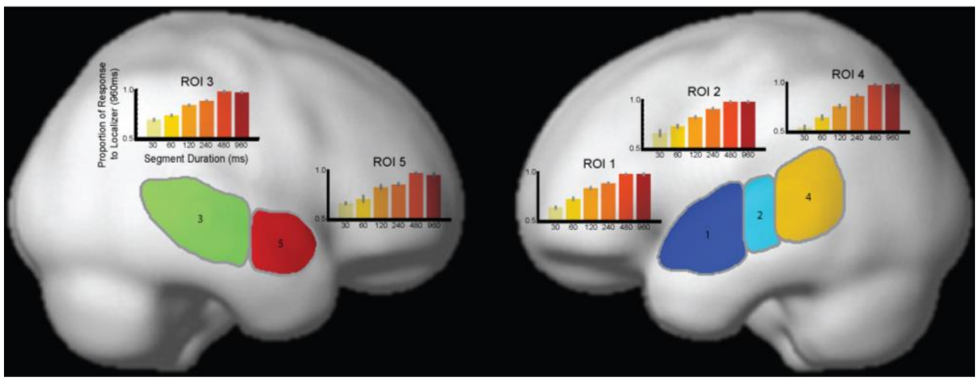
To test the importance of pitch variation, we presented quilts made from noise-vocoded speech. We generated noise-vocoded versions of each of our source speech recordings by imposing the envelopes of 10 frequency bands (ERB-spaced, covering the entire spectrum) on noise.

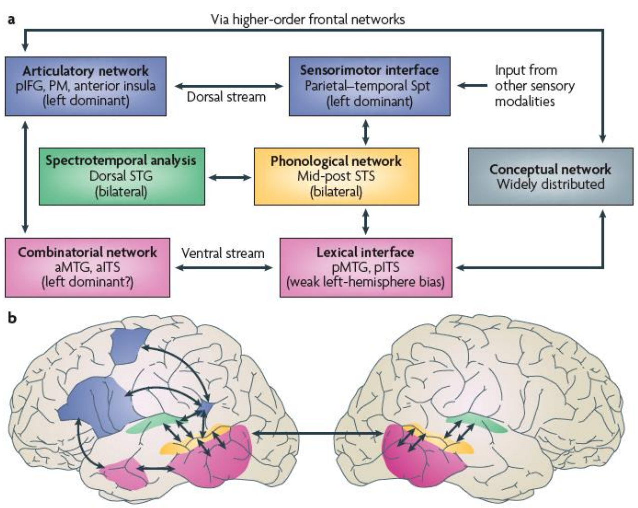


Functional ROIs revealed by a parcellation algorithm. The five color- coded fROIs are rendered onto the smoothed surface (top) and on individual axial slices (bottom) of a template brain (avg152Ts.nii in SPM). The response to the six different segment length conditions (normalized with respect to the L960 localizer condition) is plotted for each of the five fROIs. The response pattern is similar across ROIs.









Quilts

- Preserve statistical structure of speech (without linguistic structure)

Bilateral STS

- Sensitivity to speech
- Specificity to speech
- Intrinsic temporal window of <500 ms

An intermediate level between acoustics and linguistic analysis

- posit a stage/level of acoustic-phonetic analysis that generates intermediate representations prior to linguistic computation

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Outline

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What are appropriate linking hypotheses between domains?

- The experimental granularity problem

More naturalism versus more hypothesis testing?

2. The mapping problem

The parts list alignment challenge for cognitive neuroscience of language

The mapping problem

Table 1. Examples of hypothesised primitive objects/operations.

		Neuroscience
Objects		Dendrite/spine Neuron Cortical microcircuit Cortical column
Operations		Long term potentiation (LTP) Oscillation Adaptation synchronisation

Poeppel & Embick, 2005, 2014

The mapping problem

Table 1. Examples of hypothesised primitive objects/operations.

	Linguistics	Neuroscience
Objects	Distinctive feature	Dendrite/spine
	Timing slot	Neuron
	Morpheme	Cortical microcircuit
	Phrase	Cortical column
Operations	Feature spreading	Long term potentiation (LTP)
	Merge	Oscillation
	Concatenation	Adaptation
	Semantic composition	synchronisation

Poeppel & Embick, 2005, 2014

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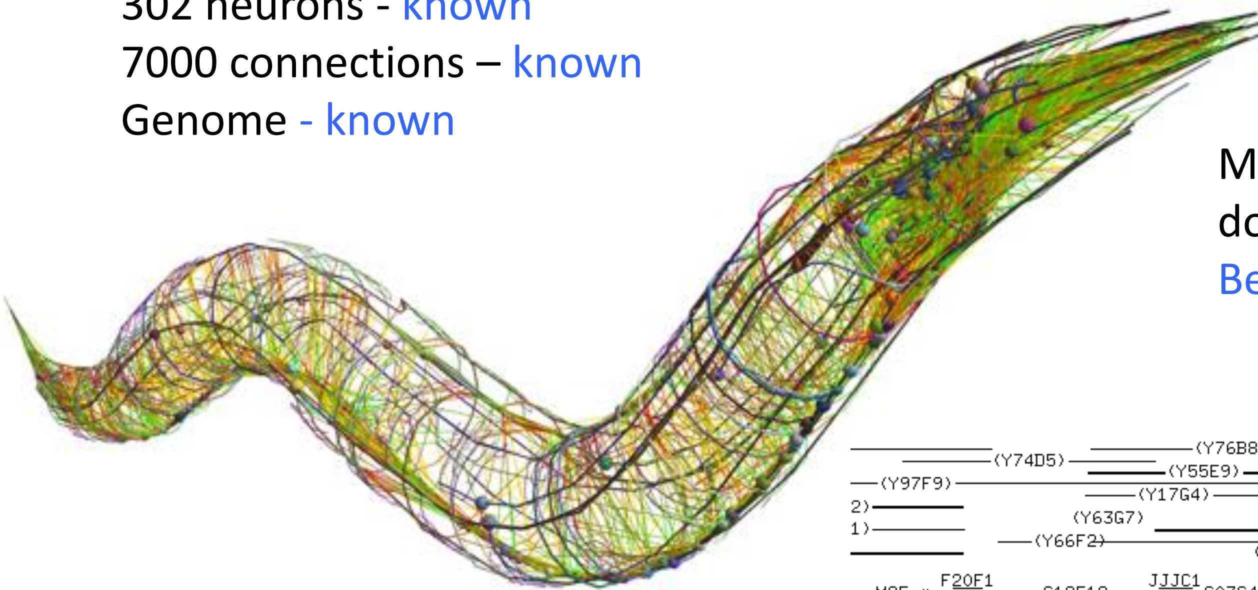
There is an absence of 'linking hypotheses' by which we explore how brain mechanisms form the basis for linguistic computation.

Aligning the alphabets or primitives or atoms or parts lists is a formidable challenge.

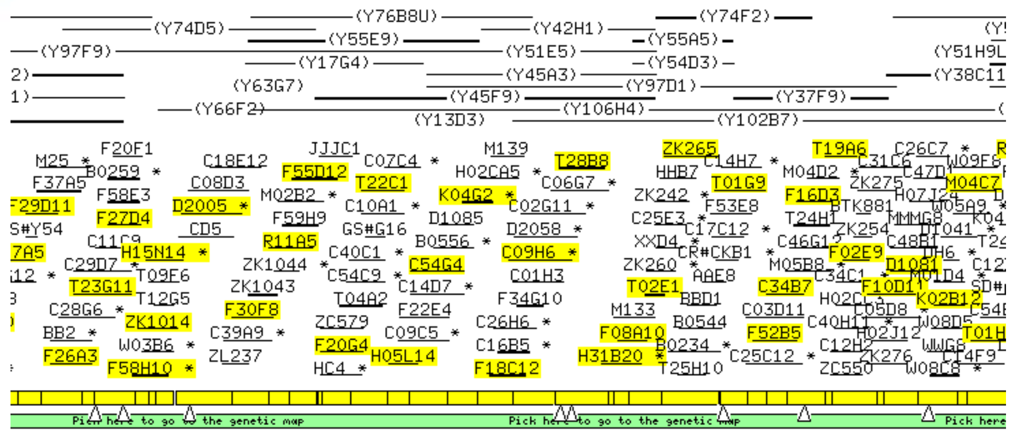
Poeppel & Embick, 2005, 2014

The c. elegans effort – a beauty and a beast

302 neurons - known
7000 connections – known
Genome - known



Model of how the worm does what it does?
Beyond our understanding!



"I think it's fair to say…that our understanding of the worm has not been materially enhanced by having that connectome available to us. We don't have a comprehensive model of how the worm's nervous system actually produces the behaviors. What we have is a sort of a bed on which we can build experiments—and many people have built many elegant experiments on that bed. But that connectome by itself has not explained anything."   *Tony Movshon, NYU, Scientific American 2012*

The mapping problem: seeking the right computational granularity

Linguistics

distinctive feature
morpheme
noun phrase
clause
concatenation
linearization
phrase-structure generation
semantic composition

?

Neuroscience

dendrites, spines
cell-assembly/ensemble
population
cortical column
long-term potentiation
receptive field
oscillation
synchronization

fractionate into
generic formal operations

identify basis for
generic formal operations

segmentation
concatenation
comparison
recursion

segmentation
concatenation
comparison
recursion

Poeppel & Embick, 2005; Poeppel 2012; Embick & Poeppel 2014

The mapping problem: seeking the right computational granularity

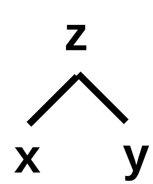
Desiderata for a model bridging neuronal mechanisms and linguistic representation

Neurobiological mechanisms that can form the basis of elemental steps involved in most linguistic computation:

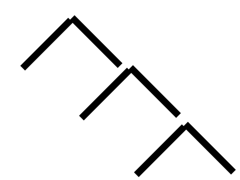
concatenation

x---y

constituency



recursion



This is the granularity - and level of abstractness - of operations that can profitably be studied in animal research as well, doing away with questions such as "are humans different or better or higher, or not" and turning to the typical questions such as: "How does this work?"

Cortical tracking of hierarchical linguistic structures in connected speech

Nai Ding, Lucia Melloni, Xing Tian, Hang Zhang, David Poeppel

Nature Neuroscience, 2016

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NYU
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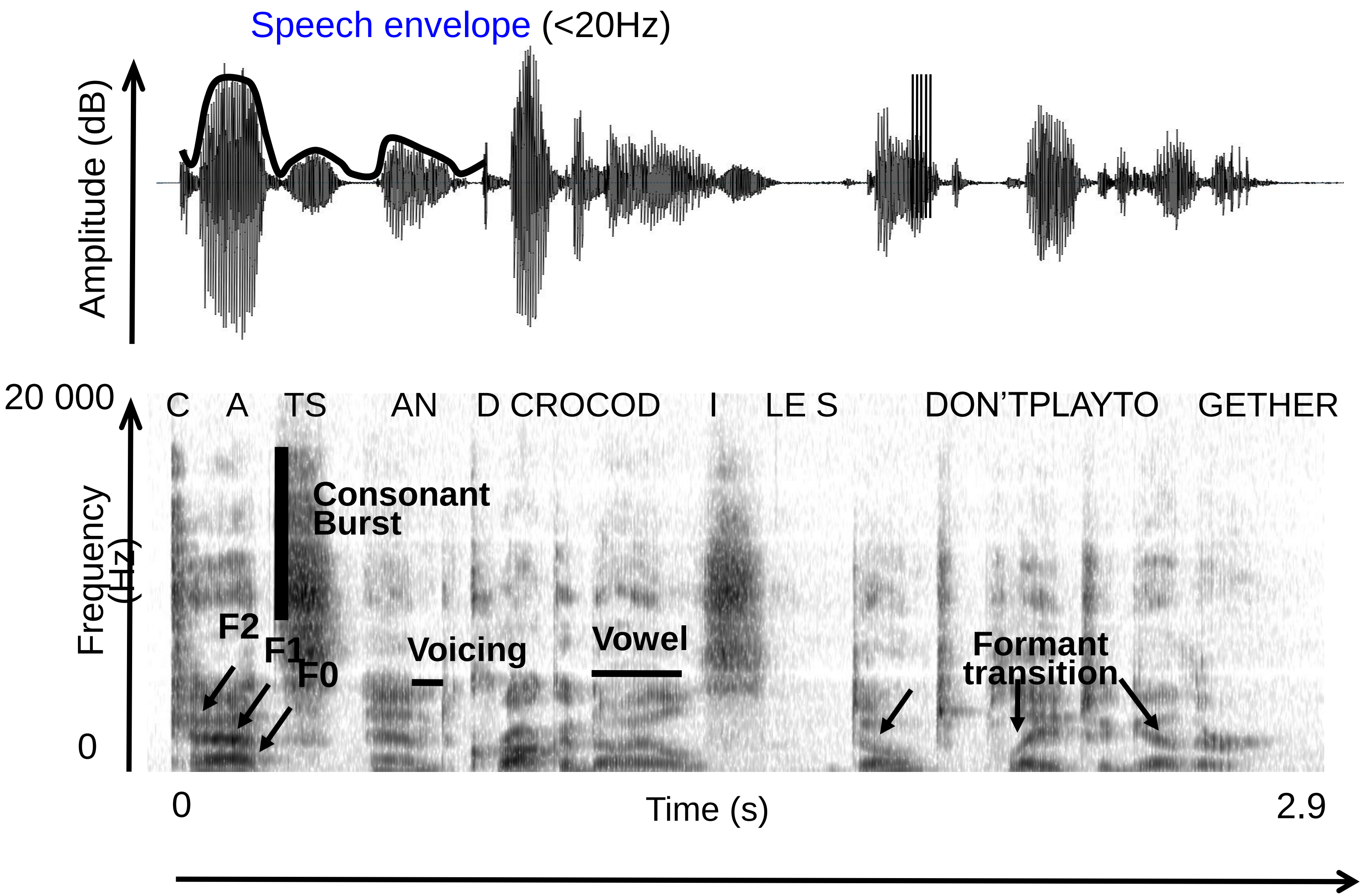
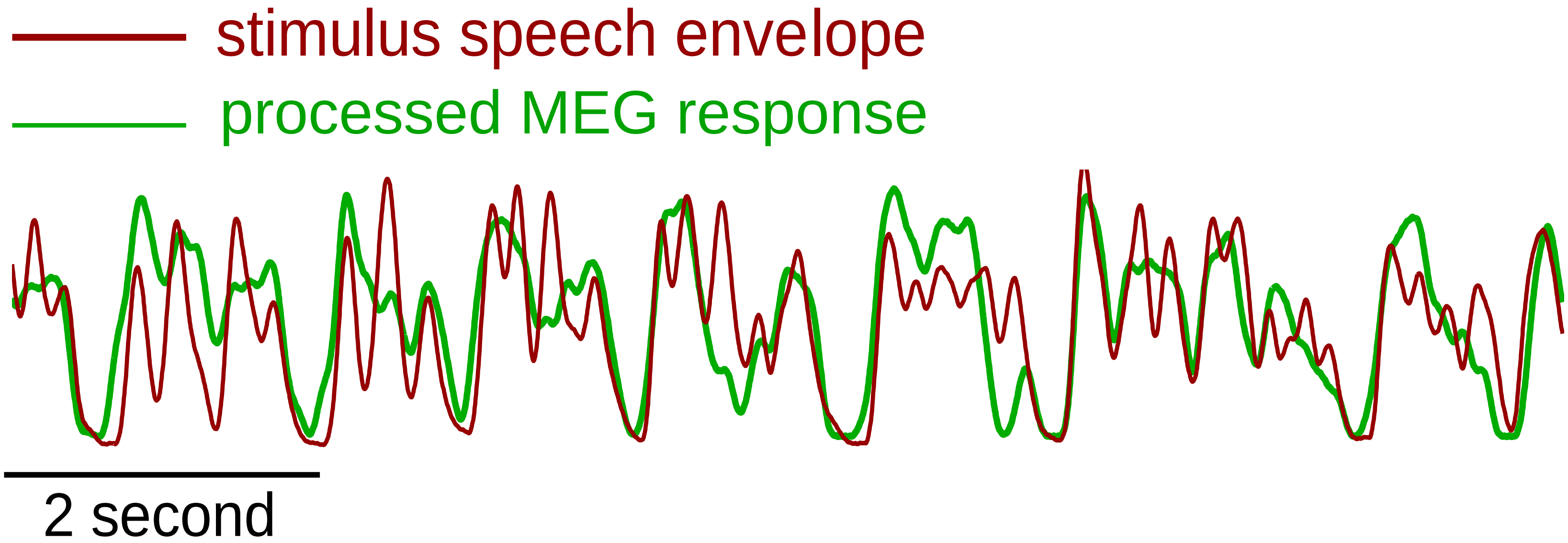


Speech envelope (<20Hz)
Amplitude (dB)
20 000
Frequency (Hz)
0
C A TS AN D CROCOD I LE S DON'TPLAYTO GETHER
Consonant Burst
F2
F1
F0
Voicing
Vowel
Formant transition
0
Time (s)
2.9

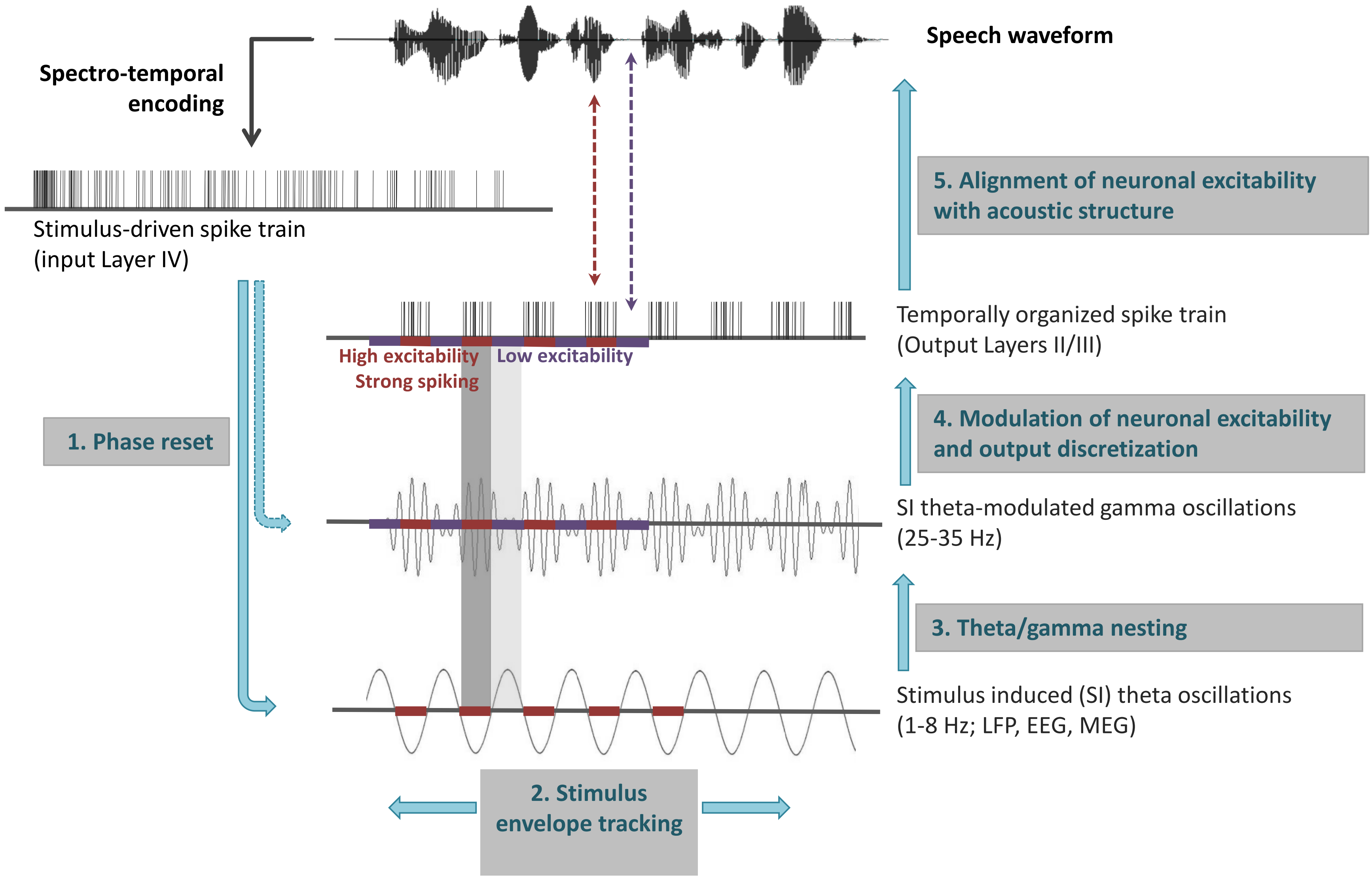
Auditory cortical activity is entrained to the envelope => syllabic rhythm.



Neural entrainment is seen in both the theta and delta bands during spoken language comprehension.

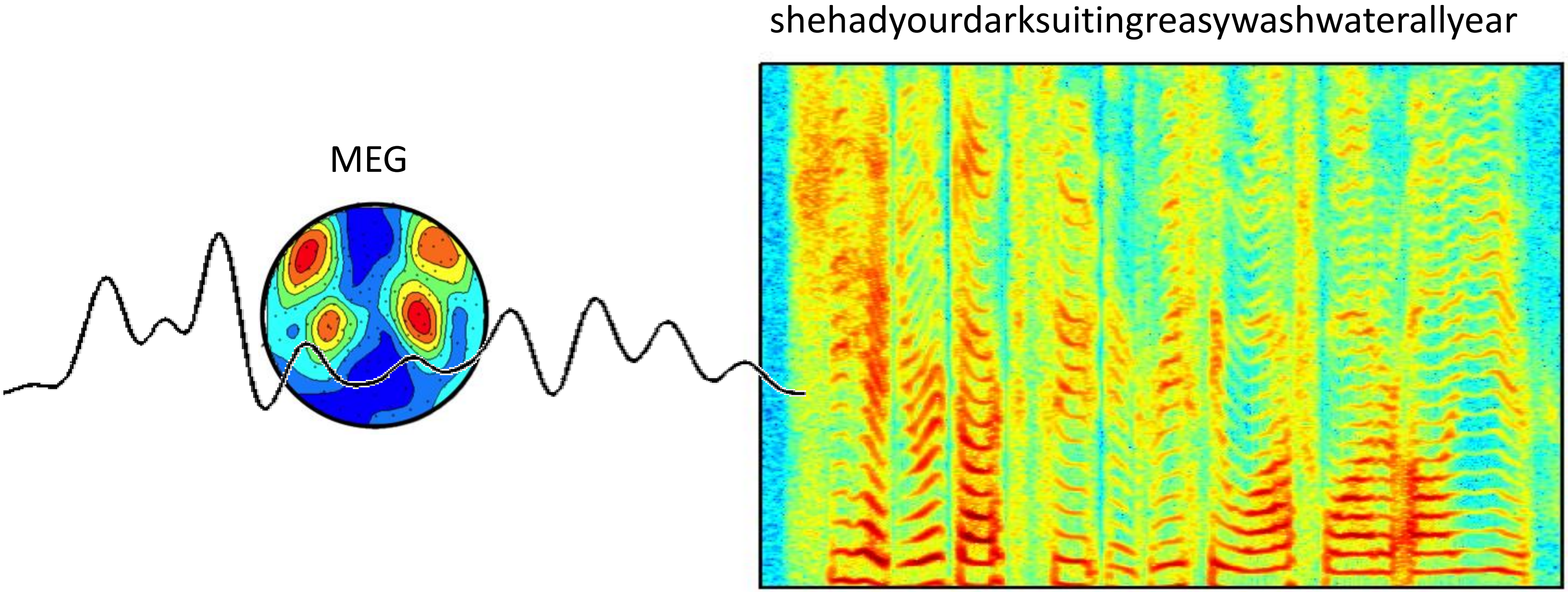
e.g. Luo & Poeppel, Neuron 2007; Ding & Simon, PNAS 2012; J Neuroscience 2013

Cortical oscillations and speech processing: emerging computational principles and operations



Giraud & Poeppel, 2012, *Nat Neurosci*

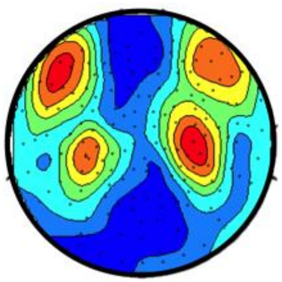
Parsing events, e.g. syllables

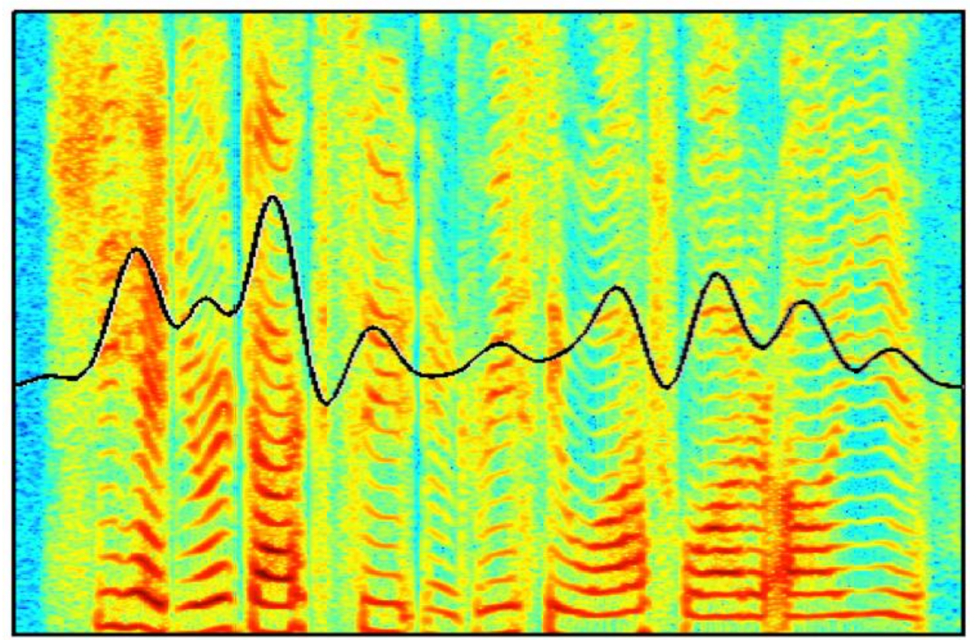


Courtesy of Keith Doelling, NYU

Parsing events, e.g. syllables

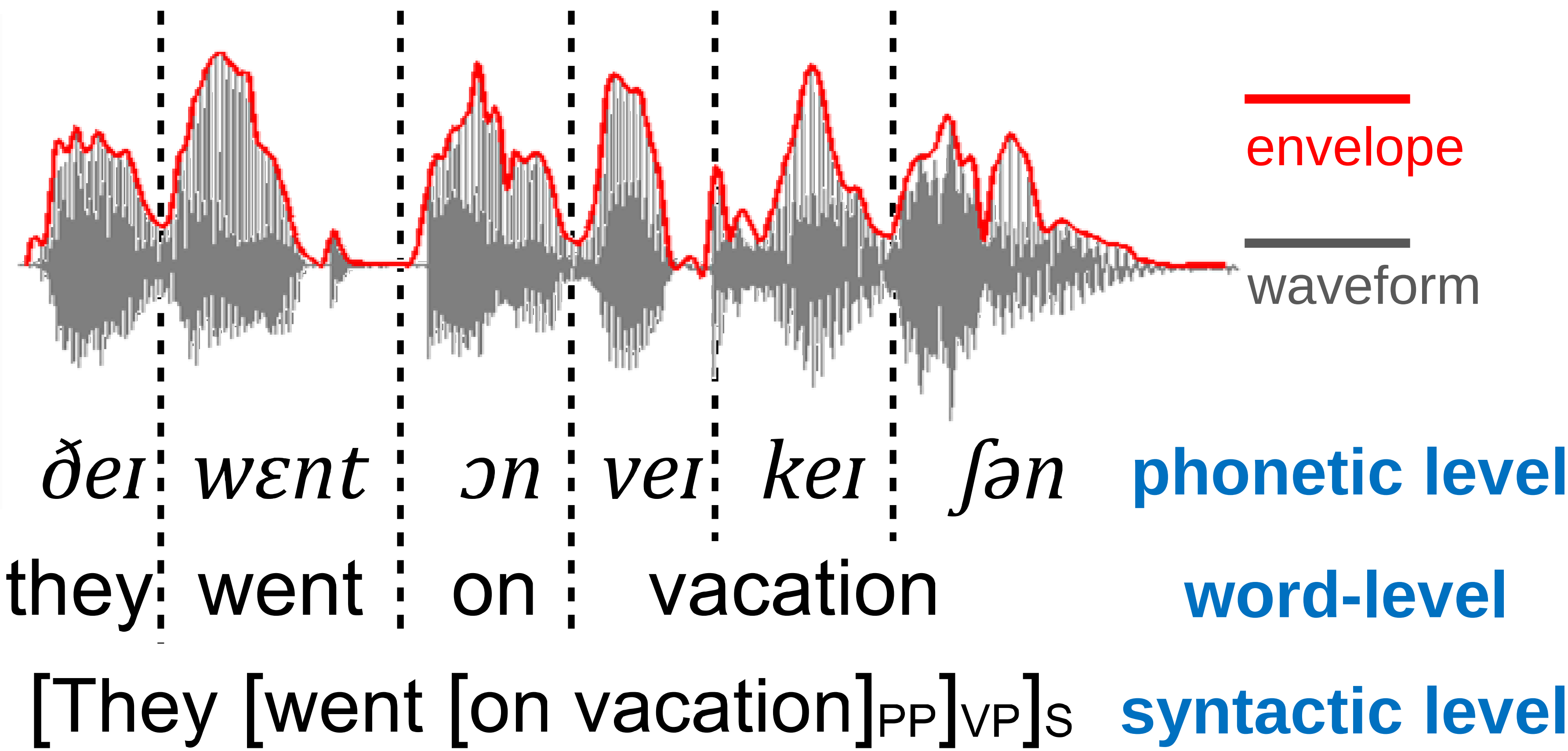
she had your dark suit in greasy wash water all year



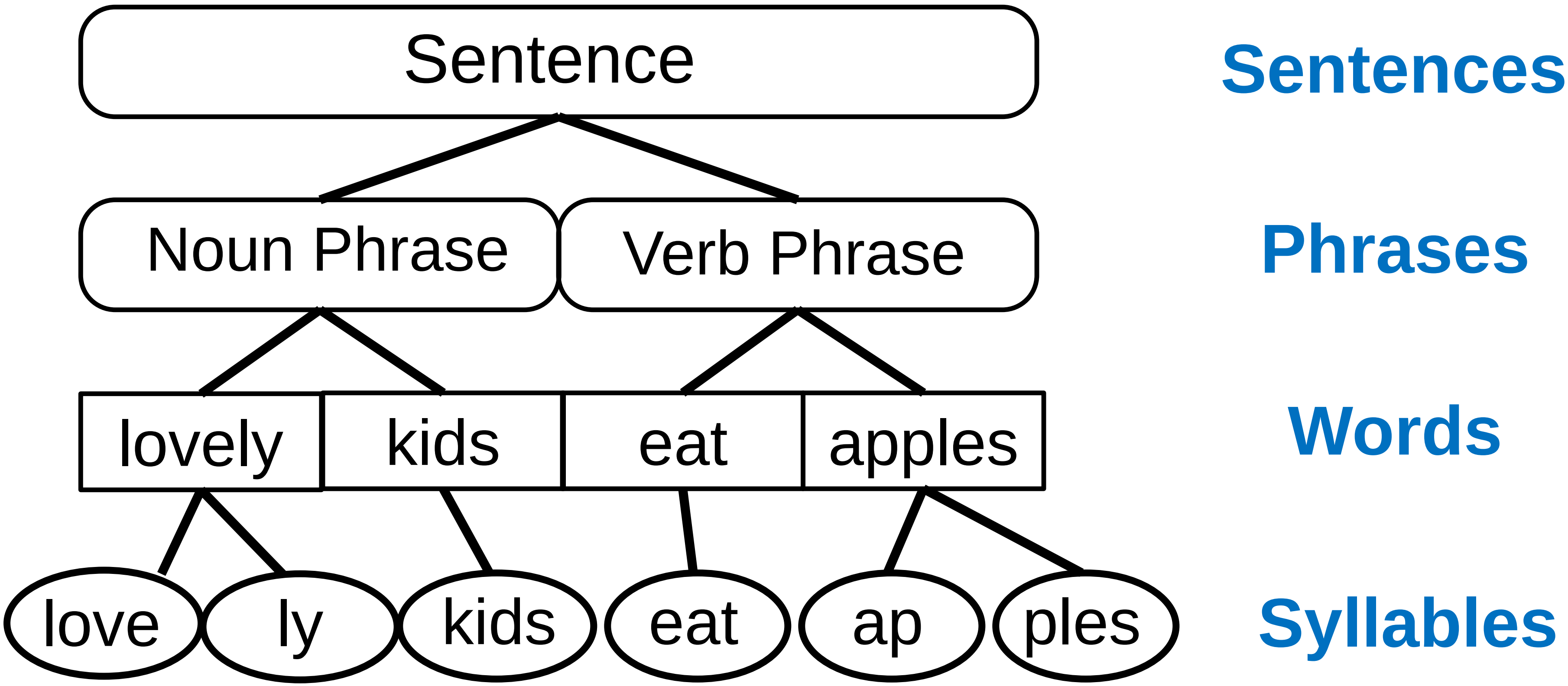


Courtesy of Keith Doelling, NYU

Boundaries between syllables are usually defined by the speech envelope, but not the boundaries between words and phrases.

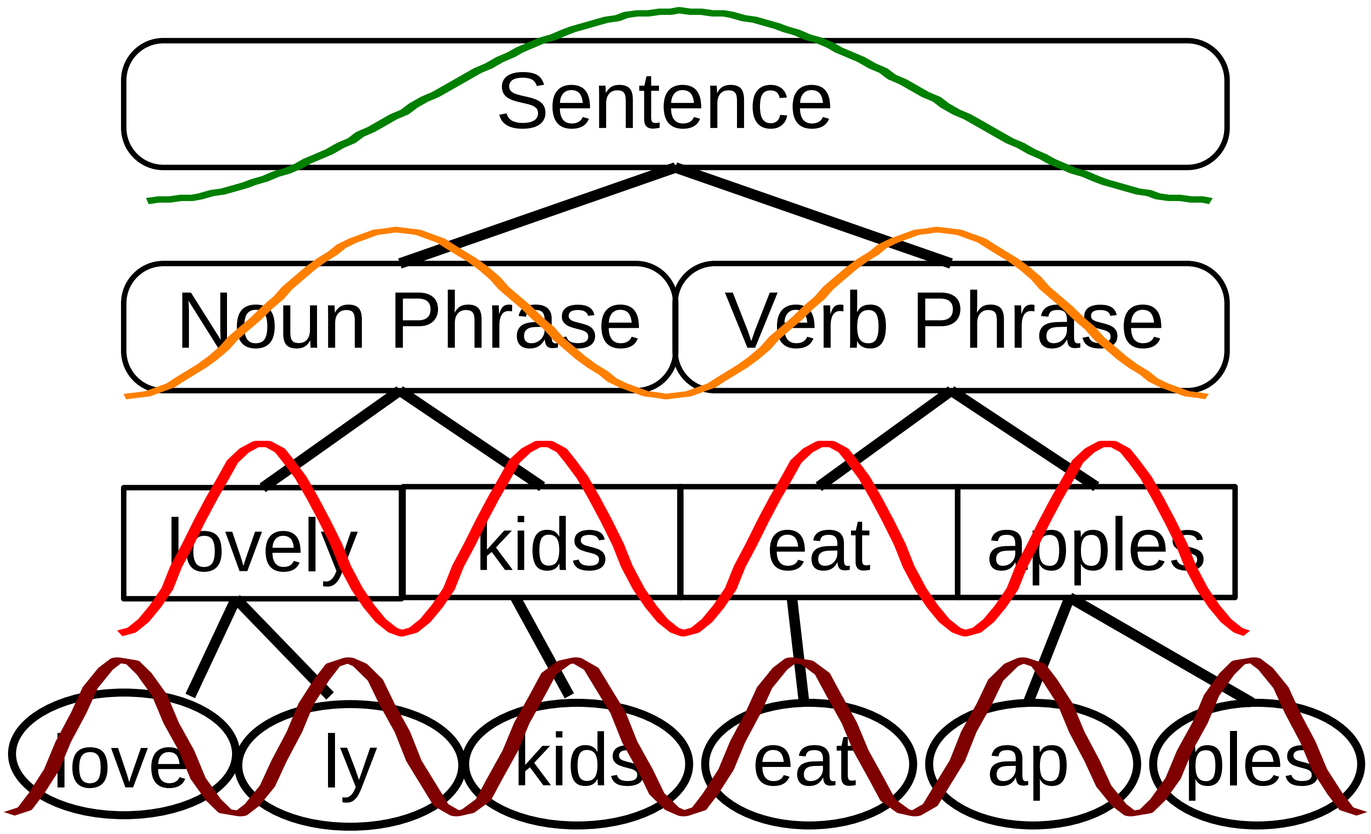


Parsing Linguistic Structures Embedded in Continuous Speech

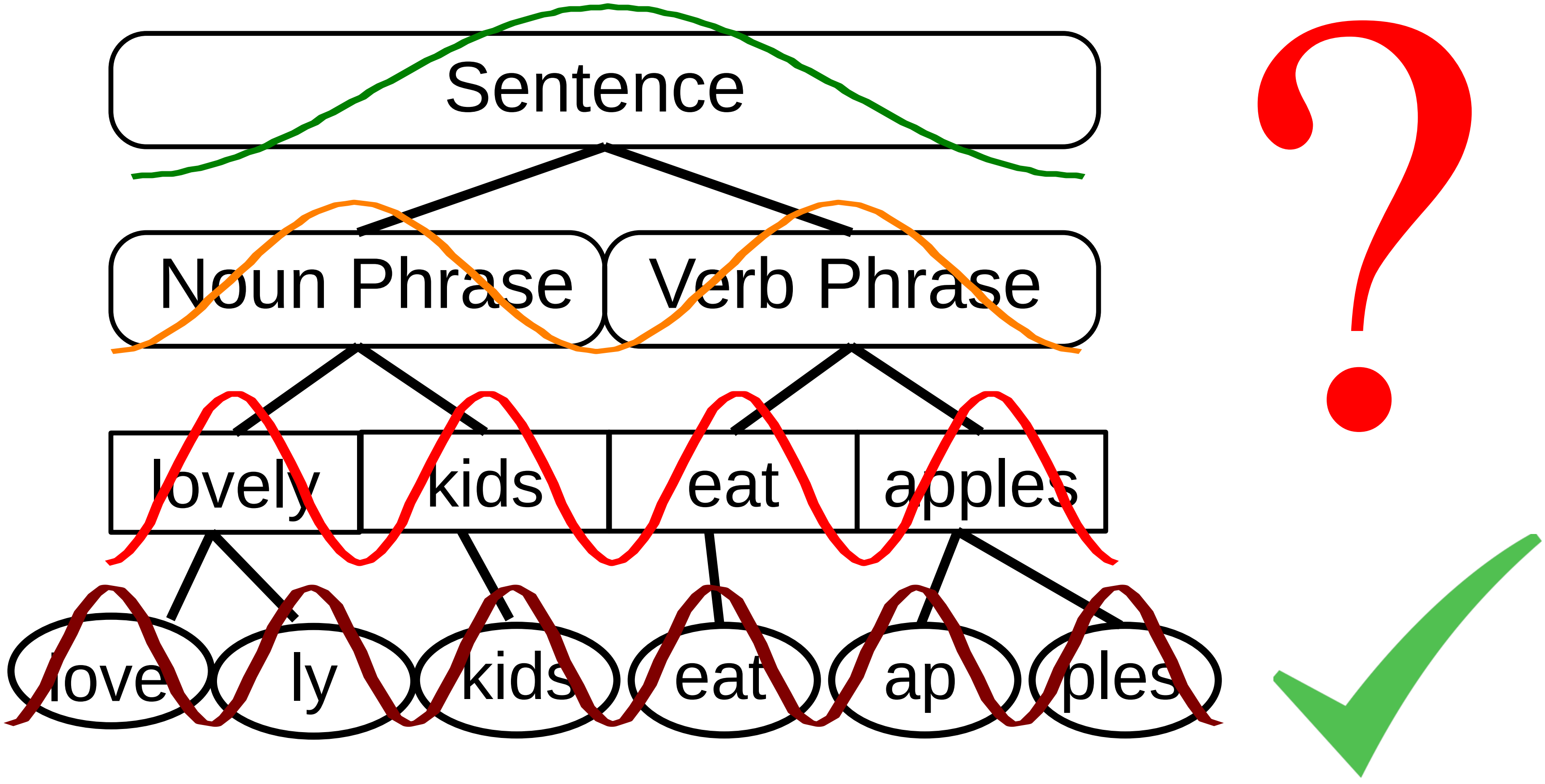


The neural code for each linguistic unit must change at the rate of that linguistic unit.

Hierarchical Entrainment to the Hierarchical Linguistic Structure?

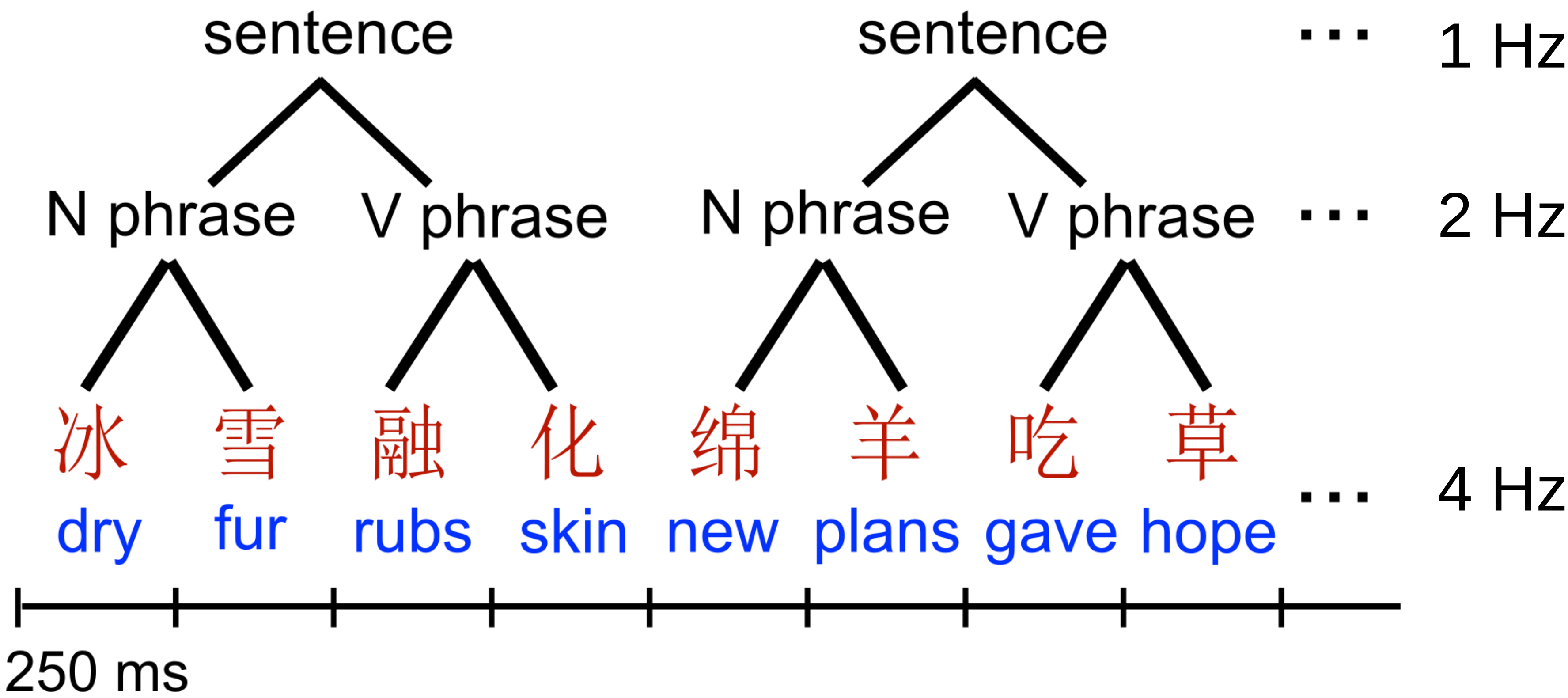


Hierarchical Entrainment to the Hierarchical Linguistic Structure?



e.g., Luo & Poeppel, 2007
Ding & Simon, 2012

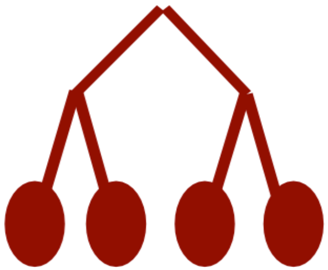
A Sequence with Hierarchical Linguistic Structures

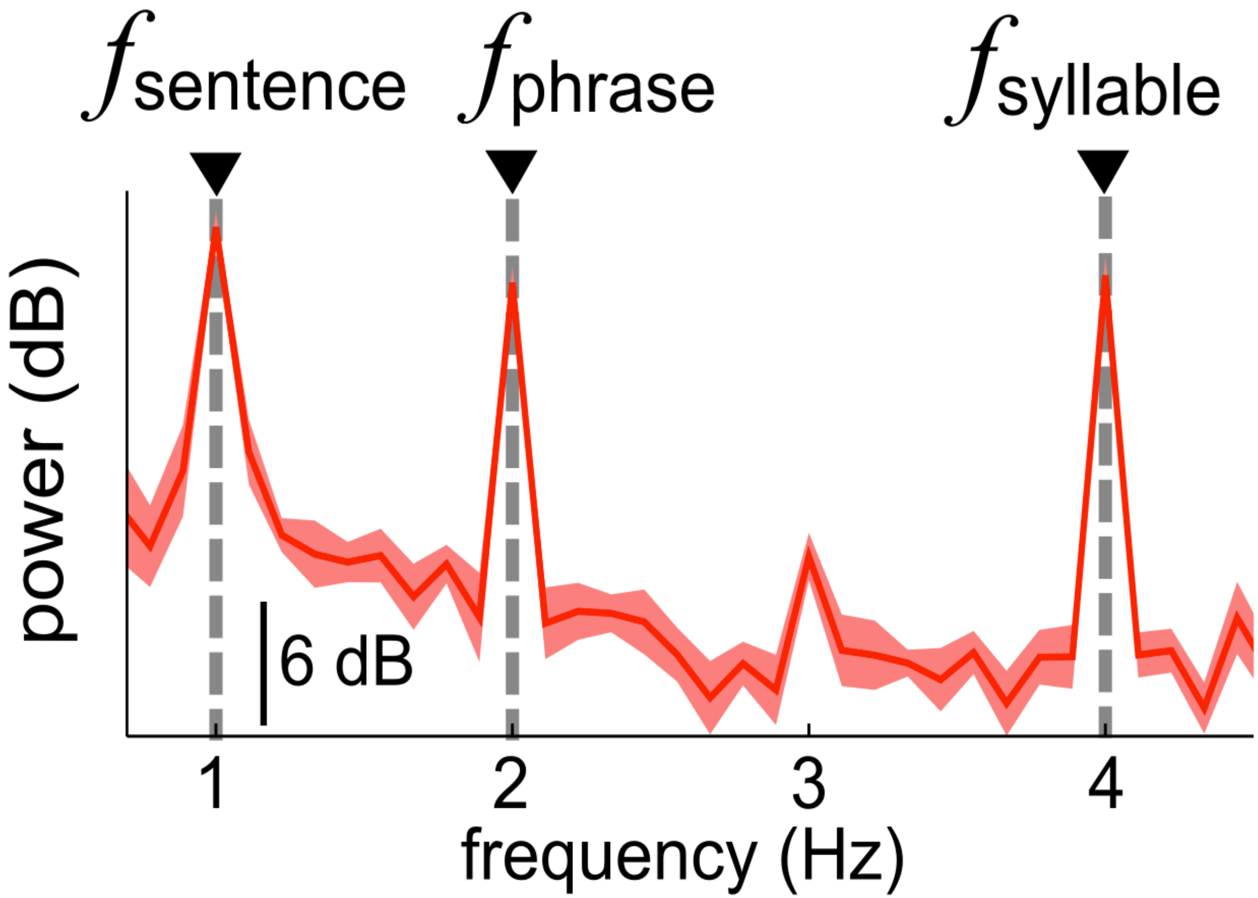


- 16 native listeners of Mandarin Chinese
- Outlier detection: occasionally, the noun phrases of two sentences will be switched, creating two nonsense sentences.
- Data processed by a spatial filter optimized to extract phase-locked activity.

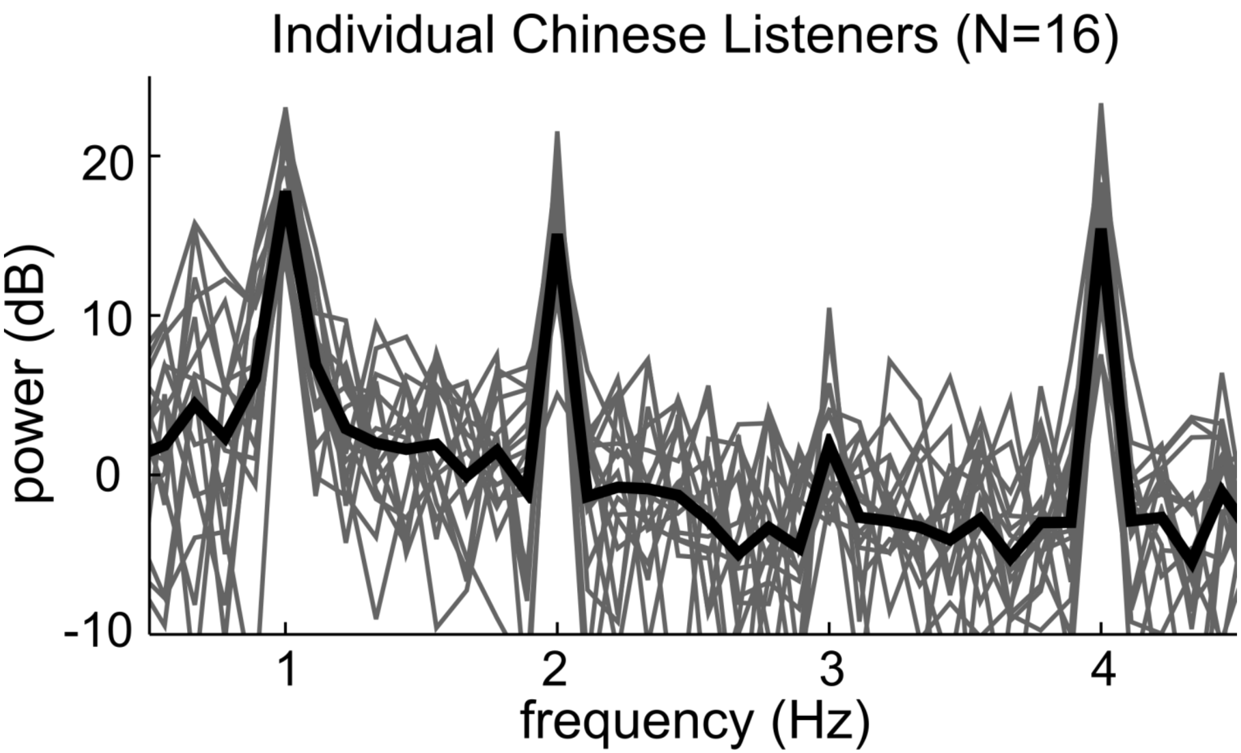
(Wang et al., J Neurophys 2012; Ding & Simon, PNAS 2012; de Cheveigné & Simon, 2008)

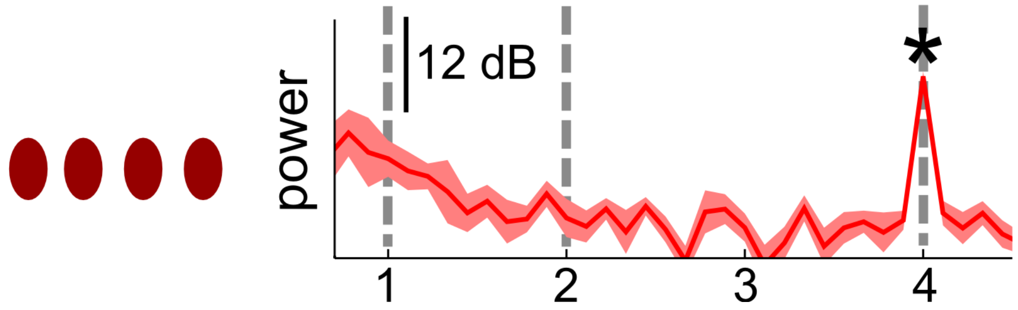
Cortical Activity Tracks Hierarchical Linguistic Rhythms



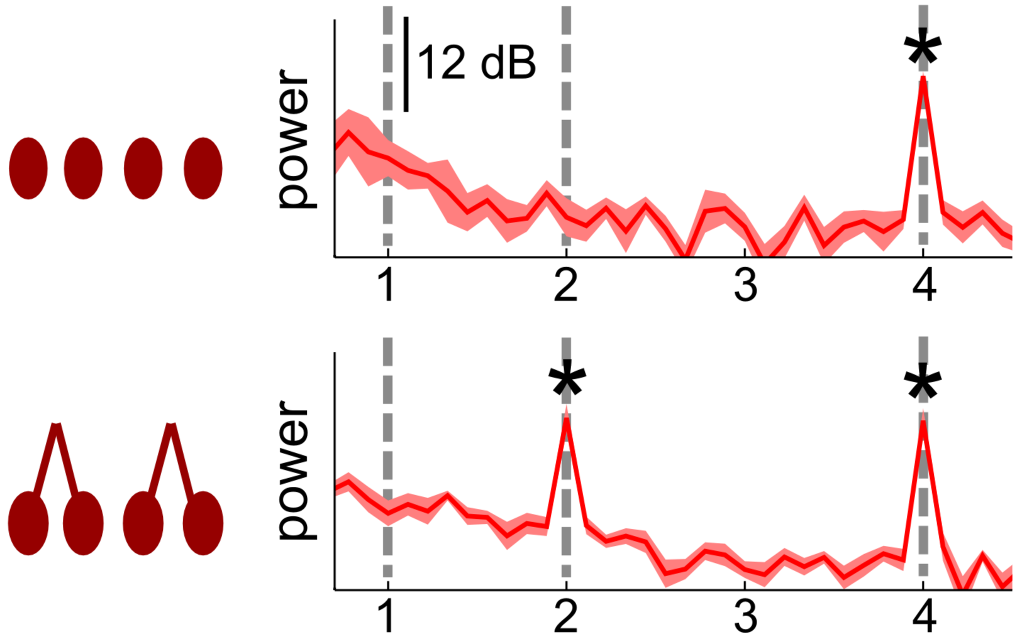


Data from Individual Listeners

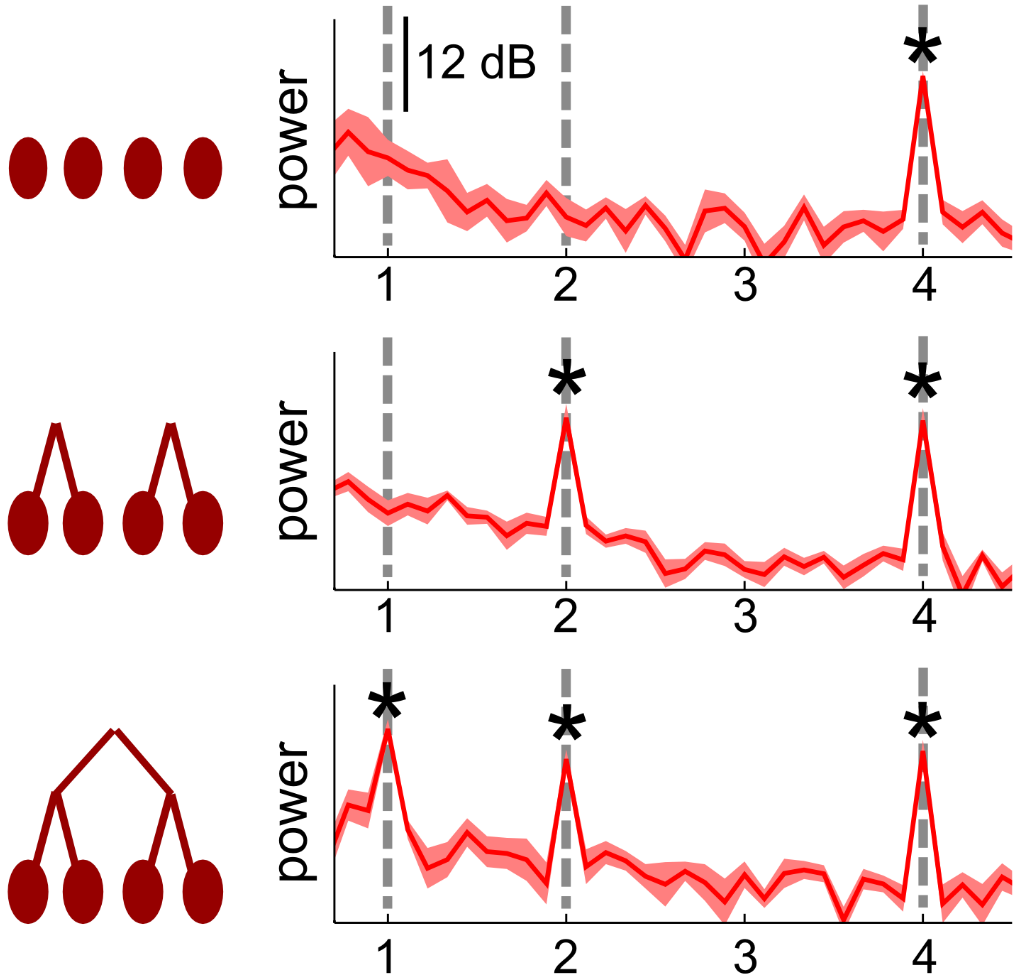




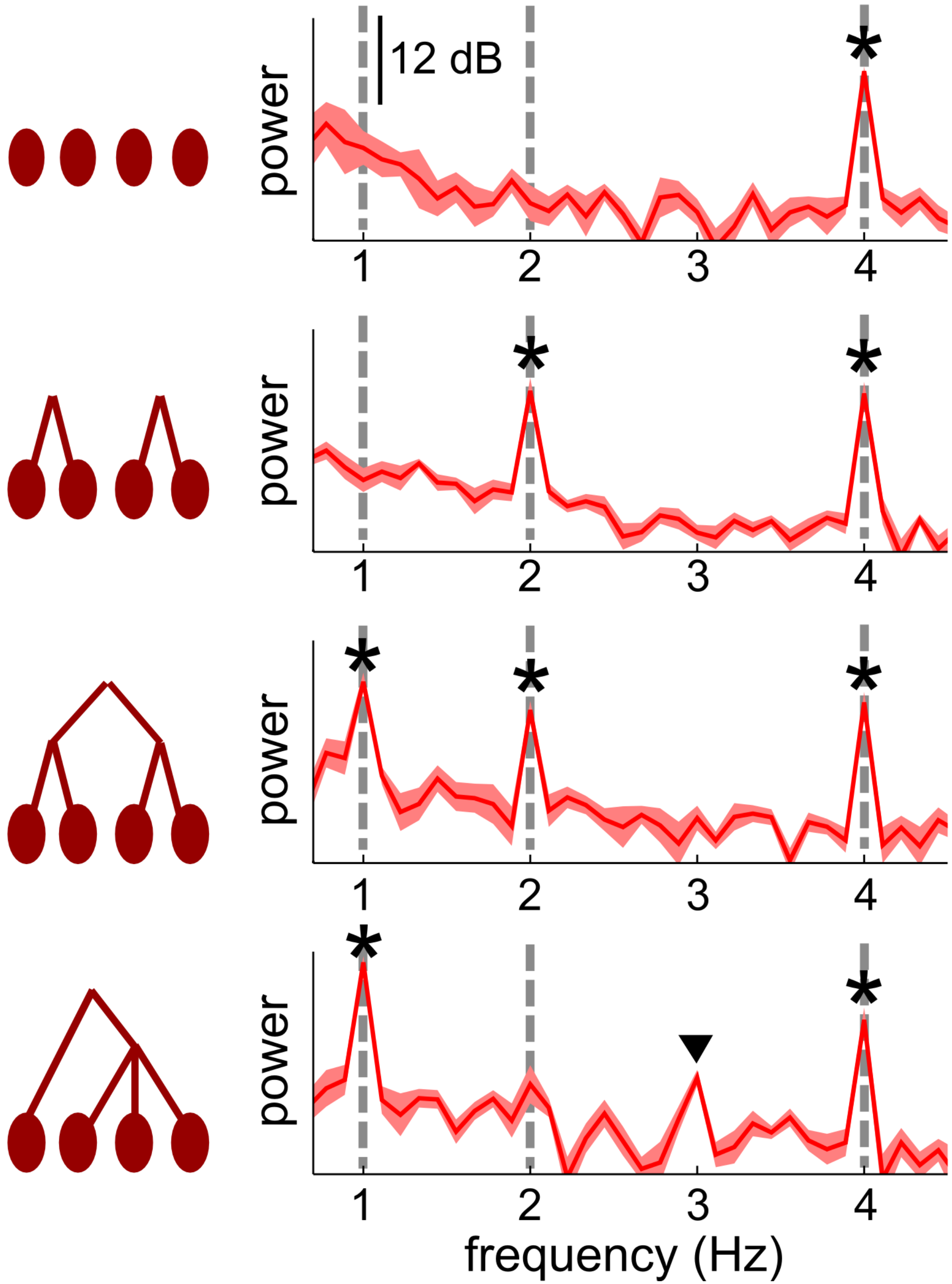
12 dB
power
*
1
2
3
4



12 dB
power
*
1
2
3
4
power
*
*
1
2
3
4

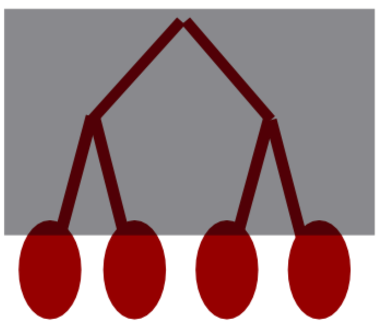


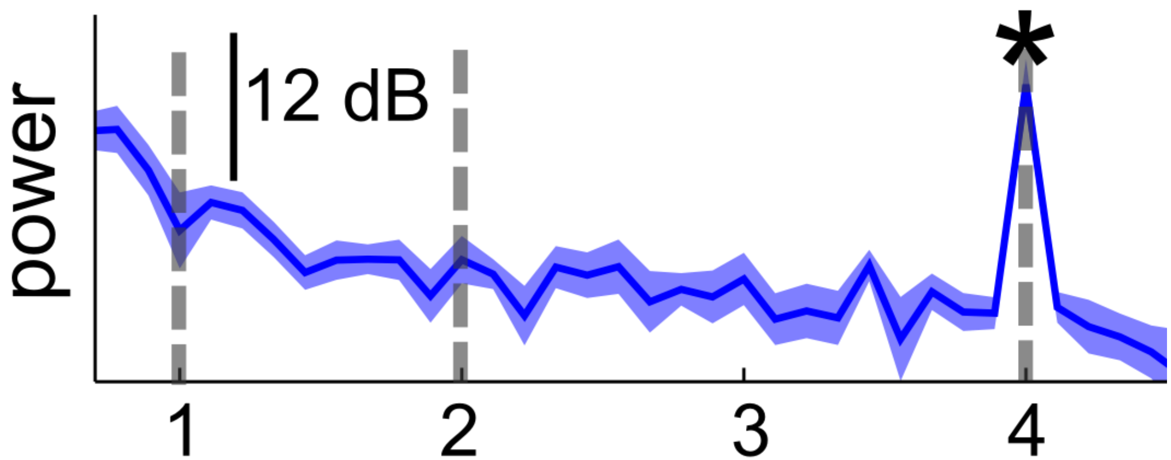
12 dB
power
power
power
*
*
*
*
*
*
1
2
3
4
1
2
3
4
1
2
3
4


12 dB
power
power
power
power
1
2
3
4
frequency (Hz)

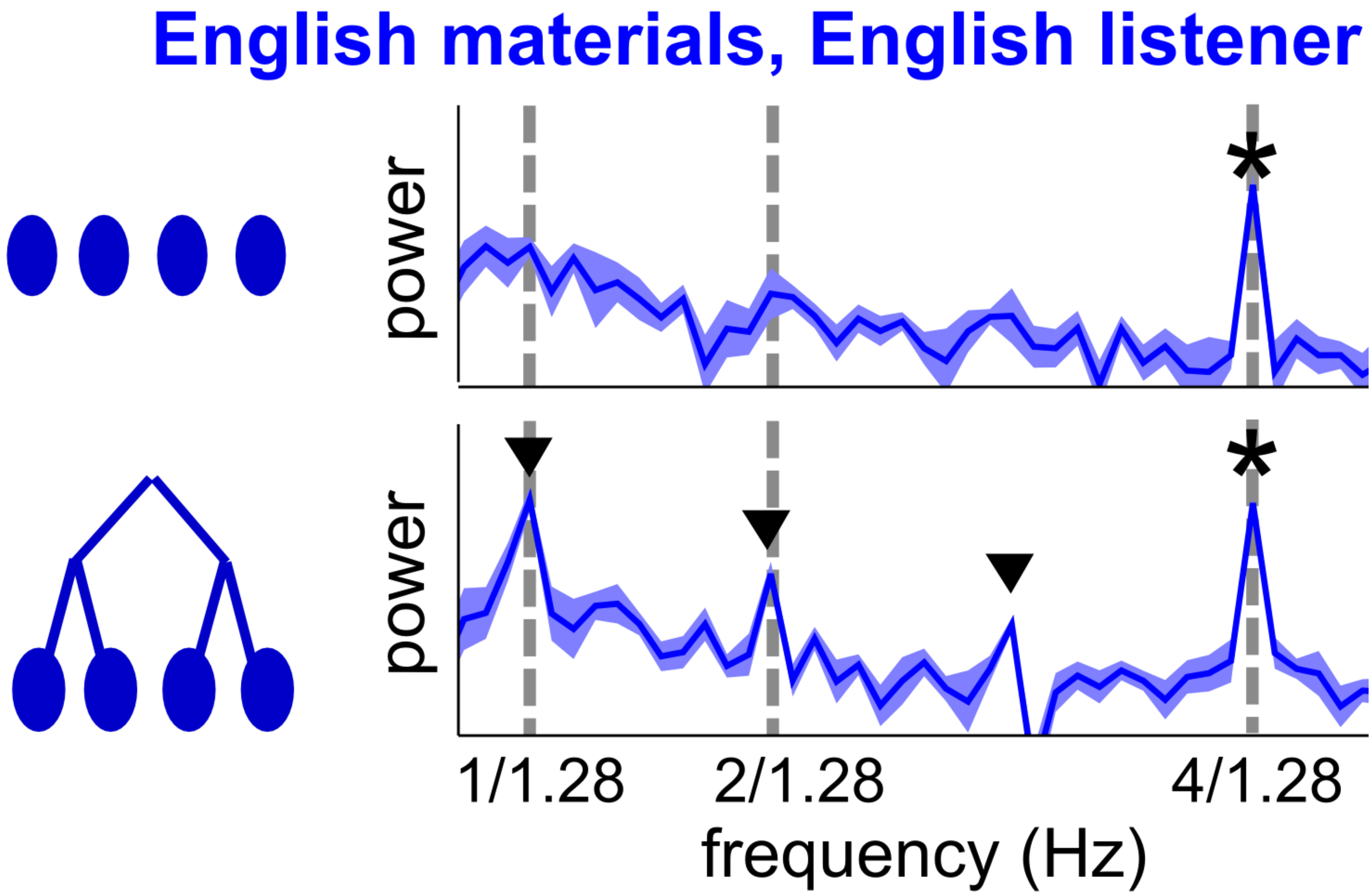
Non-speakers Only Track the Syllabic/Acoustic Rhythm

Chinese materials, English listener





Hierarchical Entrainment for English

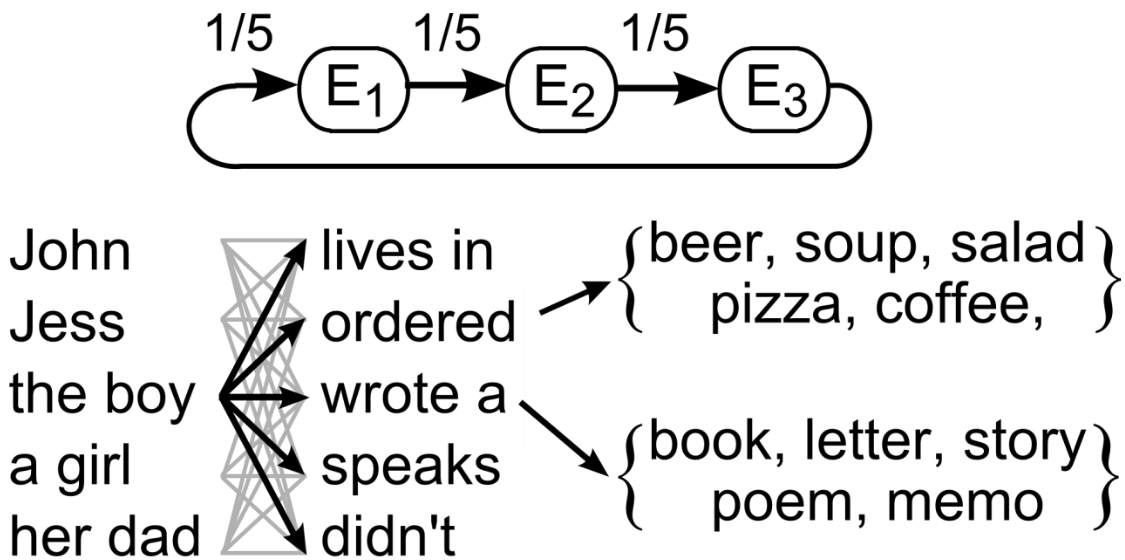


Interim Summary

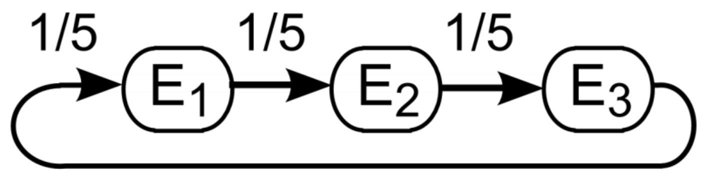
- Cortical activity is entrained to the phrasal and sentential rhythms of speech.

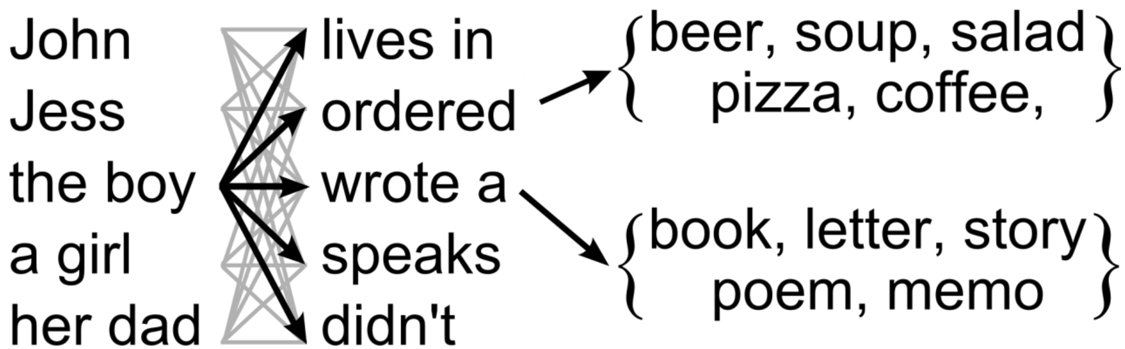
- Phrasal/sentential level entrainment is seen for both Chinese and English, and not confounded by encoding of acoustic features.

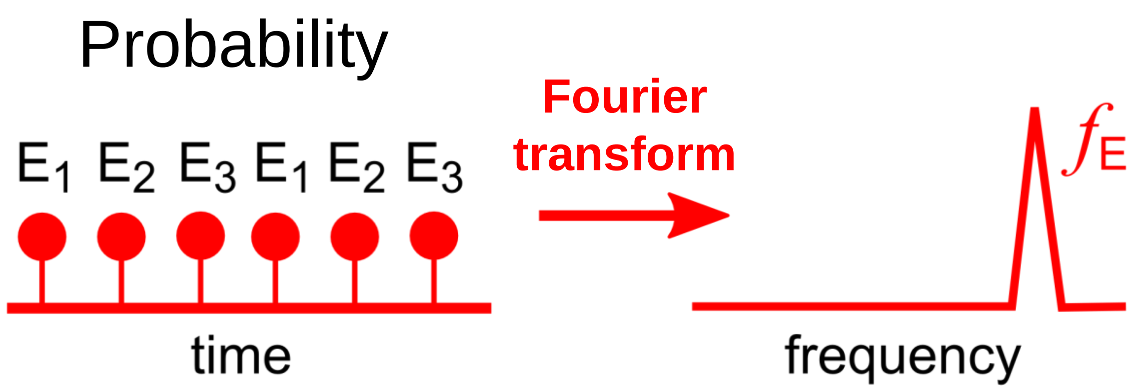
A Markov Chain Language with Constant Transitional Probability



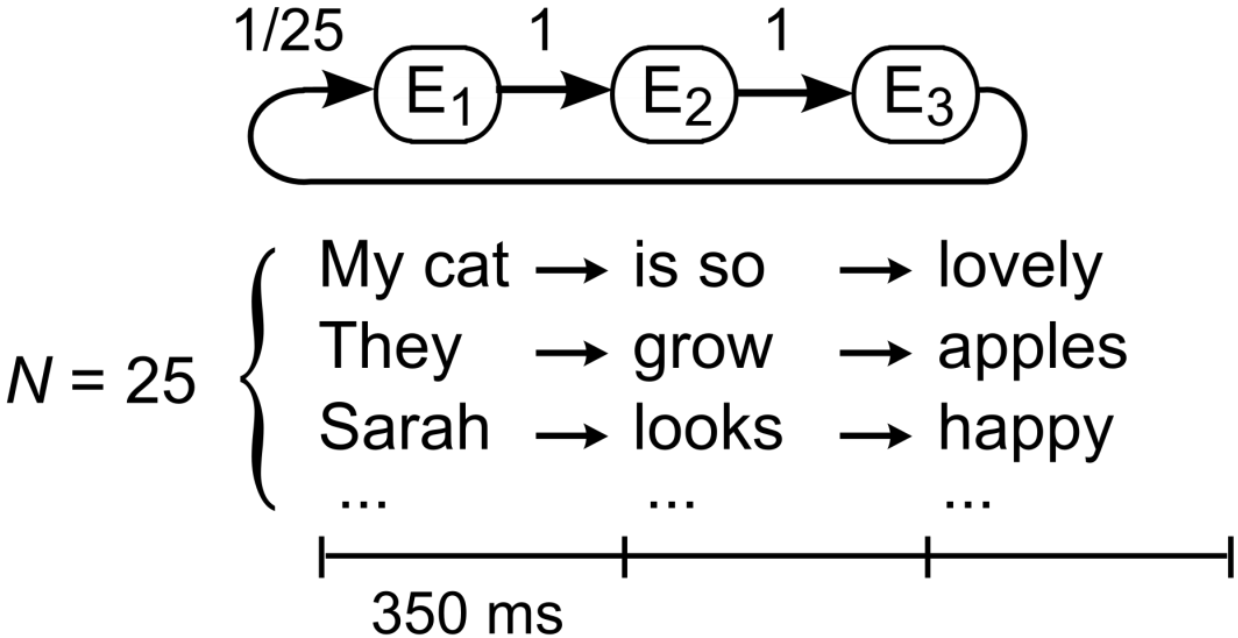
A Markov Chain Language with Constant Transitional Probability



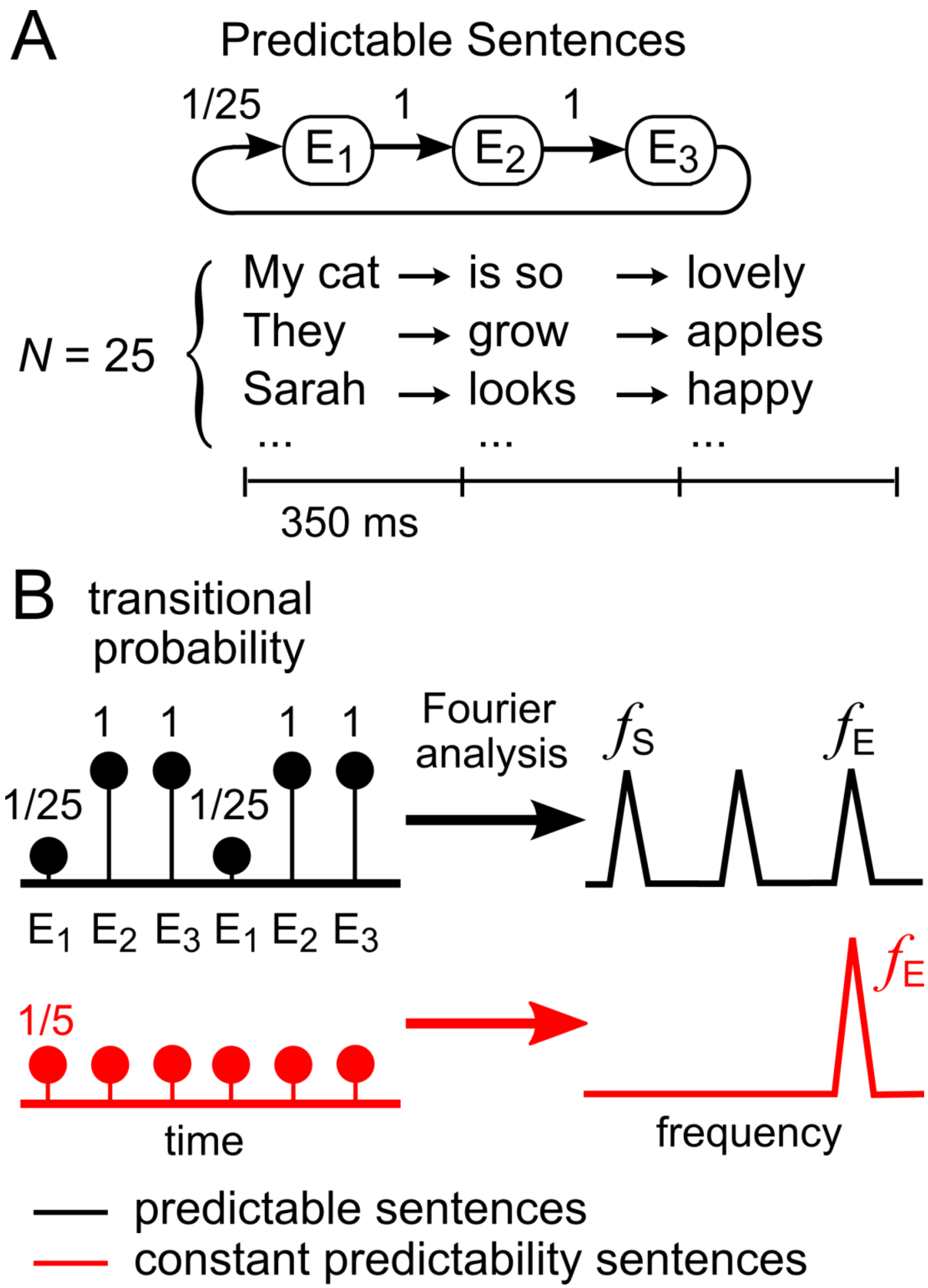




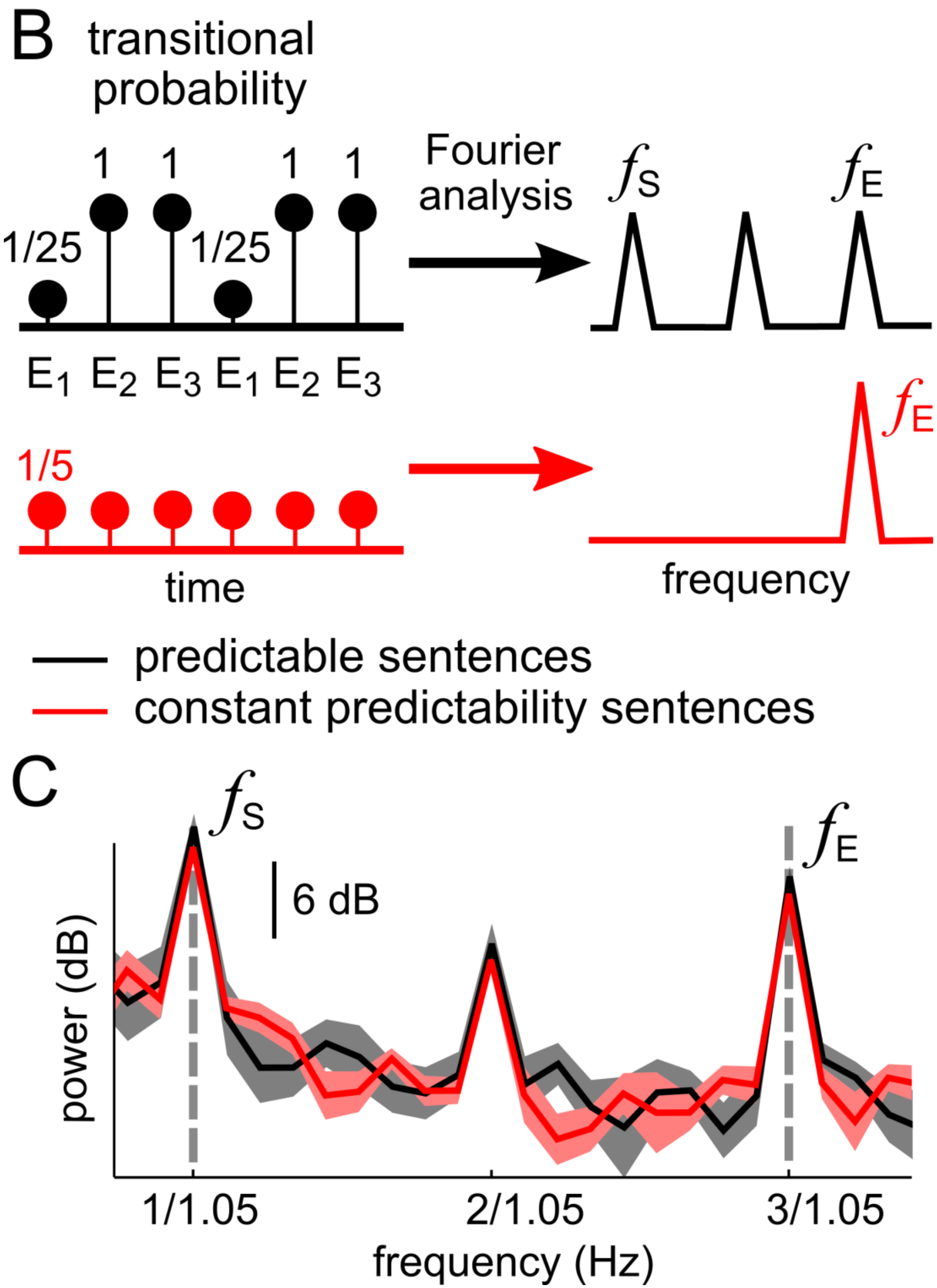
Predictable Sentences



each sentence played ~12 times



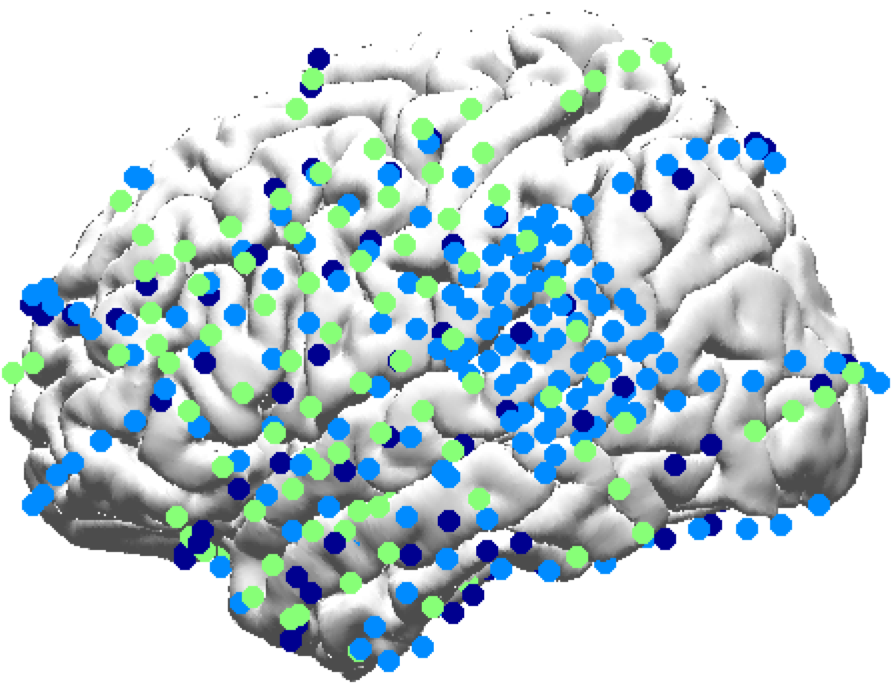
25 sentences,
each repeated ~12 times


B
transitional probability
1
1
1
1
1/25
1/25
E1 E2 E3 E1 E2 E3
1/5
time
Fourier analysis
fS
fE
fE
frequency
predictable sentences
constant predictability sentences
C
fS
fE
6 dB
power (dB)
1/1.05
2/1.05
3/1.05
frequency (Hz)

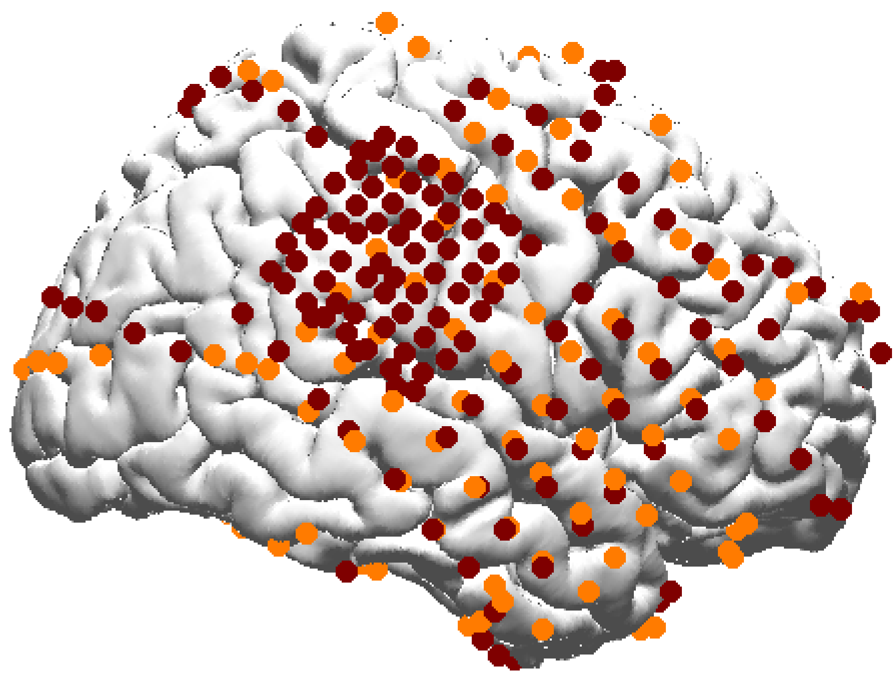
Neural Source Localization using ECoG

5 epileptic patients

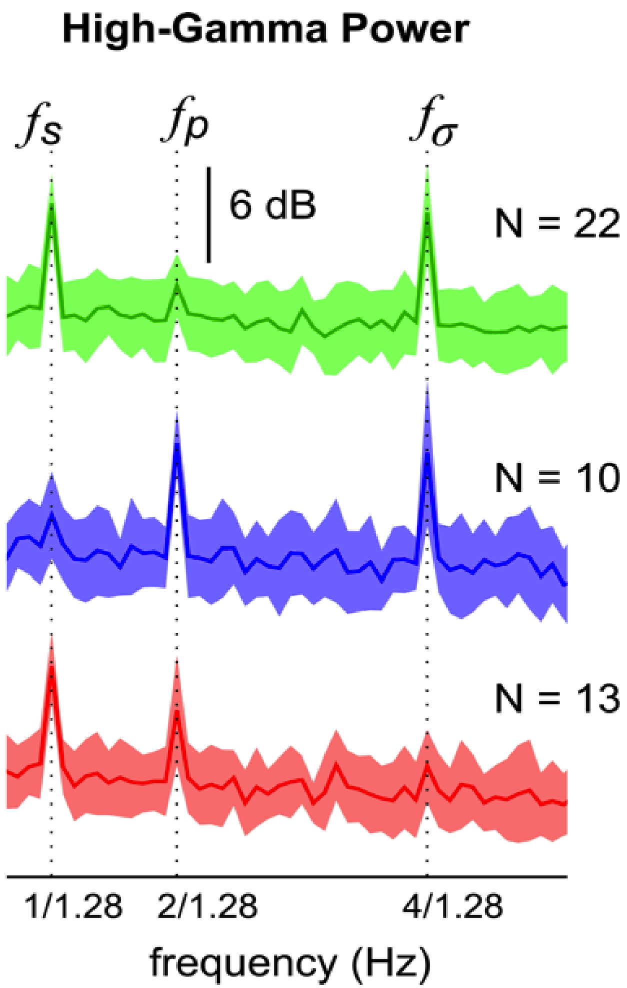
left hemisphere
(3 patients)

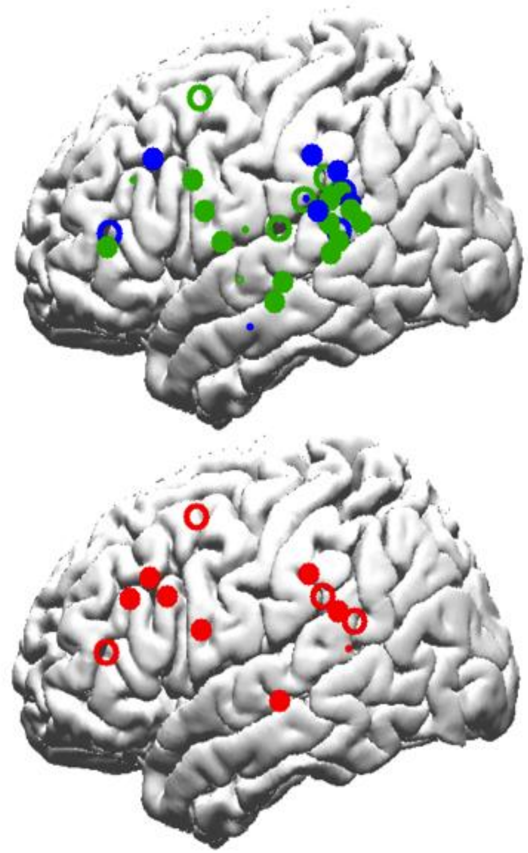


right hemisphere
(2 patients)

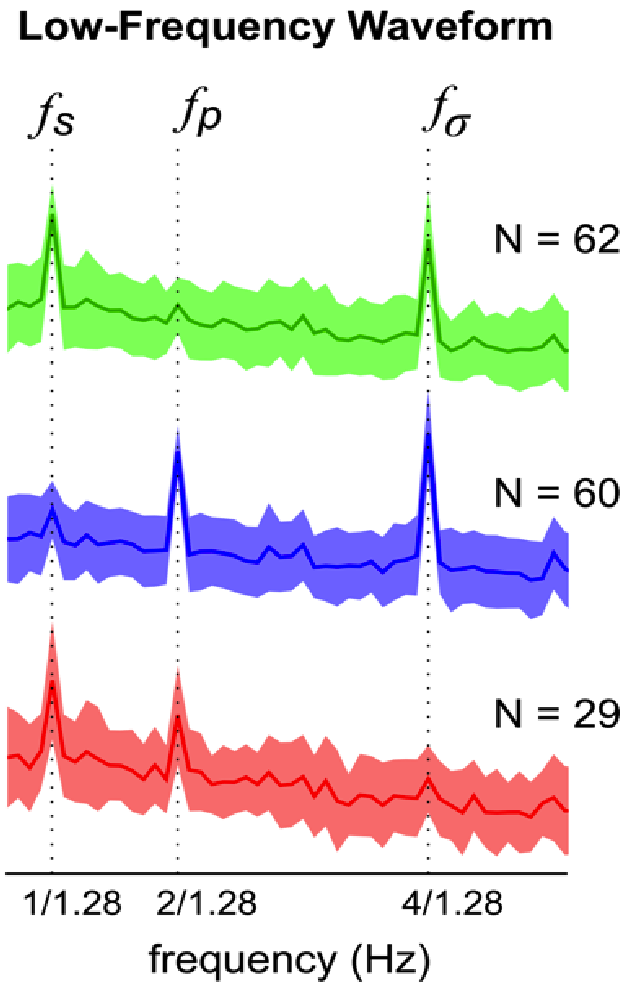


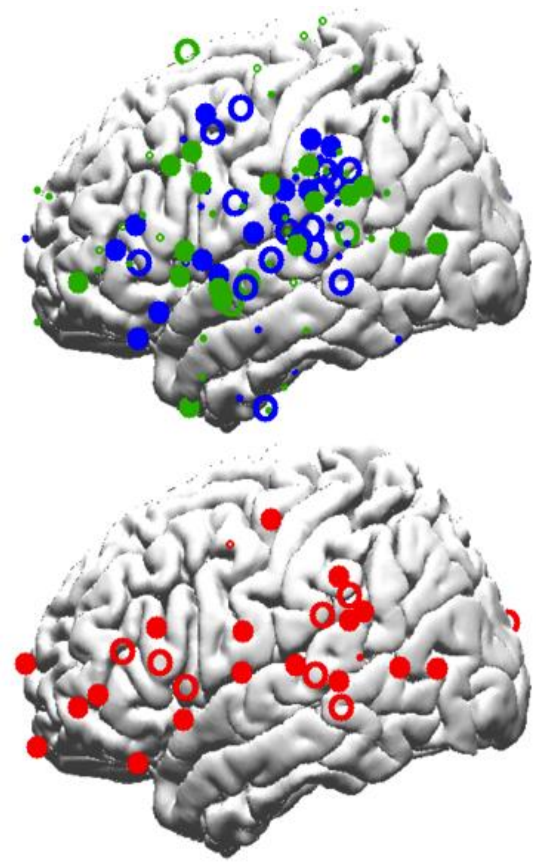
Spatially Dissociable Sentential and Phrasal Representations





Spatially Dissociable Sentential and Phrasal Representations





Summary

- Cortical circuits can generate slow rhythms matching the time scales of larger linguistic structures, even when such rhythms are not present in the speech input, which provides a plausible mechanism for online building of large linguistic structures.

- Such tracking of larger linguistic units is rule/grammar-based, not confounded by encoding of auditory features or transitional probability.

Outline

- The maps problem

Localizing what?

- The mapping problem

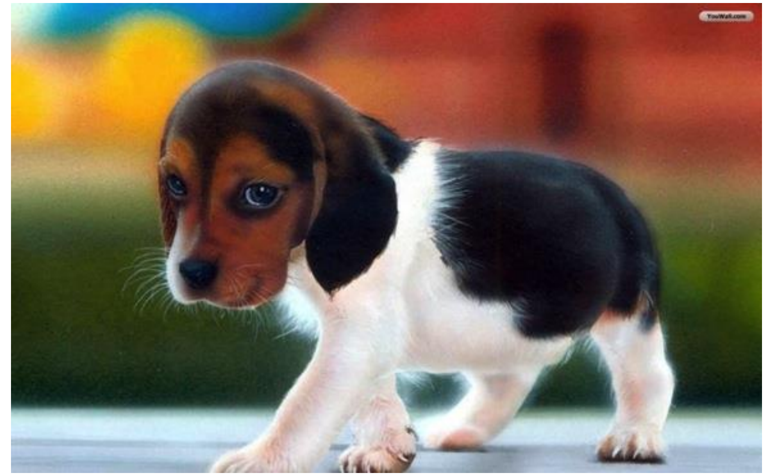
What are appropriate linking hypotheses between domains?

- The experimental granularity problem

More naturalism versus more hypothesis testing?

multisensory -- contextually dependent -- interactive

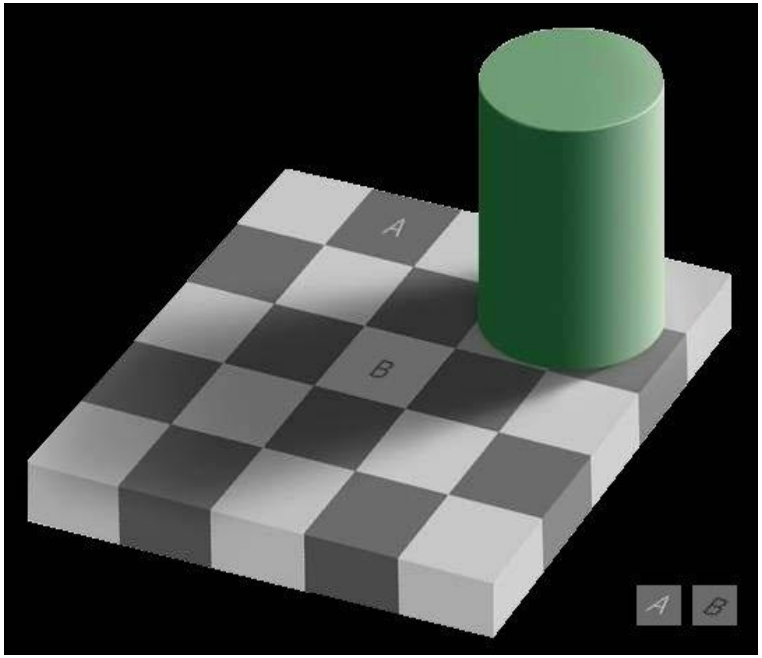
emotional

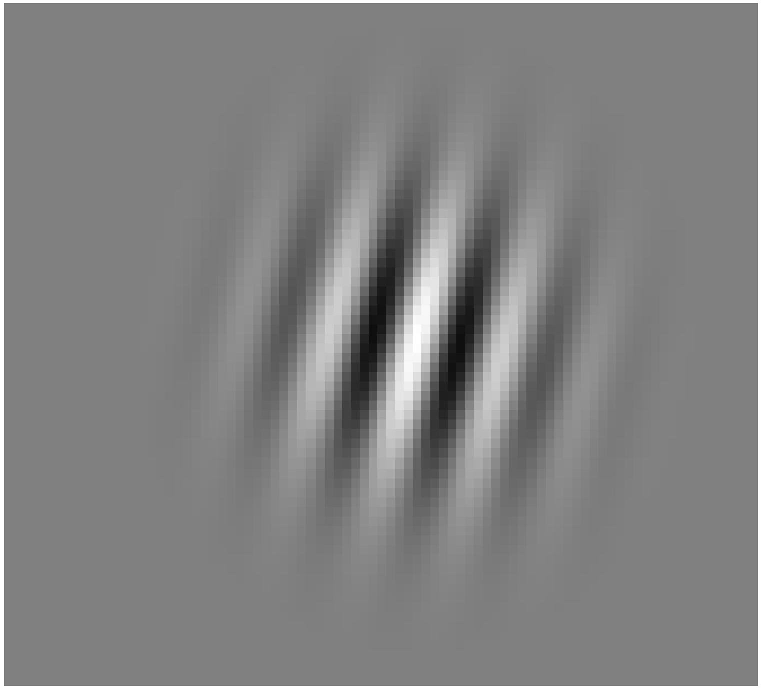


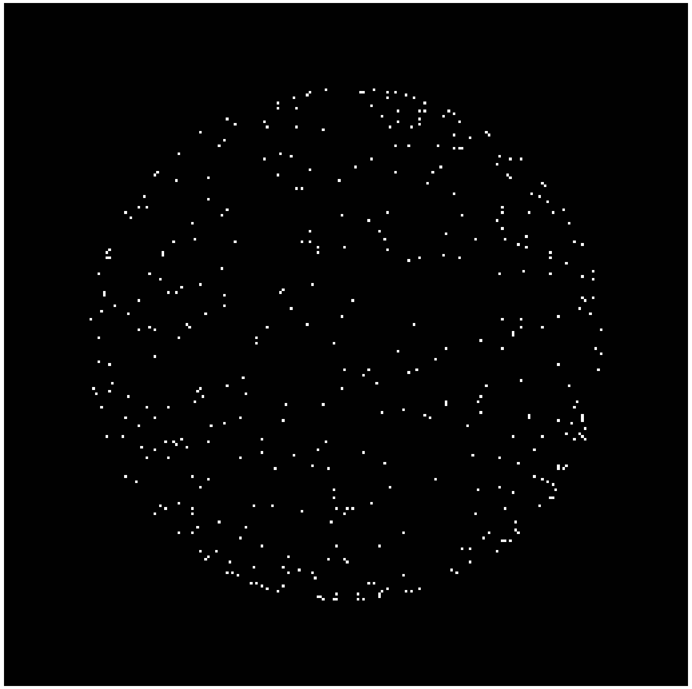
relentlessly cute

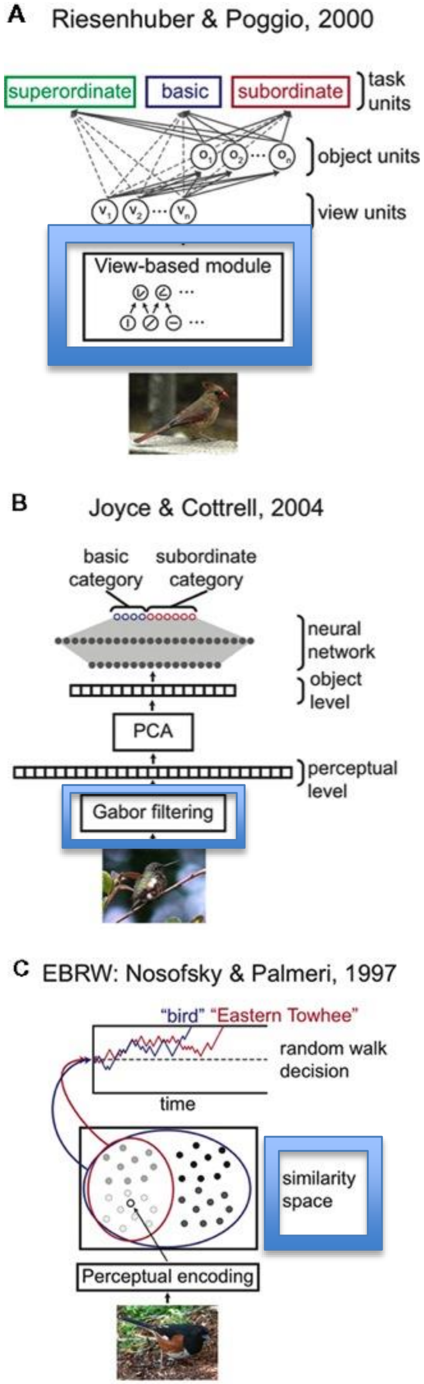
awesome

socially interactive

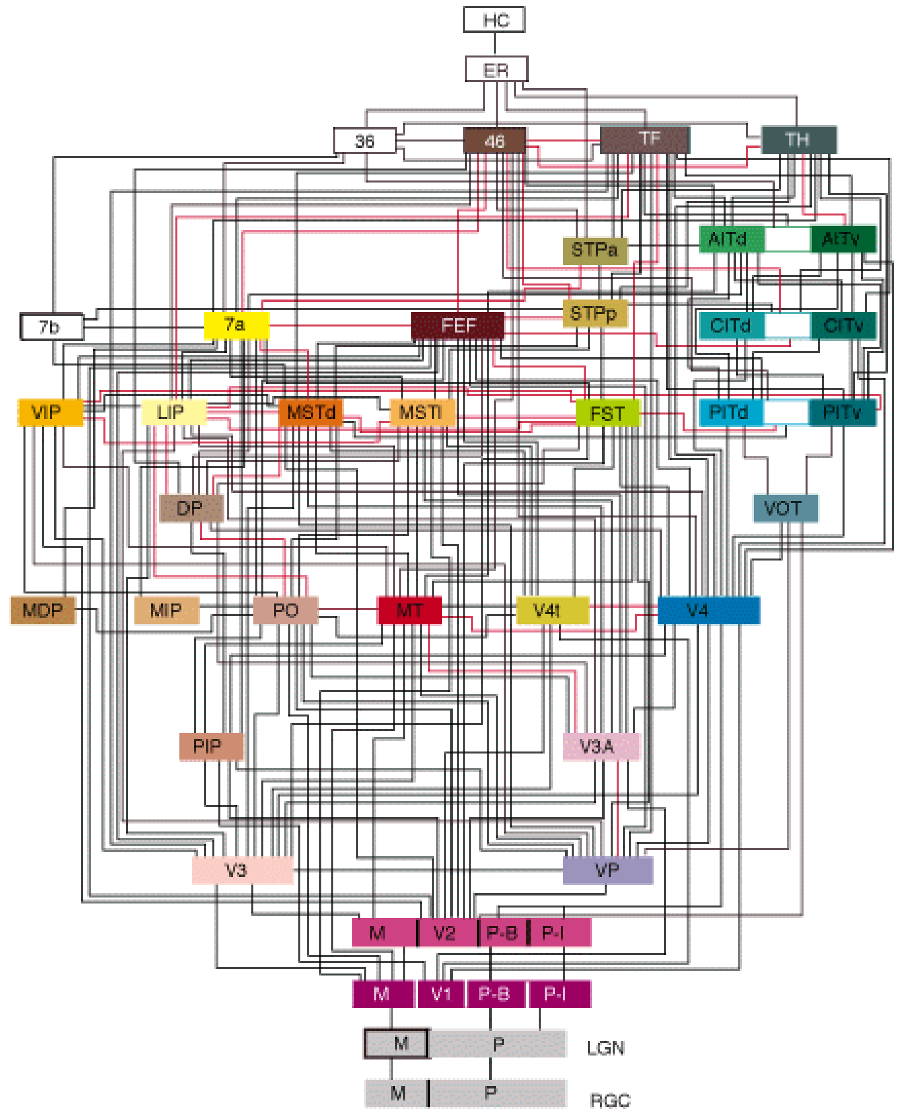

A
B
A
B

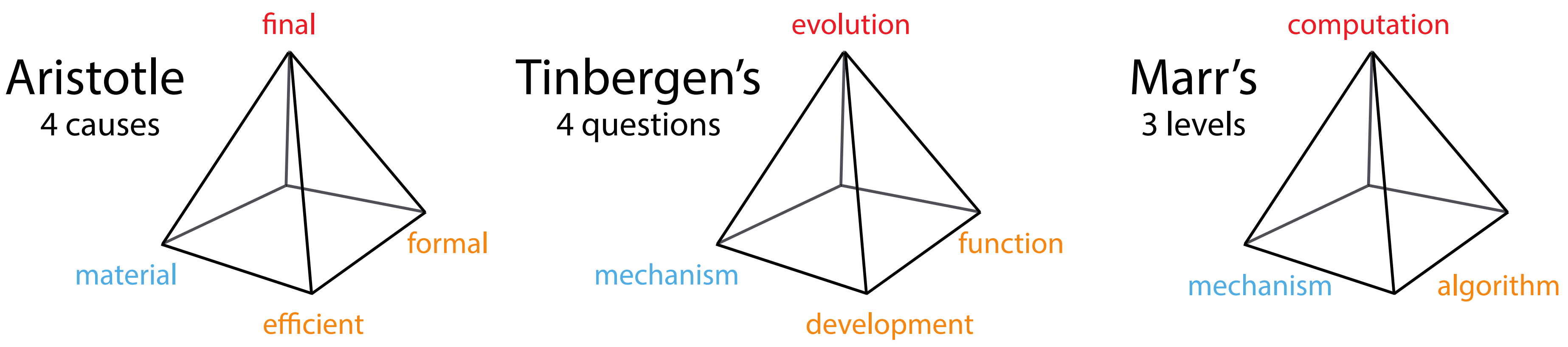






- Theoretically well motivated
- Computationally explicit
- Biologically realistic




Aristotle
4 causes
final
formal
material
efficient
Tinbergen's
4 questions
evolution
function
mechanism
development
Marr's
3 levels
computation
mechanism
algorithm

~~Outline~~ Conclusions

• The maps problem
Localization is not explanation

• The mapping problem
What are appropriate linking hypotheses?

• The world is complicated, but we still need to be ‘radical decompositionalists’ to generate explanatory understanding
Context and naturalism makes our work hard/harder

~~Outline~~ Conclusions

• The maps problem
Localization is not explanation

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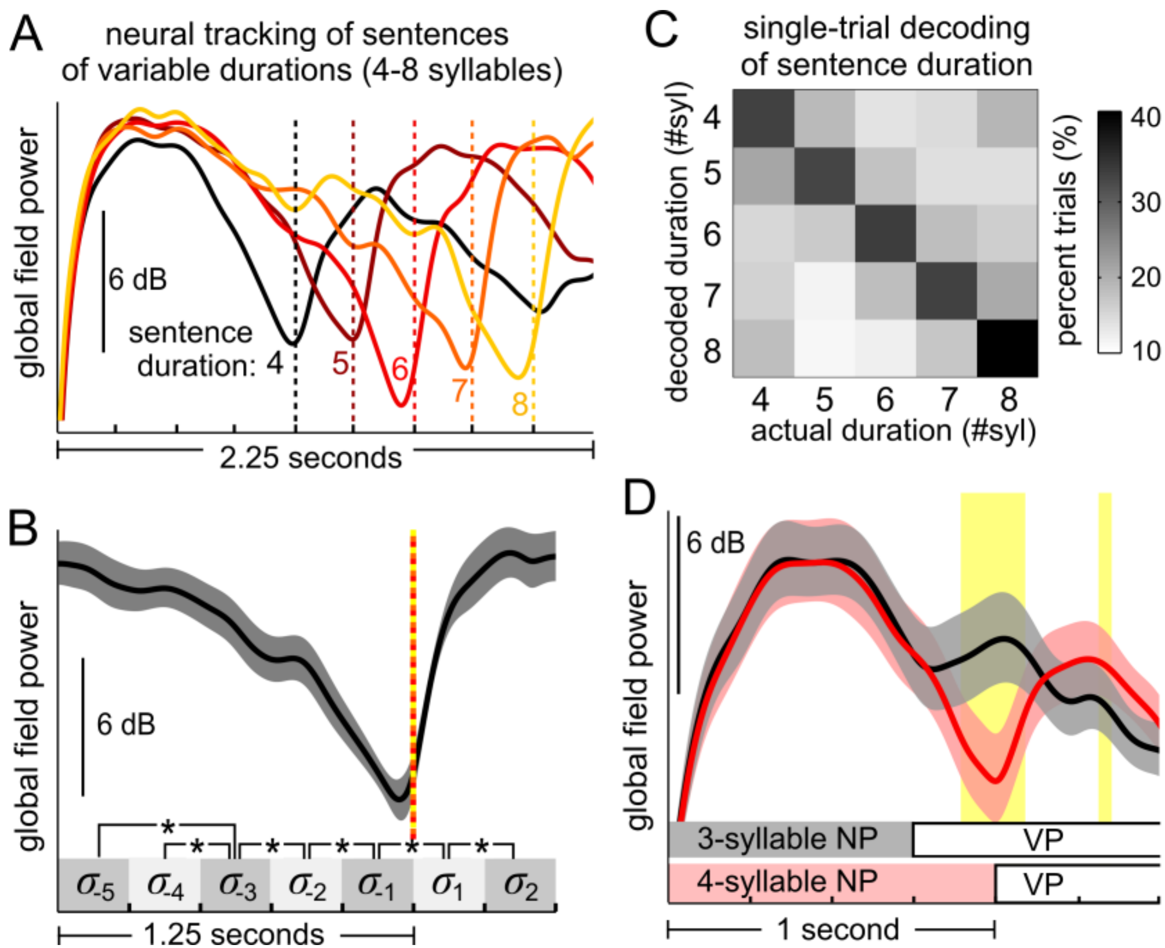
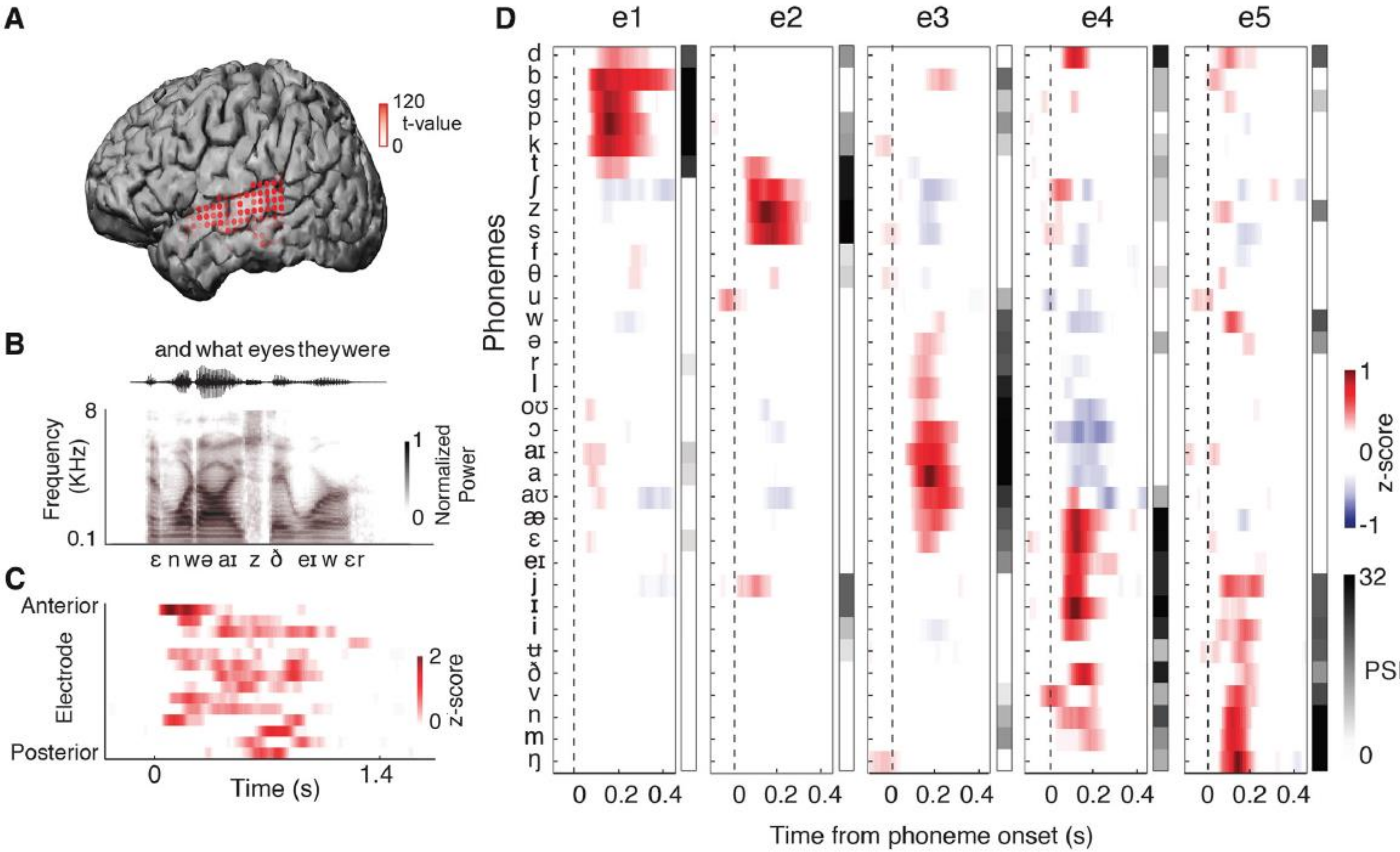
What are appropriate linking hypotheses?

• The world is complicated, but we still need to be 'radical decompositionalists' to generate explanatory understanding
Context and naturalism makes our work hard/harder

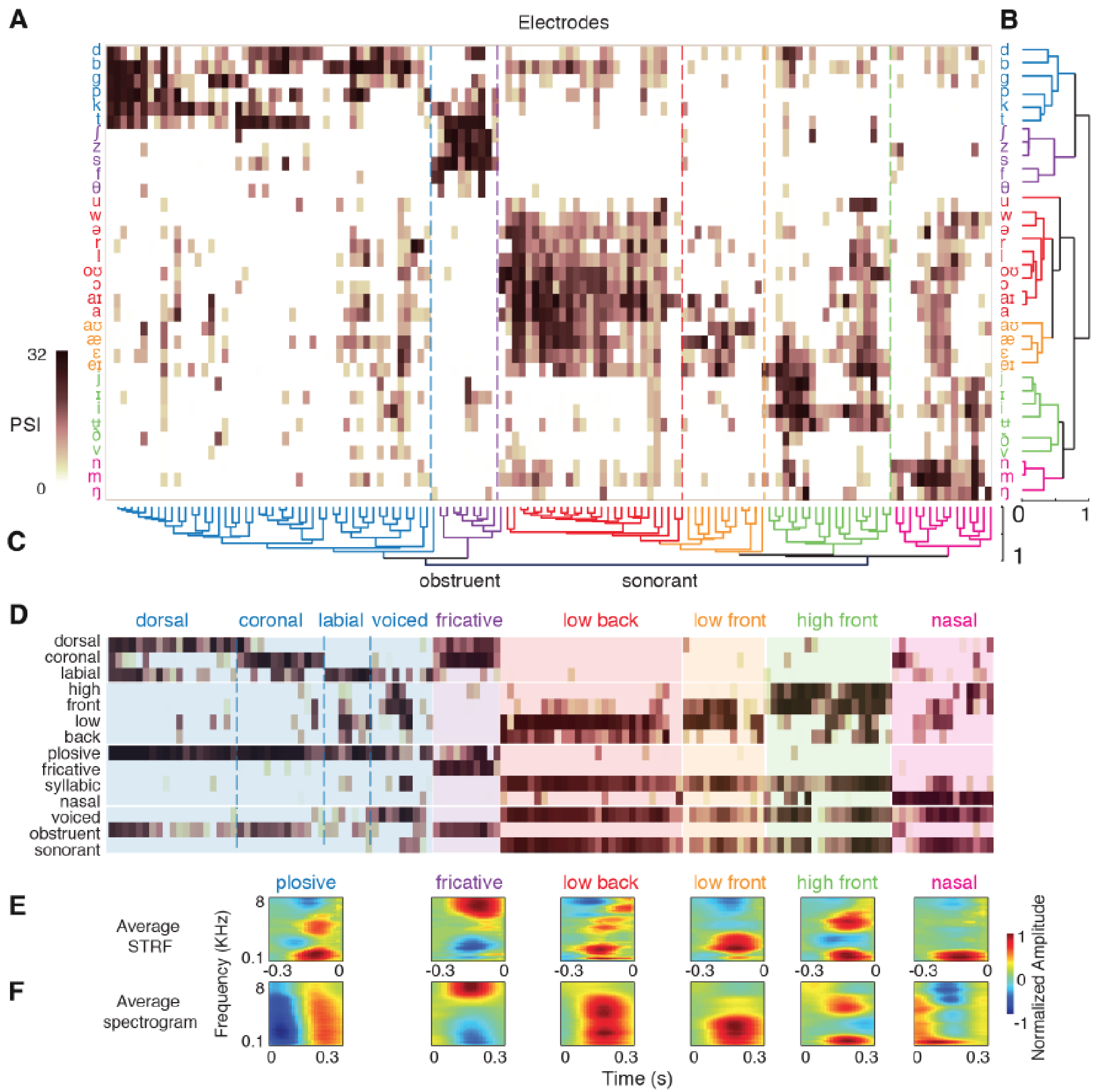
• Resolution(s)
We have ever-better spatial resolution, appropriate temporal resolution, but we could use better 'conceptual resolution'

Thanks to support from NIH, NSF, ARO, AFOSR, Max-Planck Society


A
neural tracking of sentences
of variable durations (4-8 syllables)
global field power
6 dB
sentence
duration: 4
5
6
7
8
2.25 seconds
C
single-trial decoding
of sentence duration
decoded duration (#syl)
4
5
6
7
8
actual duration (#syl)
percent trials (%)
40
30
20
10
B
global field power
6 dB
*
σ_{-5} σ_{-4} σ_{-3} σ_{-2} σ_{-1} σ_1 σ_2
1.25 seconds
D
6 dB
global field power
3-syllable NP
VP
4-syllable NP
VP
1 second

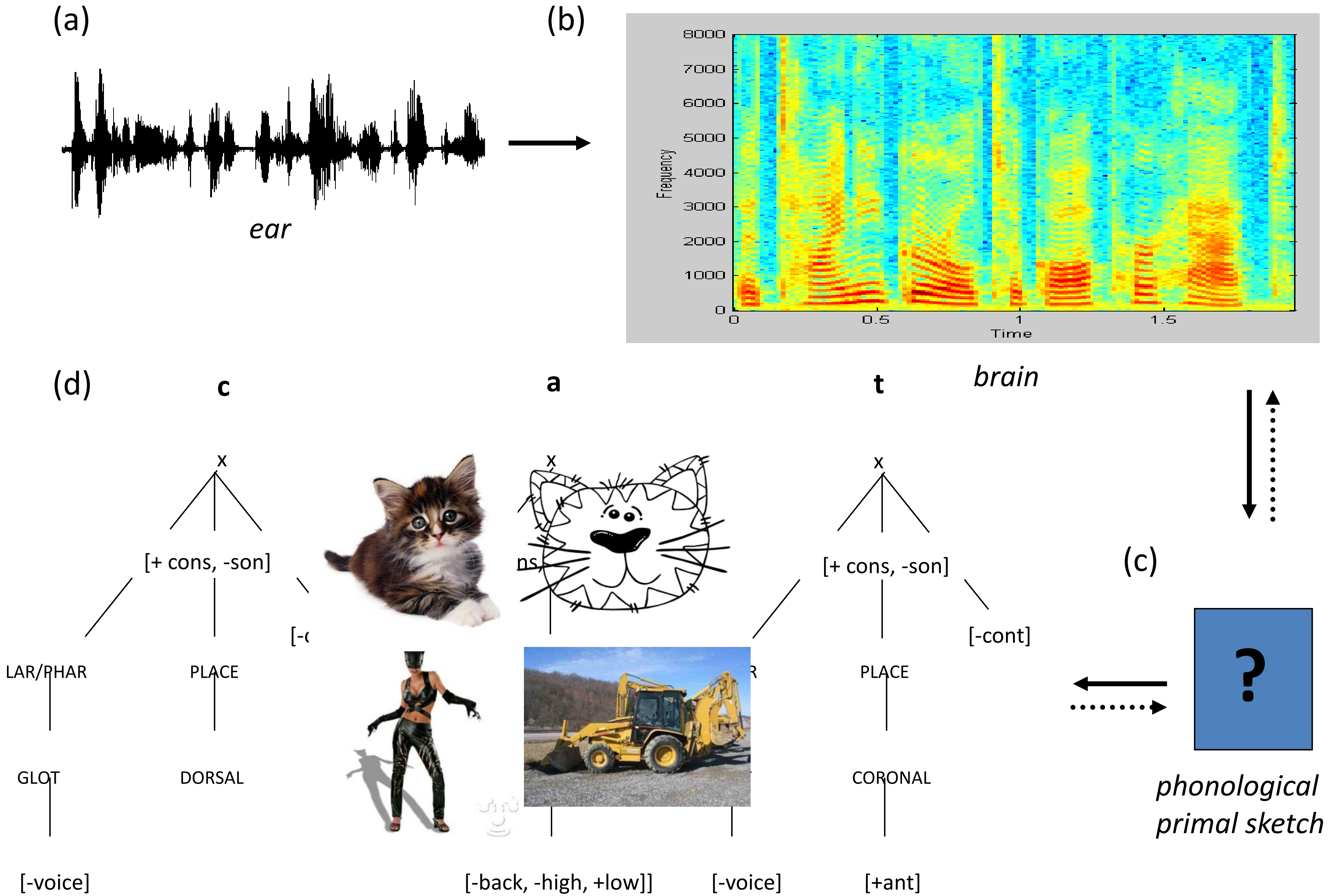


Mesgarani et al. 2014, *Science*



Mesgarani et al. 2014, *Science*

Zooming in on the problem: from vibrations in the ear to abstractions in the head



Poeppel, v. Wassenhove, Idsardi 2008

The maps problems are hard but manageable. The mapping problem (or alignment) between language and neurobiology is non-trivial

The brain 'maps' (regions/responses/coding) and
the language 'maps' (cartography of language)

are becoming increasingly detailed. Conceptual (linguistics, psychology, cognitive science, computation) and technical advances are moving us steadily forwards.

A harder challenge: The Mapping Problem

What form should the linking hypotheses take that explain how the brain forms the basis for linguistic computation? Alignment and explanation are mysterious.

New era – closer ties between linguistics, neuroscience, and computation

The spatial and temporal resolutions are increasing (imaging, invasive recording, linking to animal models, etc. …) and helping us address the maps problem.

The ‘conceptual resolution’ is what requires our attention now to address the mapping problem. Computationally explicit analyses will help in sharpening the linking hypotheses.

Connections to systems neuroscience that we should exploit more:

- links to animal models for computational subroutines
- neural coding
- genetics
- neural circuits

COGNITIVE NEUROPSYCHOLOGY, 2012, 29 (1–2), 34–55

Psychology Press
Taylor & Francis Group

The maps problem and the mapping problem: Two challenges for a cognitive neuroscience of speech and language

David Poeppel

Department of Psychology, New York University, New York, NY, USA

Language, Cognition and Neuroscience, 2014
http://dx.doi.org/10.1080/23273798.2014.980750

Routledge
Taylor & Francis Group

Towards a computational(ist) neurobiology of language: correlational, integrated and explanatory neurolinguistics

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