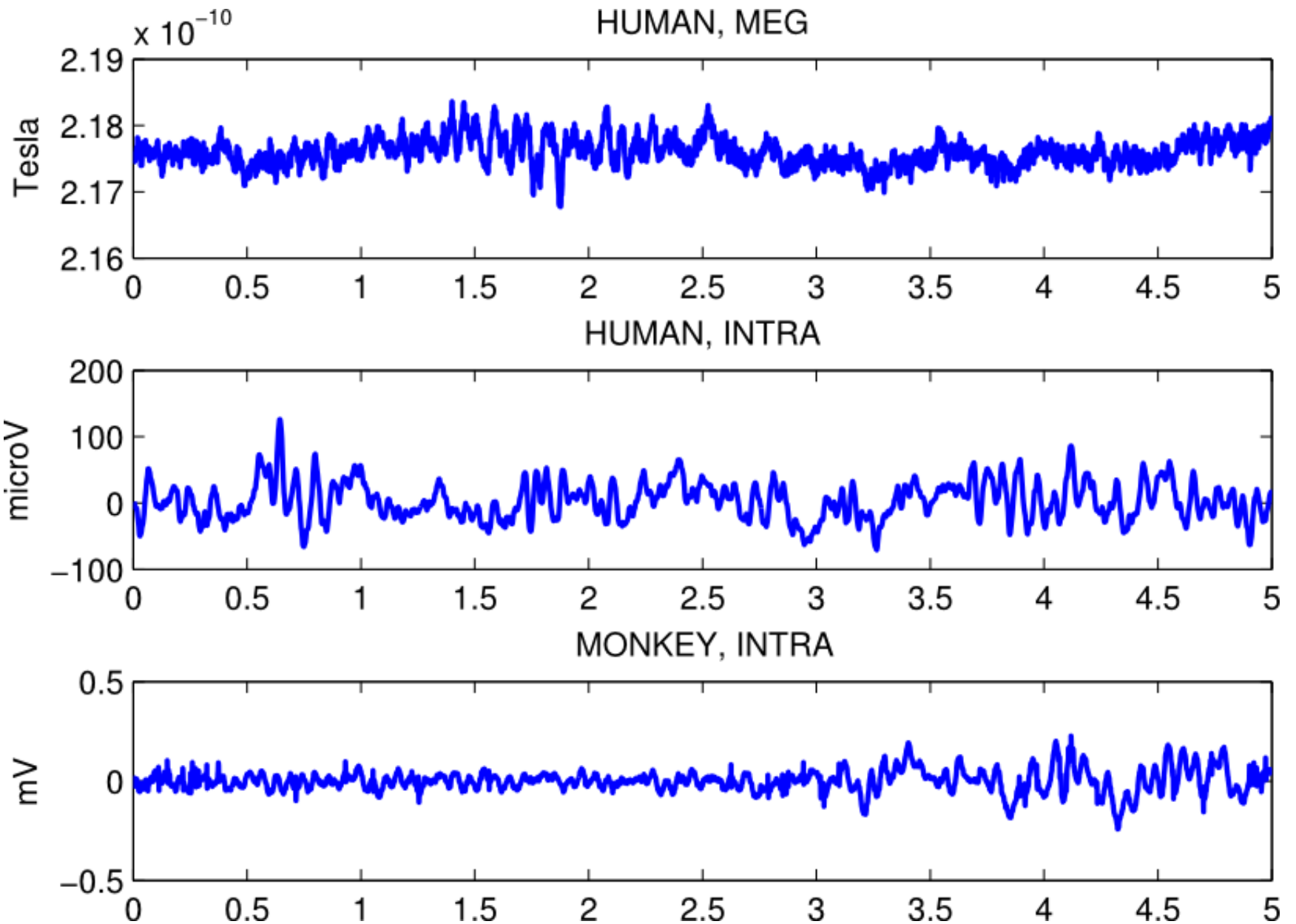


Oscillations in the brain

Florent Meyniel

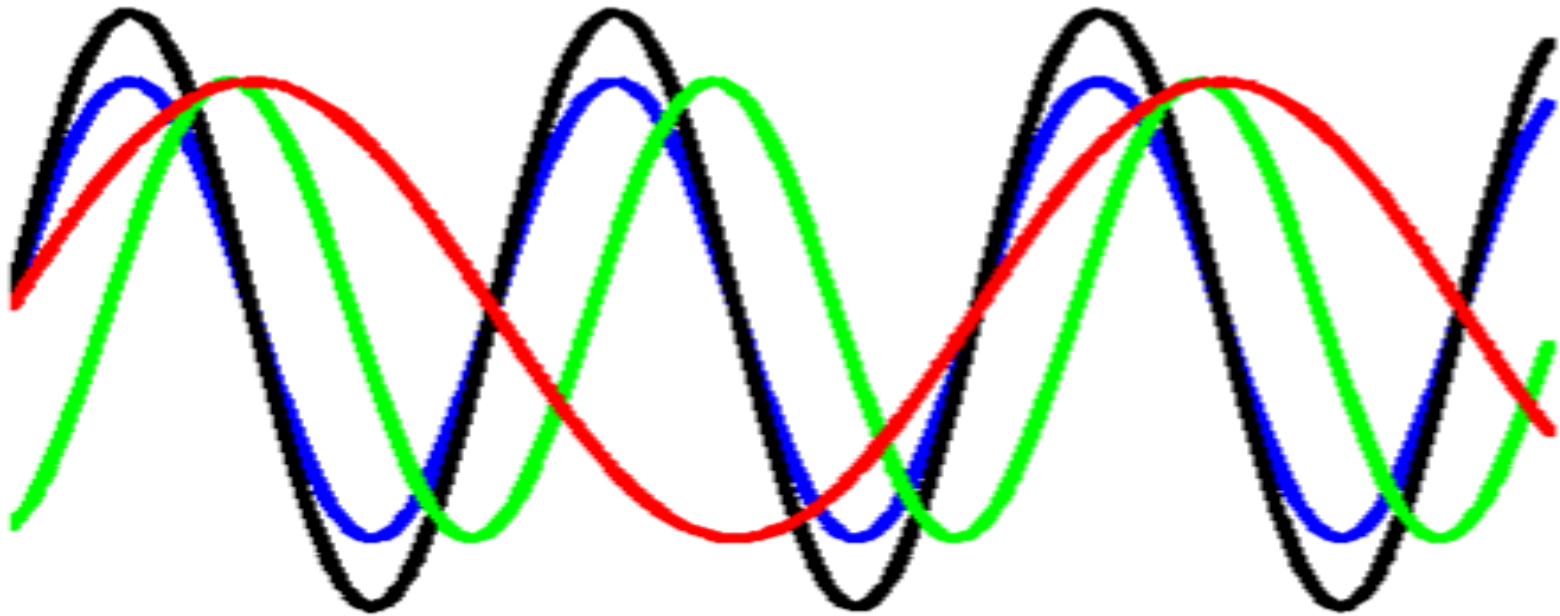
CA4 – Cogmaster 2011-2012



Thanks to Imen El Karoui (human LFP)
& Sebastien Bouret (monkey LFP)

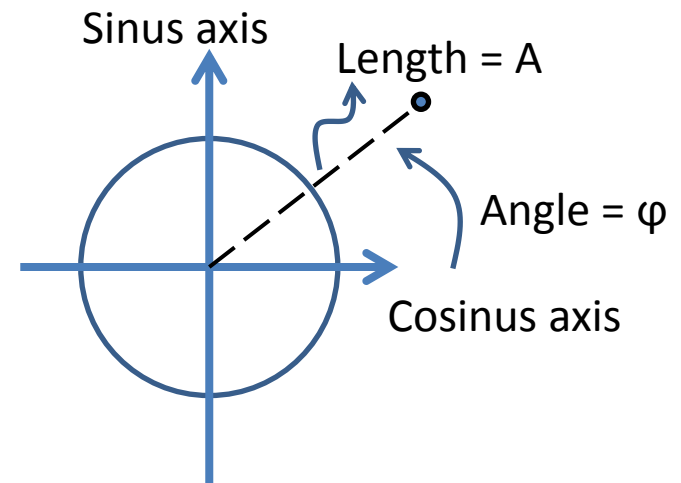
Outline of the course

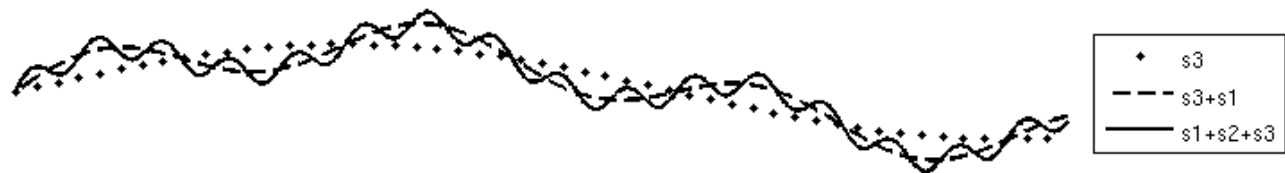
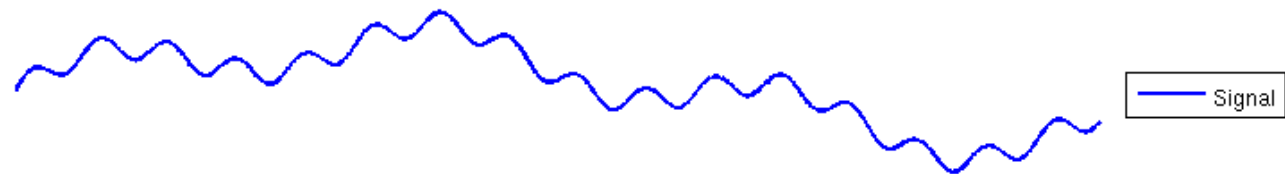
- Analyzing oscillatory signals
 - 3 fundamentals characteristics
 - The Fourier's theorems
 - Analytic tools & questions for oscillations
 - Some methodological issues
- The origin of brain oscillations
 - The single neuron level
 - The two neurons level
 - Network synchronization
 - Network architecture
 - From spikes to sensors
- Functional implication for cognition
 - A mechanistic account of neural processes
 - Rhythmicity of cognitive processes
 - Case study: beta band oscillations



$$s = A * \sin(t * 2\pi f + \varphi)$$

- **Amplitude (A)**: blue vs. black
- **Phase (φ)**: blue vs. green
- **Frequency (f)**: blue vs. red
- NB: the period $T = 1/f$
- Complex view and the trigonometric circle
 $s(t) = A(t) * [\cos(\varphi(t)) + i * \sin(\varphi(t))]$





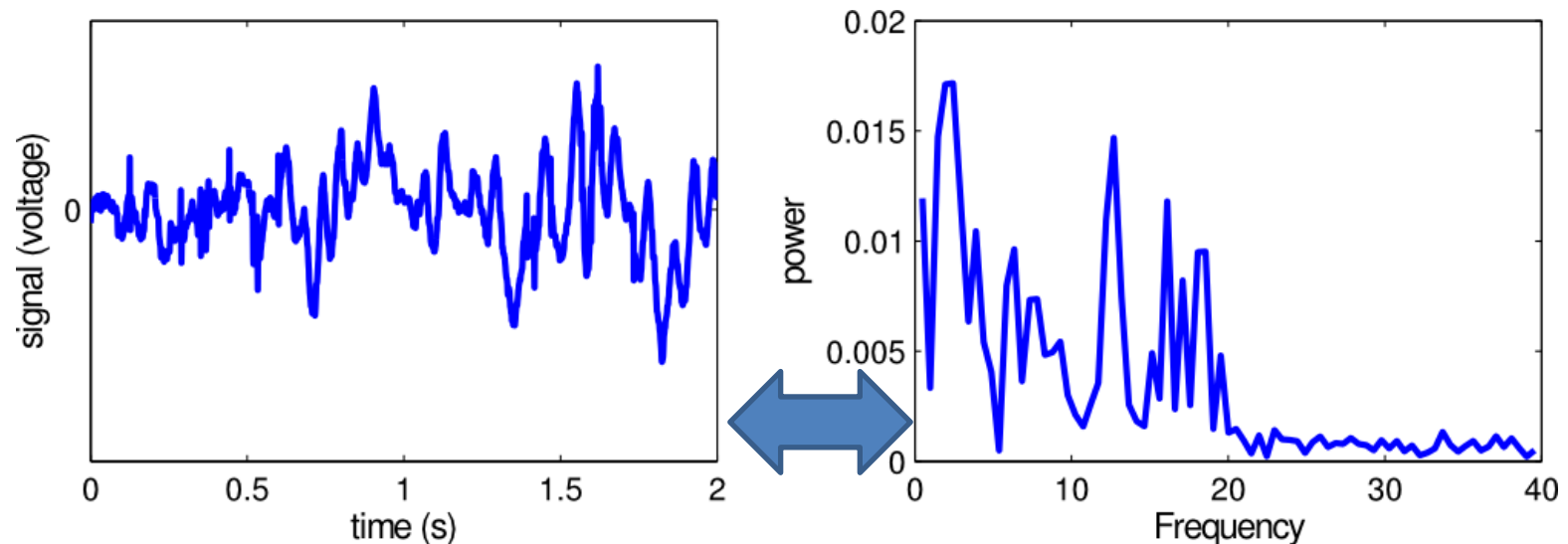
- **Spectral decomposition (Fourier series)**

- A function g can be decomposed in a unique series of sinusoids $(e^{2\pi i t p/T})_{p \in \mathbb{Z}}$

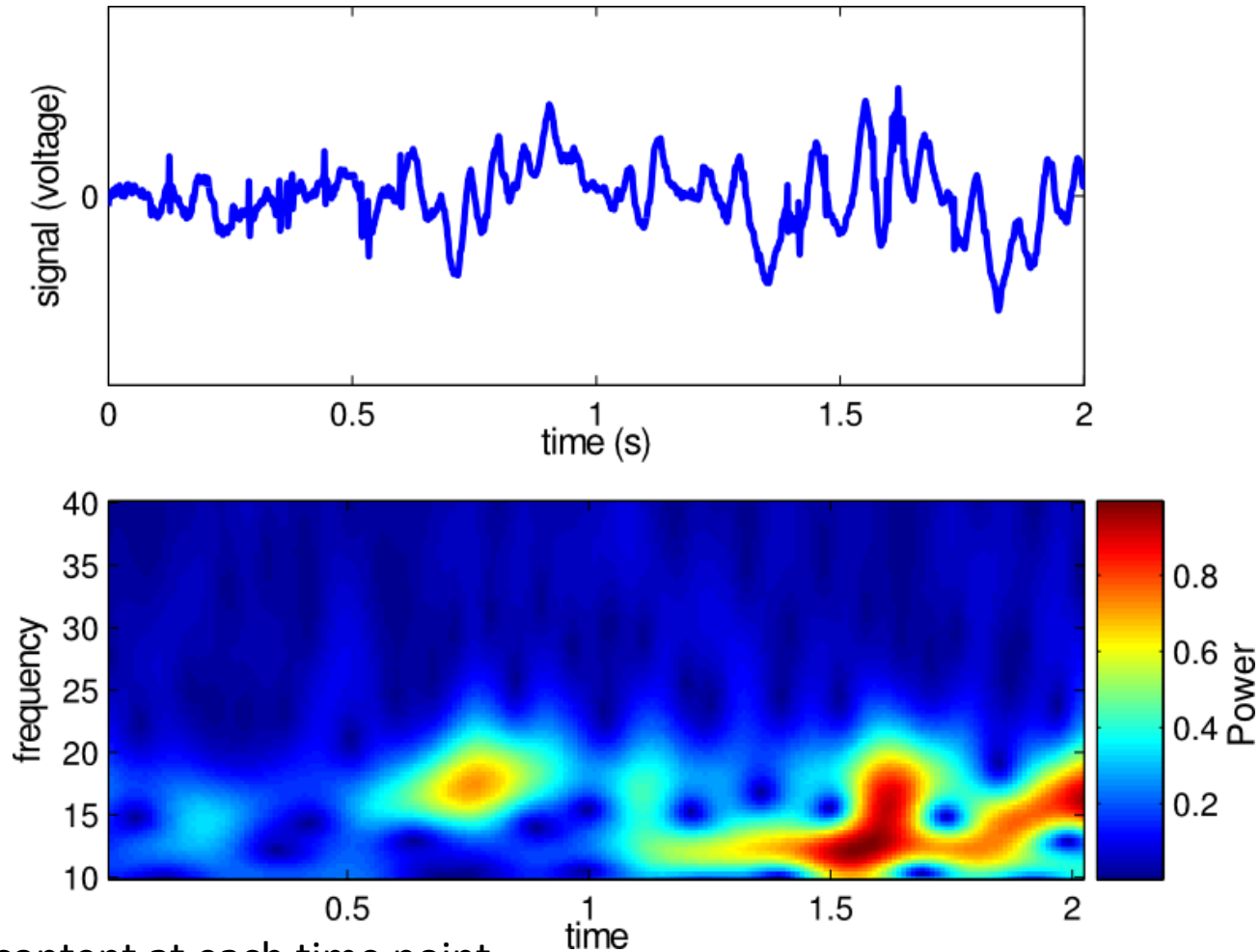
- $g(t) = \sum_{p \in \mathbb{Z}} c_p(g) e^{i2\pi t p/T}$
- With $c_p(f) = \int_0^T f(t) e^{-i2\pi t p/T} dt / T$

- **Time-frequency equivalence**

- If g is a function of time (t , second), its Fourier transform is \hat{g} a function of frequency (ξ , Hertz): $\hat{g}(\xi) = \int e^{-i2\pi t \xi} g(t) dt$
- g can be reconstructed from \hat{g} : $g(t) = \int e^{i2\pi t \xi} \hat{g}(\xi) d\xi$



Time frequency map

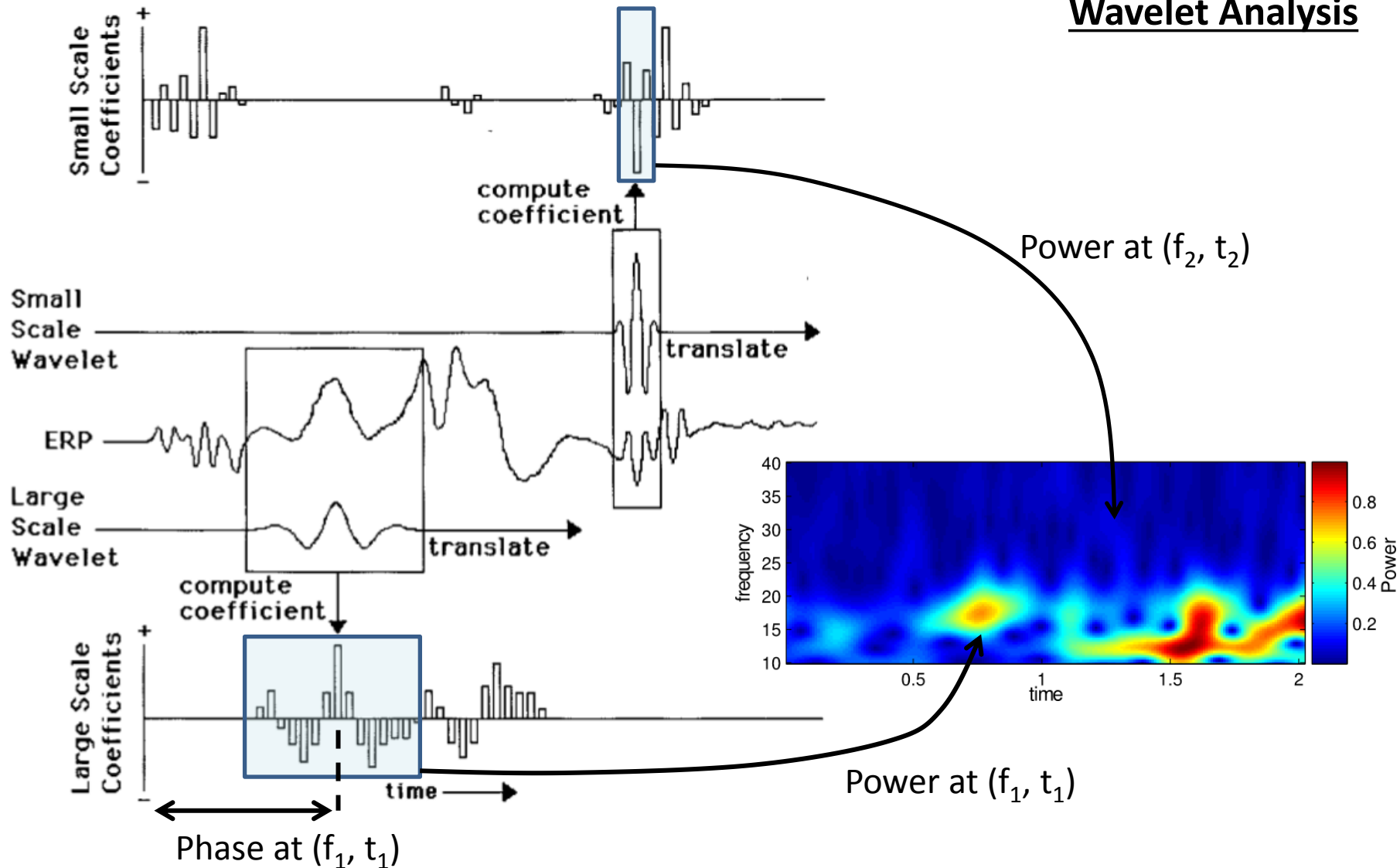


⇒ Frequency content at each time point.

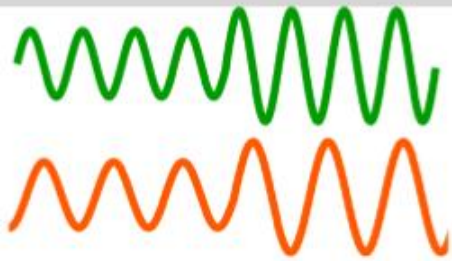
⇒ NB: note the power law, power $\rightarrow 1/f^\beta$

- **FFT (fast Fourier transform)**
 - to get the spectral power over a specific time window
 - No phase!
 - ‘per time window’
- **Hilbert transform**
 - S a signal, H its Hilbert transform (complex function), such that $s = \text{mod}(H) * \cos(\text{angle}(H))$
 - Get the phase & power for a frequency
 - ‘per frequency’
- **Wavelet analysis**
 - Get the phase & power
 - Efficient and simple computational scheme
 - ‘Both per frequency and per time’

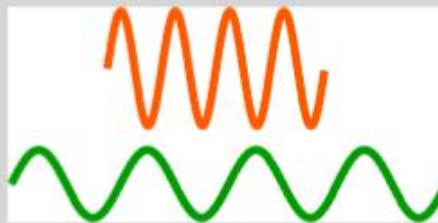
Wavelet Analysis



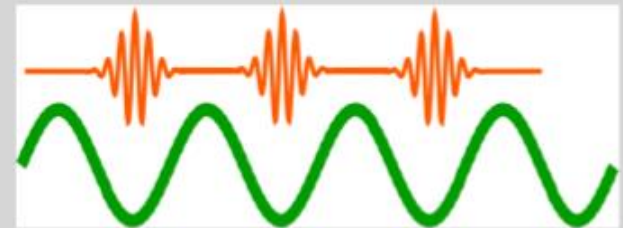
- Does a stimulus evoke a specific oscillatory response?
 - What frequency
 - What latency (same vs. different phase = evoked vs. induced)
- Are two points in the brain oscillating ‘together’?
 - Phase synchronization + same power correlation (spectral coherence)
 - Same modulation of power (power synchrony)
 - Constant phase shift (phase synchrony)
 - Phase & power coupling



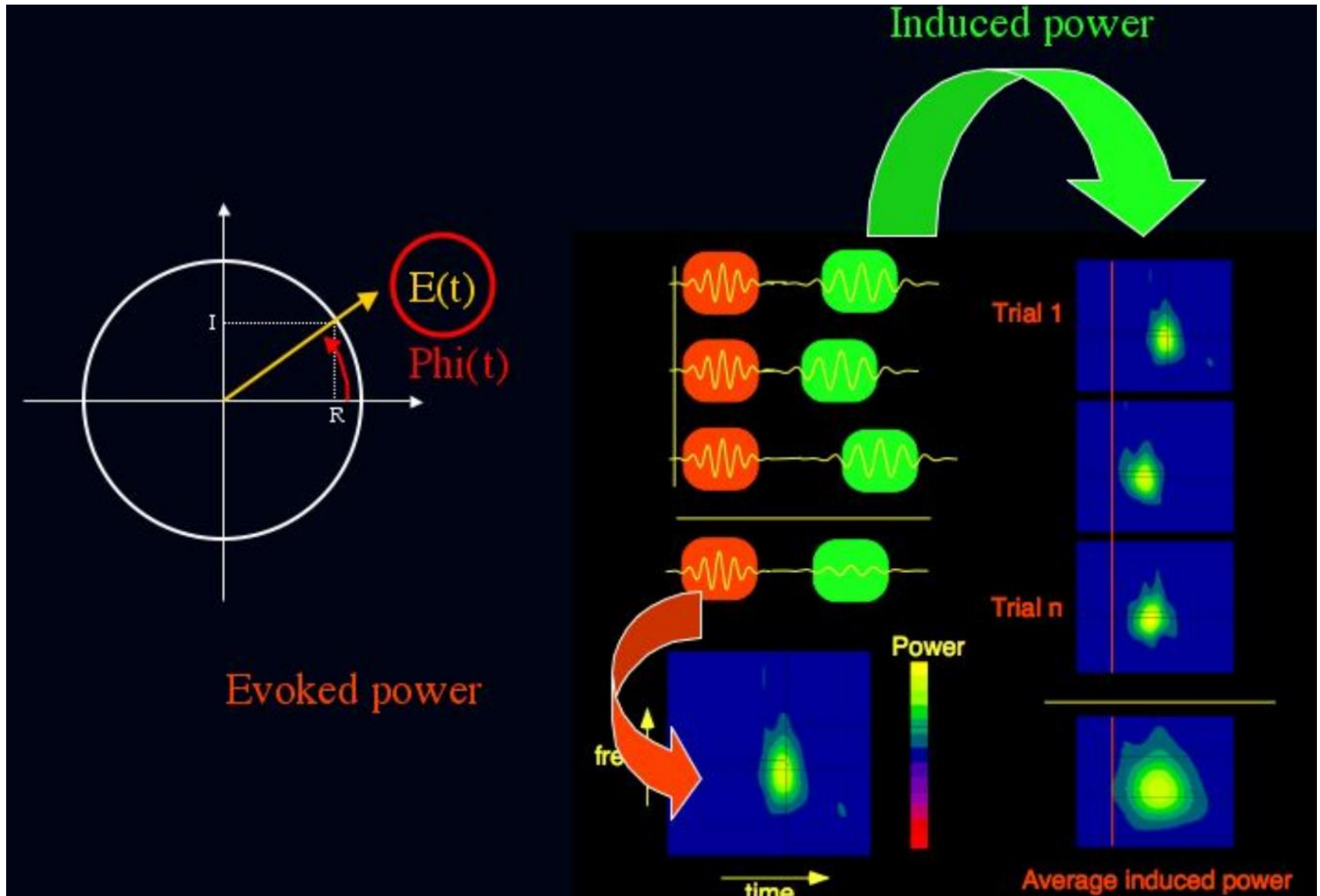
amplitude covariation



phase-locking



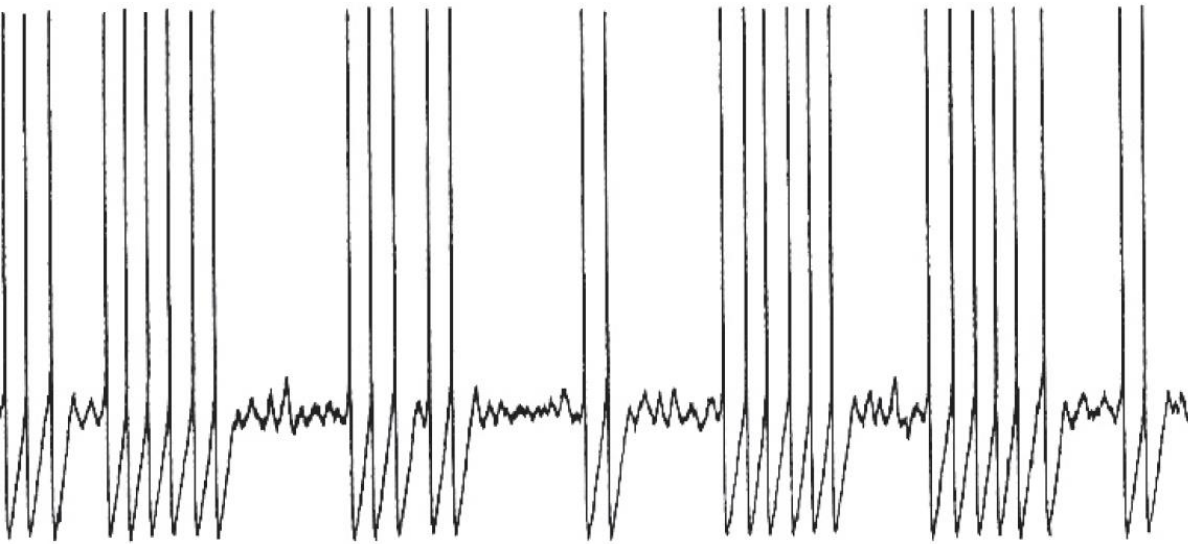
amplitude-phase locking



- 1: artifactual oscillations:
 - Stimulation, task
 - muscular artifacts (e.g. high frequency, micro saccades)
 - Volume conduction
 - Frequency dependent gain of the electrode (LFP)
- 2: Change in the power law: $1/f^\alpha$ noise, α may depend on the behavioral state (He, *Neuron* 2010)
- 3: Interpret coherence only when both signals really have a peak in their power spectrum
- 4: beware of the time window! the effect should last longer than the time window used for the analysis
- 5: Interpret phase locking only when the signals have exactly the same peak frequency
- 6: Inter-nested rhythms and cross-frequency coupling
- 7: Causality over distant signals
 - Conduction artifact!
 - Do we have good models of directionality for rhythms?
- 8: Arbitrary bands in power spectra (δ , θ , α , μ , β , γ : 0-4; 4-8; 8-12; 12-30; >30Hz), are still to be given a meaning? (Siegel, *Nature Neurosci*, 2012)

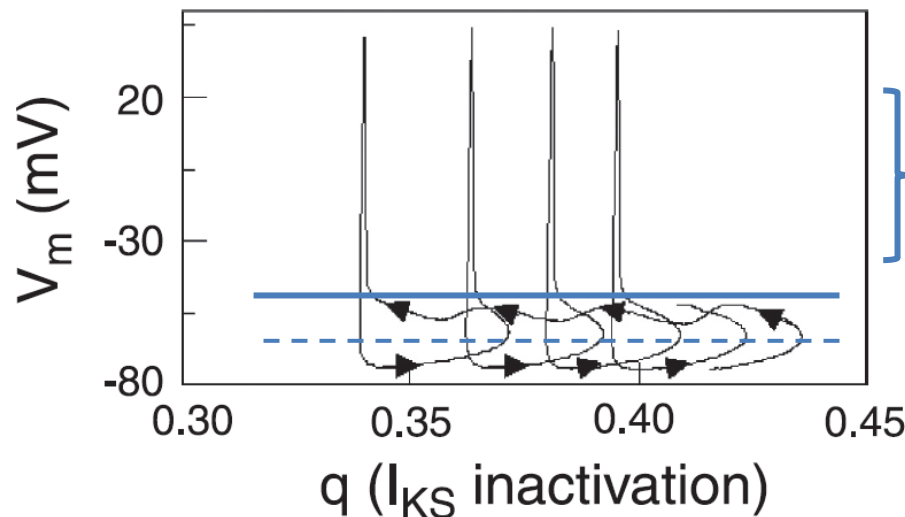
Pacemaker neurons

- auto-excitable cells with a proper frequency.
- e.g. GABA neurons in the medial septum neurons, feeds the hippocampus with theta rhythms (resonance)



20mV

500ms



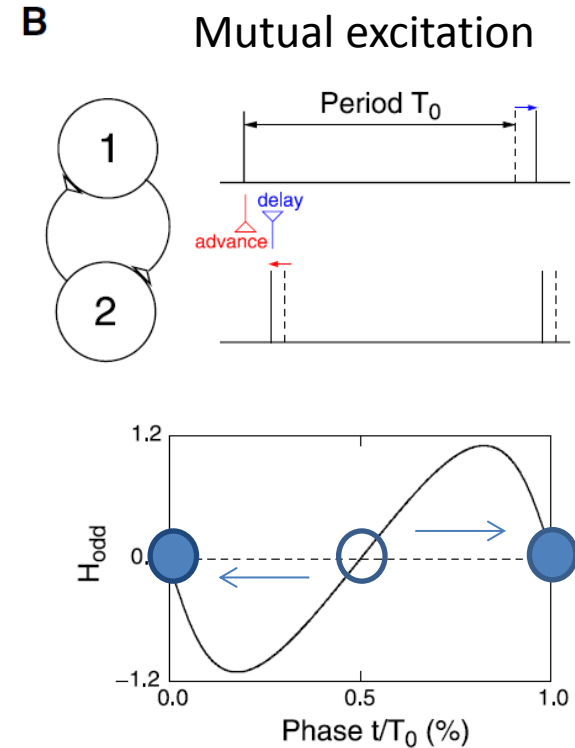
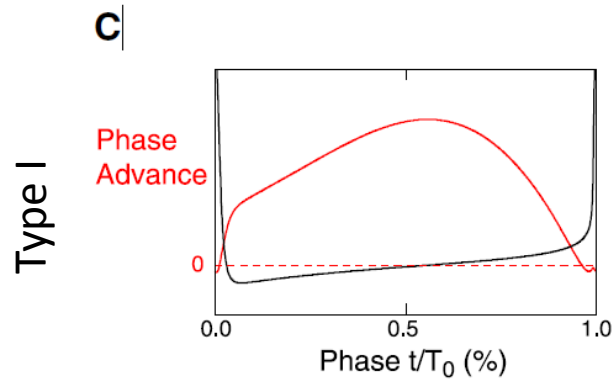
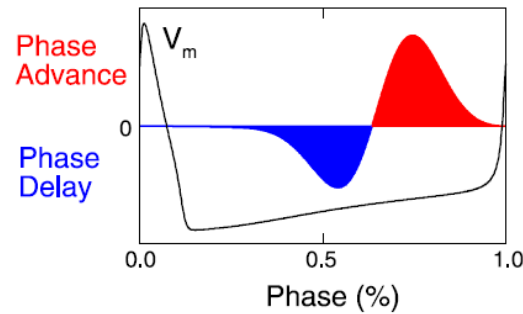
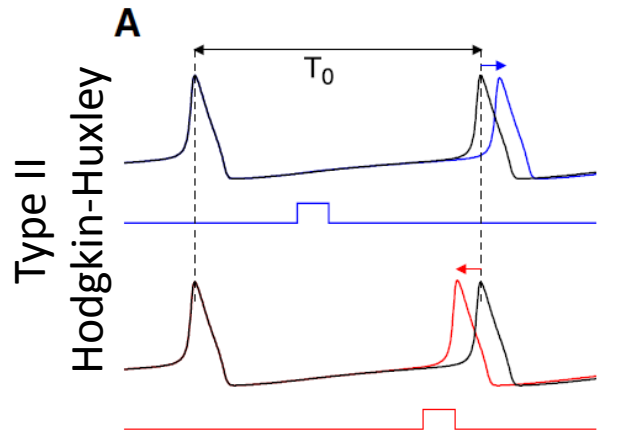
Depolarization (action-potential)

Sub-threshold activity

Hyper-polarization

Actually: few central pattern generators

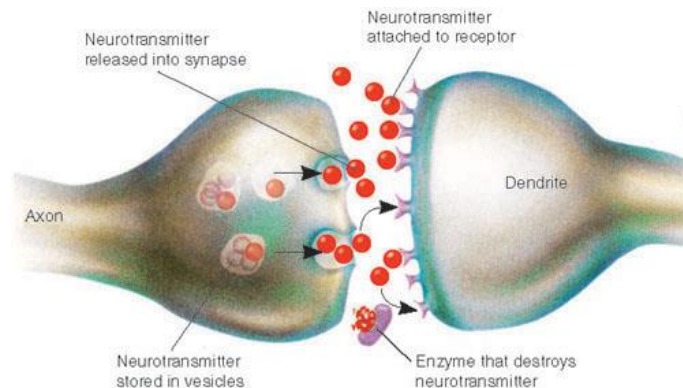
- The neuron phase response



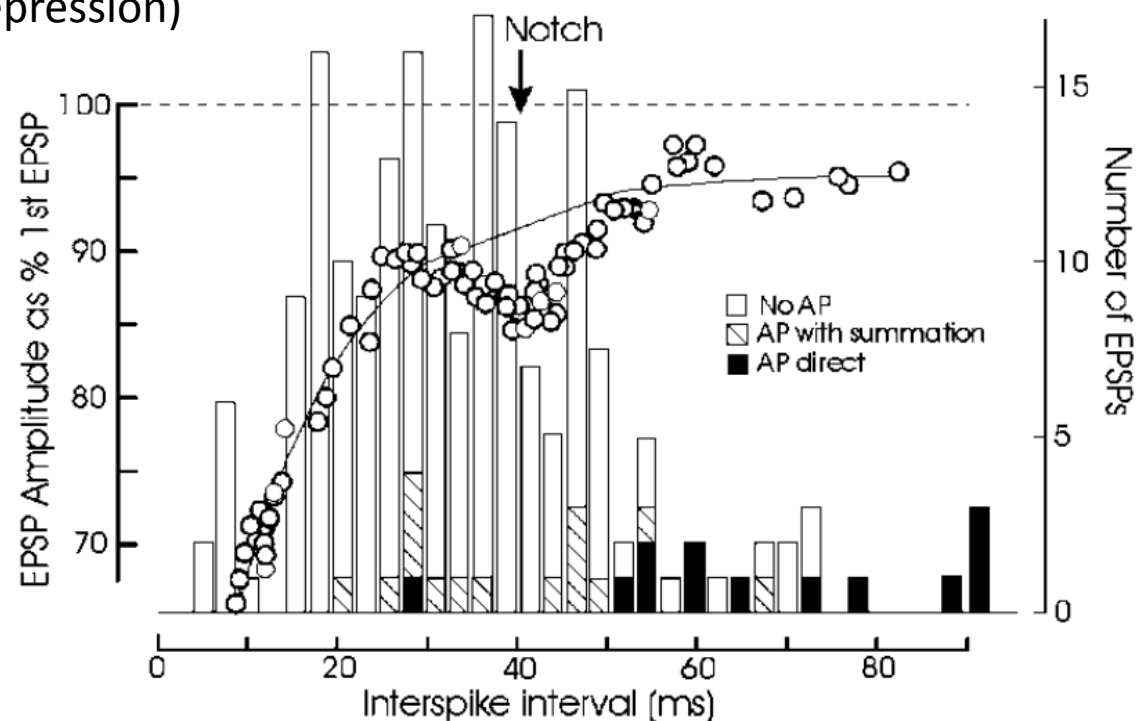
=> coupled oscillators get synchronized

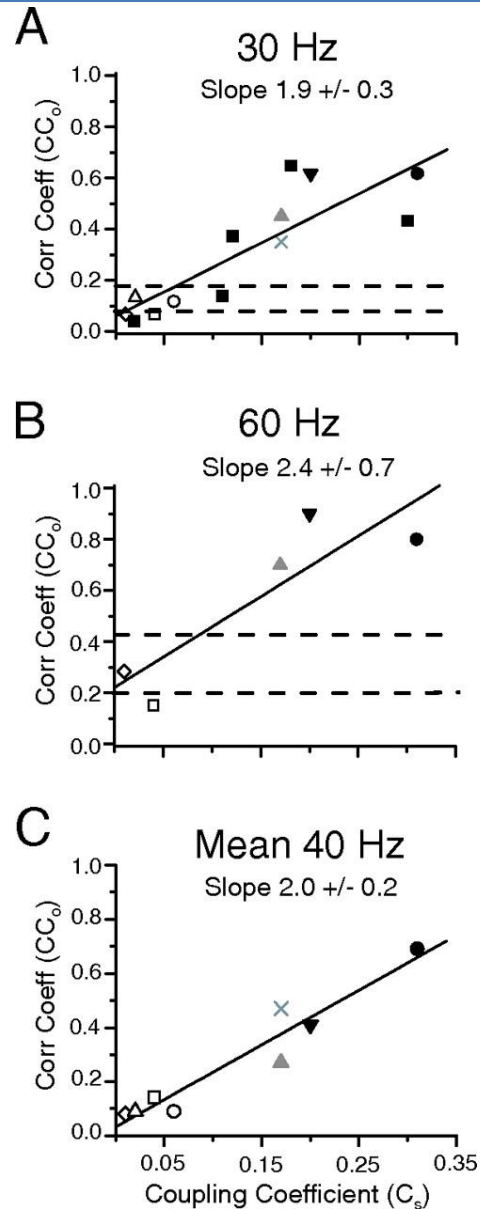
A) Thorough Chemical synapses

- recurrent excitation of pyramidal neurons with fast synapses (type II cells, cf. prev.)
=> same phase
- slow inhibitory interneurons (type I cells, cf. prev.)
=> anti-phase correlation
- Fast and strong excitation + slow or delayed inhibition feedback loop
=> gamma oscillation
- Synaptic filtering (facilitation or depression)
=> preferred frequency



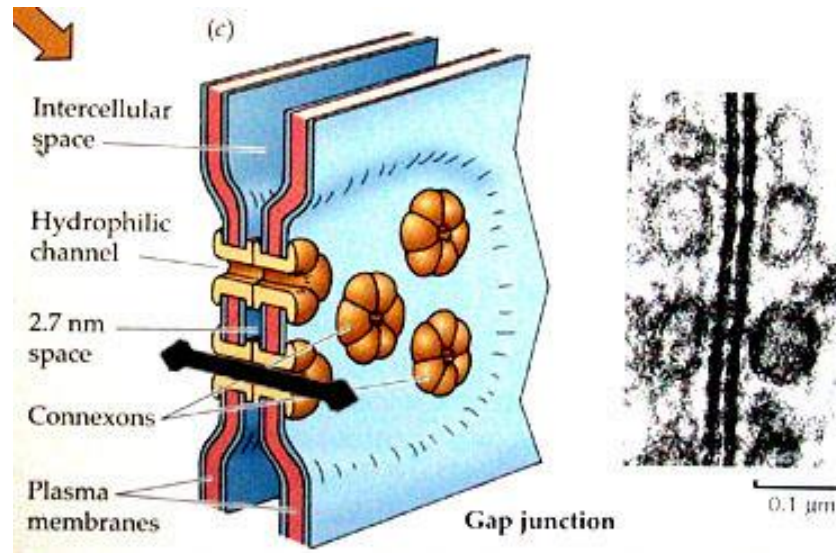
heterogeneity of neurons
↔ heterogeneity of rhythms



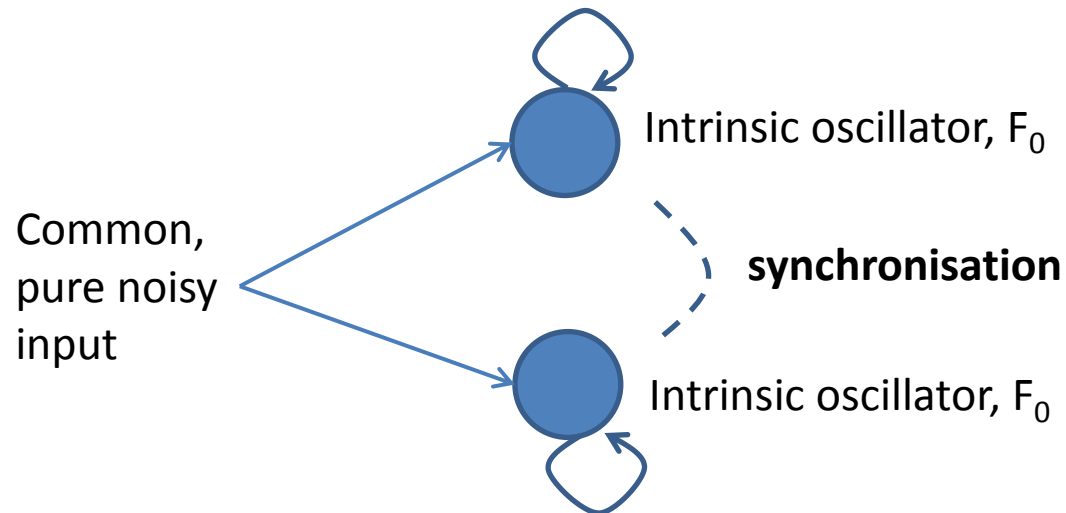


• **B) Electric coupling**

- Gap junctions: fast and bidirectional = Holy Grail of oscillations
- But: very localized
- Ex. Some GABA interneurons
- important during early stage of development with crucial properties for transient developmental brain activity

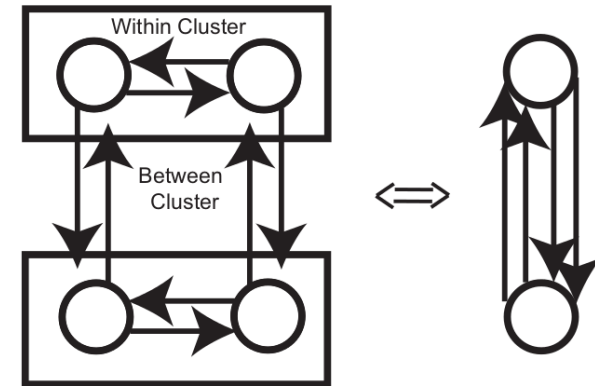


- **C) Correlation-induced stochastic synchrony**
 - networks often oscillate with oscillatory inputs
 - but also with a shared, stochastic input

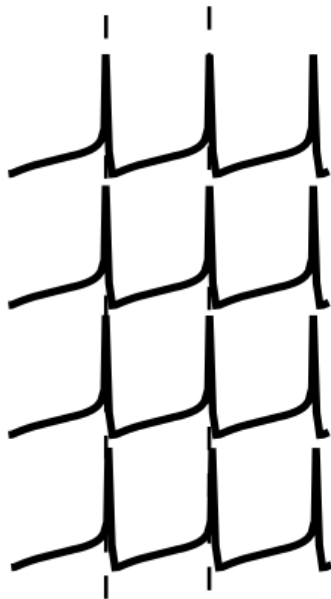


- **Clustering**

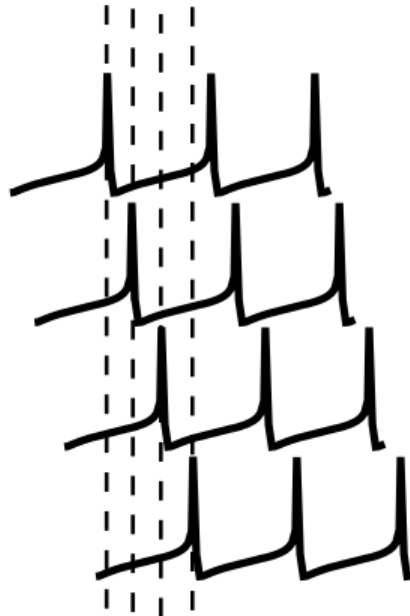
- Globally oscillating networks can break into a small number of oscillating clusters of neurons, firing intermittently



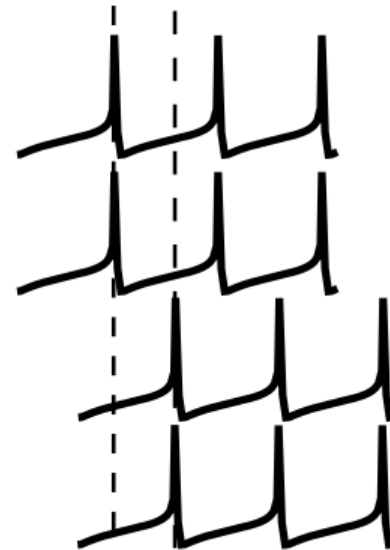
(A) SYNCHRONY



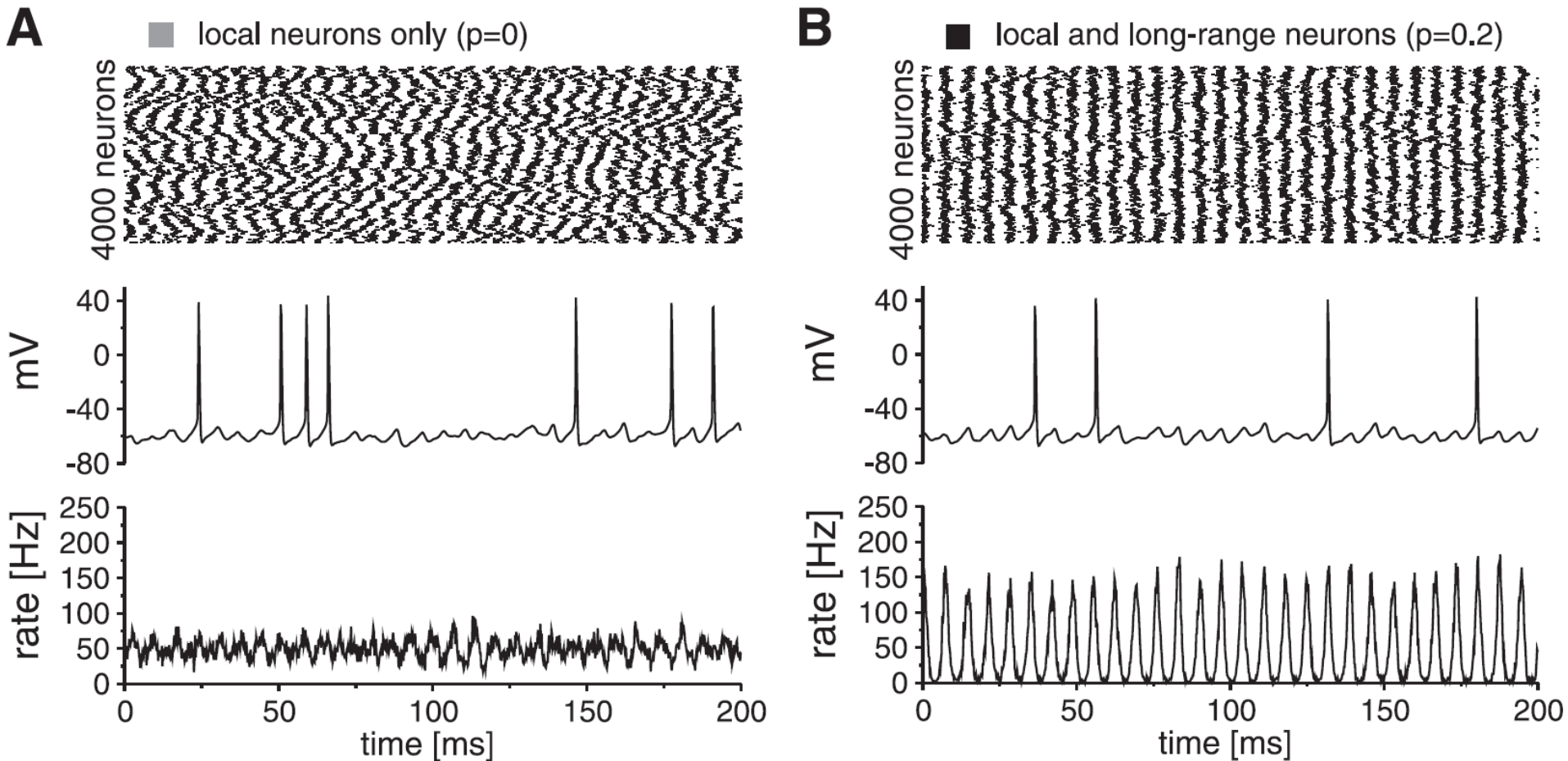
(B) SPLAY



(C) 2 CLUSTERS OF 2

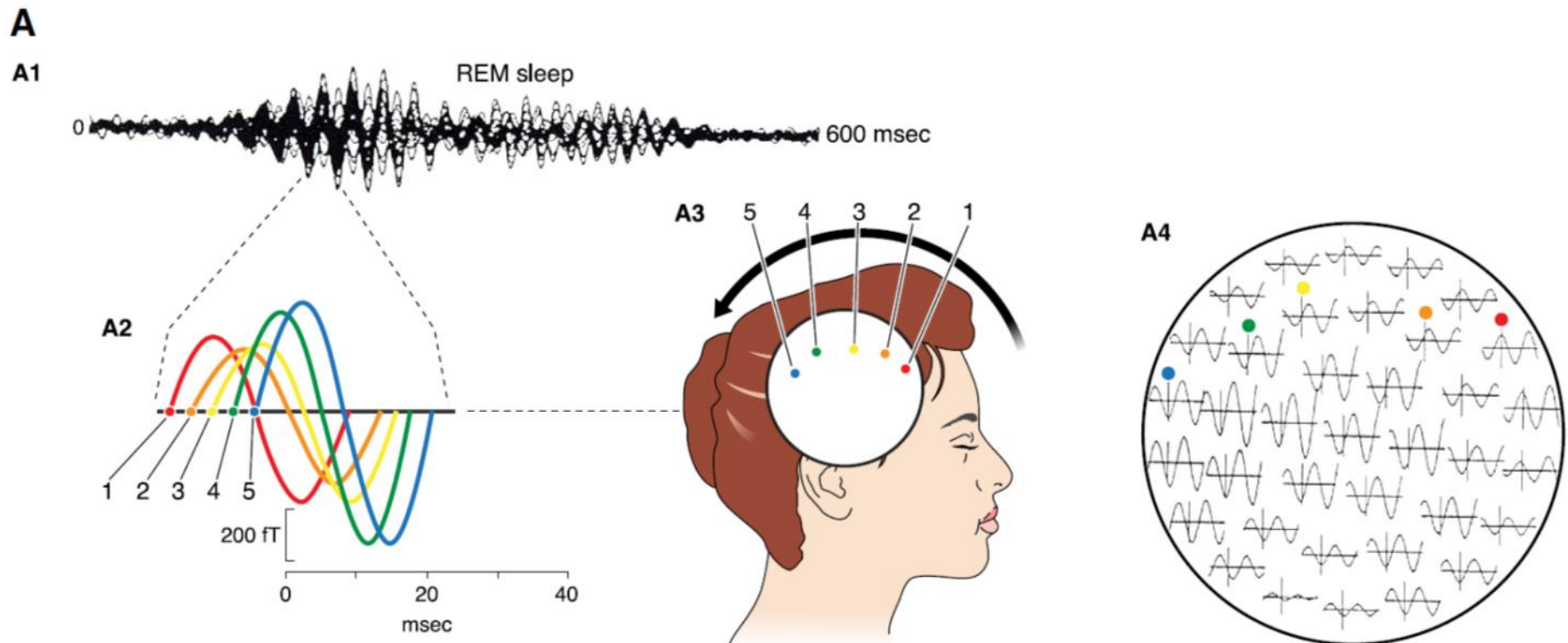


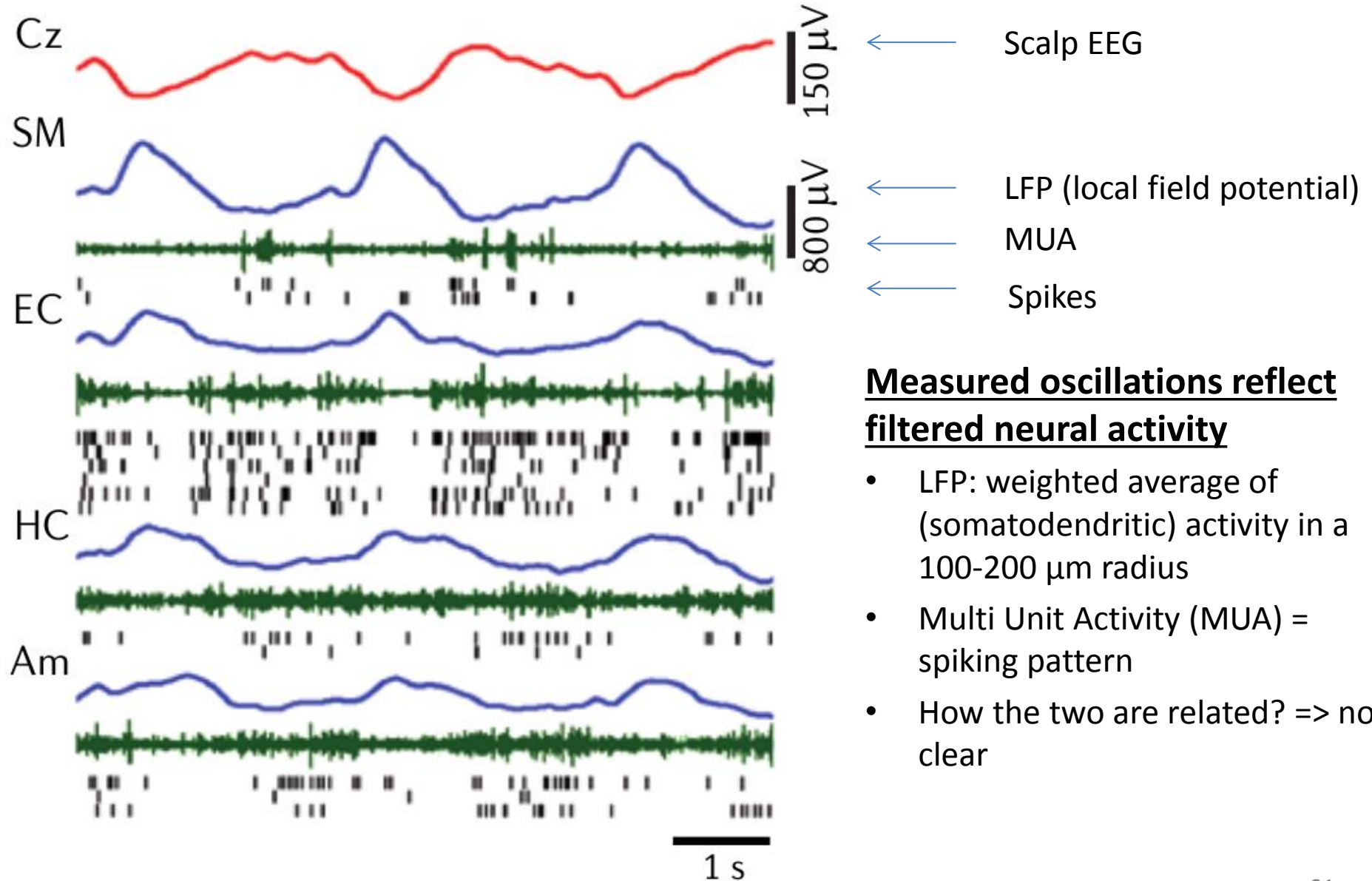
- Complex network with long range connections**



Spatially structured network

- Can produce propagating waves.
- Wave propagation (evidence at multiple scale) due to neighboring connectivity



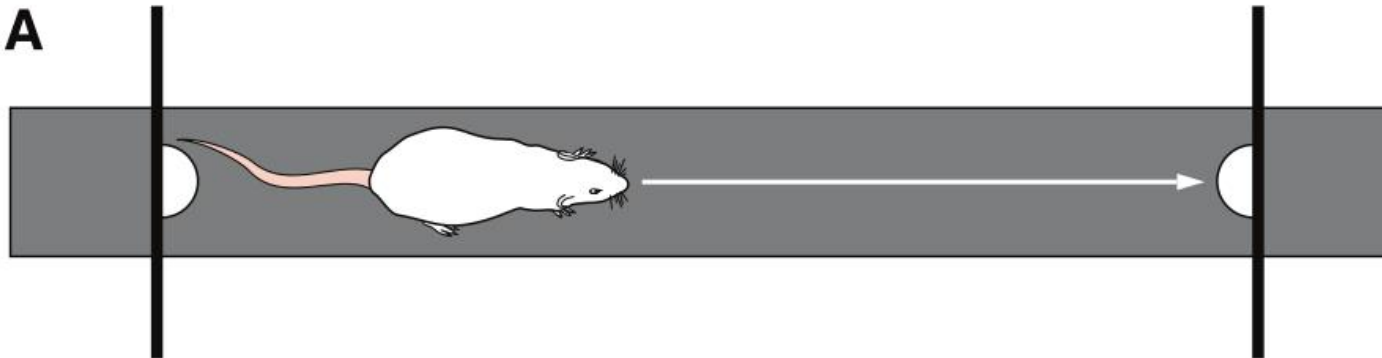


The phase code

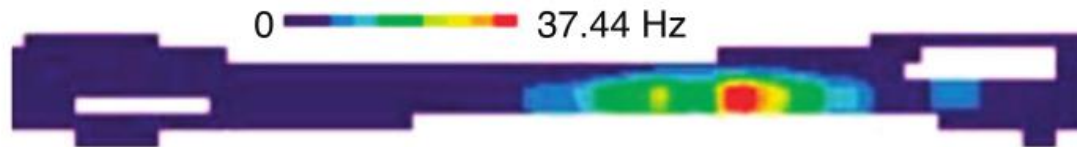
Oscillations carry additional information: time

Cf. cours Karim Benchenane

A

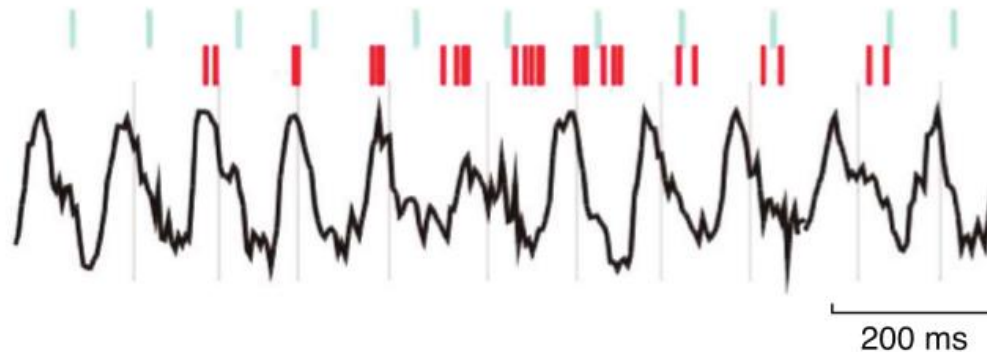


Firing
field



Symmetric response in Hz

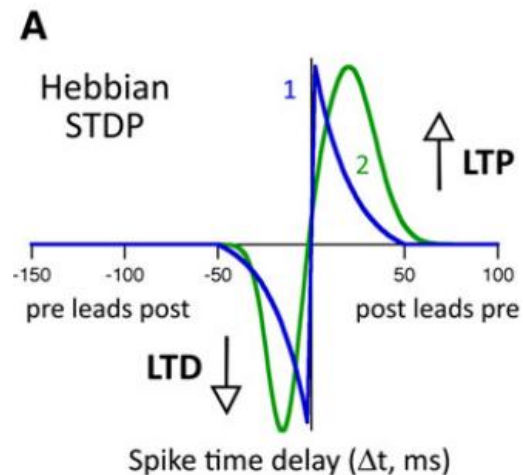
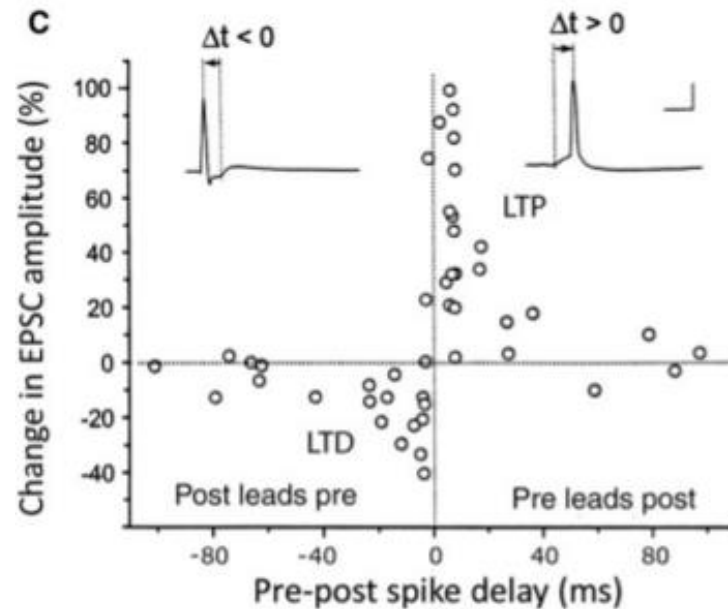
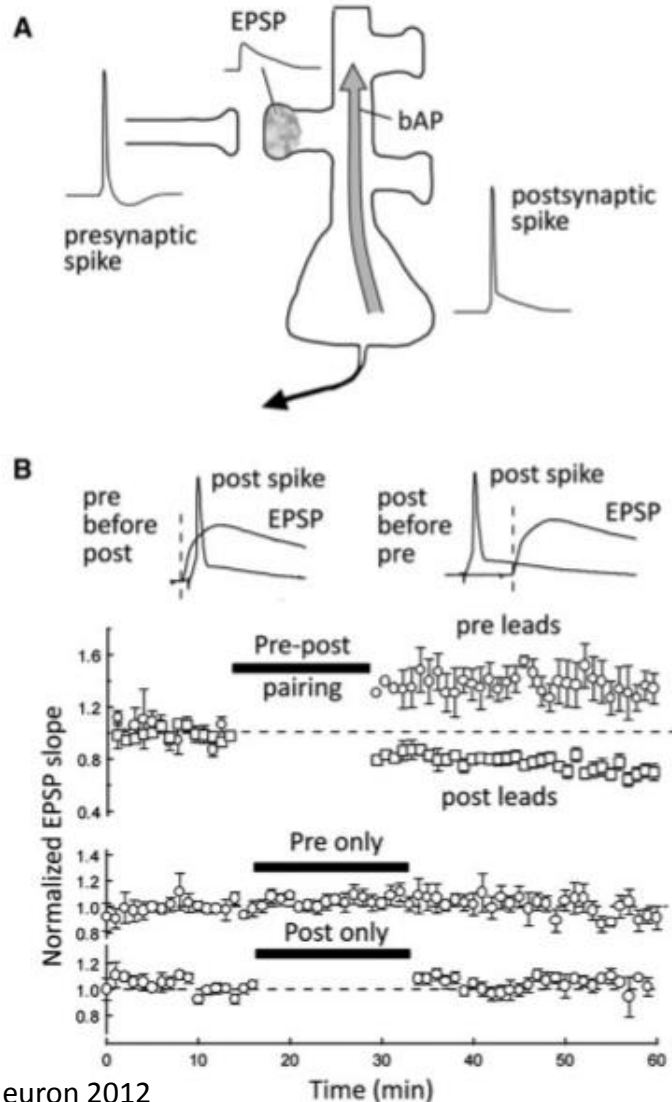
Temporal
code

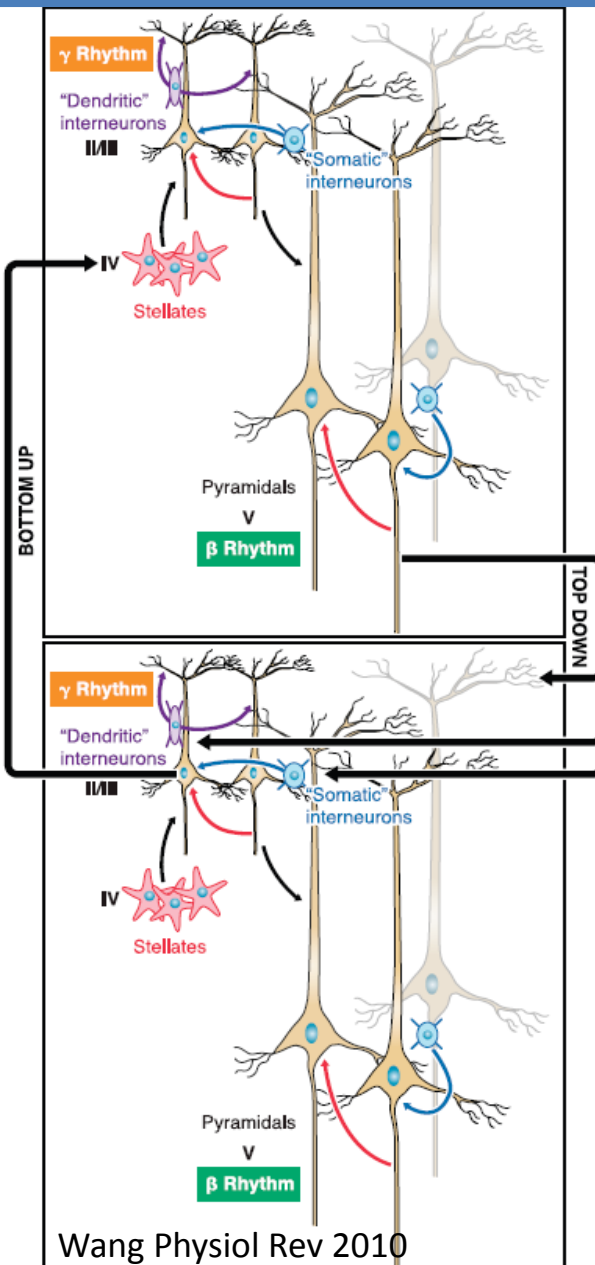


Asymmetric response
relative to theta phase

Precise timing for memory

Synaptic plasticity depends on spike timing (STDP).



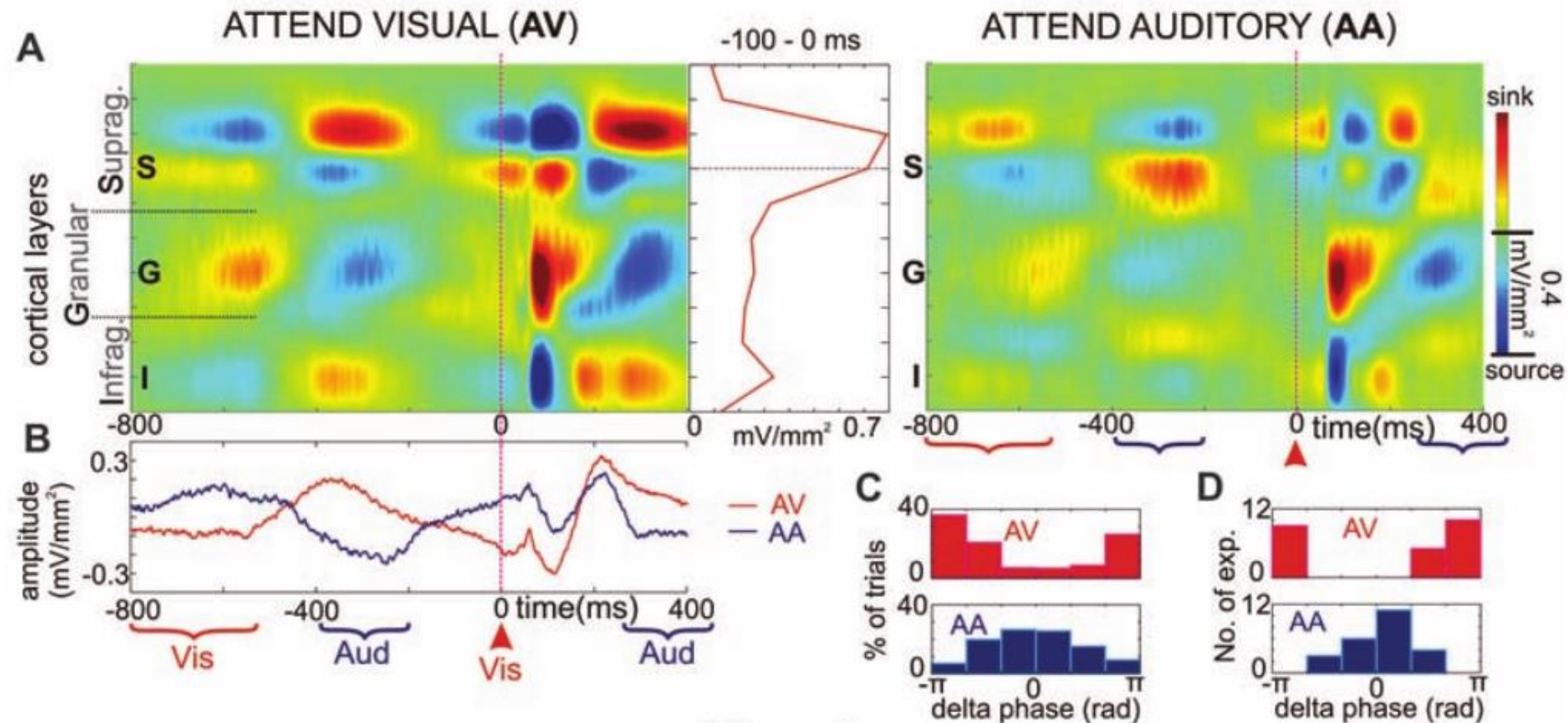


Oscillations depend on the brain architectures

- Oscillation can be layer specific:
 - beta (15-30Hz): deep layers
 - gamma (> 40Hz): superficial layers
- Feedback & feed-forward connections are also layer-specific:
 - Feed-forward
 - bottom-up signaling
 - Local processing
 - gamma
 - Feed-back
 - top-down signaling
 - Long range
 - Beta (can modulate top-down signaling).

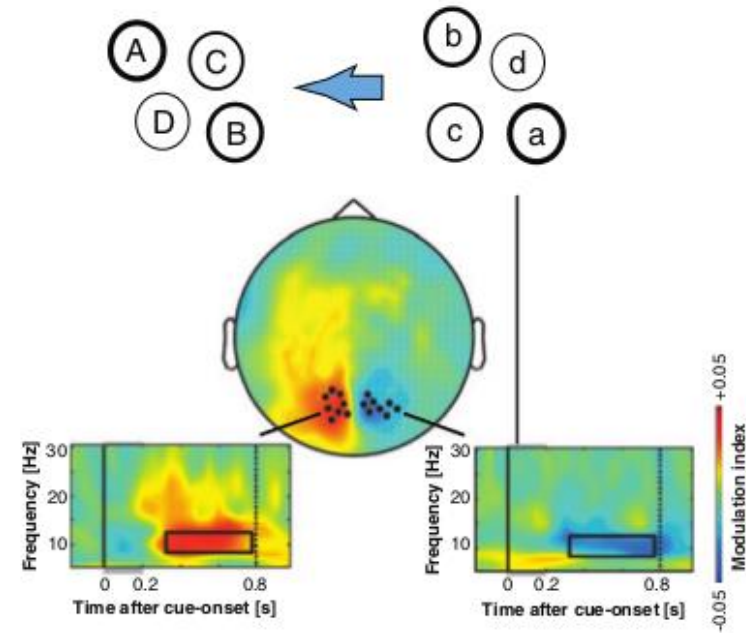
Attention selection in a perceptive stream

Low frequencies (delta) modulate the excitability of local neuronal assemblies.

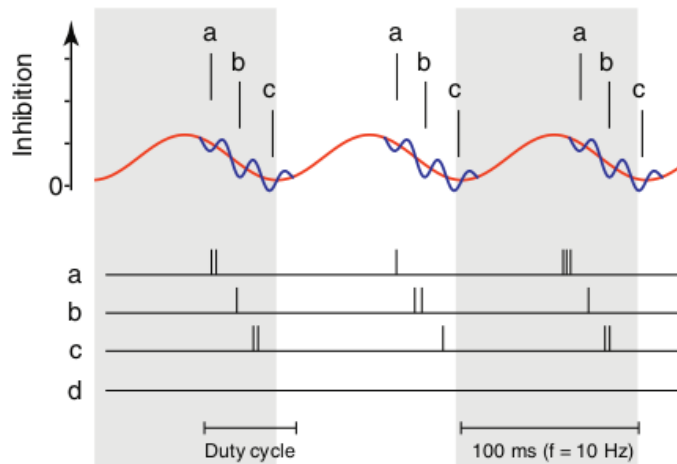


Discreetness of cognitive processes and pulsed-inhibition

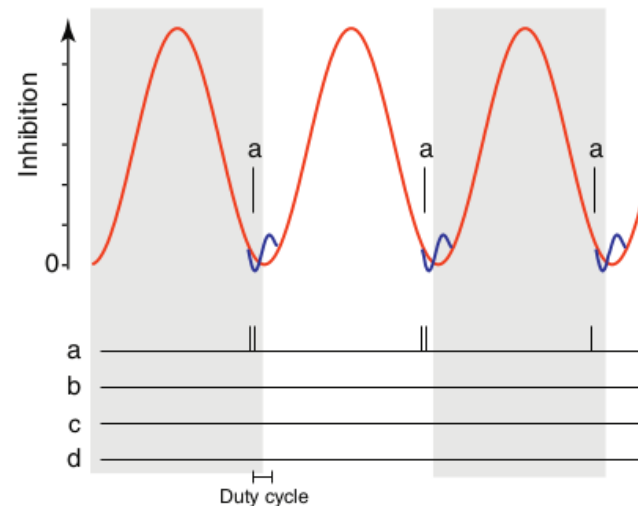
- Many cognitive processes are rhythmic. E.g. in perception: saccades, sniffing, ...
- The oscillation amplitude can control the duration allowed for processing: pulsed inhibition with alpha rhythm



Medium alpha ('medium attention')

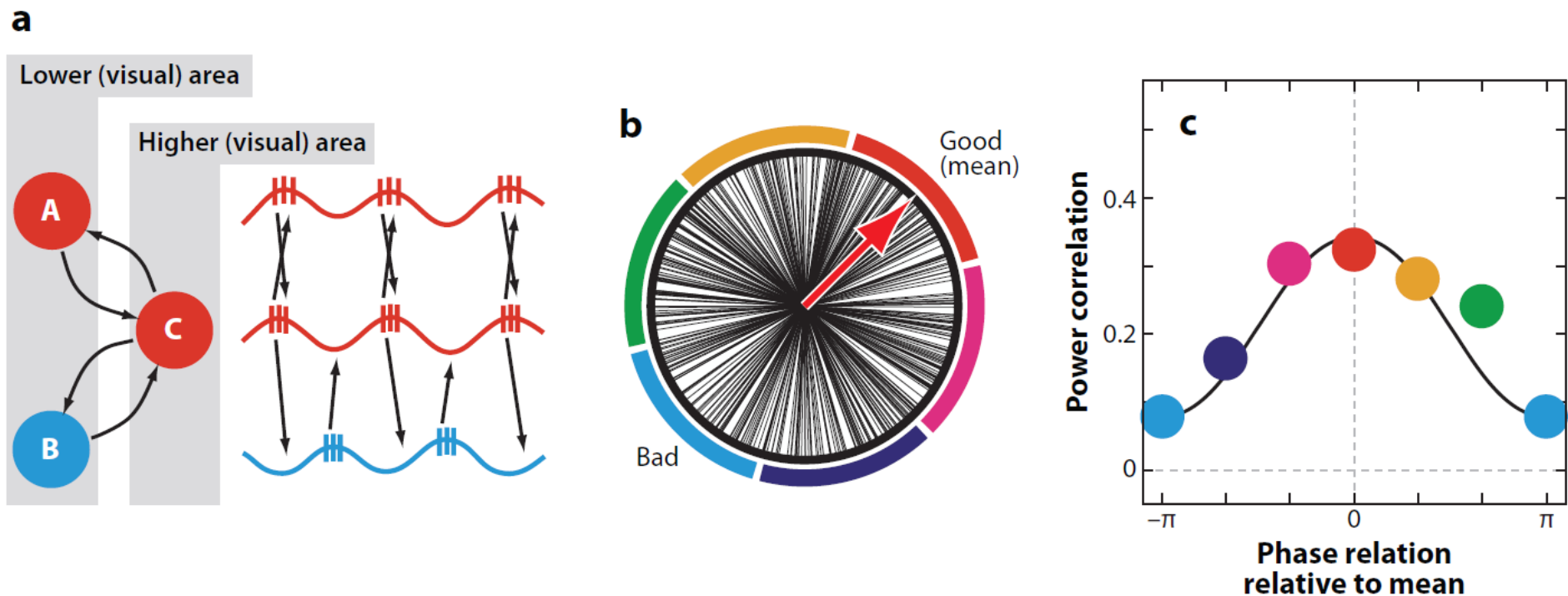


(c) High alpha ('low attention')



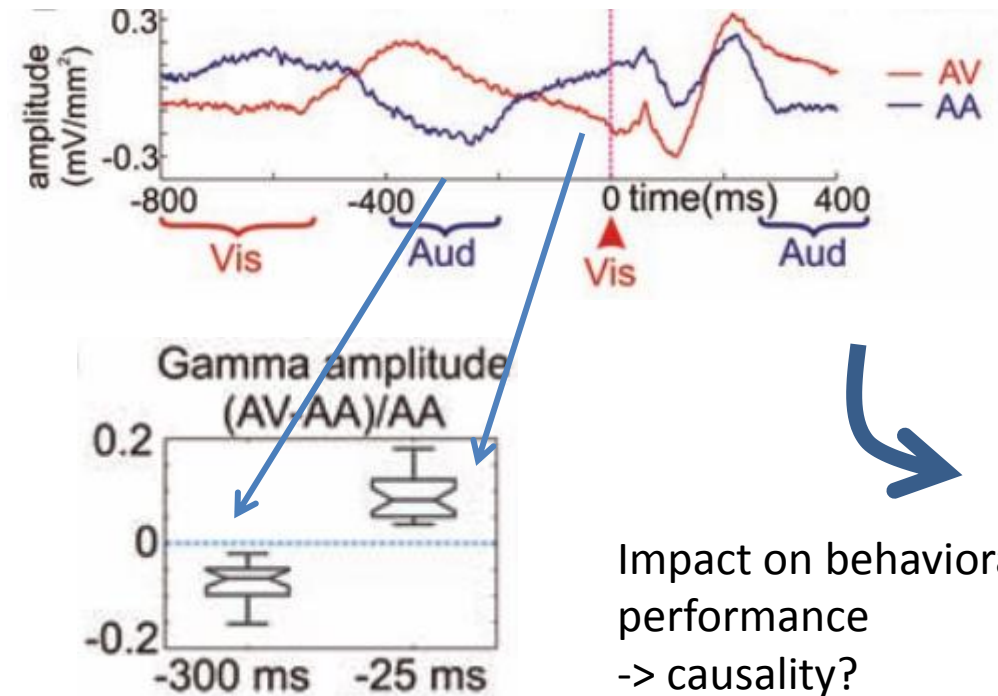
Communication-through-coherence in the gamma band

- Coherence between level can select information (functional switch)
- Gamma rhythmicity:
 - Dendritico-somatic summation at the neuronal time scale: 10 ms (coincidence detection)
 - Periodic inhibition gate the synaptic efficacy (gain modulation)

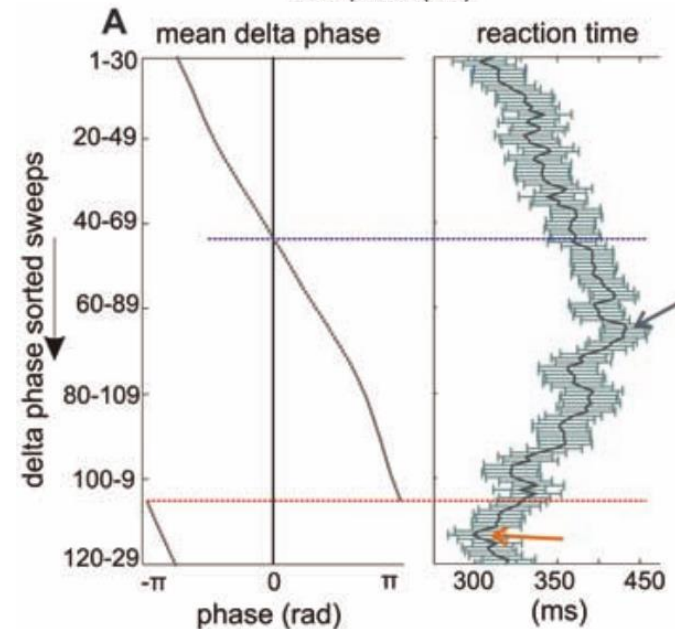
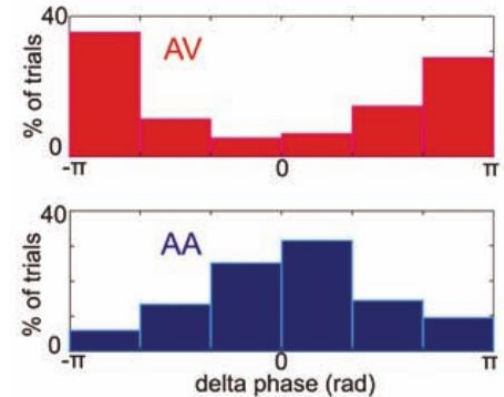


Cross-frequency coupling between high and low frequency

- high frequency (gamma) = processing
- Low frequency (delta) = attention selection



Impact on behavioral
performance
-> causality?



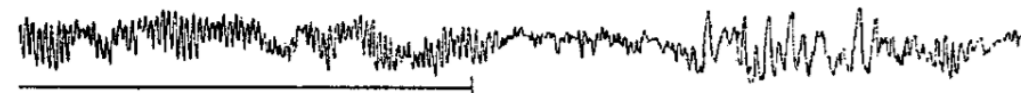
PRECENTRAL HAND



FIST CLENCHED

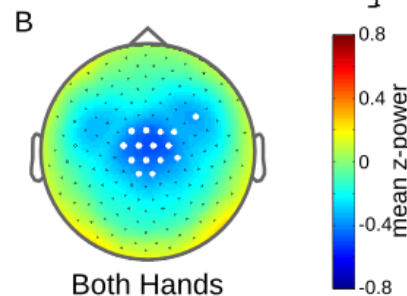
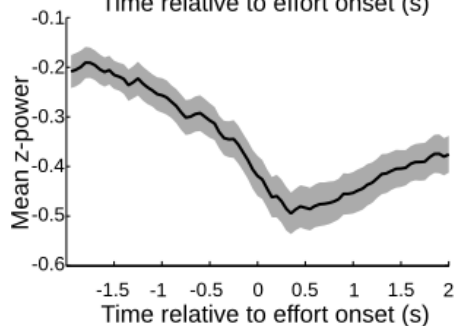
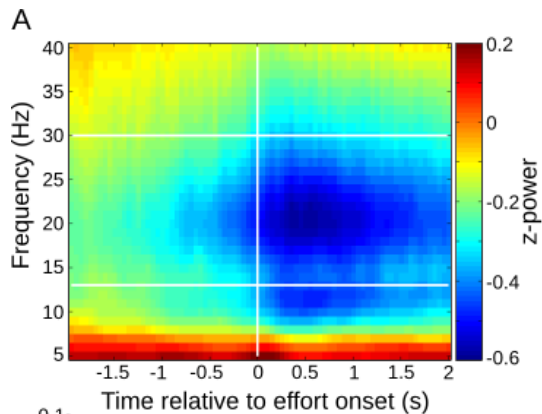
Jasper & Penfield 1949

CONTIN'D

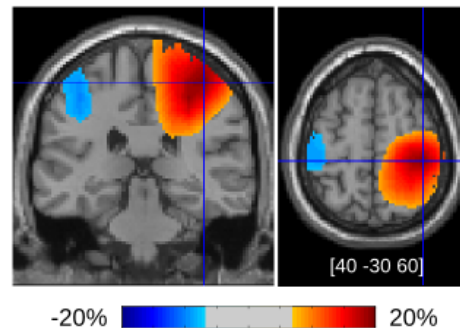


1 SEC.

RELAX



C Right Hand - Left hand

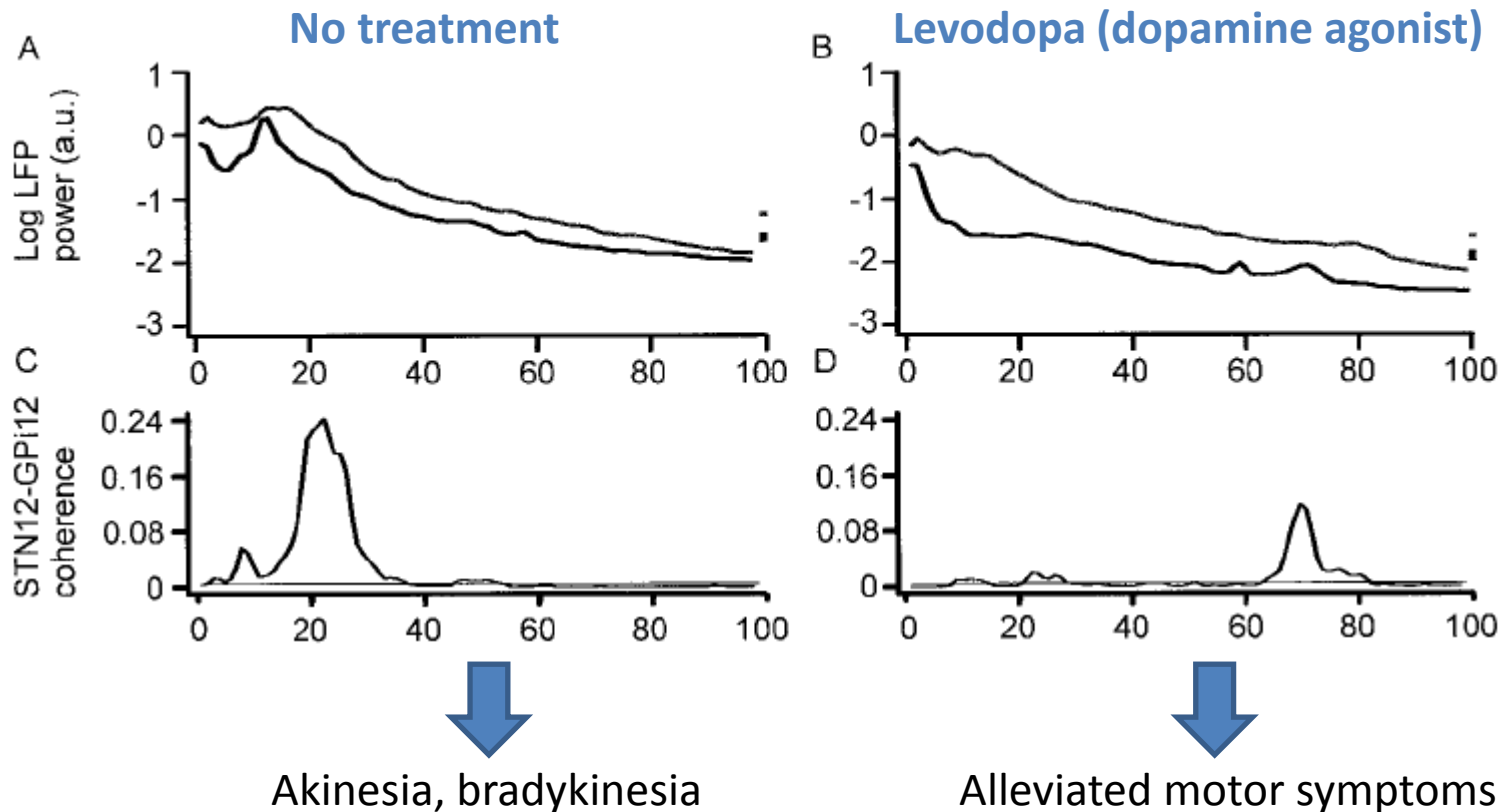


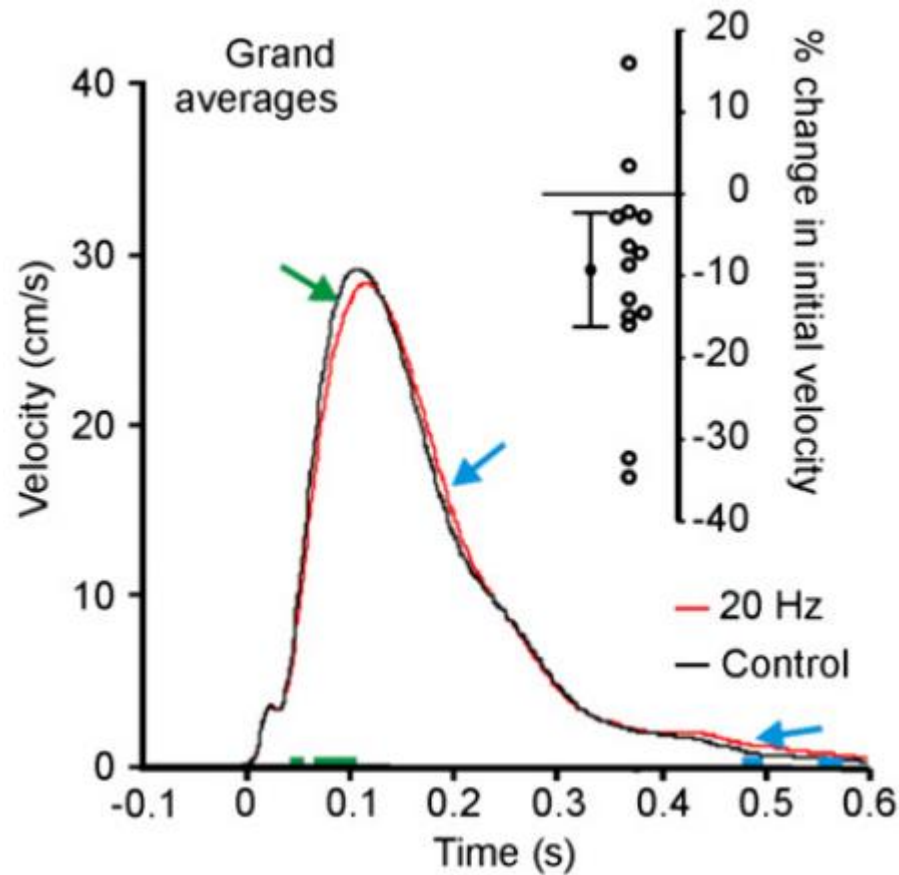
Motor beta synchrony gates motor change

- High beta synchrony when steady (either during the effort or during rest)
- For voluntary actions, the reduction of synchrony precedes the action onset

High beta synchrony prevent movement production

- Evidence from Parkinson disease patient.
- Evidence in patient and healthy participant that trial-to-trial variability in motor fluency depends on the trial-to-trial variability in beta synchrony.



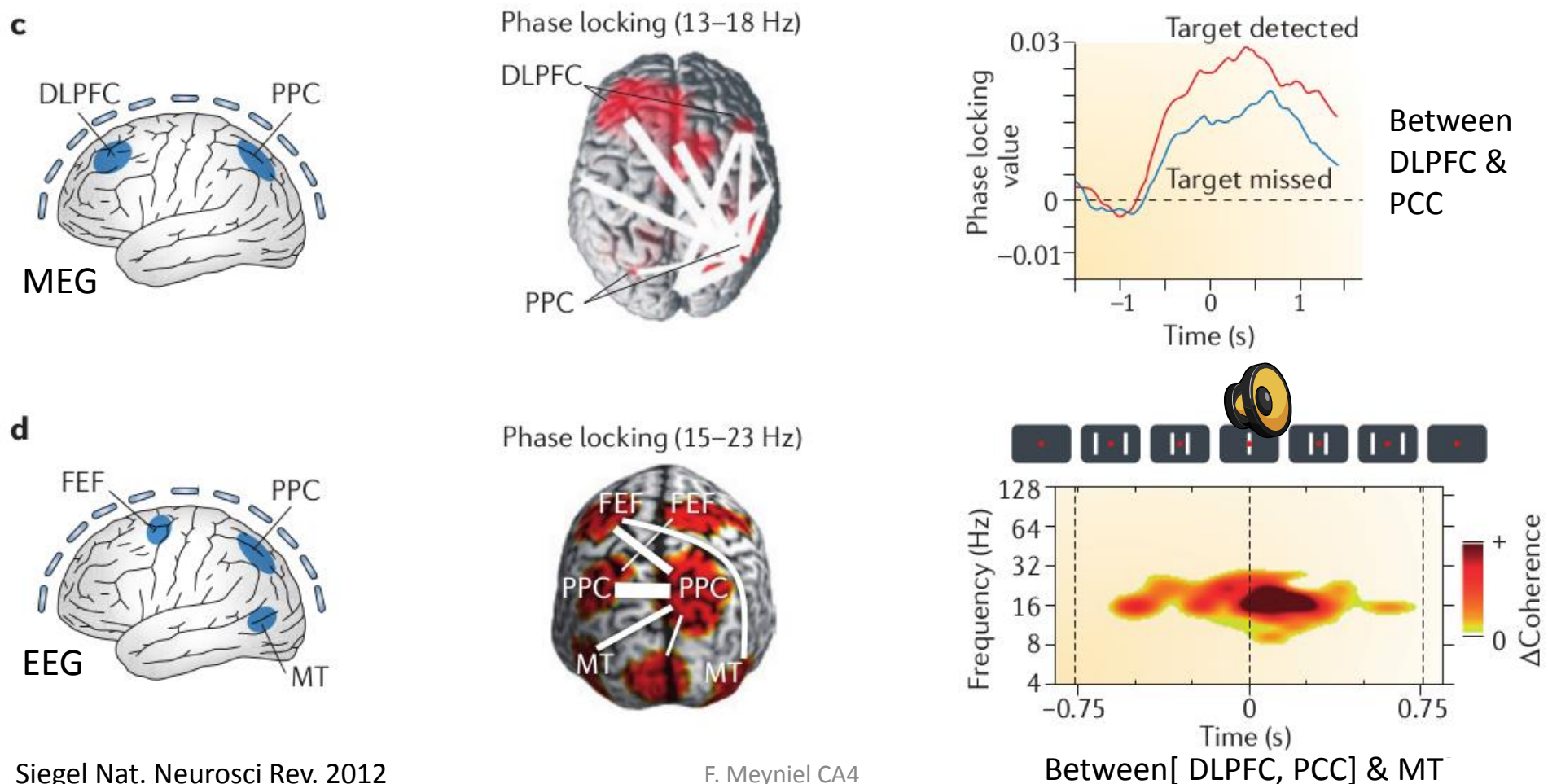


Entrained beta oscillations slow movement

- Entrained oscillation: rhythmic transcranial magnetic stimulation (TMS)
- Manipulation = evidence of causality.

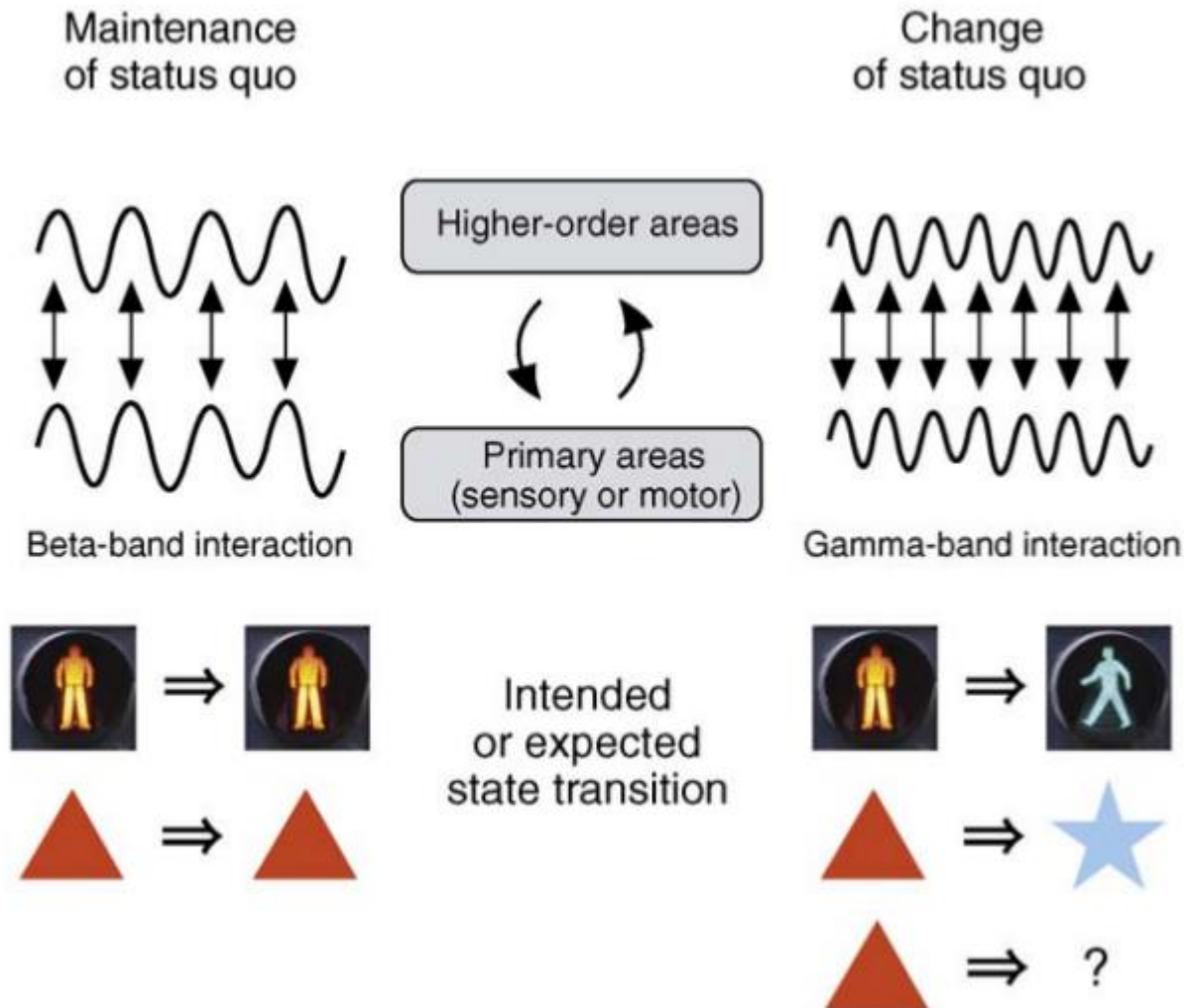
High beta synchrony during top-down processing

- Fluctuations of beta band synchrony reflect fluctuations of attention
- Those fluctuations shape our perception
- Beta band synchrony at the network level, potentially revealing functional connectivity



Proposal: Beta band synchrony promotes the status quo

beta-band activity maintains the current sensorimotor or cognitive state



Take home messages

- Oscillations and synchrony arise from intrinsic properties of synapses, neurons and networks
- Oscillations and synchrony change with many cognitive processes
- The diversity of oscillations is related to the diversity of networks and functions
- There is computational and experimental evidence that functional changes in neural networks drive changes in oscillations and synchrony
- Oscillations give an insight at the computational level, i.e. between the neural and behavioral levels.