The Nijmegen Lectures: Lecture 3

On the insufficiency of correlational cognitive neuroscience

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Language & Brain

Anyone who seriously approaches the study of linguistic behavior, whether linguist, psychologist, or philosopher, must quickly become aware of the enormous difficulty of stating a problem which will define the area of his investigations, and which will not be either completely trivial or hopelessly beyond the range of present-day understanding and technique.

Chomsky 1959

Why bother? What could we learn?

- something about how language works
- something about how the brain works
- nothing (interdisciplinary cross-sterilization)
Outline

• The maps problem

• The mapping problem

• Revisiting oscillations

• The world is complicated, but we still need to be radical decompositionalists to generate explanatory understanding
Two challenges for the neuroscience of language

1. The maps problem (*functional anatomy/physiology* of the right grain)  
   *spatial mapping, spatial resolution, temporal mapping (electrophys)*
   
   *a practical problem*

2. The mapping problem (aligning the *parts lists* or the *cognome*)  
   “*conceptual mapping*, *conceptual resolution*
   
   *a principled problem*
1. The map(s) problem

In the last 20 years, the dominant research program has become to map out the “localization of function.”

Based on new technologies such as MRI and MEG, the principal question has been “where are different functions localized”?

The **cartographic imperative** approach: lots about ‘where’ - but little ‘how’ things work.
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 ~10 subdivisions (not counting laminar specialization).

=> Monolithic generalizations about function are not even wrong.
The functional organization of the left STS: a large scale meta-analysis of PET and fMRI studies of healthy adults

Eina Liebenthal1,2*, Rutvik H. Desai2, Colin Humphries1, Merav Sabri1 and Anjali Desai1

1Department of Neurology, Medical College of Wisconsin, Milwaukee, WI, USA
2Department of Psychiatry, Brigham and Women’s Hospital, Boston, MA, USA

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 (fmSTS) subdivision was defined as a region activated by a small number of functional categories (range 1–4, mean 2.6), the functional pSTS (fpSTS) subdivision was defined as a region activated by the largest number of functional categories (range 8–14, mean 11), and the functional tSTS (ftSTS) 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 fmSTS, fpSTS, and ftSTS, respectively). The horizontal line corresponds to z = 2.807 (p < 0.005).
The Language Connectome: New Pathways, New Concepts

Anthony Steven Dick¹, Byron Bernal², and Pascale Tremblay³
Kriegstein and Giraud, 2004; Meyer et al., 2005, and the familiarity of vocalisation (Kriegstein and Giraud, 2004). These right hemisphere responses may help to explain why the perception of prosody in heard speech is associated with the right hemisphere, particularly when the language demands of the task are low (Gandour et al., 2004; Meyer et al., 2004).

Auditory processing of speech and nonspeech. Time era: 2007–2011. Extending prior findings. Bilateral superior temporal activation was reported for the acoustic analysis of speech and nonspeech sounds (Turkeltaub and Coslett, 2010; Obleser et al., 2007a, 2007b; Dick et al., 2011) and shown to be sensitive to frequency discriminations (Zaehle et al., 2008), familiarity (Raettig and Kotz, 2008; Davis and Gaskell, 2009; Kotz et al., 2010; Vaden et al., 2010). Left lateralized responses were reported for the discrimination of fast changing verbal and nonverbal sounds in the planum temporale (Elmer et al., 2011a) and for the perceptual interpretation of speech sounds in early auditory areas (Kilian-Hutten et al., 2011). In contrast, right auditory areas were associated with changes of the frequency spectrum (Obleser et al., 2008), categorical perception of familiar musical chords, and the comparison of familiar versus unfamiliar musical sequences (Klein and Zatorre, 2011; Peretz et al., 2009).
The cortical organization of speech processing

Gregory Hickok and David Poeppel

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.**

Nature Reviews Neuroscience 2007

Nature Reviews Neuroscience 2008
Figure 7. Summary of spatial distribution of voxels' tuning properties.

http://journals.plos.org/ploscompbiol/article?id=info:doi/10.1371/journal.pcbi.1003412
Plus a zoo of electrophysiological response patterns

(i.e. I am not an electrophysiological imperialist – the same kinds of good and bad things obtain in electrophysiology, because we reify responses, e.g. N1 = X, P3 = Y, N400= Z)

- Cellular-level electrophysiology
- Action potentials
- Subthreshold activity
- Rate coding
- Temporal coding
- Ensemble coding
- Spectral responses
- EEG/MEG/ECoG
- Evoked responses
- Oscillations over populations
- Power
- Phase
- Connectivity
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-
Outline

• The maps problem

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• Revisiting oscillations

• The world is complicated, but we still need to be radical decompositionalists to generate explanatory understanding
2. The mapping problem

The parts list alignment challenge for cognitive neuroscience of language
2. The mapping problem

Cognitive/linguistic models

Neurobiology

Indefrey & Levelt 2004
The mapping problem

Linguistics                           Neuroscience

Fundamental elements of representation

distinctive feature → dendrites, spines
syllable ✗ neuron
morpheme ✗ cell-assembly/ensemble
noun phrase ✗ population
clause → cortical column

Fundamental operations on primitives

concatenation → long-term potentiation
linearization ✗ receptive field
phrase-structure generation → oscillation
semantic composition → synchronization

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.
The mapping problem

Why are there no/few successful linking hypotheses?

Granularity Mismatch Problem (neurolinguistics in practice):

Linguistic and neuroimaging studies of language operate with objects of different granularity.

\[
\begin{align*}
\text{linguistics} & \quad \text{--- fine-grained distinctions} \\
\text{neuroscience} & \quad \text{--- broader conceptual distinctions}
\end{align*}
\]

Neuroscience cannot succeed in seeking “syntax” (or “phonology”) because syntax etc. are not monolithic but have many parts.

Ontological Incommensurability Problem (neurolinguistics in principle):

The units of linguistic computation and the units of neurobiological computation are incommensurable.

Therefore, an attempt at reduction makes no sense.

*Poeppel & Embick, 2005; Poeppel 2012; Embick & Poeppel 2014*
<table>
<thead>
<tr>
<th></th>
<th>Linguistics</th>
<th>Neuroscience</th>
</tr>
</thead>
<tbody>
<tr>
<td>Objects</td>
<td>Distinctive feature</td>
<td>Dendrite/spine</td>
</tr>
<tr>
<td></td>
<td>Timing slot</td>
<td>Neuron</td>
</tr>
<tr>
<td></td>
<td>Morpheme</td>
<td>Cortical microcircuit</td>
</tr>
<tr>
<td></td>
<td>Phrase</td>
<td>Cortical column</td>
</tr>
<tr>
<td>Operations</td>
<td>Feature spreading</td>
<td>Long term</td>
</tr>
<tr>
<td></td>
<td></td>
<td>potentiation (LTP)</td>
</tr>
<tr>
<td></td>
<td>Merge</td>
<td>Oscillation</td>
</tr>
<tr>
<td></td>
<td>Concatenation</td>
<td>Adaptation</td>
</tr>
<tr>
<td></td>
<td>Semantic composition</td>
<td>synchronisation</td>
</tr>
</tbody>
</table>
"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
Neuroscience needs behavior! Reversing a detrimental reductionist epistemological bias

John Krakauer, Asif Ghazanfar, Alex Gomez-Marín, Malcolm Maclver, David Poeppel forthcoming

physiology (what neurons do)  psychology/ethology (what animals do)

brain  behavior

neuroscience (how the brain explains behavior)
Another smashing success story of the Marr-type approach (a beauty):

Sound localization in the avian versus mammalian brain

• Specialized computation
• Explanatory relation between circuit and computation
• Encoding temporal information
• Detection of interaural time differences
Computational level of analysis: auditory temporal information must be used to calculate where prey or predator are located.
**Algorithmic level of analysis**: Delay lines and coincidence detectors form circuits for ITD detection

- Delay line inputs synapse on coincidence detector neurons.
- These neurons compute the new variable, ITD, and transform the time code into a place code

*Jeffress 1948*
Implementational level of analysis: Circuit in barn owls composed of delay lines & coincidence detectors

sound from the side

sound from in front

IPSi NM

NL

iso-ITD

CONTRA NM
ITD detection circuits in the barn owl conform to the Jeffress model (Carr & Konishi 1990)

NM axons form maps of ITD in dorsoventral dimension
Sound localization in the dark

predator

prey

INTERAURAL TIME DIFFERENCE

ITD (10us)

ITD (100ms)

DELAY LINES

waveform from each ear

COINCIDENT DETECTORS

tanslation to place code

(1) suggests

(2) predicts

(3) confirms

(4) explains

ITD (10us)

ITD (100ms)

Depolarizaing inhibition (gain control)

Nucleus laminaris (avian)

Hyperpolarized inhibition (temporal sensitivity)

Medial superior olive (mammalian)
Why should you care?

• A successful example of the Marr-type research program -- the biological account of a specific and complex phenotypic behavior from soup to nuts, *unifying computational, algorithmic, and implementational levels of analysis*.

• The *explanatory* relation between neuronal architecture and a particular computation: details of the circuit determine the specialization (e.g. Grothe 2003, *Nat Reviews Neurosci*).

And why should I?

• *Where we are now*: computational-representational linguistic models related to brain activation -- *weak/correlative neurolinguistics/biolinguistics*.

• *Where we want to be*: unification by mappings between the structure of neuronal circuitry and the linguistic computation performed -- *strong/explanatory neurolinguistics/biolinguistics*. 
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            constituency            recursion

x---y                     z                        

\begin{center}
\begin{tikzpicture}
\node{z} at (0,0) [below left=1cm] {
    \begin{tikzpicture}
    \node{x} at (0,0) [below left=1cm] {
        \begin{tikzpicture}
        \node{y} at (0,0) [below left=1cm]
    \end{tikzpicture}
    \end{tikzpicture}
};
\end{tikzpicture}
\end{center}

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?”
Putative primitives - the view on irreducible representations and operations from semantics (Pietroski) and syntax (Hornstein)

- **Variables**, a way to link variables
- One-place predicates, thematic roles
- Operation with the power of conjunction and existential closure

- **Concatenation** (a-directional)
- Labeling: concatenate turns into one of its constituents
- Some mechanism (copy) to deal with positional specificity of variables

The mapping problem: seeking the right computational granularity
The mapping problem: seeking the right computational granularity

Putative primitives - the view more broadly, for computational level

- differential equations
- modal logic
- category theory
- information theory

Putative primitives – a concrete attempt at linking
Boeckx, Martinez-Alvarez, Leivada 2014, J Neurolinguistics

How to handle the problem of linearization (building on Idsardi & Raimy 2013)

<table>
<thead>
<tr>
<th>Module</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Narrow syntax</td>
<td>hierarchy, no linear order, no phonological content</td>
</tr>
<tr>
<td>LINEARIZATION-1</td>
<td><strong>Immobilization</strong></td>
</tr>
<tr>
<td>Morphosyntax</td>
<td>hierarchy, adjacency, no phonological content</td>
</tr>
<tr>
<td>LINEARIZATION-2</td>
<td><strong>Vocabulary Insertion</strong></td>
</tr>
<tr>
<td>Morphophonology</td>
<td>no hierarchy, directed graph, phonological content</td>
</tr>
<tr>
<td>LINEARIZATION-3</td>
<td><strong>Serialization</strong></td>
</tr>
<tr>
<td>Phonology</td>
<td>no hierarchy, linear order, phonological string</td>
</tr>
</tbody>
</table>
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• The world is complicated, but we still need to be radical decompositionalists to generate explanatory understanding
One brief example of an attempt at a linking hypothesis, in the Marr spirit: the segmentation problem and neural oscillations

since there are no word boundary signs in spoken language the difficulty we feel in reading and understanding the above paragraph provides a simple illustration of one of the main difficulties we have to overcome in order to understand speech rather than an neatly separated sequence of letter strings corresponding to the phonological form of words the speech signal is a continuous stream of sounds that represent the phonological form of words in addition the sounds of neighboring word often overlap which makes the problem of identifying word boundaries seven harder.

Cortical oscillations (neurobiological implementation) as the mechanisms to address the segmentation problem (computational level) by phase resetting to edges (algorithm).
a. Temporal integration and multi-time resolution analysis: quantization and lateralization

Symmetric representation of spectro-temporal receptive fields in core auditory cortex

Temporally asymmetric elaboration of perceptual representations in non-primary cortex

- Proportion of neuronal ensembles
  - Left Hem
  - Right Hem

Size of temporal integration windows (ms)
[40Hz, 4Hz]
[25 ms, 250 ms]

b. Functional lateralization as a consequence of temporal integration

Analyses requiring high temporal resolution
- e.g. formant transitions
- LH

Analyses requiring high spectral resolution
- e.g. intonation contours
- RH

Many non-speech perceptual phenomena occur on the same time scales

μs phenomena
- sound localization (Jeffress)

 ms phenomena
- simultaneity thresh (Miller)
- gap detection (Plomp)
- the TMTF (Vieree)"}
- Huffman sequences (Green)
- click data (abb)

20-30 ms phenomena
- temporal order (Hirsh)
- virtual pitch onset (Terhardt)
- streaming (Bregman)
- click data (abb)
- CNNNB data (abb)

200-300 ms phenomena
- loudness processing (Green)
- pitch processing (Patterson)
- binaural TC (Grantham & Wightman)

2000+ ms phenomena
- modality & suffix effects
- periodicity detection (Julesz)
Seeing slow and seeing fast: two limits on perception

Alex O. Holcombe

Holcombe 2009, TICS
Newton, *Principia*

Our intuition

Our brain

Our brain, really
Design: evaluate coherence across single trials elicited by sentences

Similarity across trials should be larger in Within-group condition than in Across-group condition

\[
\begin{align*}
C_{\text{phase}}_{\text{within}} &> C_{\text{phase}}_{\text{across}} \\
C_{\text{power}}_{\text{within}} &> C_{\text{power}}_{\text{across}}
\end{align*}
\]

Luo & Poeppel, Neuron, 2007
Theta phase

Theta phase
A ~ 200 ms window analyzes the input signal -- The syllable as primitive

Luo & Poeppel, Neuron, 2007
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
Distribution of intrinsic cortical rhythms
Combined EEG/fMRI recordings

N=12 + 8 subjects at rest (twice 20 min.)
EEG, 32 channels, continuous acquisition.
fMRI, 1.5 T and 3 T Siemens, sparse acquisition
No auditory input beyond the MRI scanner noise.
Analyses from central electrodes to observe temporal asymmetries with minimal lateralization bias.

Giraud et al. 2007, Neuron
Combined EEG/fMRI recordings: Approach

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Segments of EEG trace

Sequence of fMRI acquisition

Continuous EEG recording (20 min.)

Sparse fMRI acquisition (20 min.)

Raw data

Estimated data (raw data convolved with hemodynamic function)

FFT

Regressors

3–6 Hz

28 – 40 Hz

Giraud et al. 2007, *Neuron*
Experiment 1 (1.5T)
A. Topography (12 subjects)

Experiment 2 (replication at 3T)
C. Topography (8 males)
Figure 2

(a) Mutual Information (bits) across different frequencies for the Left and Right Hemispheres.

(b) Comparison of Theta (3.3 Hz) and Gamma (40 Hz) bands for the Left and Right Hemispheres under Intact and Envelope Only conditions.

Cogan & Poeppel forthcoming
Acoustic landmarks drive delta–theta oscillations to enable speech comprehension by facilitating perceptual parsing

Keith B. Doelling a, Luc H. Arnal a, Oded Ghitza c, David Poeppel a,b,⁎

a Department of Psychology, New York University, USA
b NYUAD Institute, New York University Abu Dhabi, P.O. Box 129188, Abu Dhabi, UAE
c Department of Biomedical Engineering, Boston University, USA

Doelling et al. 2013, Neuroimage
Entrainment to the stimulus

Doelling et al. 2013, Neuroimage
Phase-Locked Cortical Oscillations as Potential Mechanisms of Parsing an Input Stream into Temporal Primitives of Efficient Sensory Prediction

Adapted from Peelle & Davis 2012
Cortical oscillations and speech processing: emerging computational principles and operations

1. Phase reset

2. Stimulus envelope tracking

3. Theta/gamma nesting

4. Modulation of neuronal excitability and output discretization

5. Alignment of neuronal excitability with acoustic structure

Stimulus-induced (SI) theta oscillations (1-8 Hz; LFP, EEG, MEG)

SI theta-modulated gamma oscillations (25-35 Hz)

Temporarily organized spike train (Output Layers II/III)

Speech waveform

Stimulus-driven spike train (input Layer IV)

High excitability

Strong spiking

Low excitability

Spectro-temporal encoding

Giraud & Poeppel, 2012, Nat Neurosci

Cortical oscillations and speech processing: emerging computational principles and operations.
Zooming in on the problem: from vibrations in the ear to abstractions in the head

Giraud & Poeppel, 2012, Nat Neurosci

Ghitza and Greenberg, 2011, Frontiers
Parsing events, e.g. syllables

Courtesy of Keith Doelling, NYU
Parsing events, e.g. syllables

Courtesy of Keith Doelling, NYU
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
Outline

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• Revisiting oscillations

• The world is complicated, but we still need to be radical decompositionalists to generate explanatory understanding
multisensory -- contextually dependent -- interactive
emotional
to
relentlessly cute

awesome

socially interactive
- Theoretically well motivated
- Computationally explicit
- Biologically realistic
Aristotle
4 causes
- material
- efficient

Tinbergen’s
4 questions
- final
- formal
- mechanism
- development
- function
- evolution

Marr’s
3 levels
- computation
- mechanism
- algorithm
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

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

David Embick* and David Poeppelb,c

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@davidpoeppel http://www.talkingbrains.org/ http://psych.nyu.edu/clash/poeppellab/
• The maps problem
Localization is not explanation

• The mapping problem
What are appropriate linking hypotheses?

• Revisiting oscillations
Low-frequency oscillations provide an administrative service
On computation, but not (yet) (direct) insight on representation

• The world is complicated, but we still need to be radical
Decompositionalists to generate explanatory understanding
Context and naturalism makes our work hard/harder/hardest
Concluding advice for young researchers

Rejection of rejection letter (Chapman & Slade, 2015, British Medical Journal)

Dear Professor [insert name of editor]

[Re: MS 2015_XXXX Insert title of your important study here]

Thank you for your rejection of the above manuscript.

Unfortunately we are not able to accept it at this time. As you are probably aware we receive many rejections each year and are simply not able to accept them all. In fact, with increasing pressure on citation rates and fiercely competitive funding structures we typically accept fewer than 30% of the rejections we receive. Please don’t take this as a reflection of your work. The standard of some of the rejections we receive is very high.

In terms of the specific factors influencing our decision the failure by Assessor 1 to realise the brilliance of the study was certainly one of them. Simply stating “this study is neither novel nor interesting and does not extend knowledge in this area” is not reason enough. This, coupled with the use of Latin quotes by Assessor 2, rendered an acceptance of your rejection extremely unlikely.

We do wish you and your editorial team every success with your rejections in the future and hope they find safe harbour elsewhere. To this end, may we suggest you send one to [insert name of rival research group] for consideration. They accept rejections from some very influential journals.

Please understand that our decision regarding your rejection is final. We have uploaded the final manuscript in its original form, along with the signed copyright transfer form.

We look forward to receiving the proofs and to working with you in the future.
Yours sincerely
Thanks to support from NIH, NSF, ARO, AFOSR, Max-Planck Society
A syllable is a unit of organization for a sequence of speech sounds. A syllable is typically made up of a syllable nucleus (most often a vowel) with optional initial and final margins (typically, consonants).

\[\sigma\]

\[
\text{Onset} \quad \text{Rhyme}
\]

\[
\text{Nucleus} \quad \text{Coda}
\]

\[
c \quad a \quad t
\]

\[
s \quad i \quad \text{ng}
\]

Definition: The theta-syllable is a theta-cycle long speech segment located between two successive vocalic nuclei.

Ghitza 2013
**A Marr’s-eye-view on lateralization in speech perception**

Following David Marr (1982), *Vision*

### Computational characterisation
A continuously varying input stream has to be segmented or chunked into units of the appropriate temporal granularity to make contact with stored representations (~words, composed of segments, syllables, morphemes …)

### Algorithmic hypotheses
- Multi-time resolution processing: analyze the input at multiple scales, e.g. featural, segmental, syllabic analyses (Poeppel)
- Temporal versus spectral analyses (Zatorre)

### Implementational analyses
Different temporal integration constants in neuronal ensembles; asymmetric distribution of neuronal ensembles across hemispheres

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[Diagram and annotations]

- **Right hem**
- **Left hem**
- **Temporal resolution**
- **Spectral resolution**

**Proportion of neuronal ensembles**

- **LH**
- **RH**

- **250 ms**
- **25 ms**

- **250 ms**
- **25 ms**

**Temporal resolution**

- **LH**: 250 ms
- **RH**: 25 ms

---

**LAR/PAR**

- **PLACE**
- **DORSAL**
- **GLDT**
- **[-voice]**

- **[+ cons, -son]**
- **[-cont]**