from TIMING *to* MEANING *in the Human Brain*

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1. Information & Neural oscillations

2. Timing
   Building endogenous temporal references inspite of entrainment
   Counter-acting intrinsic structural biases for serial ordering with oscillations

3. Meaning: Endogenous speech parsing under volitional control

lack of meaning in information theory

The fundamental problem of communication is that of reproducing at one point either exactly or approximately a message selected at another point. Frequently the messages have *meaning*; that is they refer to or are correlated according to some system with certain physical or conceptual entities. These semantic aspects of communication are irrelevant to the engineering problem. The significant aspect is that the actual message is one *selected from a set* of possible messages. The system must be designed to operate for each possible selection, not just the one which will actually be chosen since this is unknown at the time of design.

Shannon (1948) A mathematical theory of communication

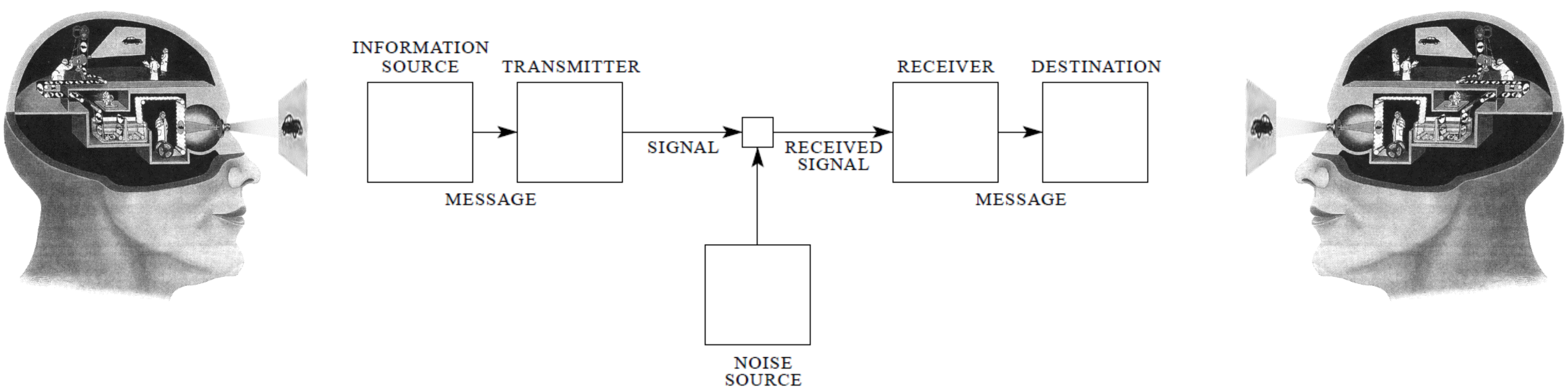
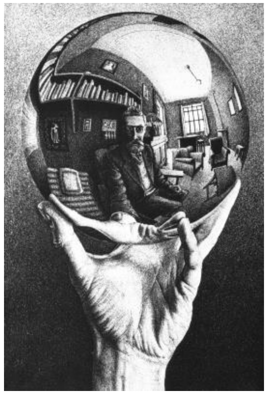
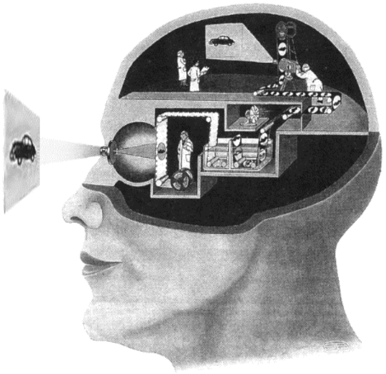


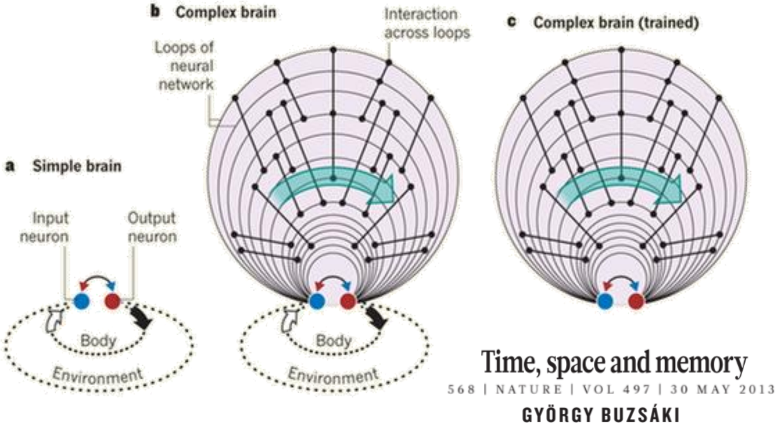
Fig. 1—Schematic diagram of a general communication system.



self-referential



meaning assignment



semi-autonomy

Some underminded aspects in neuroscience to account for:

(1) the brain analyzes information through its own knowledge-based decoder

(2) to understand the neural code, brain activity should be characterized in the brain's own time metrics

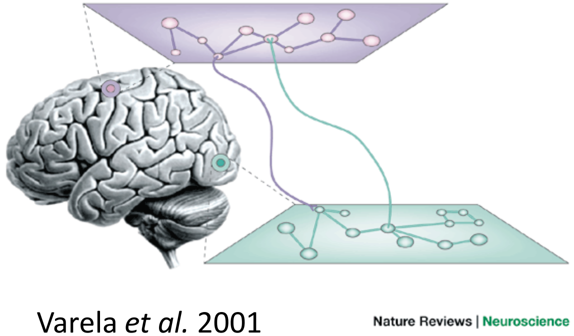
Question: do oscillations implement the time metrics onto which information content is mapped / analyzed / vectorized?

van Wassenhove, 2016, 2017a,b

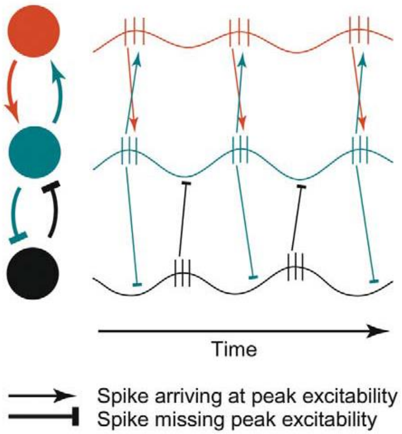
Communication-Through-Coherence (CTC) hypothesis

phase synchrony between neural populations supports integration of information across large-scale brain regions

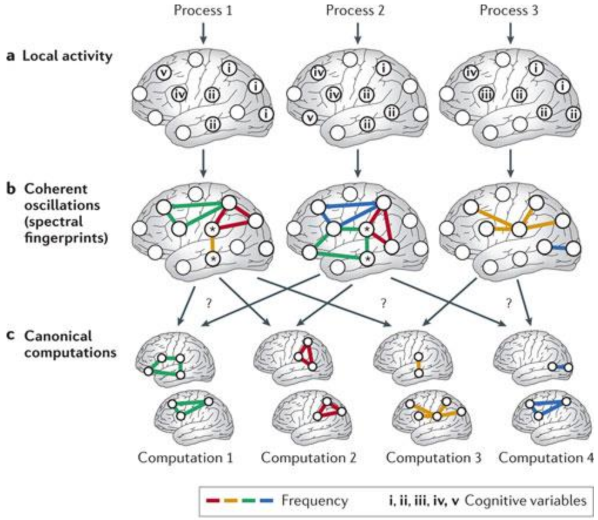
Freeman, Singer, Llinas,… Varela et al., 2001; Engel & Singer, 2001; Fries, 2005, 2015; Siegel et al., 2012; Akam et al., 2014; Bastos et al., 2015; […]



Varela *et al.* 2001



Fries 2005



Siegel *et al.* 2012

Entrainment with delay is the general mechanism that sets up phase relations subserving CTC both for unidirectional communication and for <u>bidirectional</u> communication.

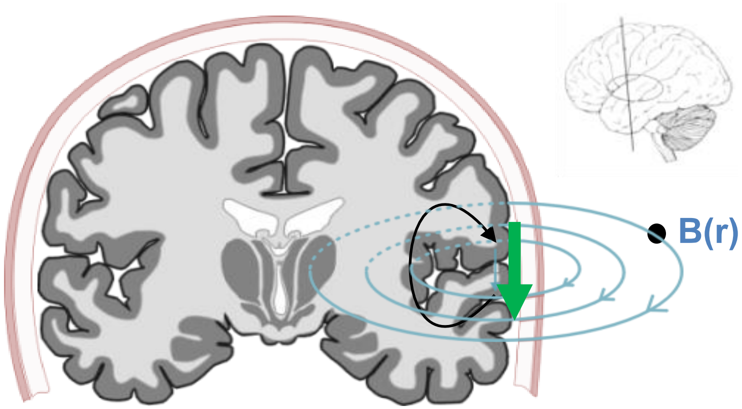
- Fries 2015

➔ *CTC hypothesis of asymmetrical i/o predicts that neural delays enable matching the phase at which spiking is likeliest, thereby providing endogenous functionality to the underlying anatomical structure*

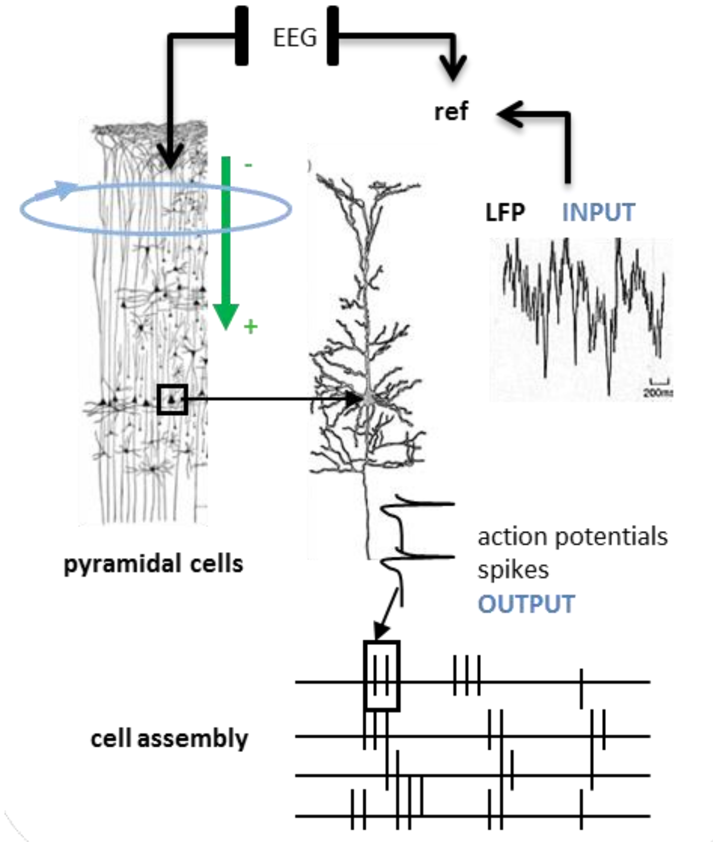
Non-invasive time-resolved neuroimaging in humans

MEG mainly records population activity located in sulci. [brain activity in pT (10^{-12} T) | earth in µT]

EEG mainly records population activity located in gyri. [µV]

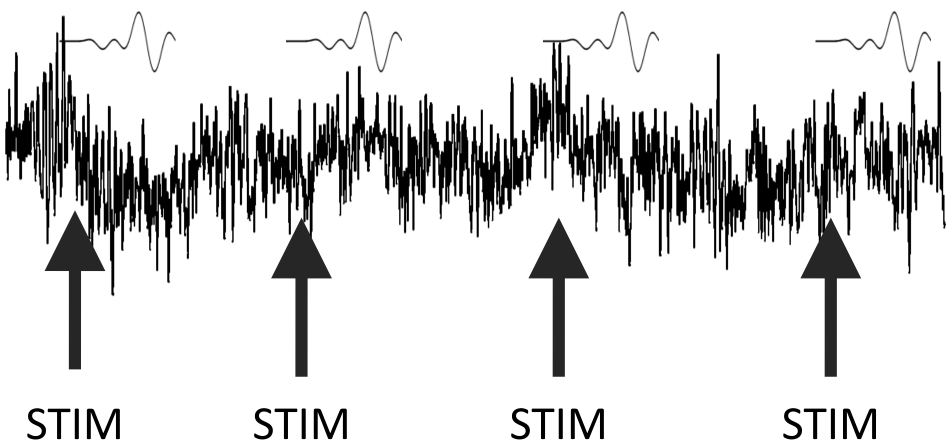


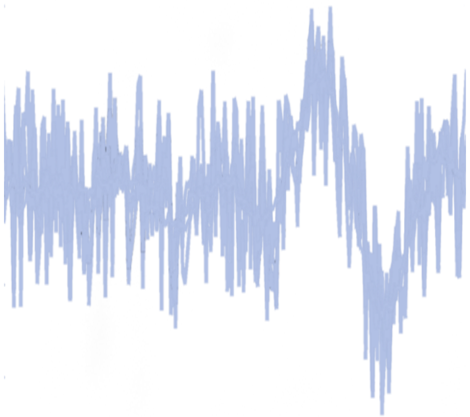
coronal section
human brain



BRAIN	≈ 10^{11} neurons
CORTEX	≈ 10^{10} neurons
PYRAMIDAL NEURONS	**≈ 85% (8.5^{10})**
SYNAPSES	≈ 10^4 to 10^5
CORTICAL SURFACE	≈ 3000 cm^2
Temporal resolution	**≈ 1 ms**
Spatial resolution	**≈ 0.5 cm^2**
Sensitivity	≈ 10^7 à 10^9 neurons *i.e.*~ **50 000 neurones/10 nAm**

Time-locked processing (evoked activity)





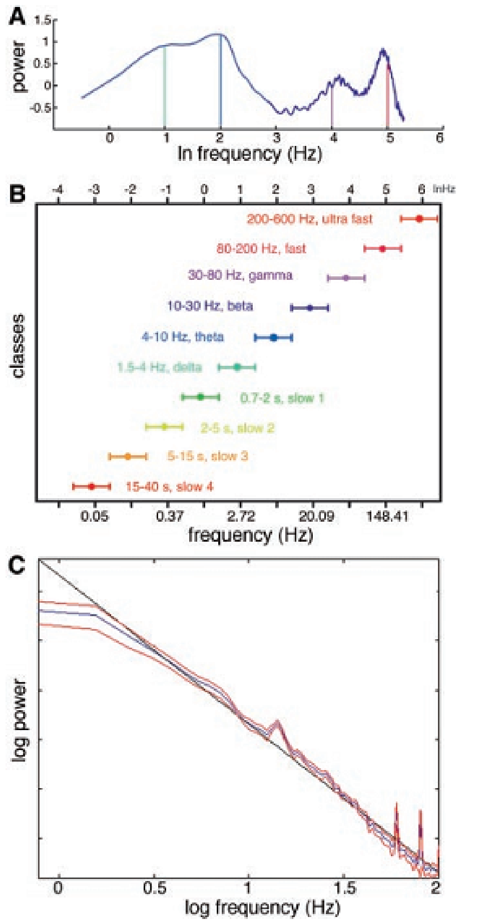
Event Related Field/Potential (ERF/P)

macroscopic brain activity

arrythmic (scale-free) + rhythmic (time-scaling oscillations)

Neuronal Oscillations in Cortical Networks

Science György Buzsáki[1*] and Andreas Draguhn[2]

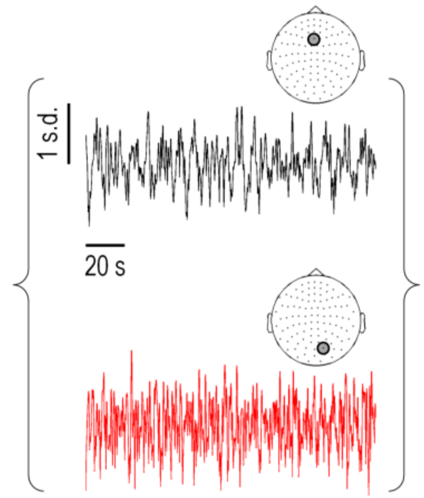


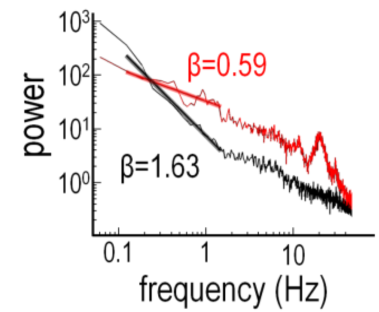
The log-dynamic brain: how skewed distributions affect network operations

REVIEWS

György Buzsáki[1,2] and Kenji Mizuseki[1,3]

264 | APRIL 2014 | VOLUME 15





P Ciuciu

P Abry

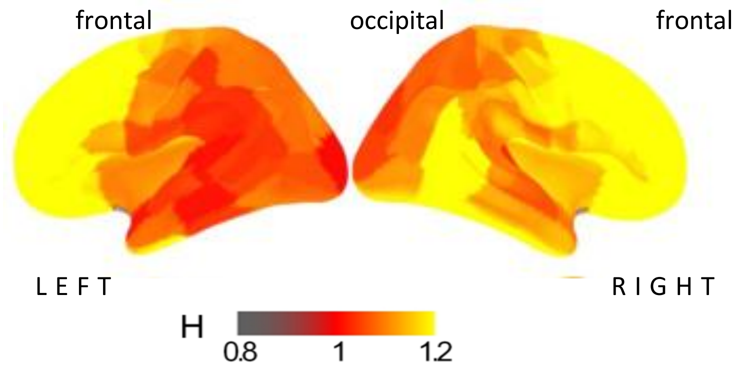
Zilber et al 2012
Ciuciu *et al 2018*

Natural logarithmic relationship between brain oscillators

Markku Penttonen[a], György Buzsáki[b,*]

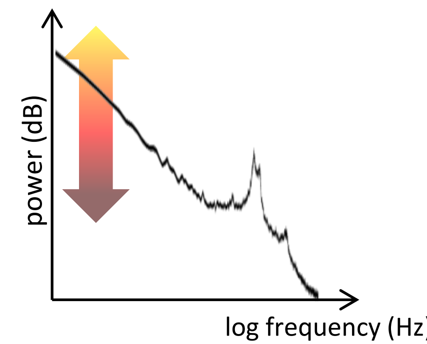
"From our analysis a general principle emerged: discrete oscillation bands form a geometric progression on a linear frequency scale and thus a linear progression on a natural logarithmic scale. Furthermore, the numerous brain oscillators fill all frequency bands from ultra-slow to ultra-fast frequencies without major gaps

temporal structure of human brain activity



LaRocca *et al* 2018

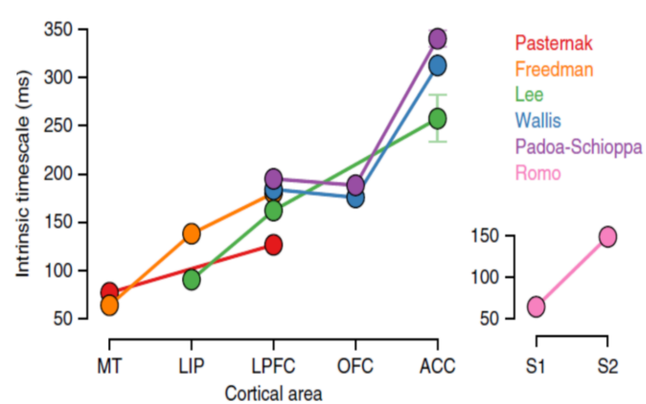
resting-state MEG



A hierarchy of intrinsic timescales across primate cortex

John D Murray[1,2], Alberto Bernacchia[2,3], David J Freedman[4], Ranulfo Romo[5,6], Jonathan D Wallis[7,8], Xinying Cai[9,10], Camillo Padoa-Schioppa[10], Tatiana Pasternak[11,12], Hyojung Seo[2], Daeyeol Lee[2] & Xiao-Jing Wang[1,2,9]

nature neuroscience

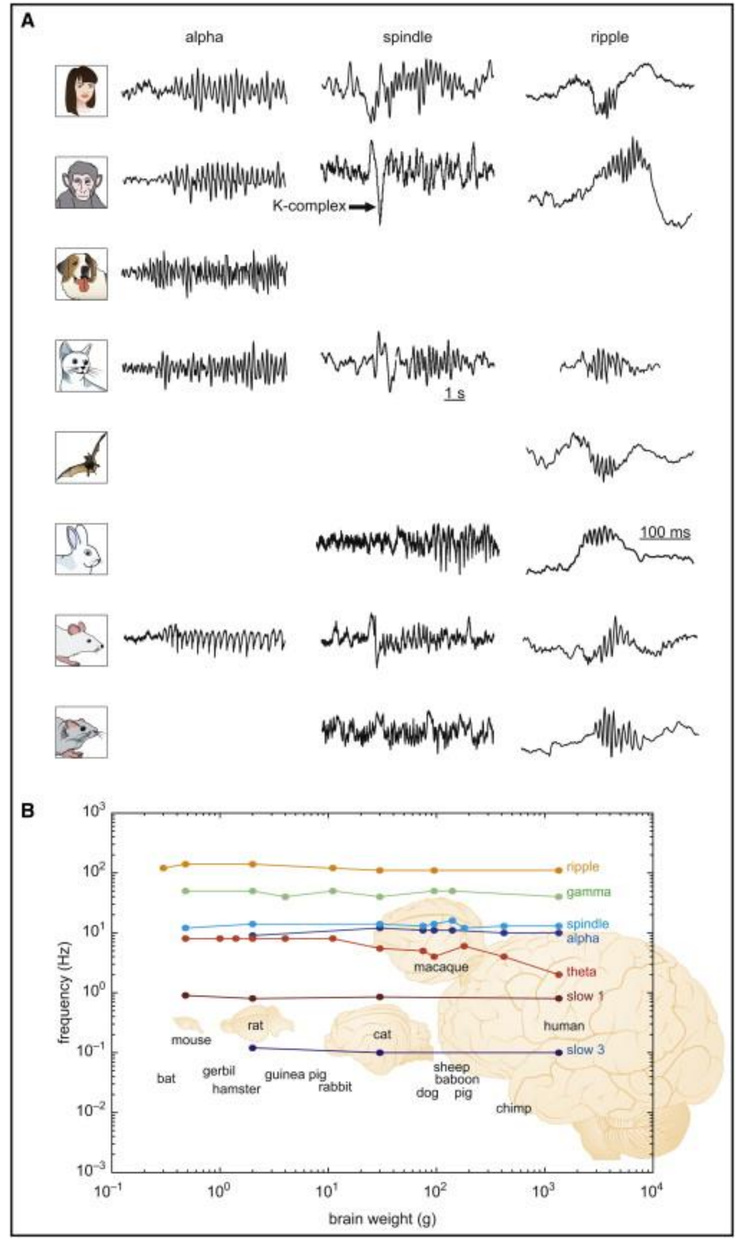


Zilber et al 2012
He 2014
LaRocca et al 2018
Deghani et al …

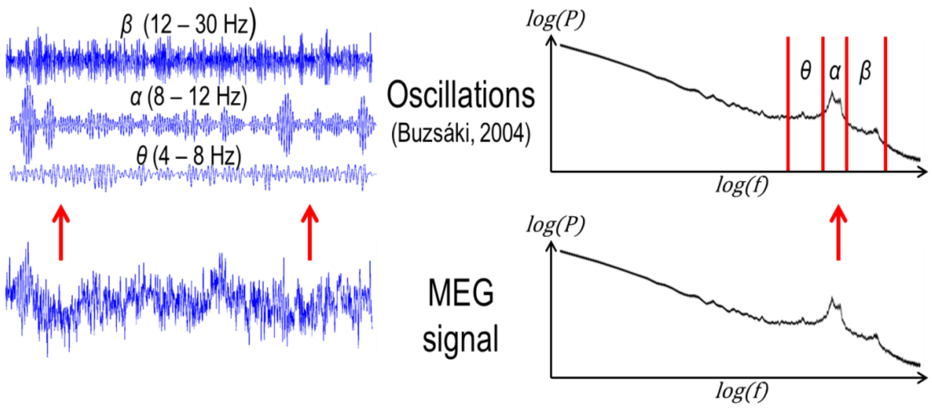
Scaling Brain Size, Keeping Timing:

Evolutionary Preservation of Brain Rhythms

György Buzsáki, Nikos Logothetis, and Wolf Singer



working hypothesis: oscillatory structures in (human) brain activity provide natural temporal metrics for information processing in the brain by breaking long-range temporal autocorrelations



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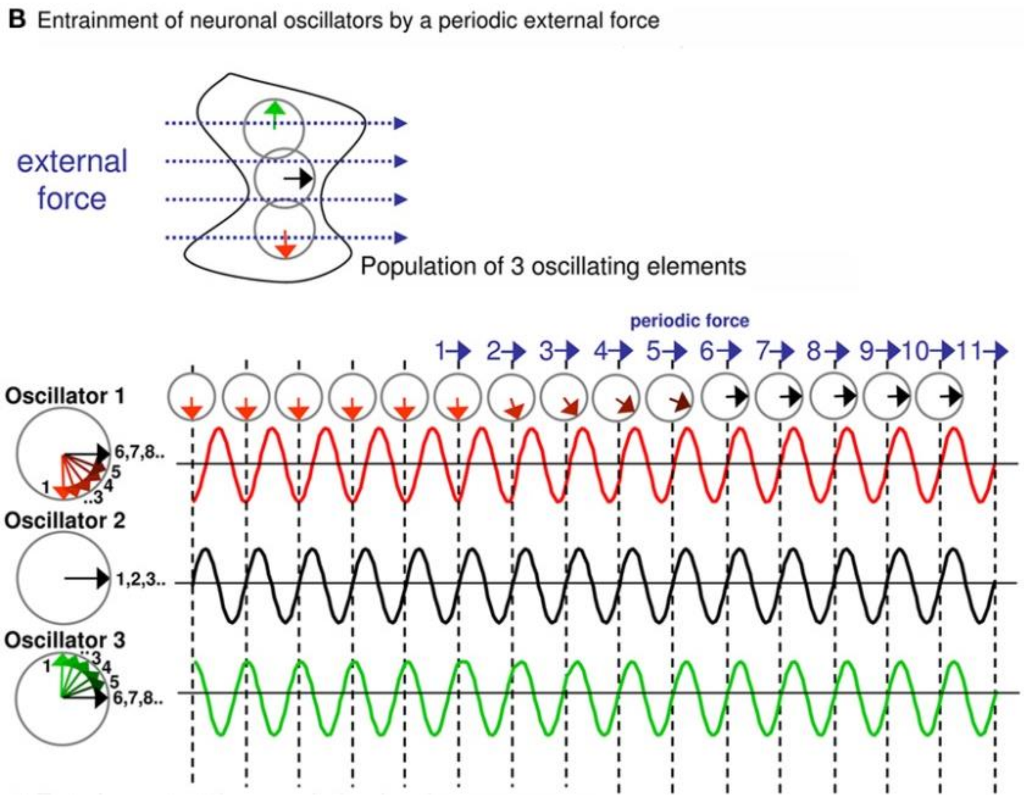
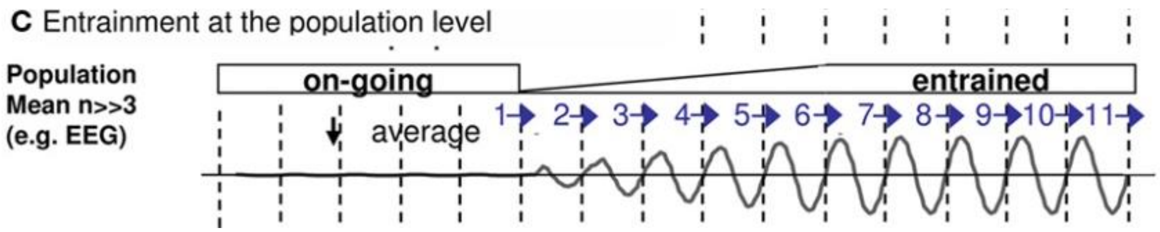
Entrainment of cortical response to sensory inputs



Thut et al 2012

Consistent with CTC
sensory entrainment predicts an increase of power and PLV as a function of the duration of the entrainement.



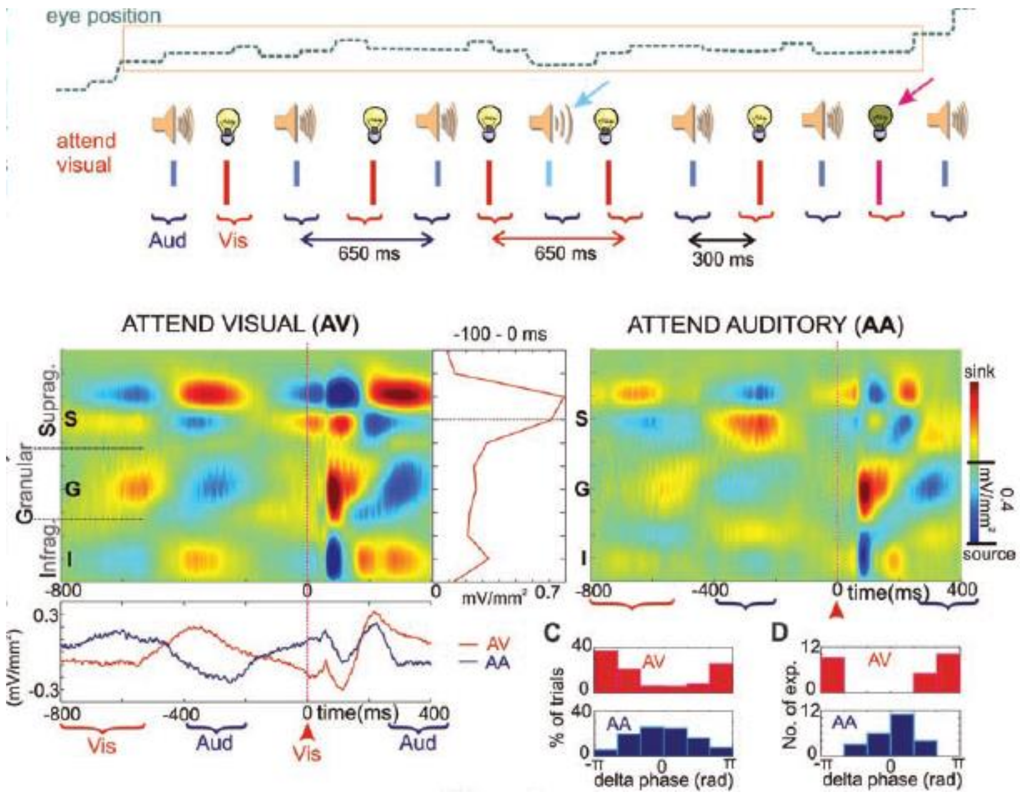
Thut et al 2011

Les consistent with bidirectional CTC
endogenous control of brain responses does not *a priori* predict stationarity in the latency of brain response.

~ passive resonance to inputs

in temporal entrainement, although ‘attention selection’ enables switching from one to the other sensory modality, the entrained response *is locked to* the exogenous temporal structure of sensory inputs

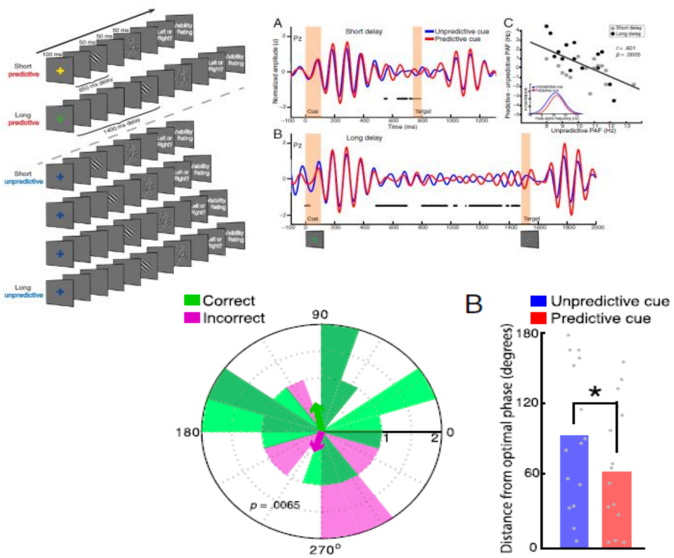
Entrainment of Neuronal Oscillations as a Mechanism of Attentional Selection
Peter Lakatos, *et al.*
Science **320**, 110 (2008);
DOI: 10.1126/science.1154735



(little evidence for) endogenous modulation of phase-response in humans

Top-down control of the phase of alpha-band oscillations as a mechanism for temporal prediction

Jason Samaha[a,1], Phoebe Bauer[b], Sawyer Cimaroli[a], and Bradley R. Postle[a,c]

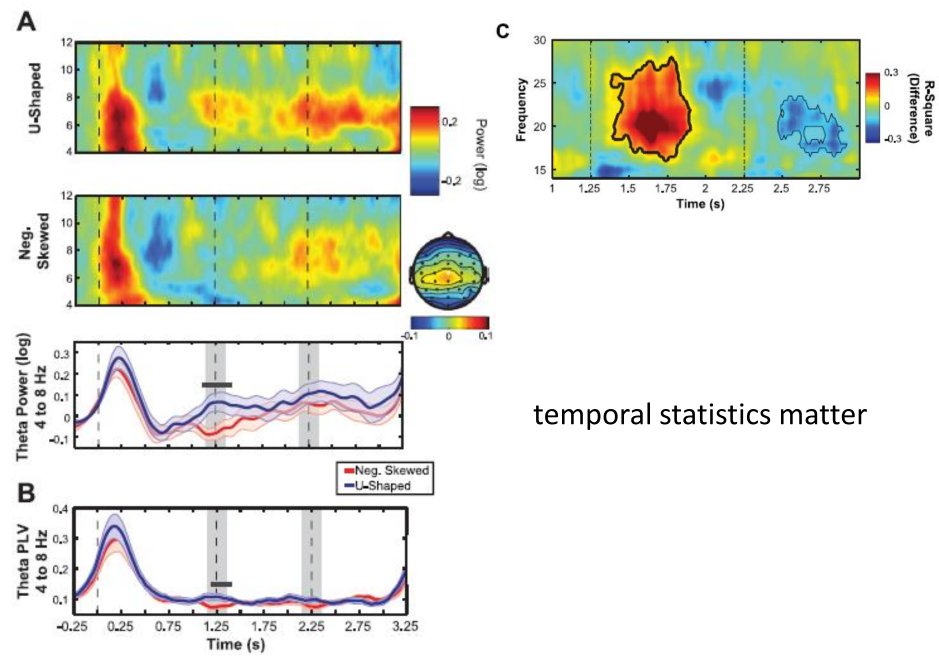


internal prediction matters

J Neurophysiol 106: 2964–2972, 2011.
First published September 7, 2011; doi:10.1152/jn.00157.2011.

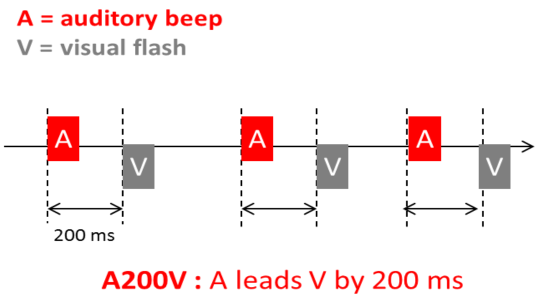
Endogenous modulation of low frequency oscillations by temporal expectations

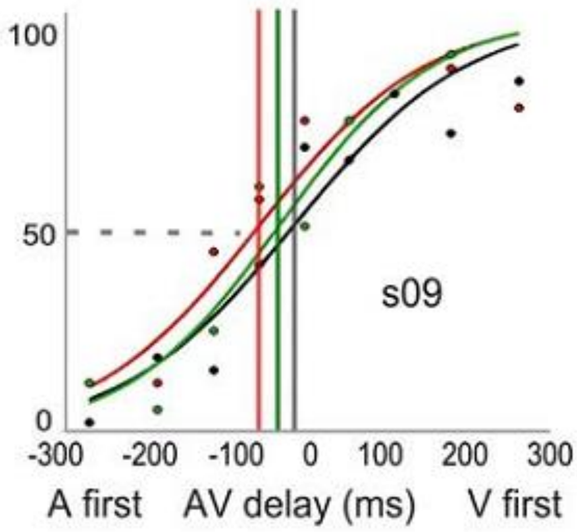
Andre M. Cravo,[1] Gustavo Rohenkohl,[2,3] Valentin Wyart,[2] and Anna C. Nobre[2,3]



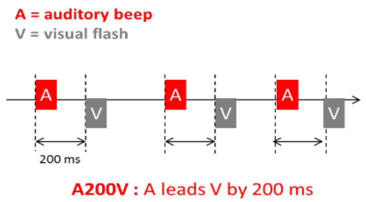
temporal statistics matter

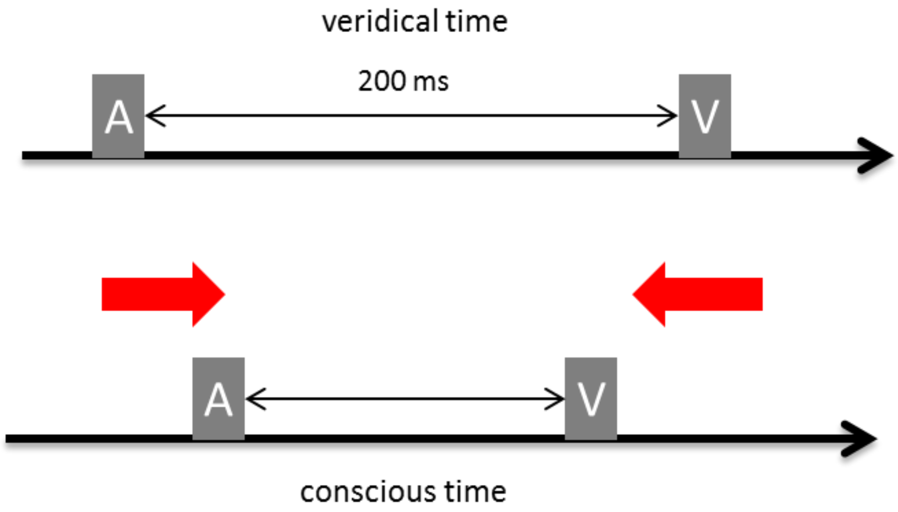
building simultaneity across sensory modalities





Kösem et al 2014





Kösem et al 2014

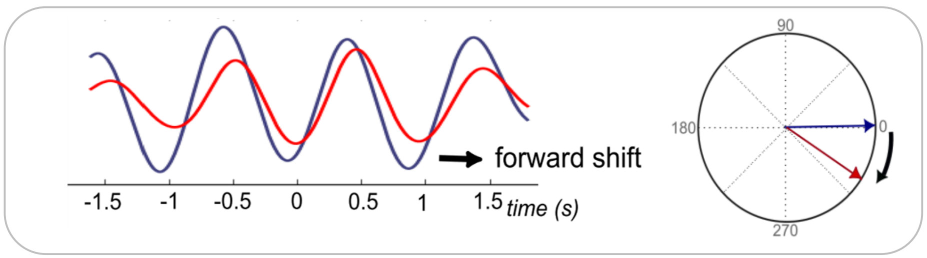
WH1: entrainment is passive (initial and final ϕ are arbitrary [var ϕi, var ϕf] <u>or</u> stationary [ϕi = ϕf])

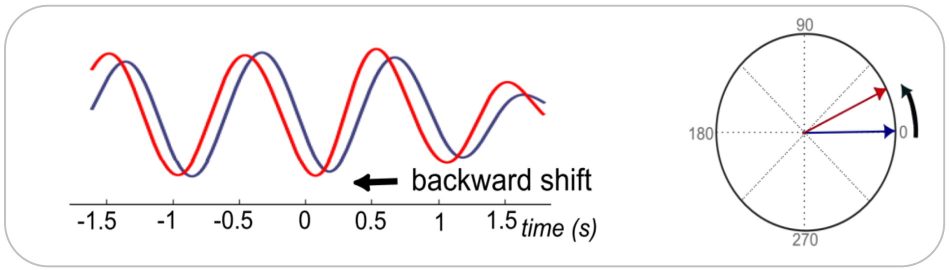
vs.

WH2: entrainment is active and computationally relevant for time perception

ϕi = before

ϕf = after



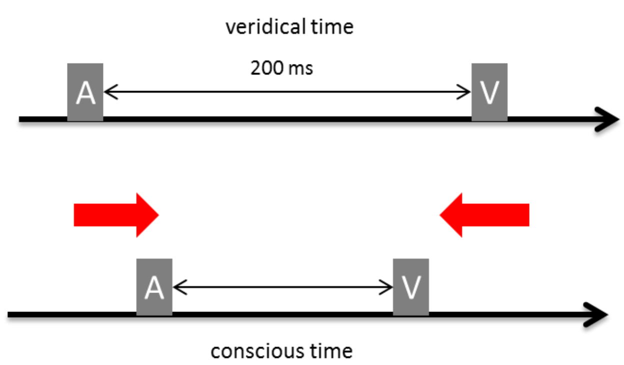


auditory cortex

advance the analysis of A in time

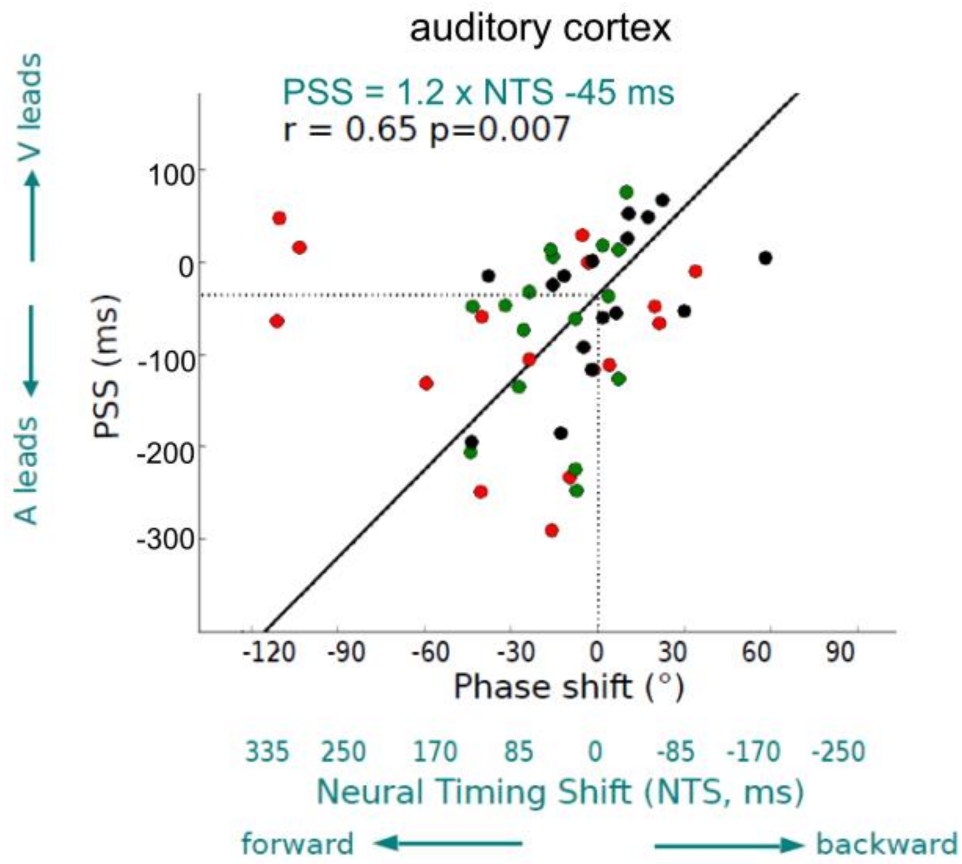
visual cortex

delay the analysis of V in time



Kösem et al 2014

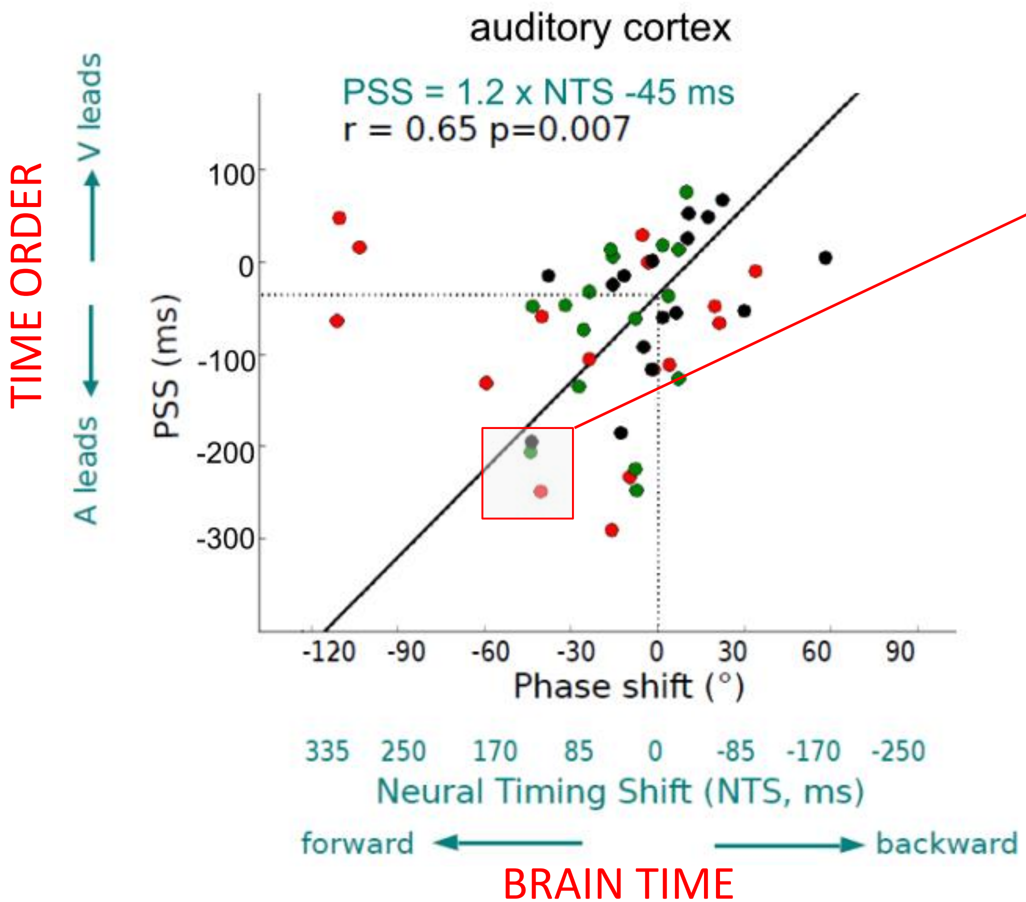
The non-stationarity of entrained phase responses linearly predicts perceived order



the more negative the phase difference,
the more forward in time the auditory analysis
the more A must precede V to be perceived as simultaneous

Kösem et al 2014

the non-stationarity of entrained phase responses linearly predicts perceived order



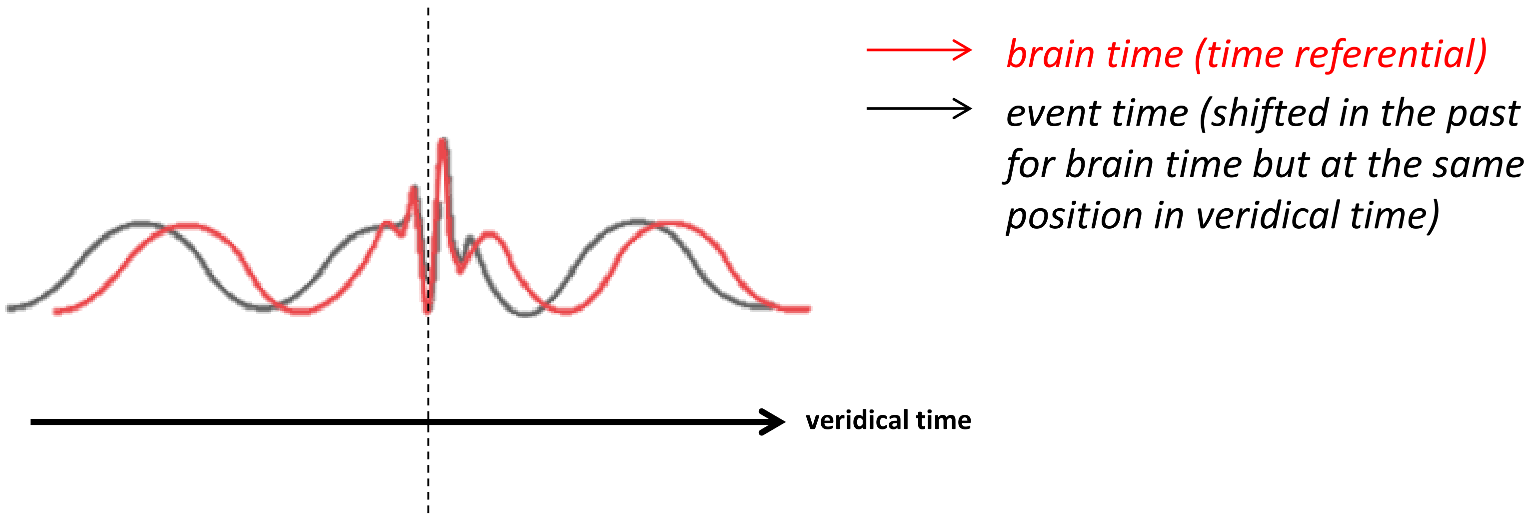
phase delays in the auditory response moves the analysis of the sound forward in time

a negative PSS indicates that the participant required the sound to be presented earlier than the visual event to report simultaneity

the more negative the phase difference,
the more forward in time the auditory analysis
the more A must precede V to be perceived as simultaneous

Kösem et al 2014

our claim is not that 1 Hz oscillation encodes time, rather,
that the phase response entrained to external rhythms can be endogenously modified
and this change is reflected in participants' conscious time (order) perception



evidence for non-stationarity of phase response suggests temporal
autonomization through endogenous control

van Wasssenhove (CON, 2016)

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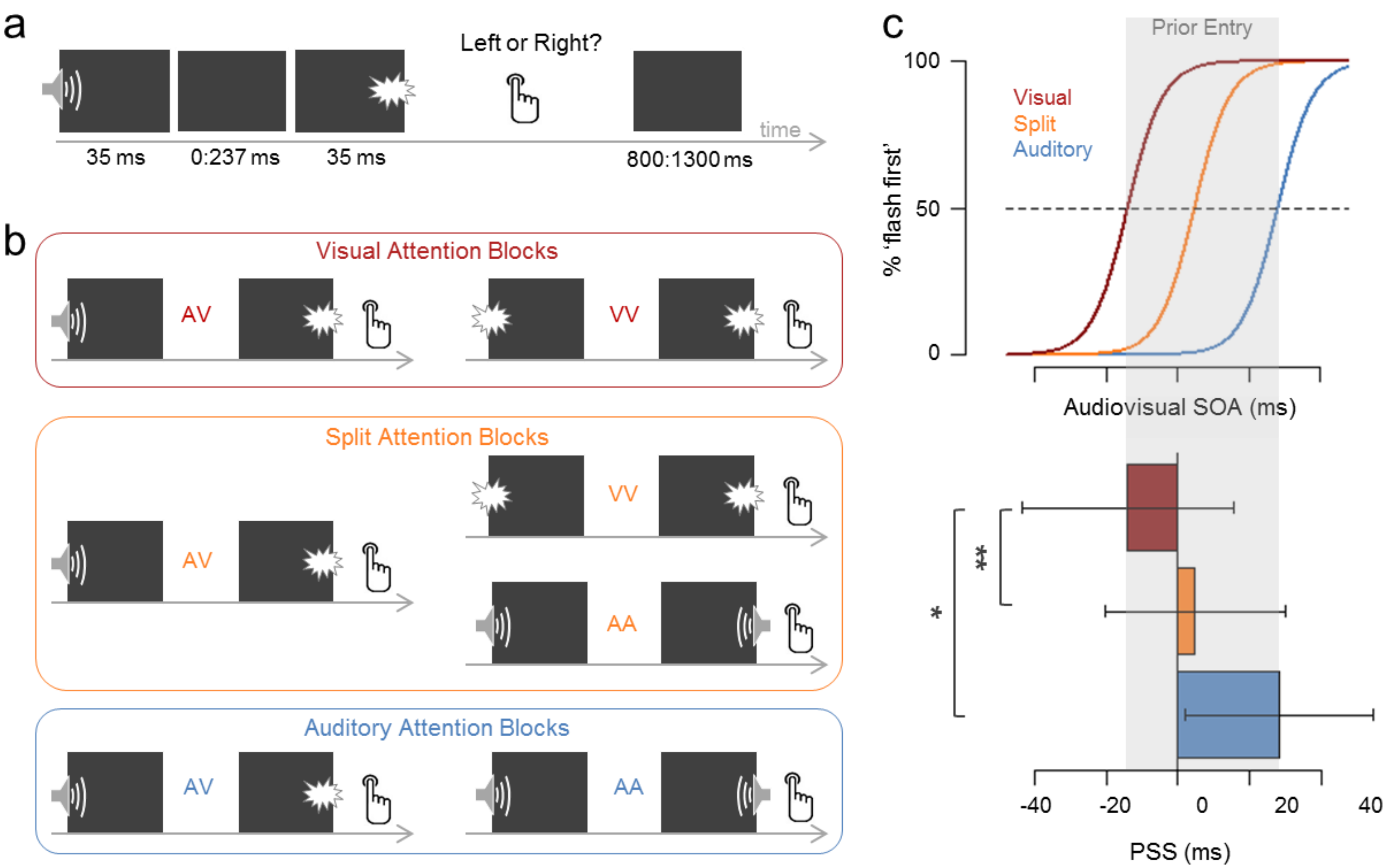
assessing the stability of order perception



spatialized paradigm adapted from Spence et al (2001)

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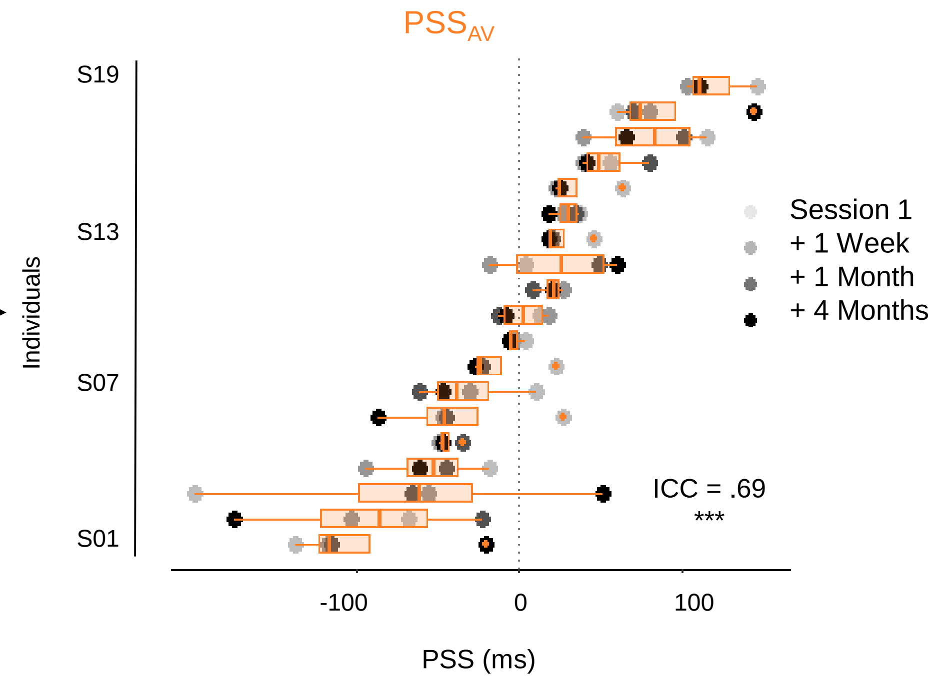
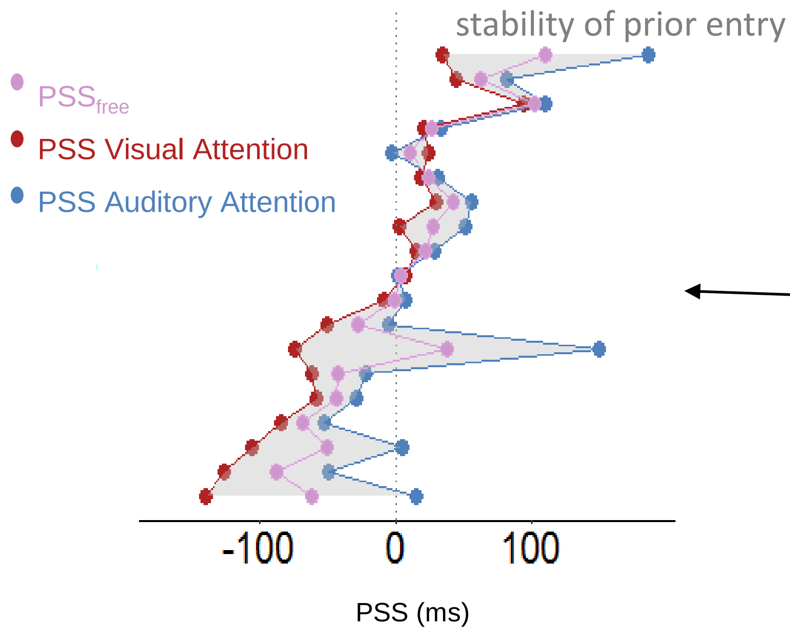
an individual's temporal order* bias is stable over time

** audiovisual, visual, auditory, & spatial*





attention compensates but does not fully eradicate an individual's order bias

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to make sense, reordering of inputs in internal time metrics
phase-dependency & coupling with gamma sequence encoders

Perceptual Cycles

Rufin VanRullen[1,2,*]

Trends in Cognitive Sciences, October 2016, Vol. 20, No. 10

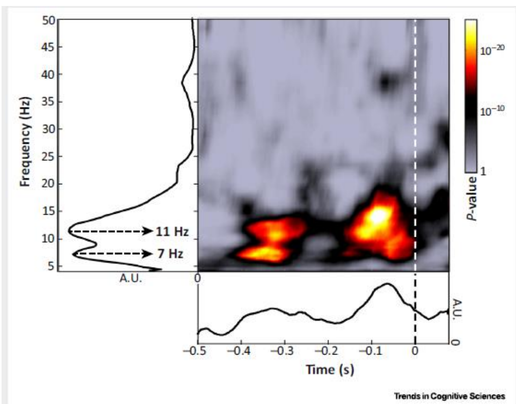
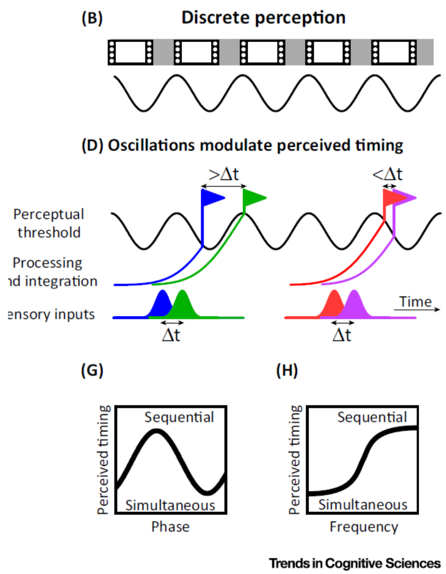


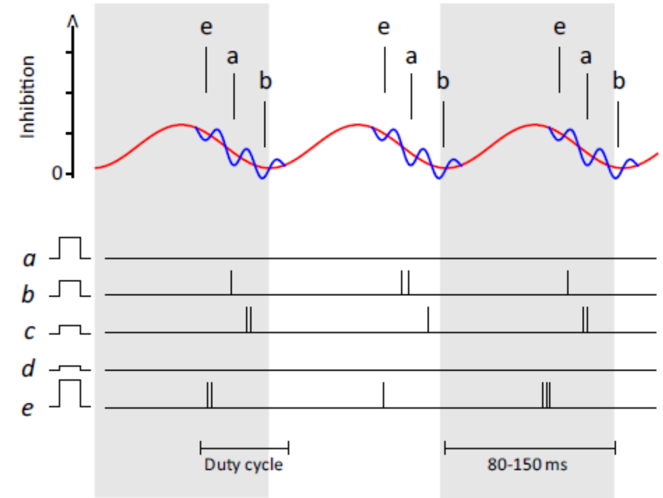
Figure I. Compilation of 10 Independent EEG Studies of Phase-Dependent Perception from Our Laboratory. All studies had in common: 9–18 observers; a randomized inter-stimulus interval, guaranteeing unpredictable

10 studies showing theta ~7 or alpha ~11 Hz prestimulus phase-dependency taken as evidence for rhythmic or discrete perception

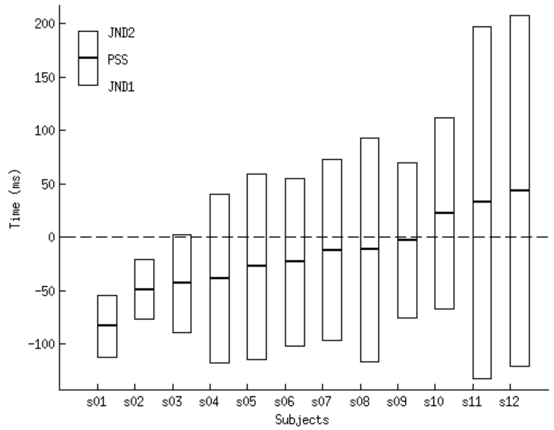


Temporal coding organized by coupled alpha and gamma oscillations prioritize visual processing

Ole Jensen, Bart Gips, Til Ole Bergmann*, and Mathilde Bonnefond*

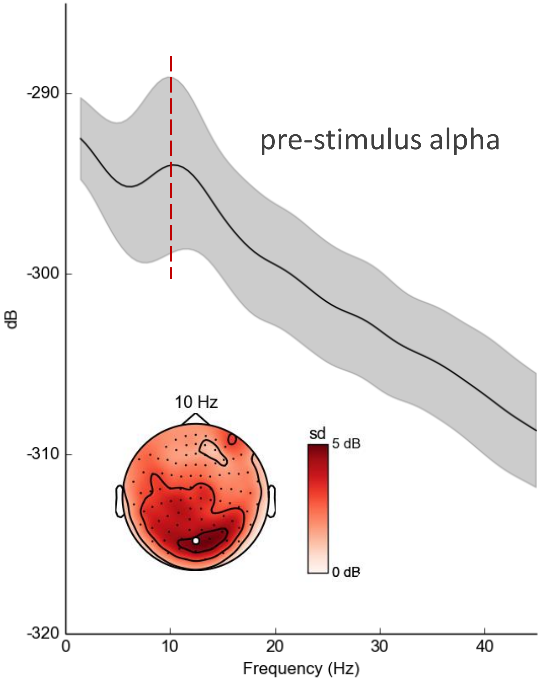


inter-individual PSS variability



maximally ambiguous stimulus = individual's PSS

Which of A or V was presented first?



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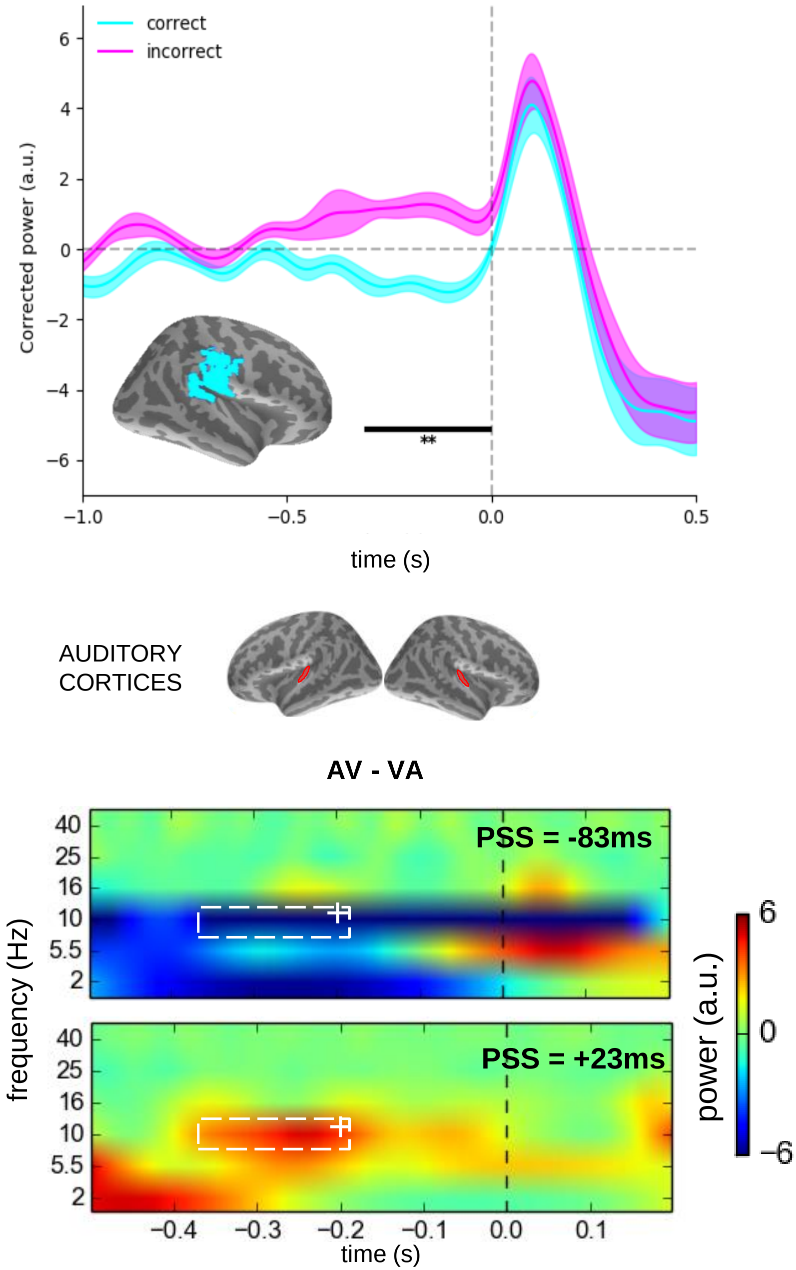

(1) a ↘ of prestim alpha power in auditory cortices was associated with correct performance irrespective of veridical order

⇔ no insight on order perception :

PSS^- : **audio first** given AV stimuli

PSS^+ : **visual first** given VA stimuli

(2) the signed magnitude difference of prestimulus alpha power informed on an individual's percept

⇔ a ↘ of prestim alphain audictoyr cortex for a participant requiring A to precede V (PSS^-) was associated with perceiving AV

conversely, an increase of prestim alpha for a participant requiring V to precede A (PSS^+) to perceive simultaneity was associated with perceiving VA

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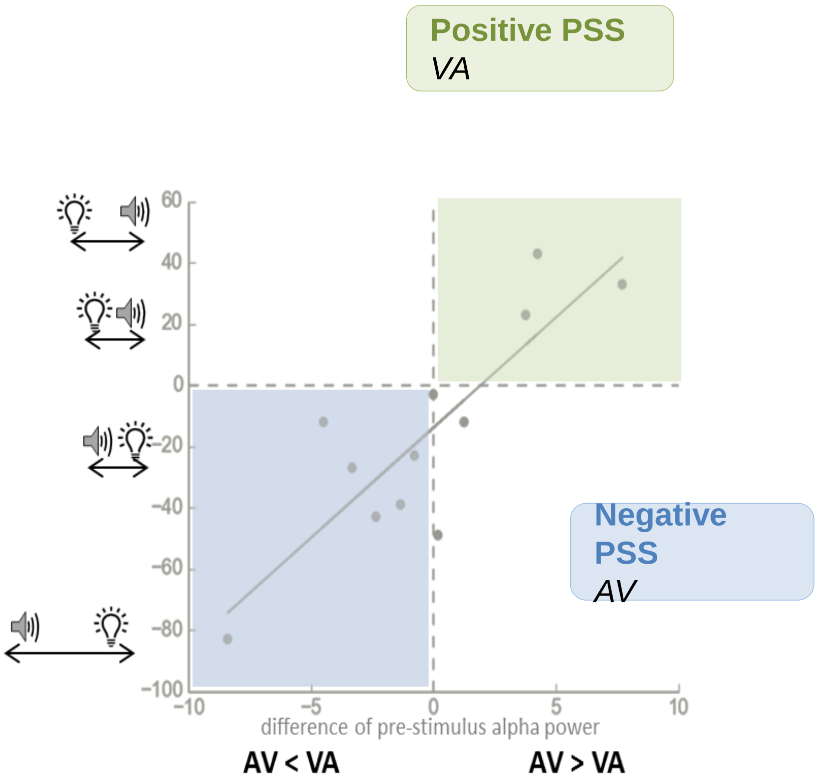
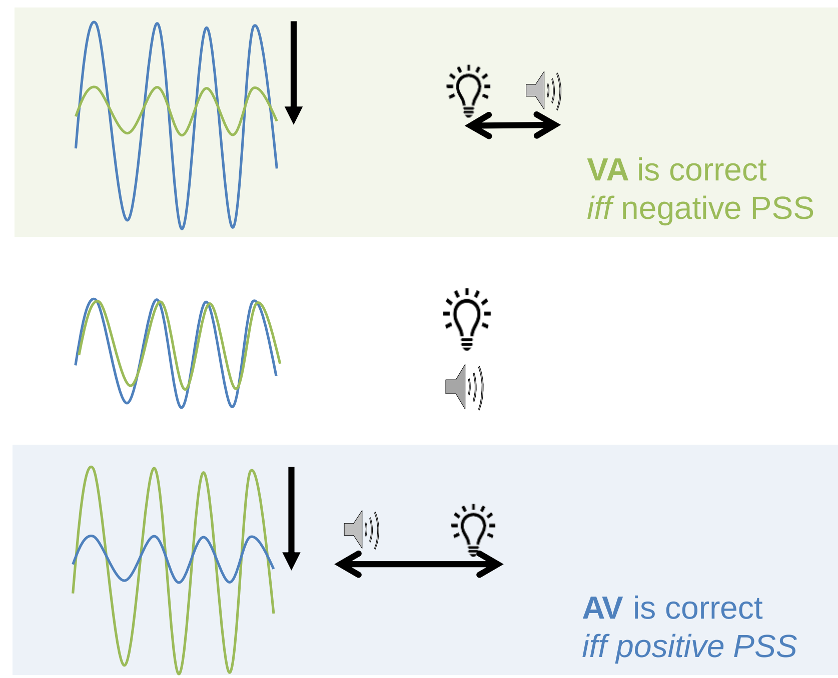
no phase-dependency of time order in the absence of entrainement
rather, the magnitude of alpha power decrease may counteract structural bias



(2) the **signed magnitude** difference of prestimulus alpha power predicts an individual's order percept



higher prestimulus alpha [incorrect] ⇔ follows structural bias, inhibition of sensory evidence
consistent with Iemi et al (2016); Chaumon & Busch (2014); van Dijk et al (2008)

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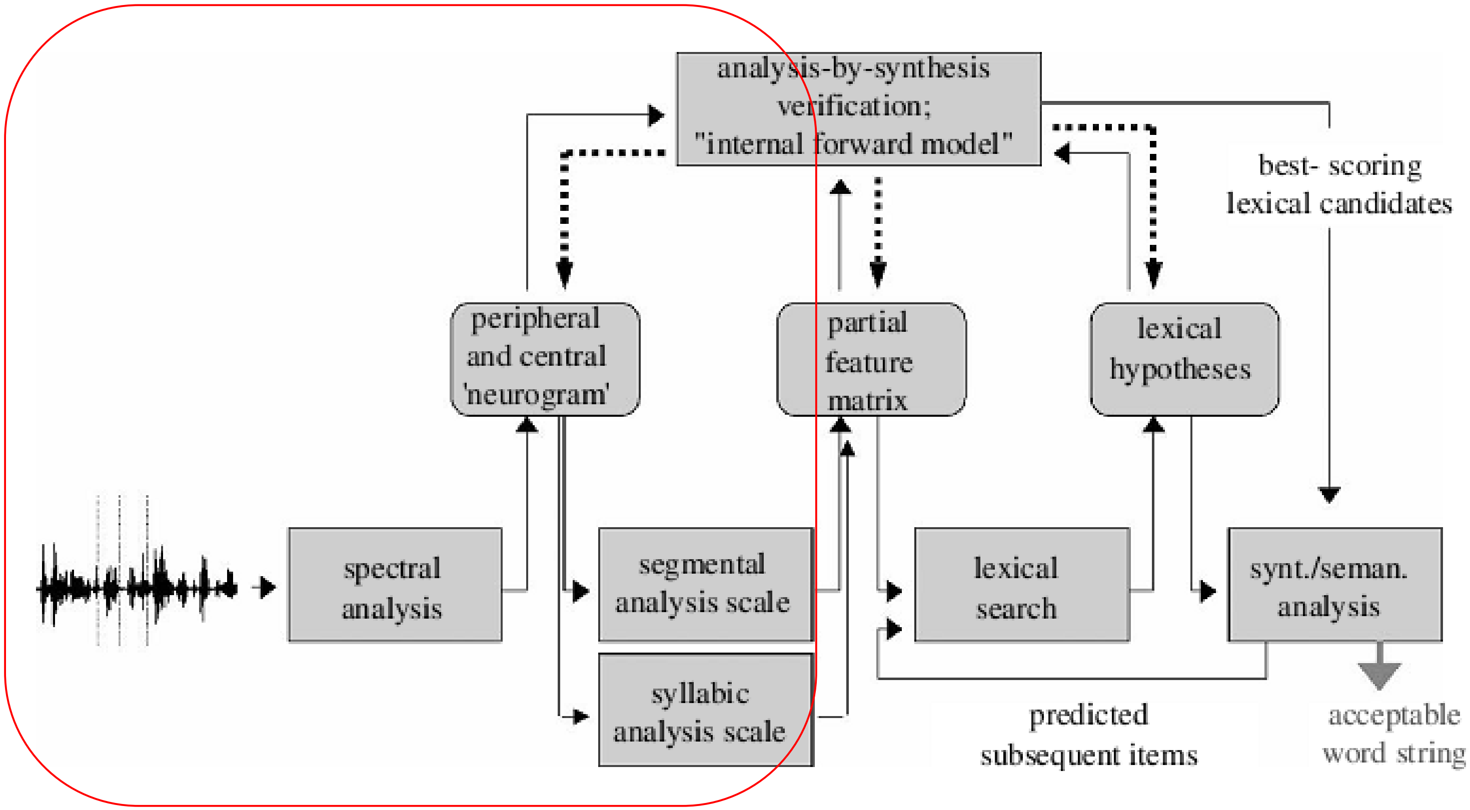
speech representations require tailored discretization of sensory inputs

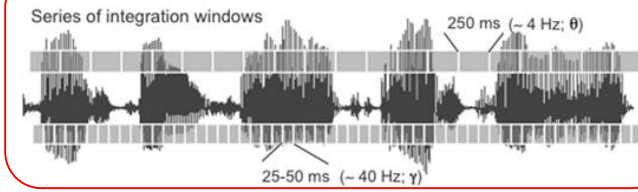
Speech perception at the interface of neurobiology and linguistics

David Poeppel[1,2,*], William J. Idsardi[1] and Virginie van Wassenhove[3]

Phil. Trans. R. Soc. B (2008) **363**, 1071–1086



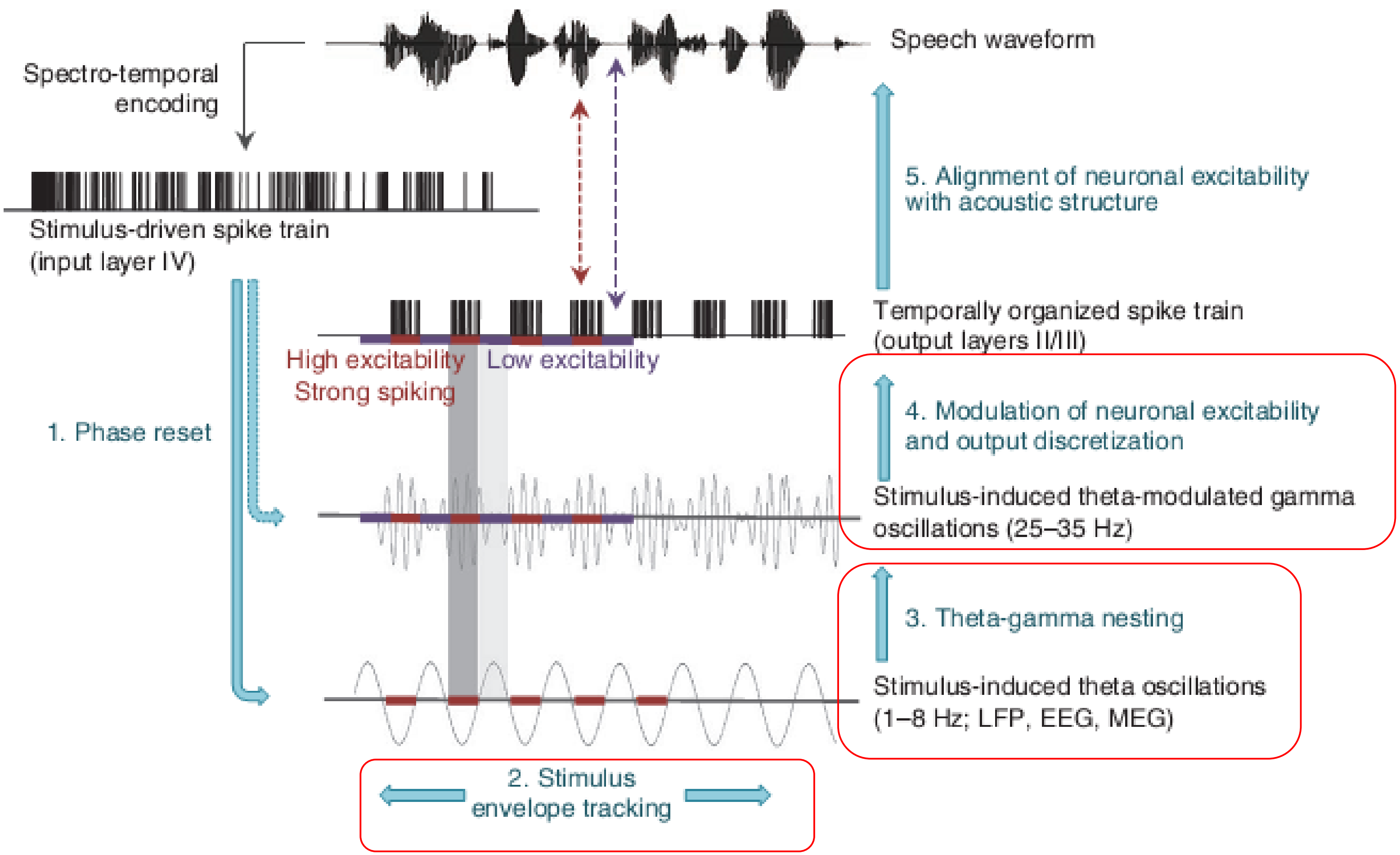
critical role of neural oscillations
parsing &| integrating



Cortical oscillations and speech processing: emerging computational principles and operations

Anne-Lise Giraud[1] & David Poeppel[2]

nature neuroscience

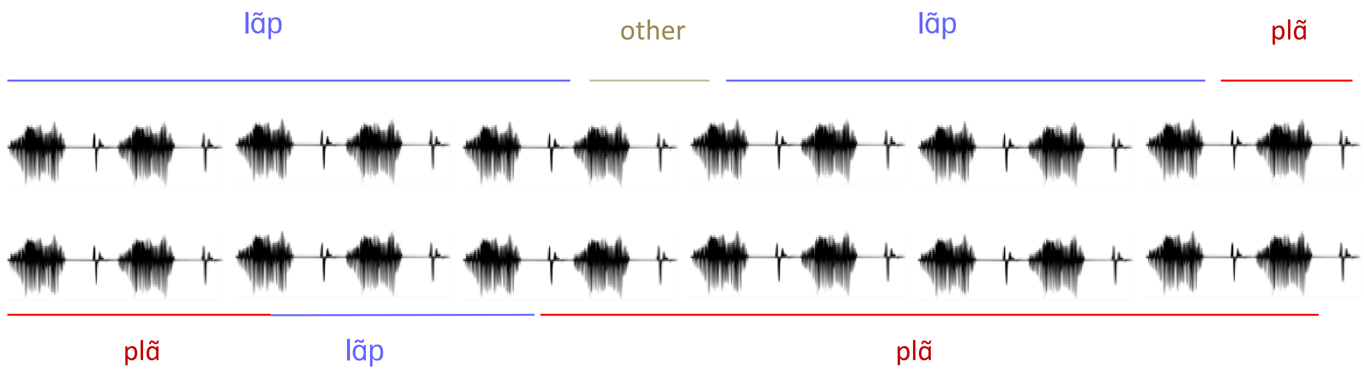


bistable speech • paradigm

INSTRUCTIONS

maintain [lãp]

maintain [plã]



verbal transformation paradigm from Basirat et al 2012, Phil Trans R Soc B: Biol Sci

Kösem et al 2016 *J Neurophys*

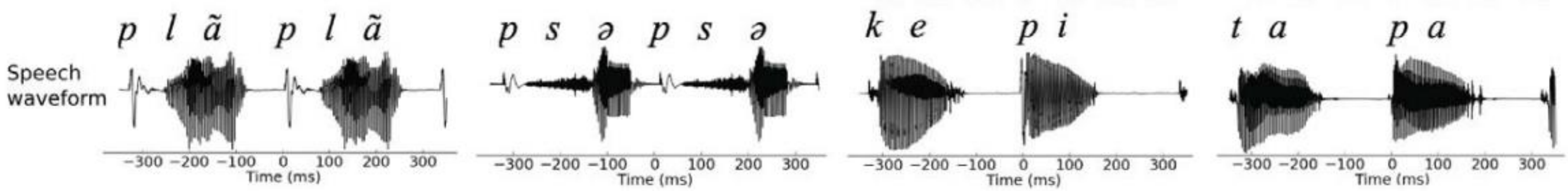
Kösem & van Wassenhove 2016 *Language, Cognition & Neuroscience*

volitional control • maintain one or the other percept

STIMULI TESTED

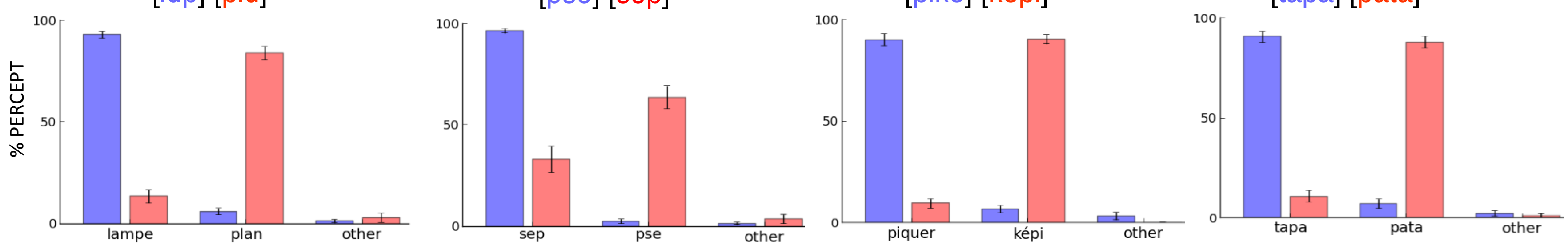
MONOSYLLABIC | BISYLLABIC

WORD [lãp] [plã] | NON-WORD [psə] [səp] | WORD [pike] [kepi] | NON-WORD [tapa] [pata]



MONOSYLLABIC | BISYLLABIC

WORD [lãp] [plã] | NON-WORD [psə] [səp] | WORD [pike] [kepi] | NON-WORD [tapa] [pata]

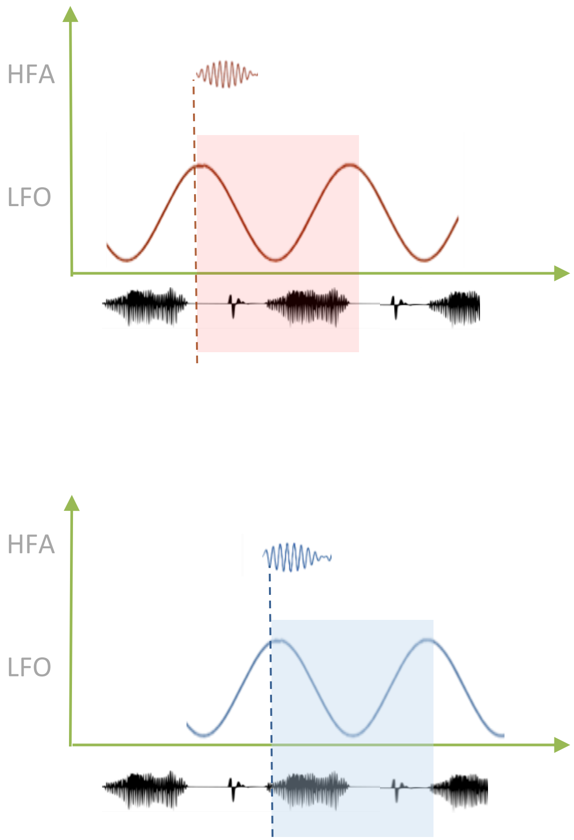


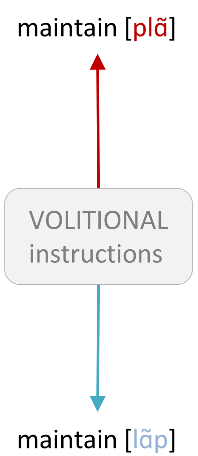
Kösem et al 2016 *J Neurophys*

working hypotheses

ACOUSTIC PARSING | SAMPLING

no change in acoustics
⇔
change in speech segmentation





working hypotheses

ACOUSTIC PARSING | SAMPLING

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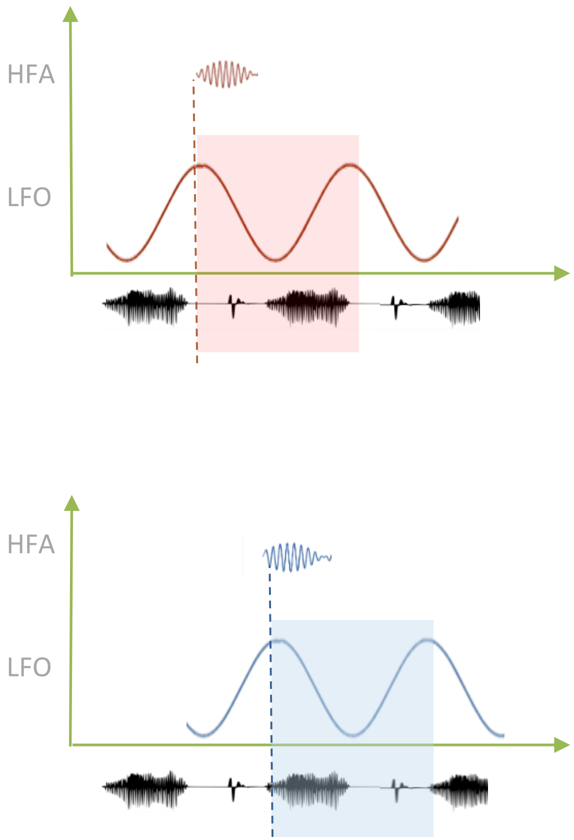
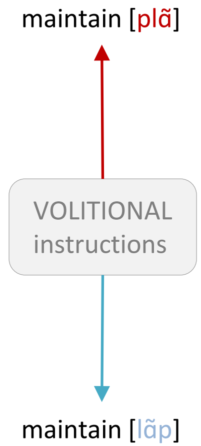
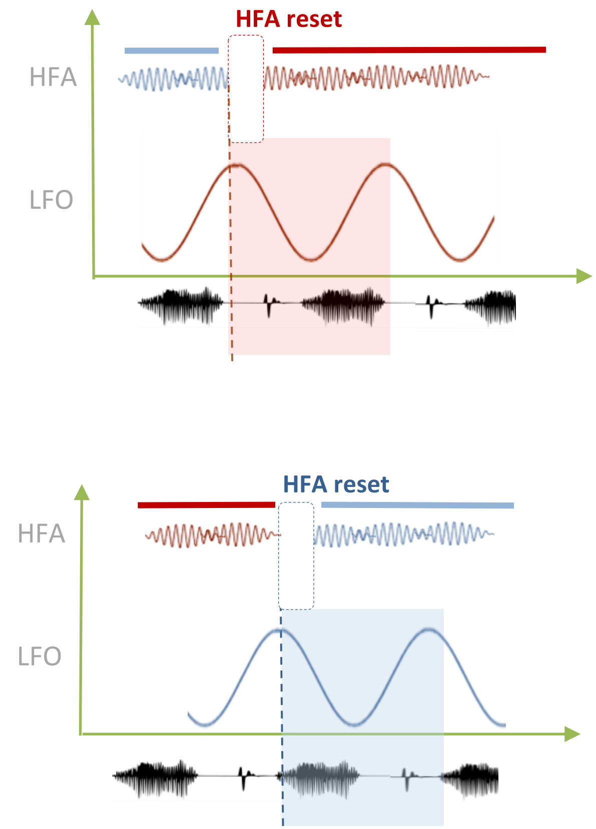


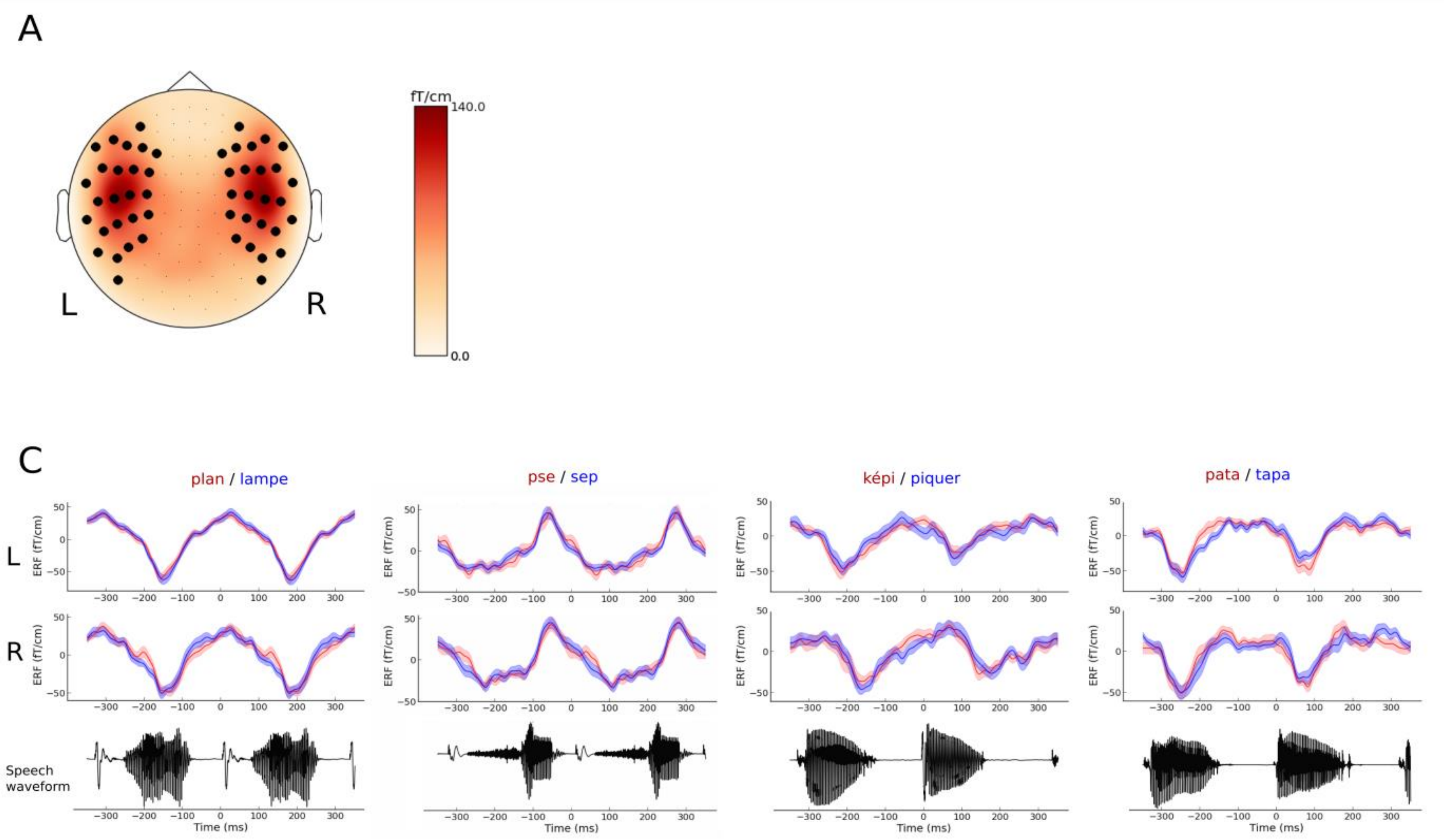


LINGUISTIC PARSING

no change in acoustics
⇔
change in speech segmentation
+
change in the discretization of speech content

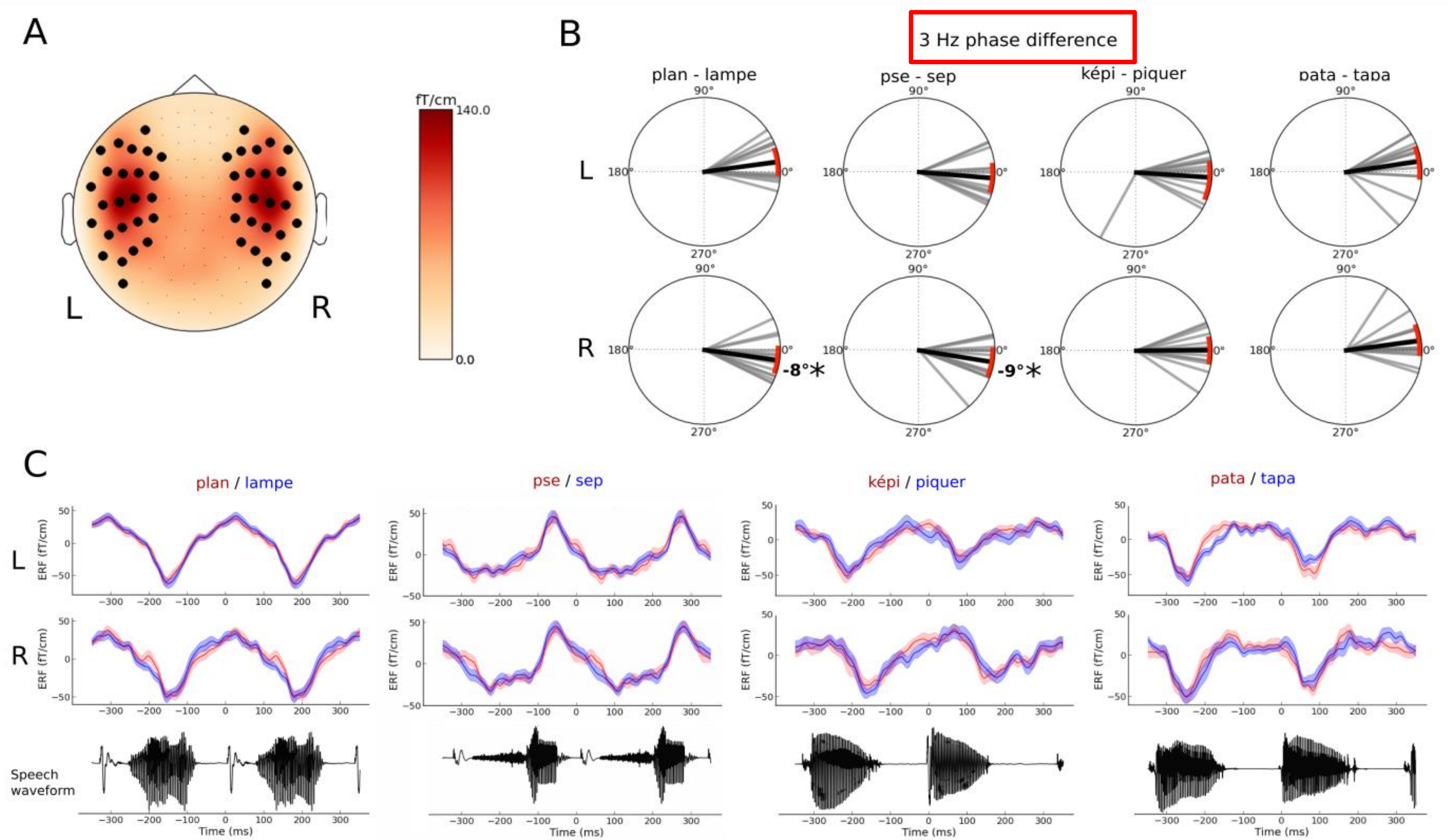


low-frequency oscillations did not robustly reflect perceived speech 1/4



Kösem et al 2016 *J Neurophys*

low-frequency oscillations did not robustly reflect perceived speech 2/4



Kösem et al 2016 *J Neurophys*

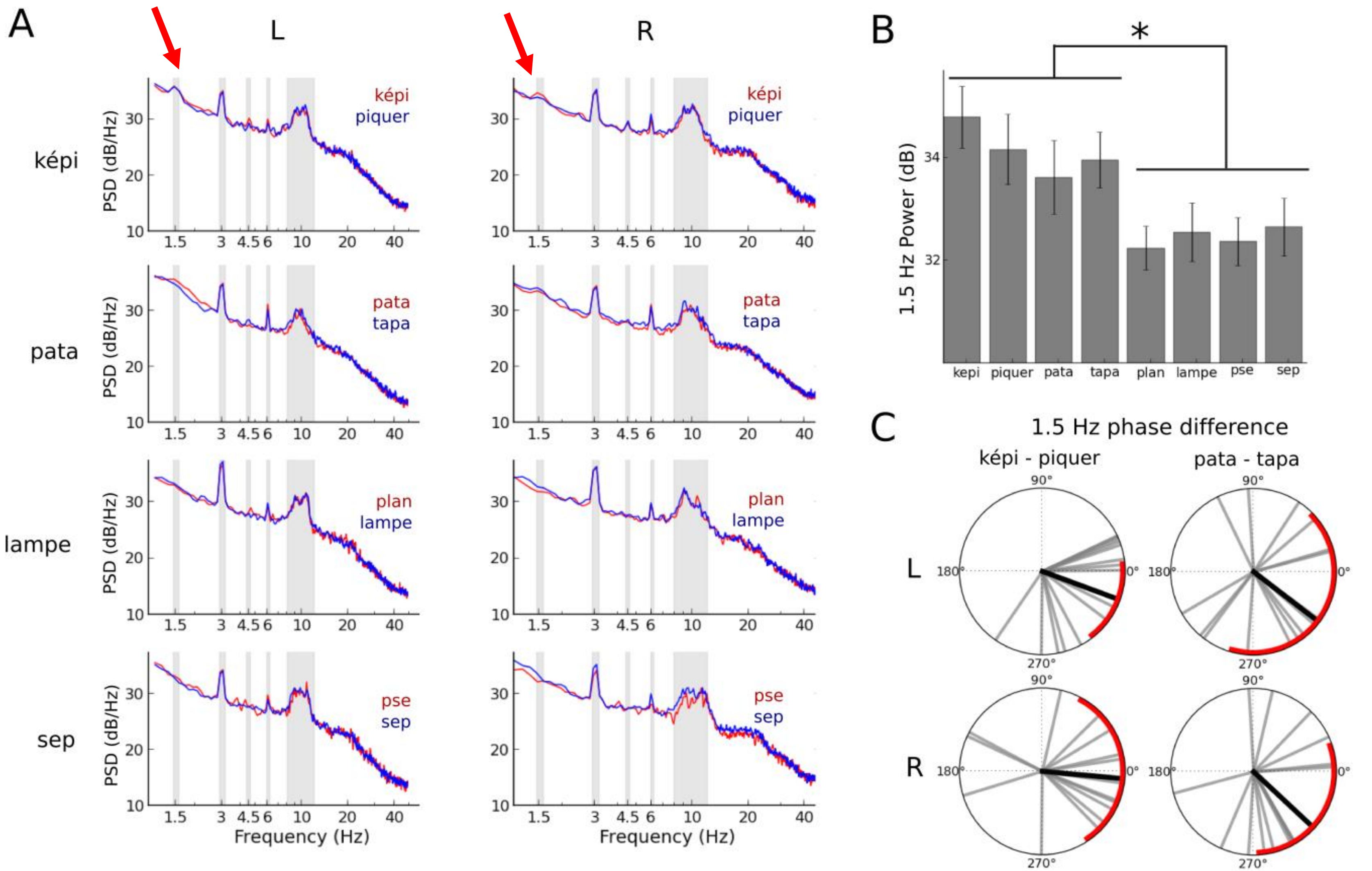
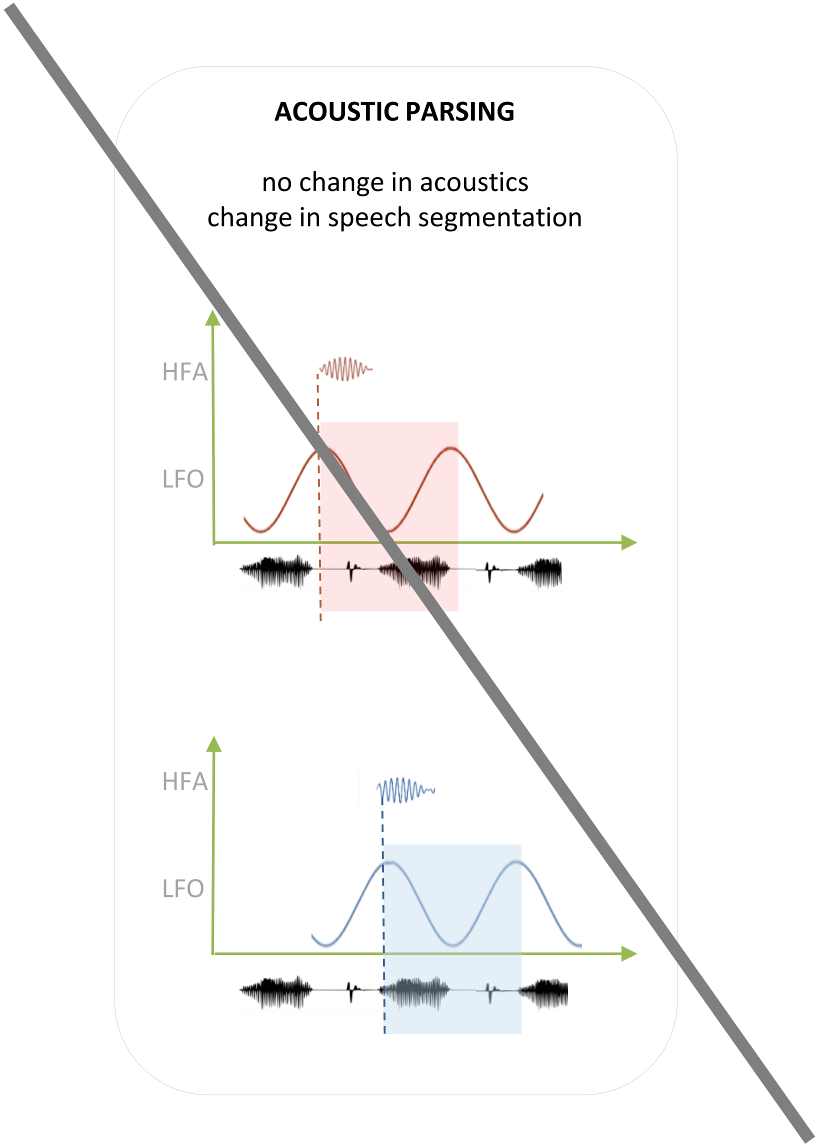
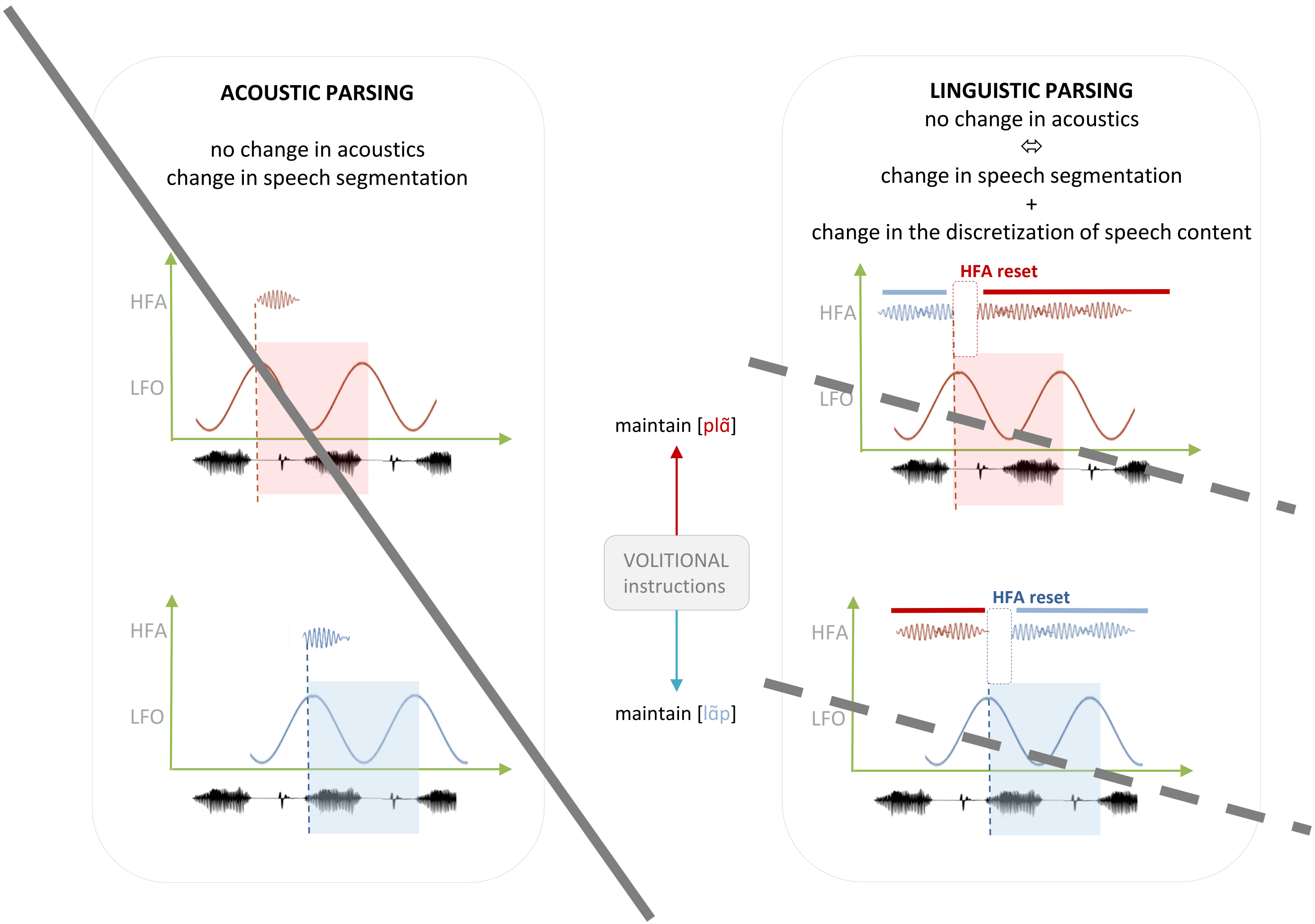


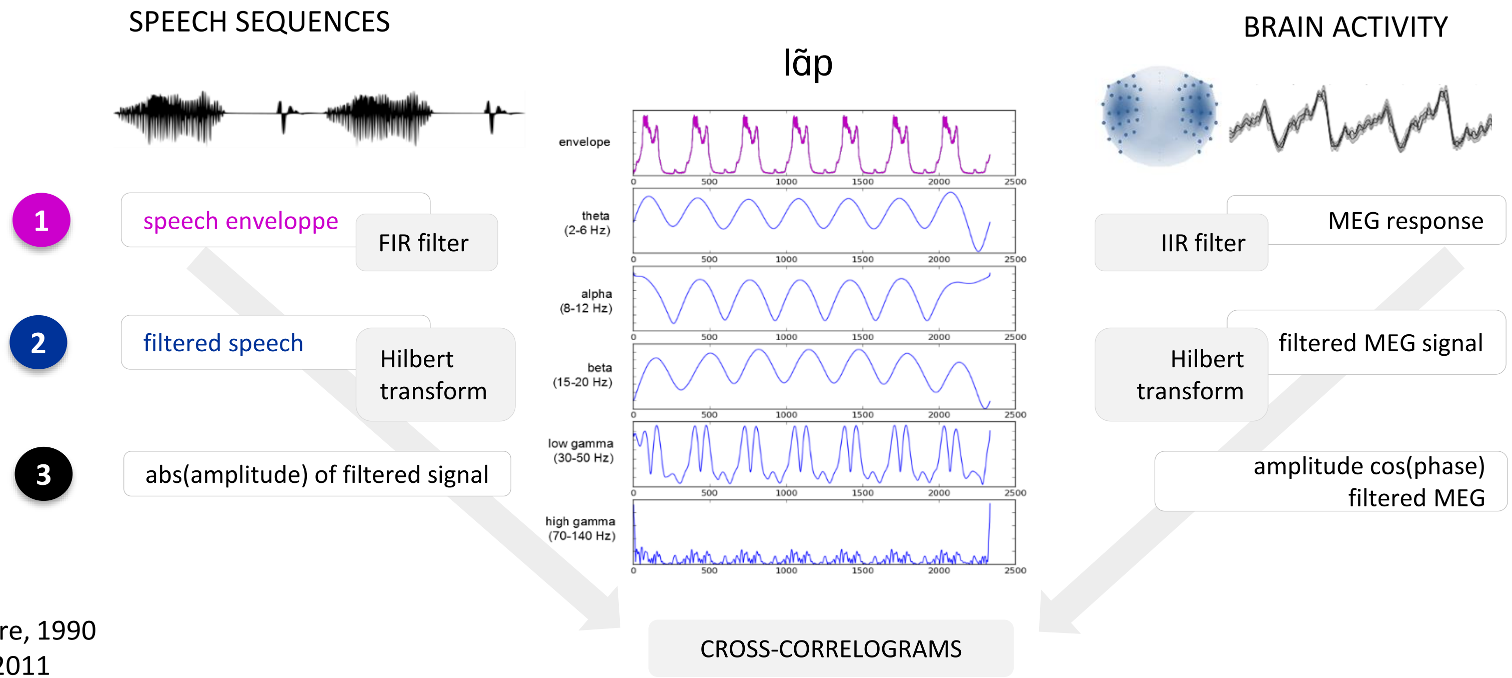
Figure 4: Frequency power spectra of the envelopes of the acoustic stimuli. The 1.5 Hz sub-harmonic in the bisyllabic stimuli sequences could readily be seen in contrast to the monosyllabic stimuli. The 1.5 Hz component was also stronger in "képi" sequence compared to "pata" sequence.

Kösem et al 2016 *J Neurophys*


ACOUSTIC PARSING
no change in acoustics
change in speech segmentation
HFA
LFO
HFA
LFO

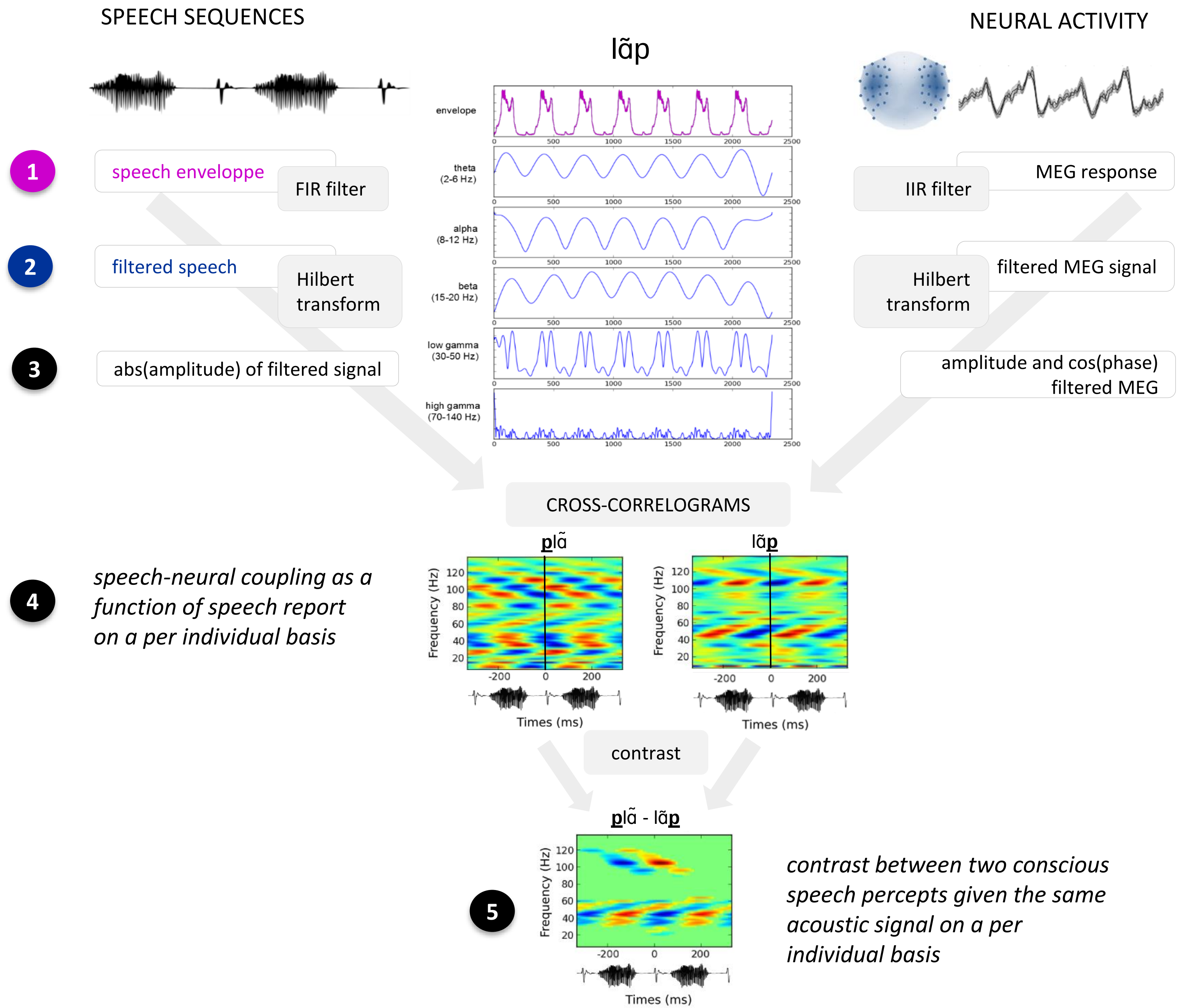

ACOUSTIC PARSING
no change in acoustics
change in speech segmentation
HFA
LFO
HFA
LFO
maintain [plã]
VOLITIONAL instructions
maintain [lãp]
LINGUISTIC PARSING
no change in acoustics
⇔
change in speech segmentation
+
change in the discretization of speech content
HFA reset
HFA
LFO
HFA reset
HFA
LFO

METHODS



Glasberg & Moore, 1990
used in Ghitza , 2011

METHODS


SPEECH SEQUENCES
lãp
NEURAL ACTIVITY
envelope
theta (2-6 Hz)
alpha (8-12 Hz)
beta (15-20 Hz)
low gamma (30-50 Hz)
high gamma (70-140 Hz)
1
speech enveloppe
FIR filter
MEG response
IIR filter
2
filtered speech
Hilbert transform
filtered MEG signal
Hilbert transform
3
abs(amplitude) of filtered signal
amplitude and cos(phase) filtered MEG
CROSS-CORRELOGRAMS
plã
lãp
Frequency (Hz)
Times (ms)
4
speech-neural coupling as a function of speech report on a per individual basis
contrast
plã - lãp
5
contrast between two conscious speech percepts given the same acoustic signal on a per individual basis

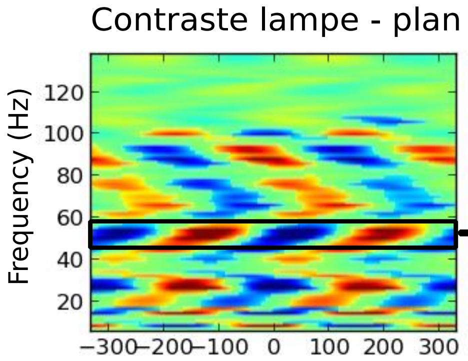
the latency of GAMMA activity *w.r.t* entrained THETA distinguishes conscious speech percepts

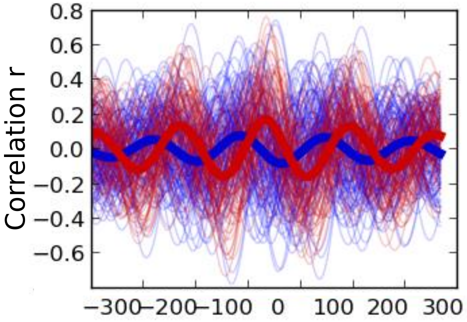
cross-correlation
(auditory speech signal X auditory cortex response)

gamma range

distinct phase of the
gamma response envelope

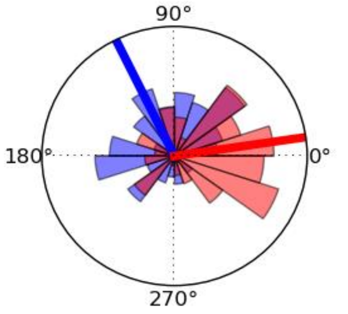
participant 1





lampe
trial
average

plan
trial
average

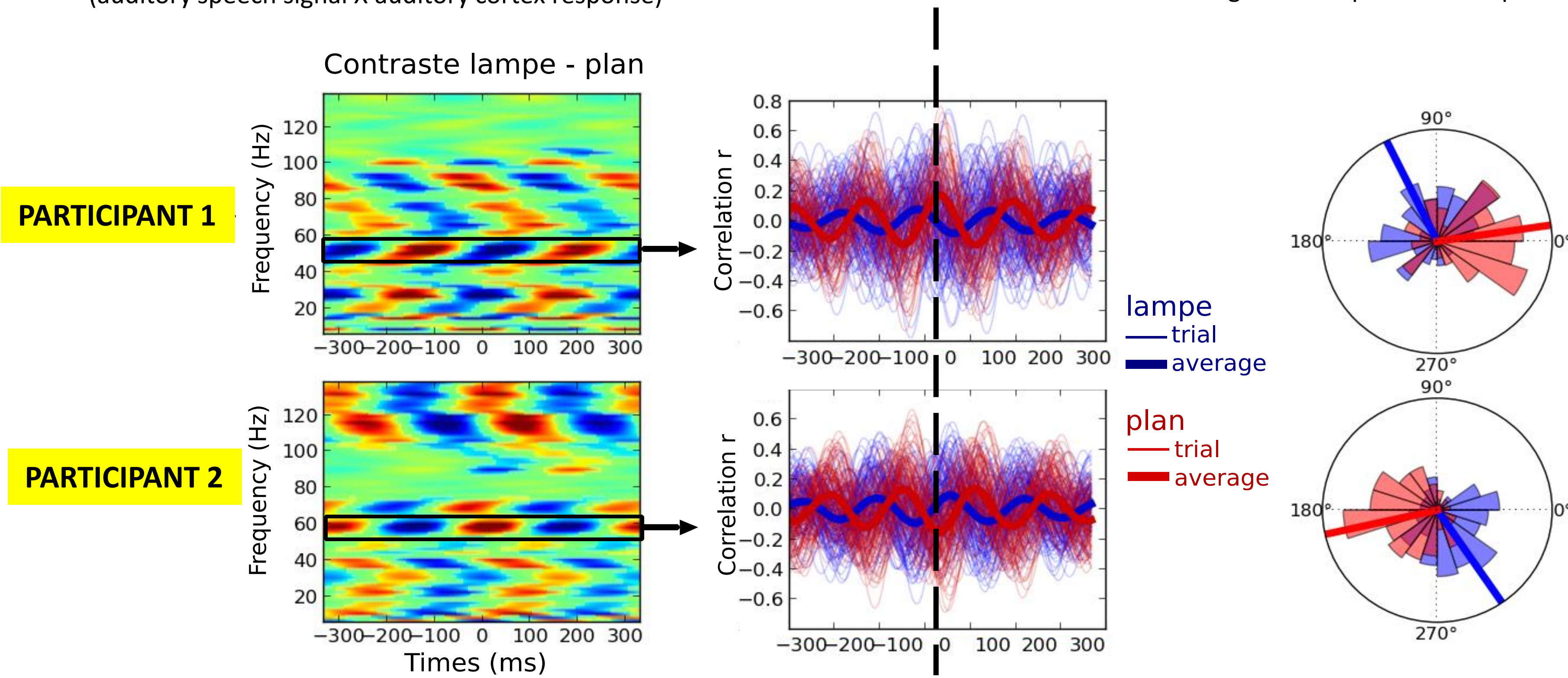


on a *per individual* basis

cross-correlation
(auditory speech signal X auditory cortex response)

gamma range

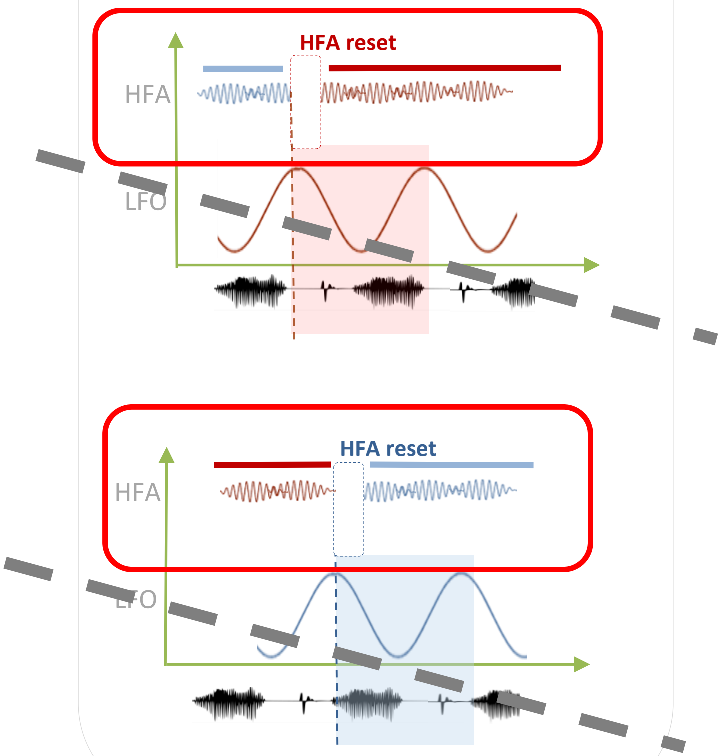
distinct phase of the
gamma response envelope



what are the origins of endogenous changes of gamma latency?

LINGUISTIC PARSING

no change in acoustics
change in speech segmentation
change in the discretization of speech content



Rhythms for Cognition: Communication through Coherence

Neuron
Perspective

Pascal Fries[1,2,*]

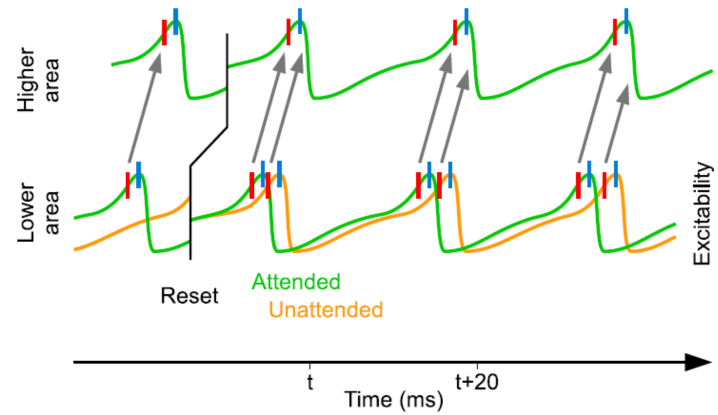
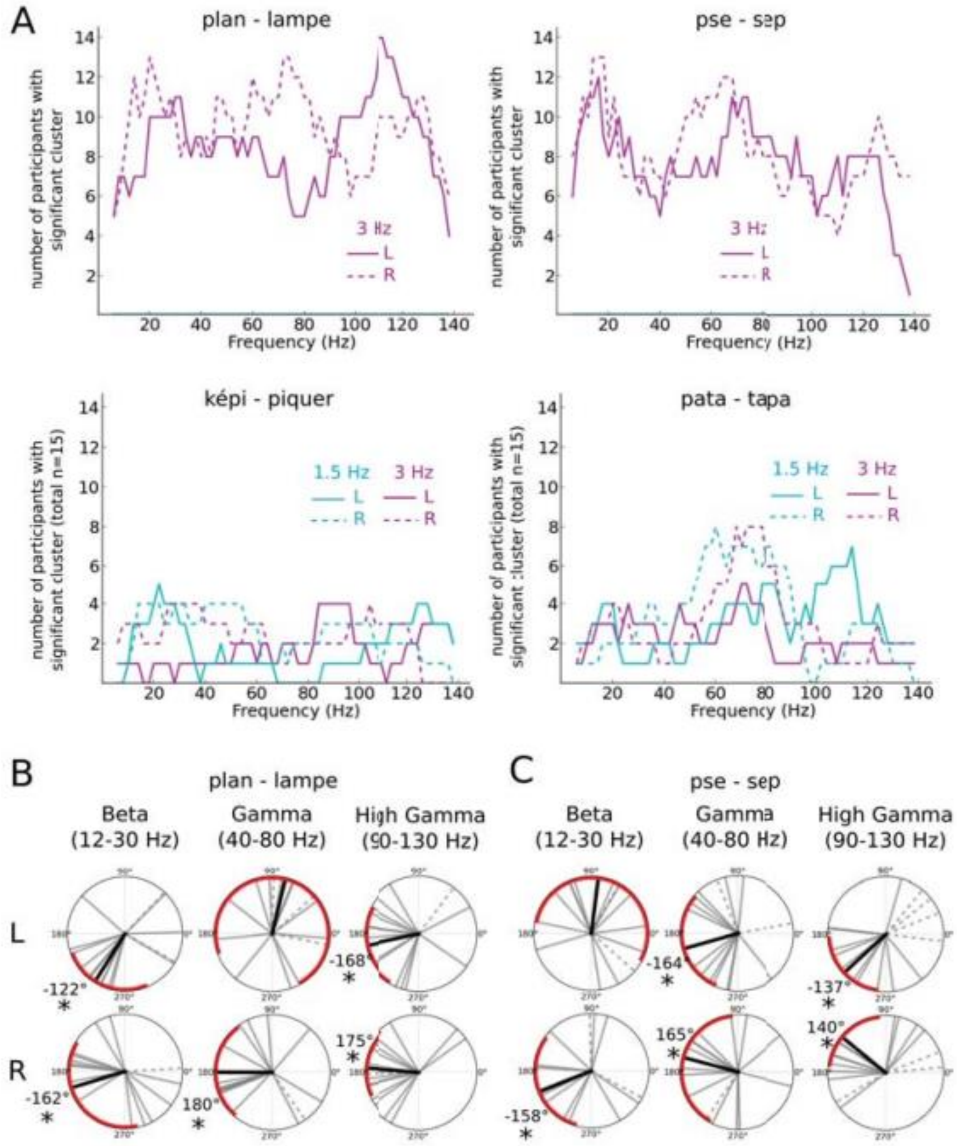


Figure 7. Theta-Rhythmic Phase Reset Turns Gamma-Frequency Differences into Latency Differences
In the lower area, after a reset, the gamma rhythms representing different stimuli start at the same phase. The gamma rhythm representing the attended stimulus (green) is faster than the gamma rhythm representing the unattended stimulus (orange). This frequency difference translates into a latency difference. The input from the attended representation reaches the higher area first, transmits its representation, and triggers inhibition to shut out the competing unattended representation.

beta predictions as proposed by speech models?

significant differences in cross-correlograms [12 - 130 Hz] between percepts are captured by the phase of the neural-speech tracking.



TAKE HOME MESSAGES

1. Non-stationarities of oscillatory activity are a partial autonomization of mental representations *w.r.t.* to the environment.

2. Inter-individual differences in oscillatory brain responses may be key to subjective awareness.

3. Low frequency neural responses alone can not inform on an individual's conscious percept during volitional control of bistable speech.

4. The latency of high frequency neural activity in time *w.r.t.* speech-tracking informed on an individual's speech percept consistent with an endogenous hierarchical control of attended speech.

Dr Anne Kösem

Dr Laetitia Grabot

erc

PROJET FINANCÉ PAR L'ANR – ANR – PROJECT FUNDED BY THE ANR

Campus Paris Saclay

FONDATION DE COOPERATION SCIENTIFIQUE

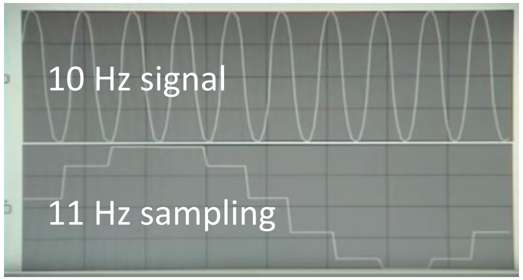
MARIE CURIE ACTIONS

timely

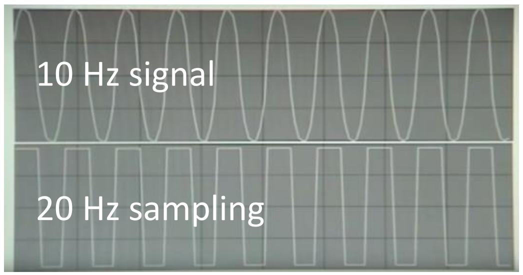
cost

EUROPEAN COOPERATION IN SCIENCE AND TECHNOLOGY

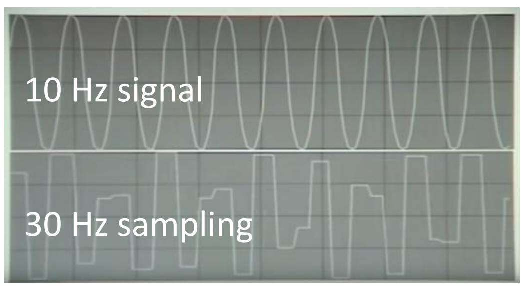
sampling



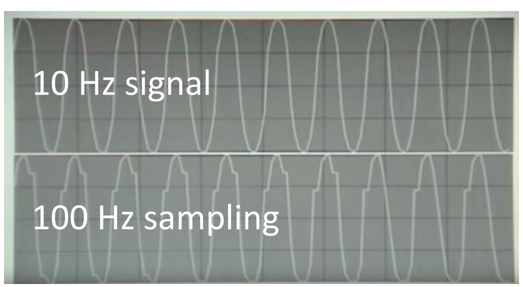
no brainer



near freq recovery



amplitude loss

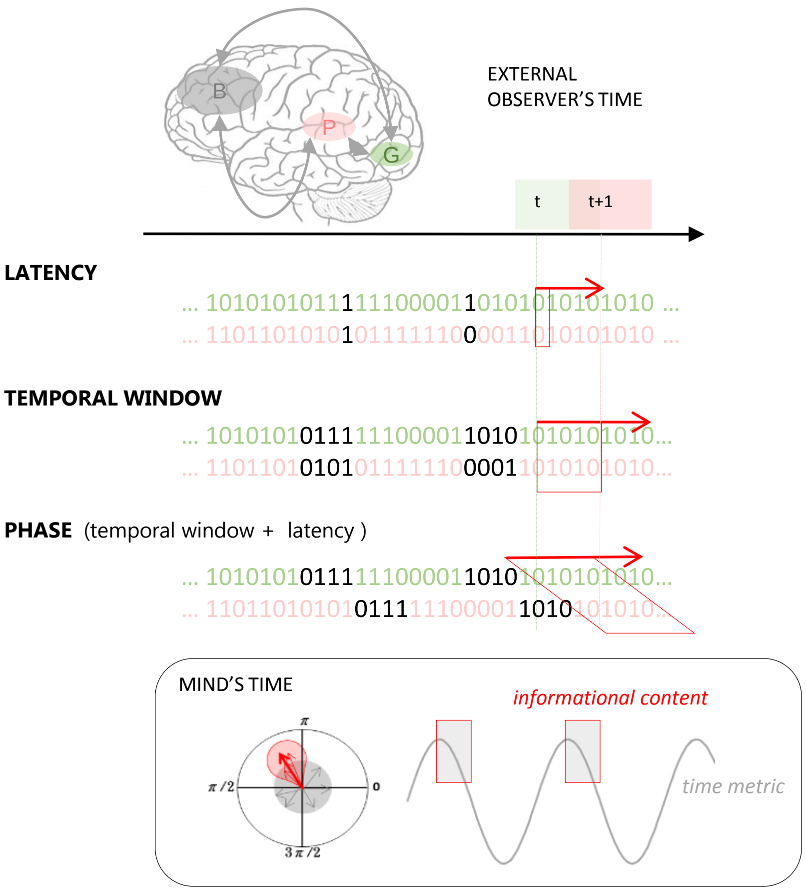


signal recovery

if
the computational implementation of neural oscillations is sampling
then
proximal informational content is much slower than was is currently considered

http://video-demos.colostate.edu/
https://youtu.be/Fy9dJgGCWZI

*sampling ≠ parsing



sampling = process by which a continuous time series is transformed into a discrete-time sequence of signals ⇔ from external to endogenous representation (Fs issue)

parsing = analysis of a sequence of symbols according to internal rules of a formal grammar ⇔ internal process

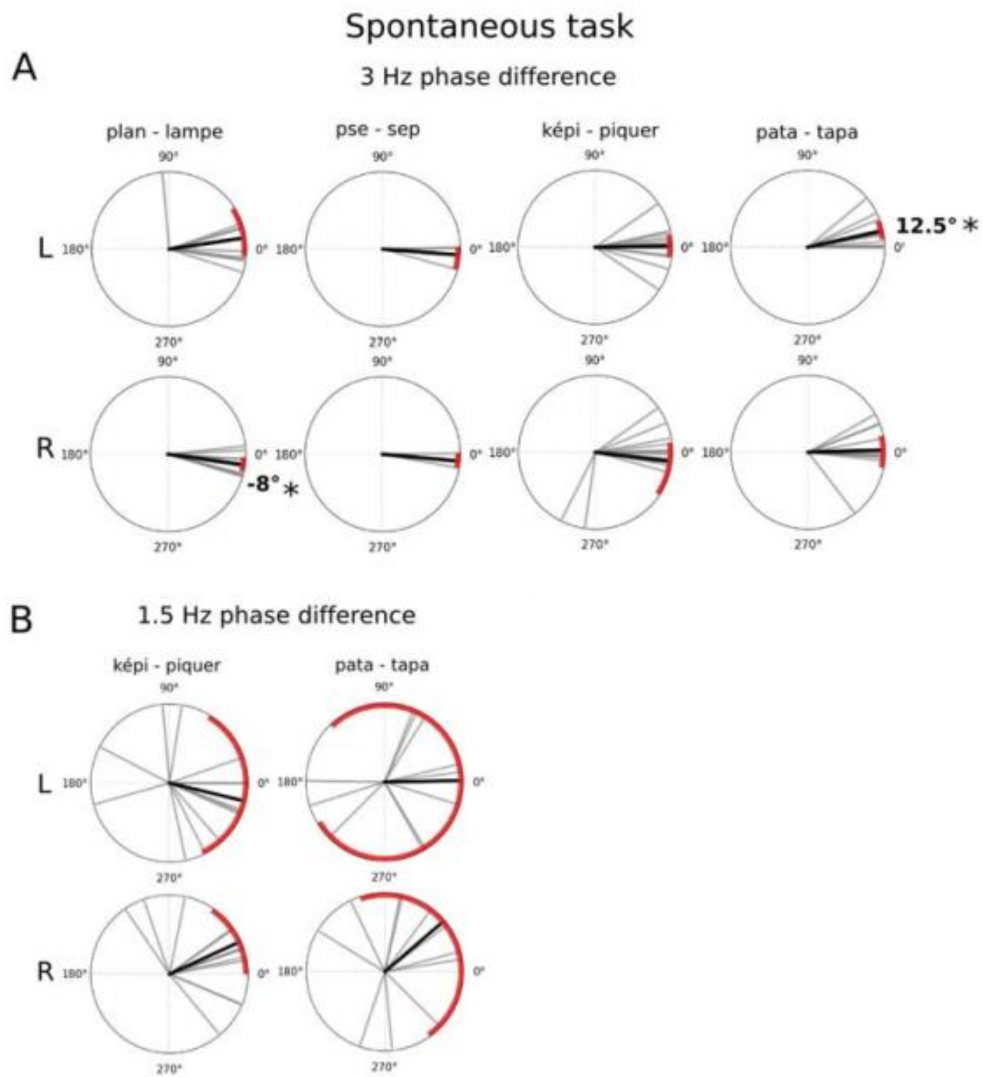
van Wassenhove 2017 *Psych Journal*
van Wassenhove 2017 *J Consciousness Studies*

one of my current obsession*s*

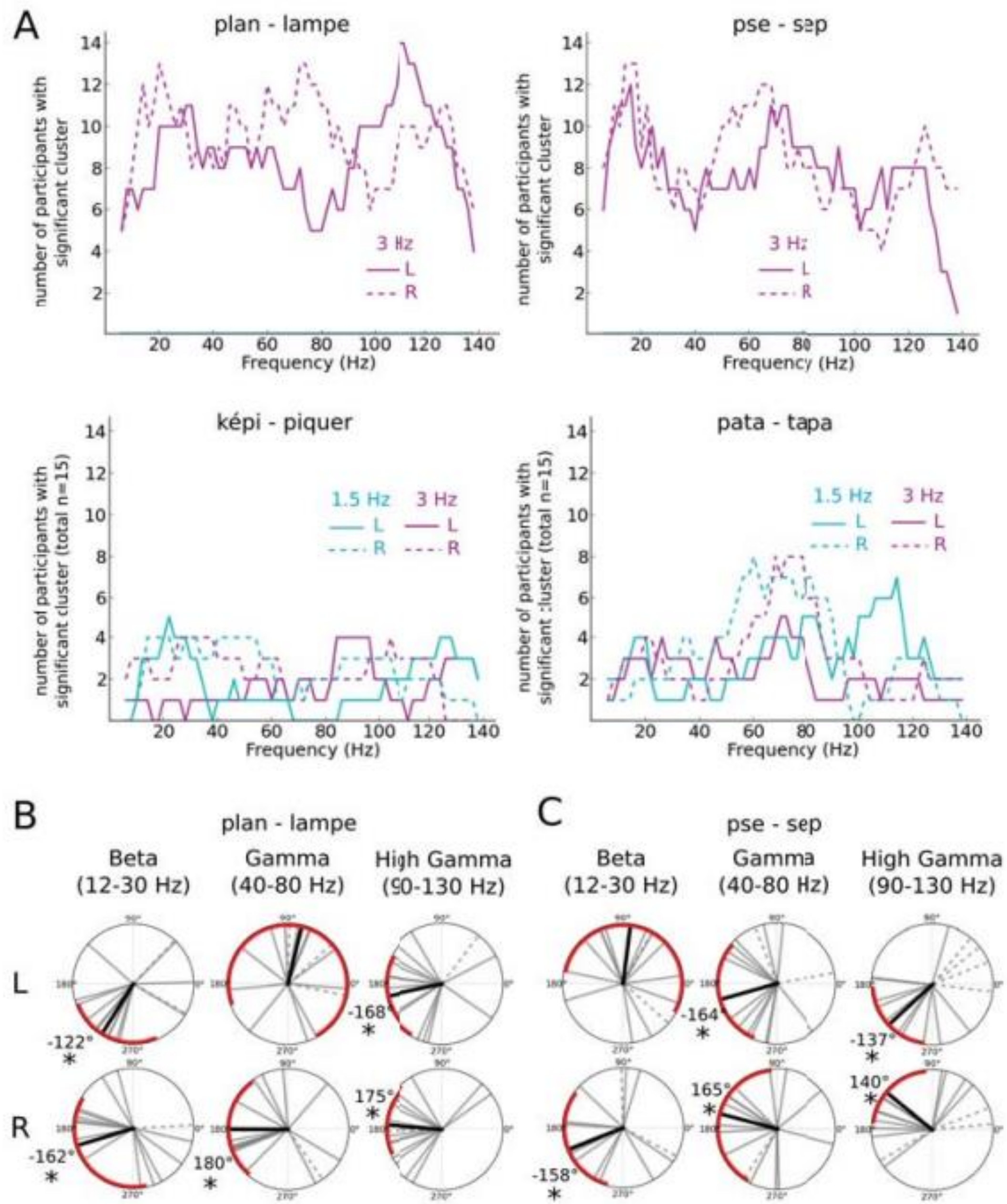
[…] Unlike artificial ad-hoc computing systems, the brain is architecturally defined by its dynamic scales or temporal regimes that have been shaped by evolutionary demands and biological constraints. These temporal regimes constrain the properties of large-scale neural computations yet current formalizations of brain functions seldom incorporate time as a predictive variable for computations - **i.e. mathematical models seldom make predictions as to the time a given computation may or should actually take to achieve its goals. Temporal constraints tend to be incorporated *a posteriori* leaving aside the questions of whether particular processes should require many or few processing steps, more or less time, and whether representing time itself should be a computational requirement for cognition**. *[…]*

Time consciousness in a computational mind/brain (2017)

Journal of Consciousness Studies


Spontaneous task
A
3 Hz phase difference
plan - lampe
pse - sep
képi - piquer
pata - tapa
L
R
12.5° *
-8° *
90°
180°
0°
270°
B
1.5 Hz phase difference
képi - piquer
pata - tapa
L
R

significant differences in cross-correlograms [12 - 130 Hz] between percepts are captured by the phase of the neural-speech tracking.



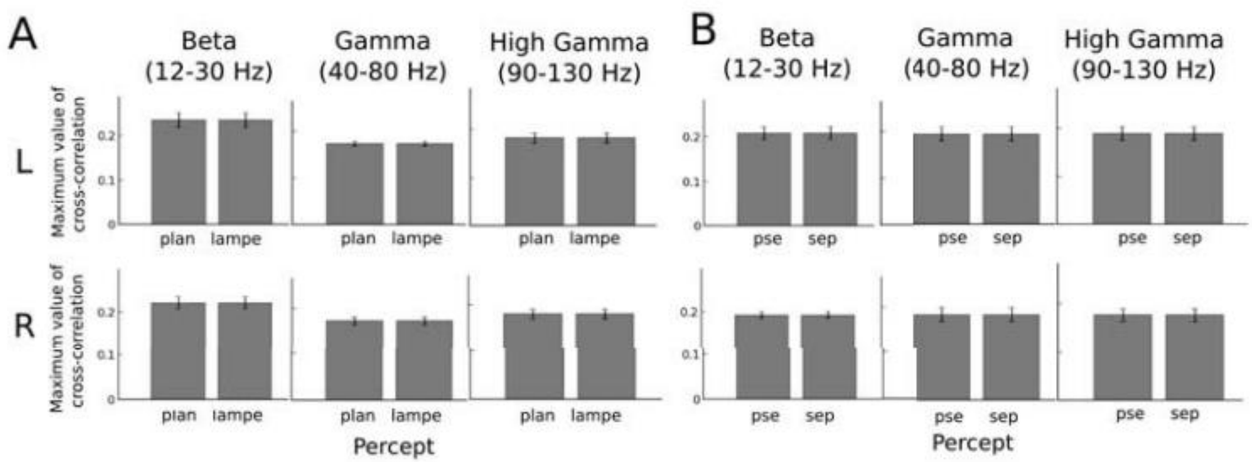
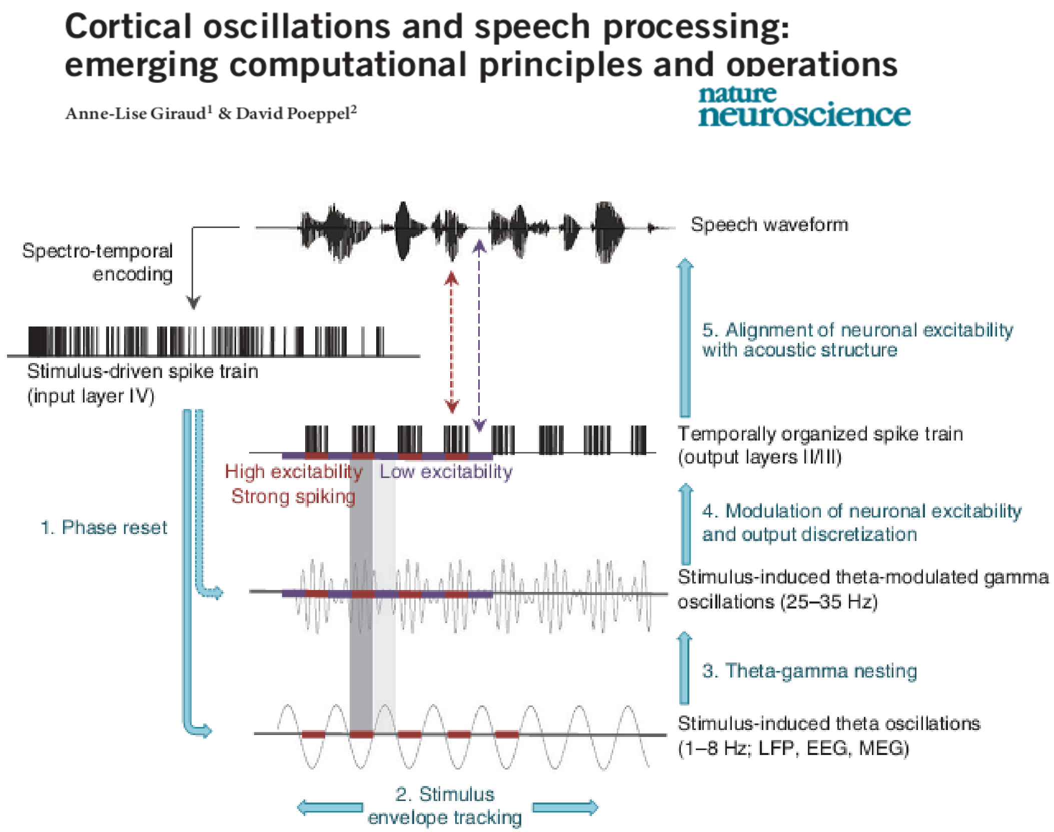


Figure 7: Mean maximum value of cross-correlation across participants in beta, gamma and high gamma bands. The maximum value of cross correlation did not significantly change between "lampe" and "sep" sequences (F[1,14]<1), between hemispheres (F[1,14]<1) and between target frequencies (F[2,28]<1). Crucially, the maximal value of cross-correlations did not differ between percept conditions (F[1,14]<1).



Kösem & van Wassenhove (in press) Language, Cognition and Neuroscience

theta oscillations primarily reflect early sound processing and phonological processing
delta oscillations reflect the encoding of sound properties as well as abstract syntactic structures
high gamma activity encode phonological, lexical and syntactic

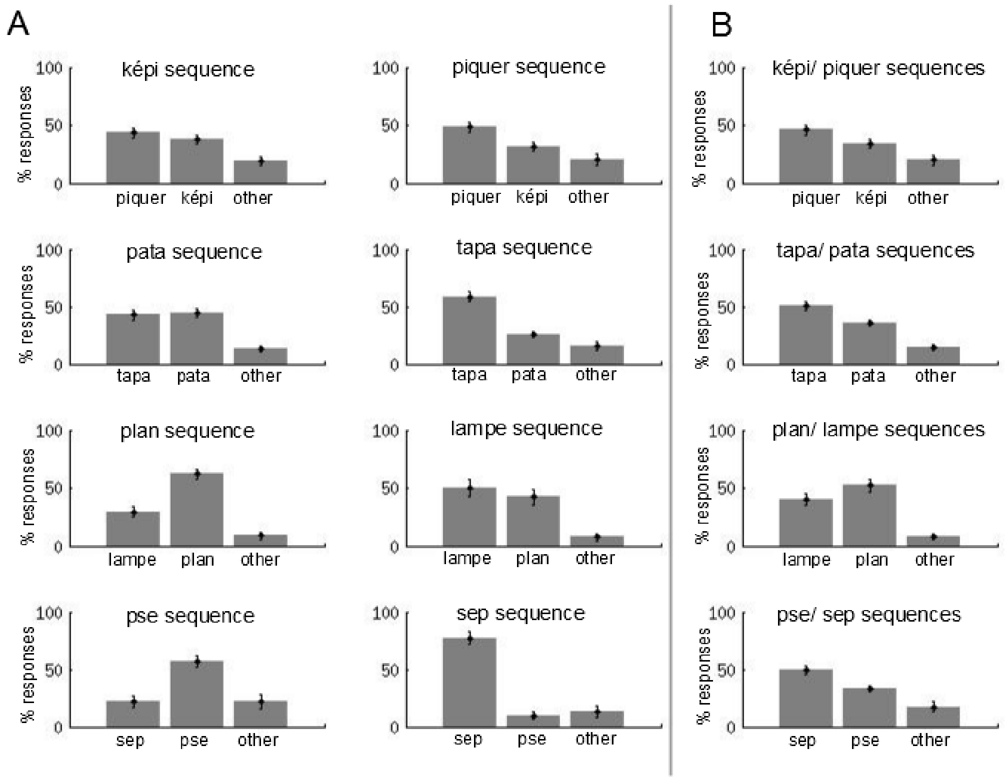
Implication of low-frequency neural entrainment has been associated with

→ increased speech intelligibility (Ahissar et al., 2001; Ding & Simon, 2013a; Doelling et al., 2014; Gross et al., 2013; Peelle, Gross, & Davis, 2013; Pérez, Carreiras, Gillon Dowens, & Duñabeitia, 2015;Rimmele, Zion Golumbic, Schröger, & Poeppel,2015)

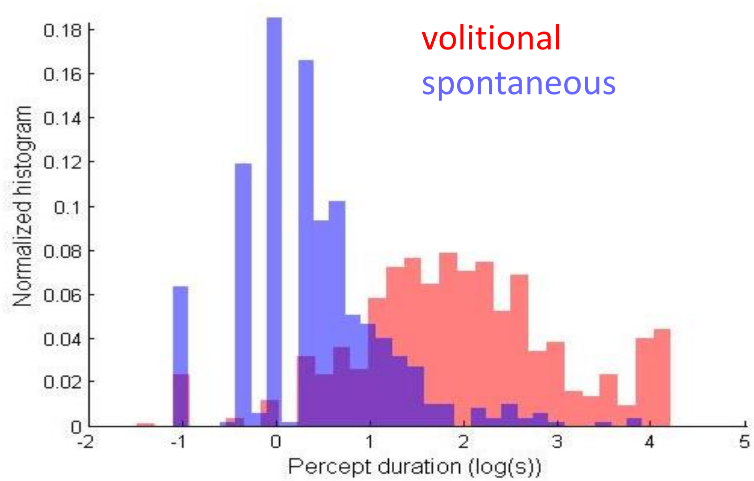
→ but the benefits disappear when acoustic cues are controlled for (Howard & Poeppel, 2010; Millman et al., 2015; Peña & Melloni, 2012; Zoefel & VanRullen, 2015a)

Kösem, van Wassenhove (LCN, 2017)

spontaneous conditions

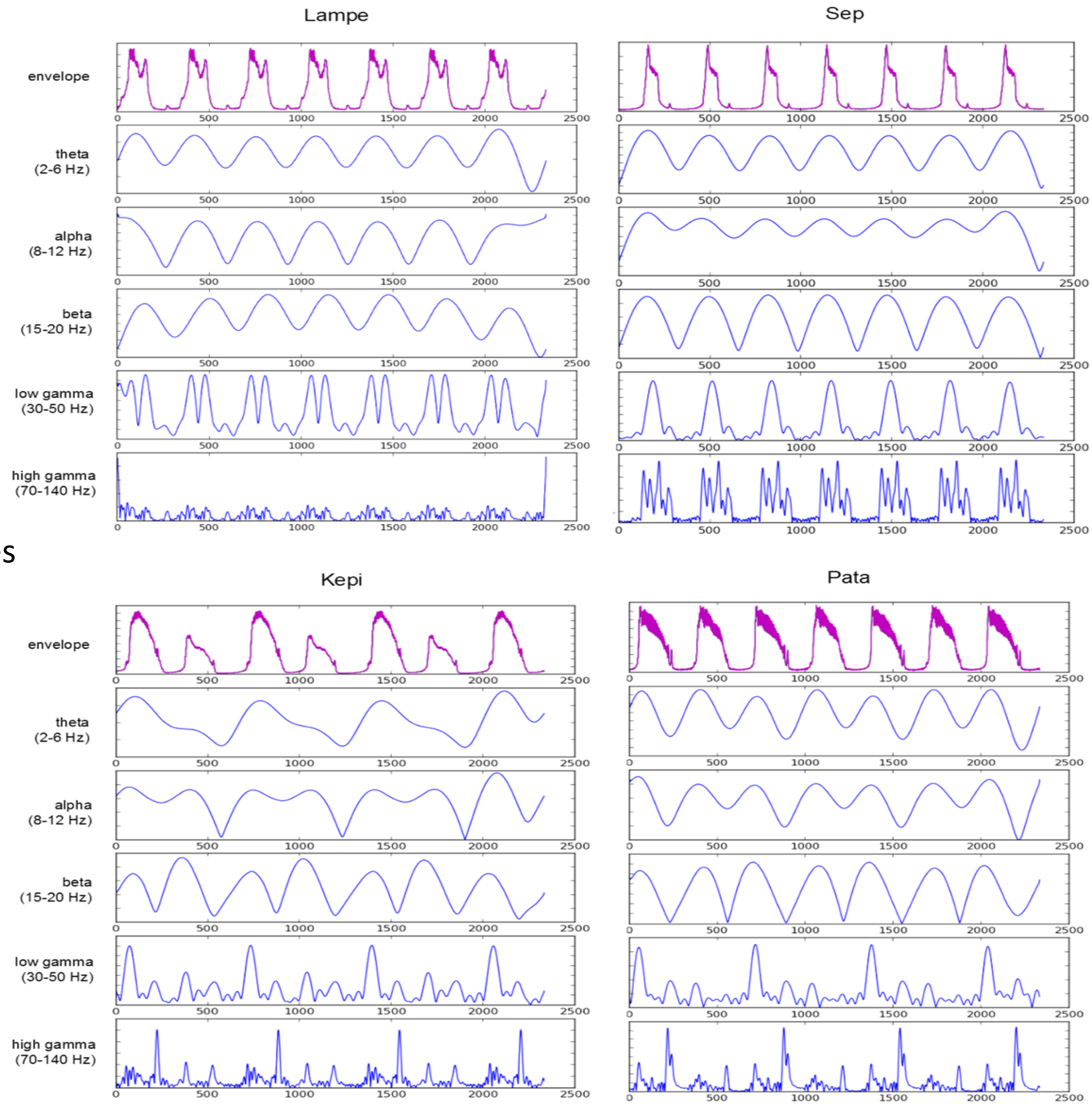


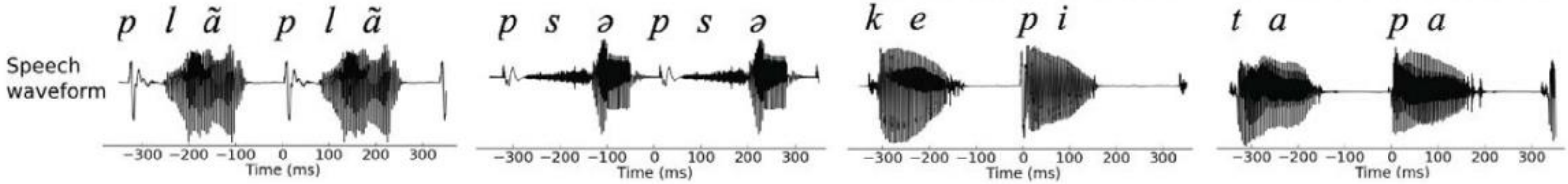
percept duration

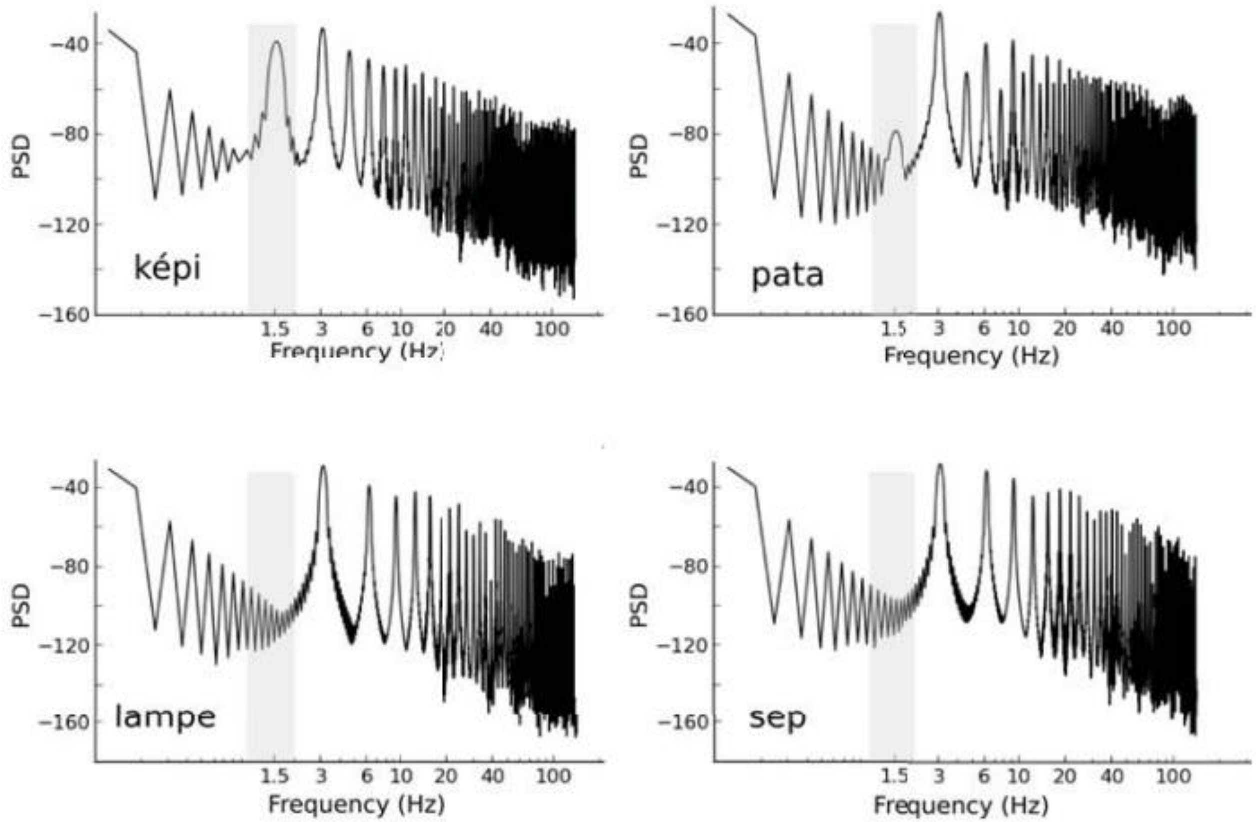


Outputs of cochlear model applied to each speech sequences 250 Hz to 3 KHZ

Glasberg & Moore, 1990
Ghitza, 2011




p l ã p l ã
p s ə p s ə
k e p i
t a p a
Speech waveform
Time (ms)


PSD
Frequency (Hz)
képi
pata
lampe
sep