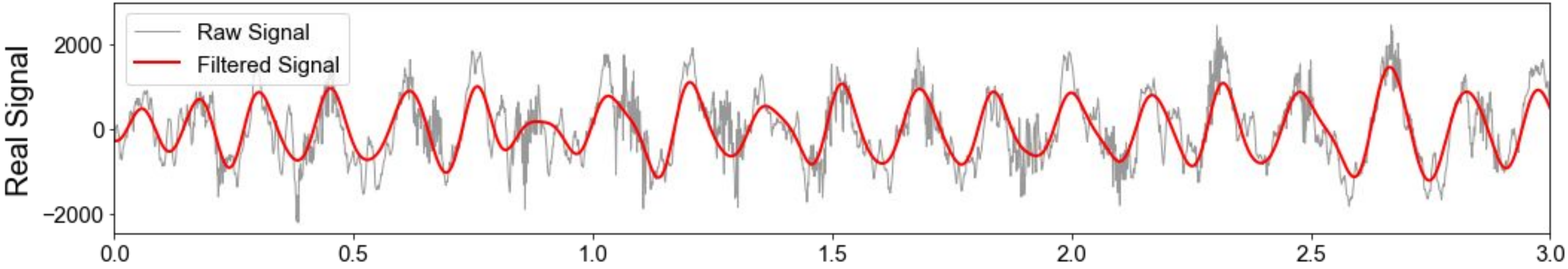
Lecture 8

Last time…

Bandpass filters

Bandpass filters keep signal components in a frequency range (e.g., theta 4–12 Hz) and suppress components outside it.

There are also **highpass** (keep high frequencies), **lowpass** (keep low frequencies), **bandstop** (stop certain frequencies, aka notch).



Two kinds of filters: FIR and IIR

Finite Impulse Response (FIR)

$$\boxed{\sum_{k=0}^{M} b_k x(n-k)}$$

current and past inputs

Infinite Impulse Response (IIR)

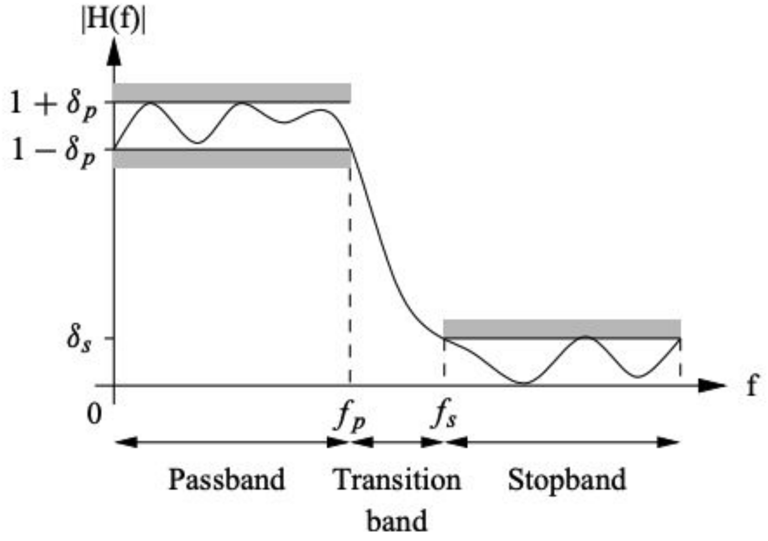
$$\boxed{\sum_{k=0}^{M} b_k x(n-k)} - \boxed{\sum_{k=1}^{N} a_k y(n-k)}$$

current and past inputs

past outputs

Filter design tradeoffs

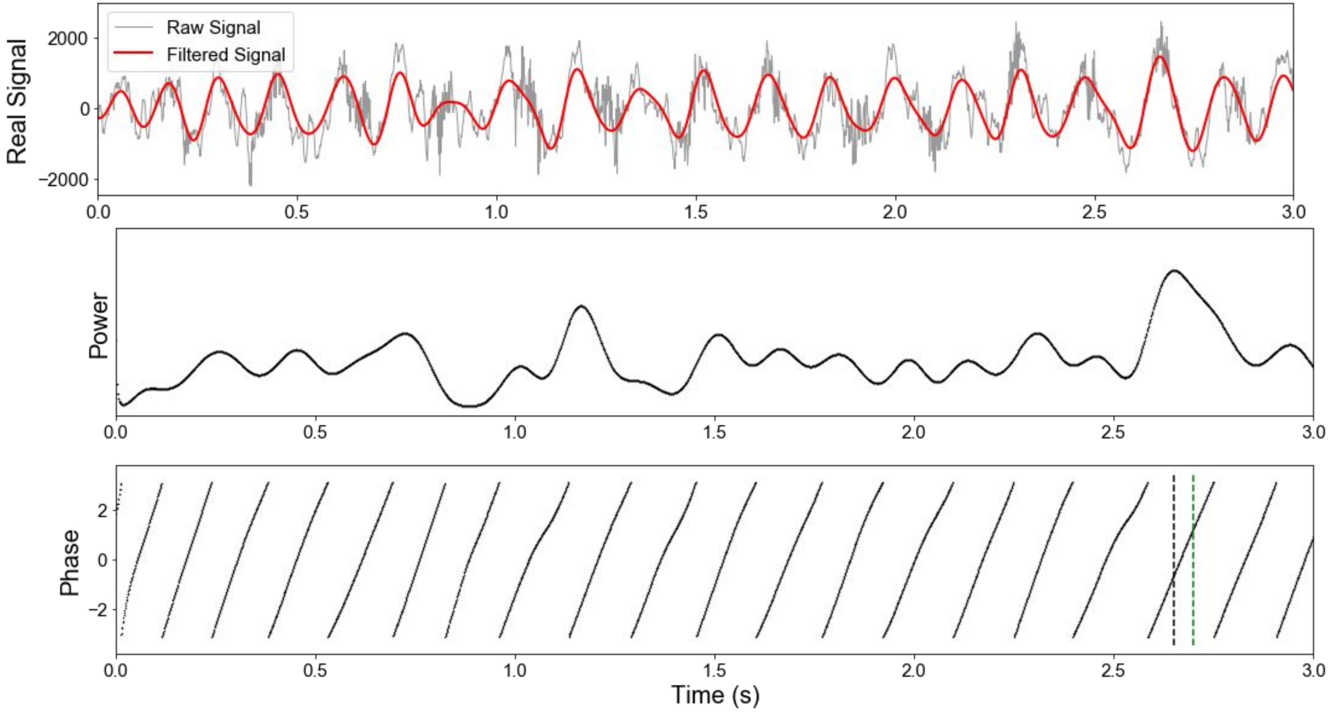
1. Ripple in the pass-band
2. Attenuation of the stop-band
3. Steepness of roll-off
4. Filter order (i.e., length for FIR filters)
5. Time-domain ringing



Key takeaways

- FIR filters are easier to design and deal with
- Filters also have a time-frequency trade off
- You should use acausal filters to prevent distortion of phase (unless doing real time)
- You should always check your filter characteristics before using (frequency magnitude response, impulse response, etc).

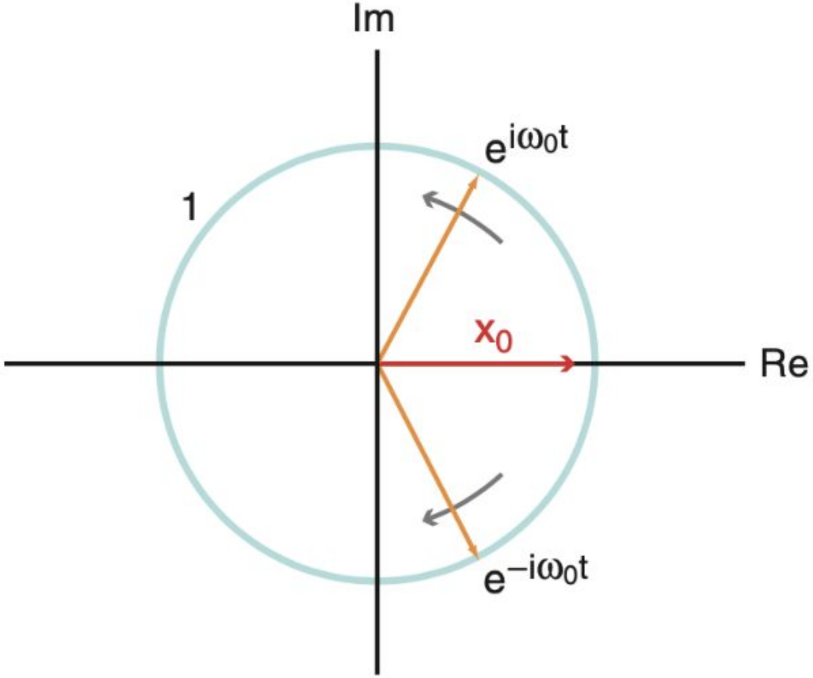
Sometimes we want the instantaneous phase and power of a signal in a particular frequency band



Hilbert transform

Original signal $x_0 = 2\cos(2\pi f_o t) = e^{i\omega_0 t} + e^{-i\omega_0 t}$

Complicated (2 complex exponentials)



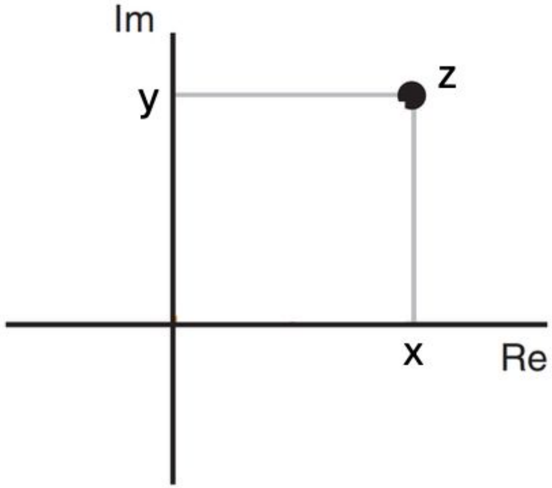
Analytic signal $z_0 = 2e^{i\omega_0 t}$

Simple (1 complex exp)

A point in the complex plane

Hilbert transform

Analytic signal $z = x + iy$ A point in the complex plane



$$z(t) = A(t)\, e^{i\,\phi(t)}$$

amplitude phase

Get the **amplitude** and **phase** from the analytic signal

Ex.

$z_0(t) = 2e^{i\omega_0 t}$ $A(t) = 2$ $\phi(t) = \omega_0\, t$

Key Takeaways

- Think of the Hilbert transform as a coordinate transformation that is convenient for making the analytic signal (time domain to phasor circular coordinates)
- We can also think of it as zeroing out the negative frequency Fourier coefficients and doubling the positive frequency Fourier coefficients
- NB: **scipy.signal.hilbert** does not compute the Hilbert transform, it computes the analytic signal

Coherence: equations

Put it all together ...

$$\kappa_{xy,\,j} = \frac{|< S_{xy,\,j} >|}{\sqrt{< S_{xx,\,j} >}\sqrt{< S_{yy,\,j} >}}$$

In polar coordinates

cross-spectrum of x & y, depends on trial averaged amplitudes, phase differences.

$$= \frac{\left| \sum_{k=1}^{K} A_{j,k} B_{j,k} \exp\left(i\Phi_{j,k}\right) \right|}{\sqrt{\sum_{k=1}^{K} A_{j,k}^{2}} \sqrt{\sum_{m=1}^{K} B_{j,m}^{2}}}$$

x trial averaged spectrum, at frequency index j

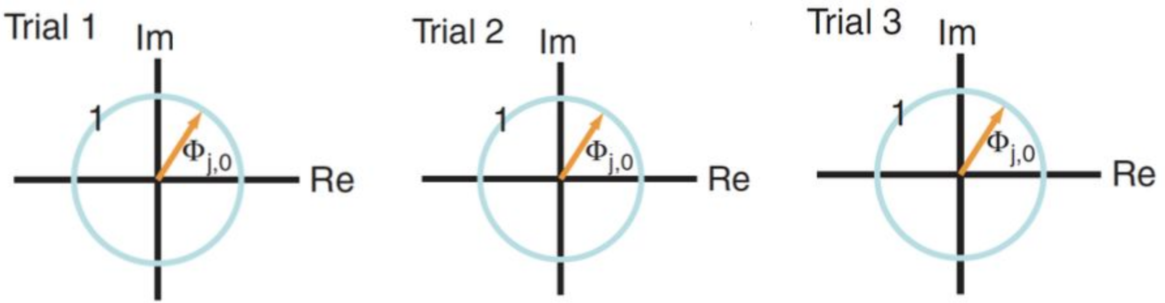
y trial averaged spectrum, at frequency index j

Coherence: intuition

$$\kappa_{xy,j} = \frac{1}{K}\left|\sum_{k=1}^{K}\exp\left(i\Phi_{j,k}\right)\right|$$

Case 1: Phases align across trials. $\boxed{\Phi_{j,k} = \Phi_{j,0}}$

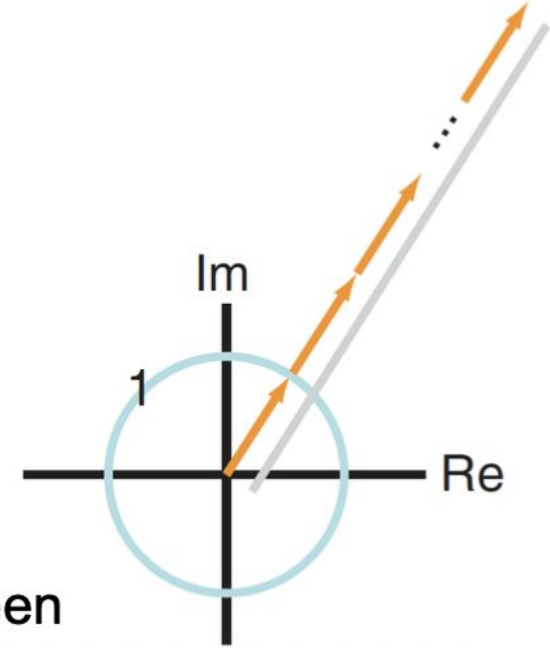
Plot $\exp\left(i\Phi_{j,k}\right)$ in the complex plane.



sum these vectors end to end across trials

divide by K

$$\kappa_{xy,j} \approx 1$$



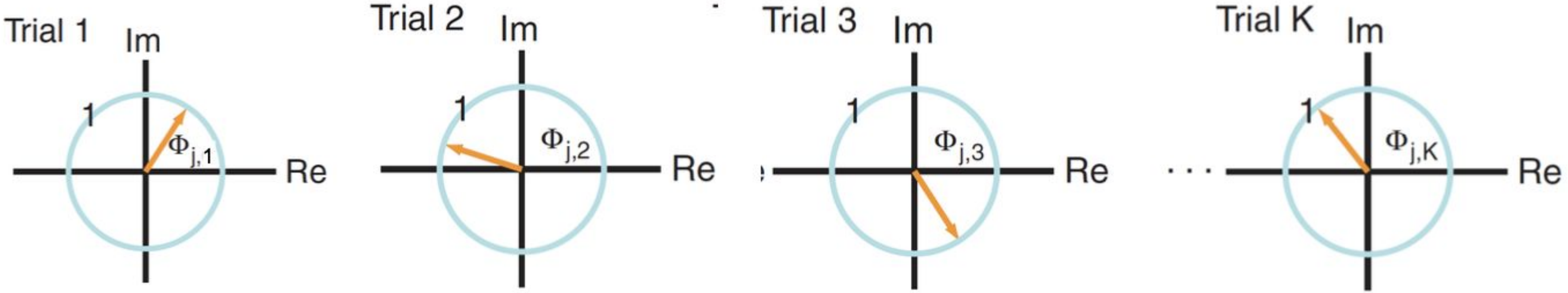
<u>strong coherence</u> - constant phase relation between the two signals across trials at frequency index j.

Coherence: intuition

$$\kappa_{xy,j} = \frac{1}{K}\left|\sum_{k=1}^{K} \exp\left(i\Phi_{j,k}\right)\right|$$

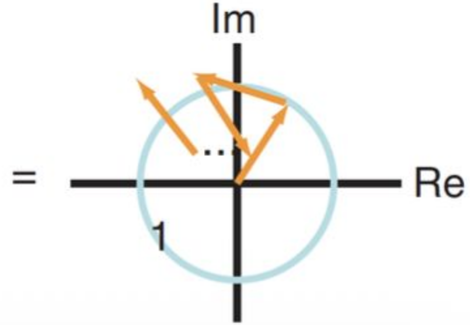
Case 2: Random phase differences across trials.

Plot $\exp\left(i\Phi_{j,k}\right)$ in the complex plane.



sum these vectors end to end across trials

divide by K $\qquad \kappa_{xy,j} \approx 0$



weak coherence - random phase relation between the two signals across trials at frequency index j.

Coherence: summary

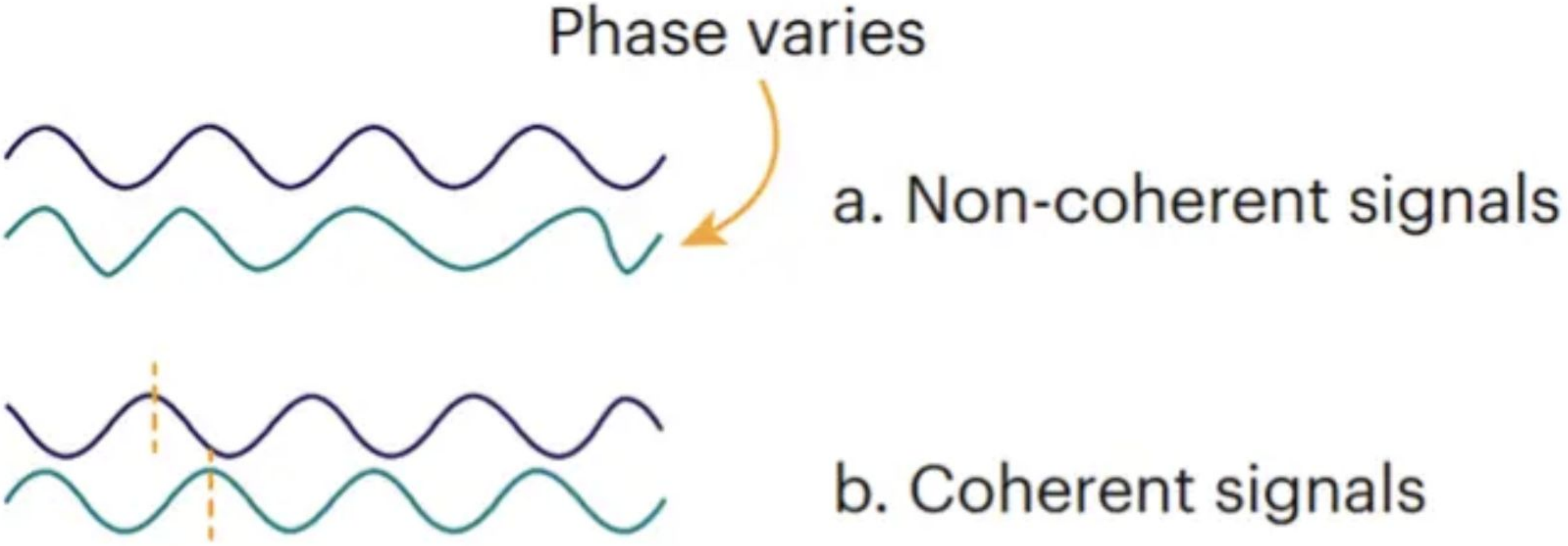
$$0 \leq \kappa_{xy,j} \leq 1$$

0: no coherence between signals x and y at frequency index j

1: strong coherence between signals x and y at frequency index j .

The coherence is a measure of the phase consistency between two signals at frequency index j across trials.

Coherent vs. Incoherent signals



https://www.keysight.com/blogs/en/inds/2023/01/06/the-importance-of-phase-coherent-rf-signal

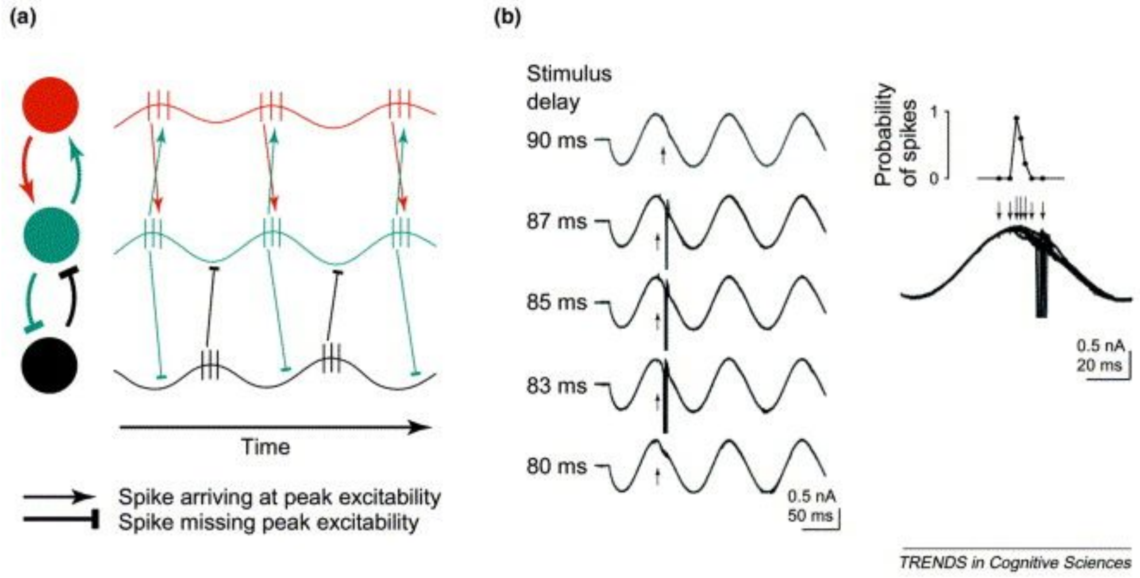
Key Takeaways

- Coherence measures phase consistency of two signals in the frequency domain
- You need to have multiple trials or tapers to compute coherence (otherwise it will be trivially one)
- The Fourier transform of the cross-correlation is coherence (coherence is correlation in the frequency domain)
- Didn’t mention last time: cohereograms - can compute across time

This time…

- Communication through coherence
- Potential issues with coherence
- Related measures of measuring coupling between signals
  - Phase locking value
  - Phase lag index
- Spike-LFP relationships
  - Phase tuning curves
  - Circular statistics
  - Non-parametric spike field coherence
  - Parametric spike field coherence (harmonic Poisson regression)
- Cross frequency coupling

Communication through coherence



Communication through coherence: When two regions' LFPs are phase-aligned, they create time windows of high excitability so that spikes arriving from one region are more effective at driving responses in the other.

Fries, P. (2005, 2015)

Potential issues with coherence

Common sources: coherence is frequency domain correlation, a third common source can drive correlation between two signals

Volume conduction: A single electrical source can be sensed by multiple electrodes

Phase Locking Value

Coherence depends on the power of each signal.

In phase locking value, we ignore the power and only consider the phase relationship

Coherence: equations

This is what we'll compute:

$$\kappa_{xy,\,j} = \frac{|< S_{xy,\,j} >|}{\sqrt{< \boxed{S_{xx,\,j}} >}\sqrt{< S_{yy,\,j} >}}$$

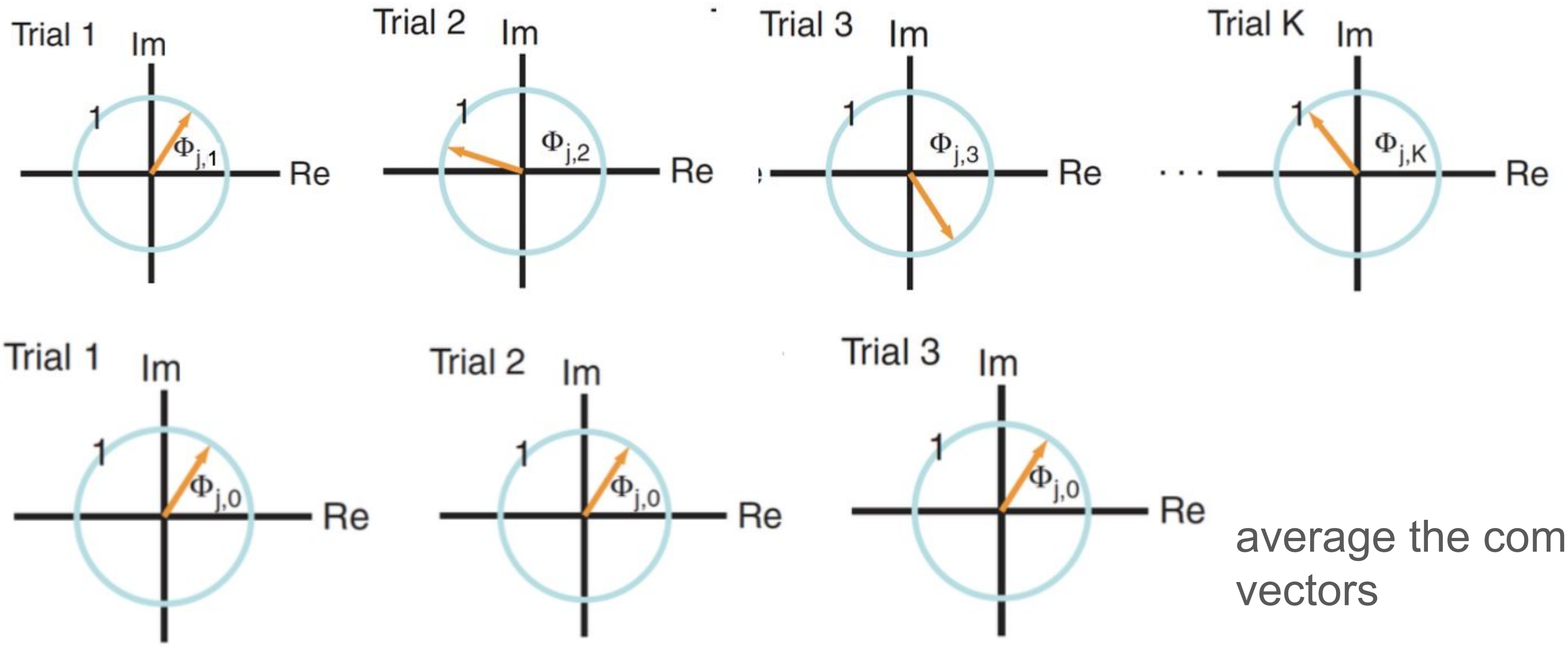
$S_{xy,j}$ = Cross-spectrum at frequency index j

$S_{xx,j}, S_{yy,j}$ = Auto-spectra at frequency index j

$< S >$ = Average of S over trials

Lachaux, J.P. et al. (1999).

Phase locking value



average the complex vectors

The problem

This means we treat all the vectors as having the same power

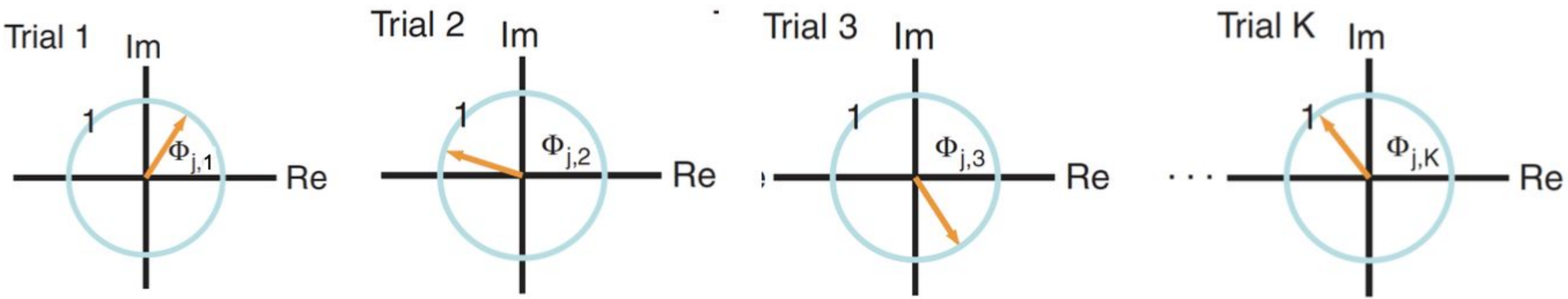
If we have a lot of trials with small power vectors, we are scaling these up and making them important.

This could be a much noisier estimate.

Phase Lag Index

The phase lag index is **the average sign of the imaginary component of the cross-spectrum**.

The imaginary component sets **in-phase or anti-phase signals to zero** and the sign scales it to have the same magnitude regardless of phase.

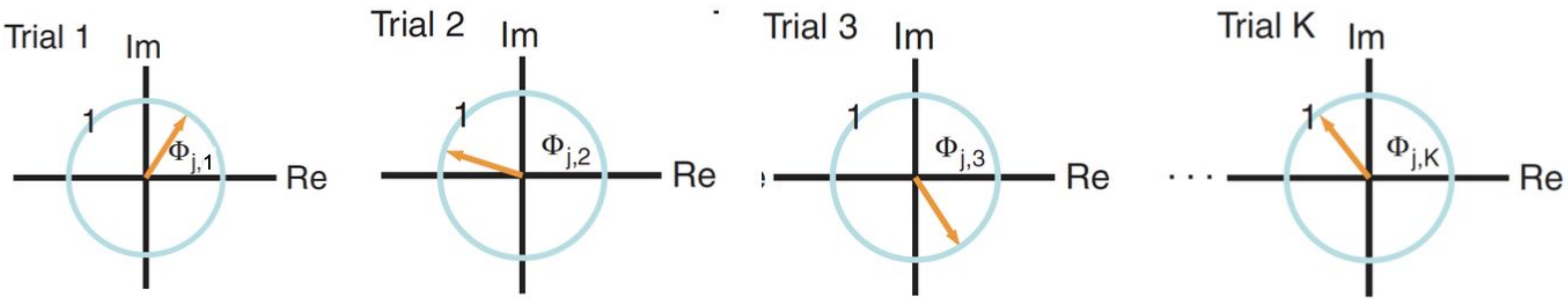


Stam et al. (2007)

Phase Lag Index

Q: Why would we want to set in-phase or anti-phase components to zero?

A: Volume conduction (Assumes volume-conducted sources arrive at sensors at the same time, resulting in a cross-spectrum with phase angle of 0 (perfectly in-phase) or π (anti-phase) if the sensors are on opposite sides of a dipole source).



Other similar measures

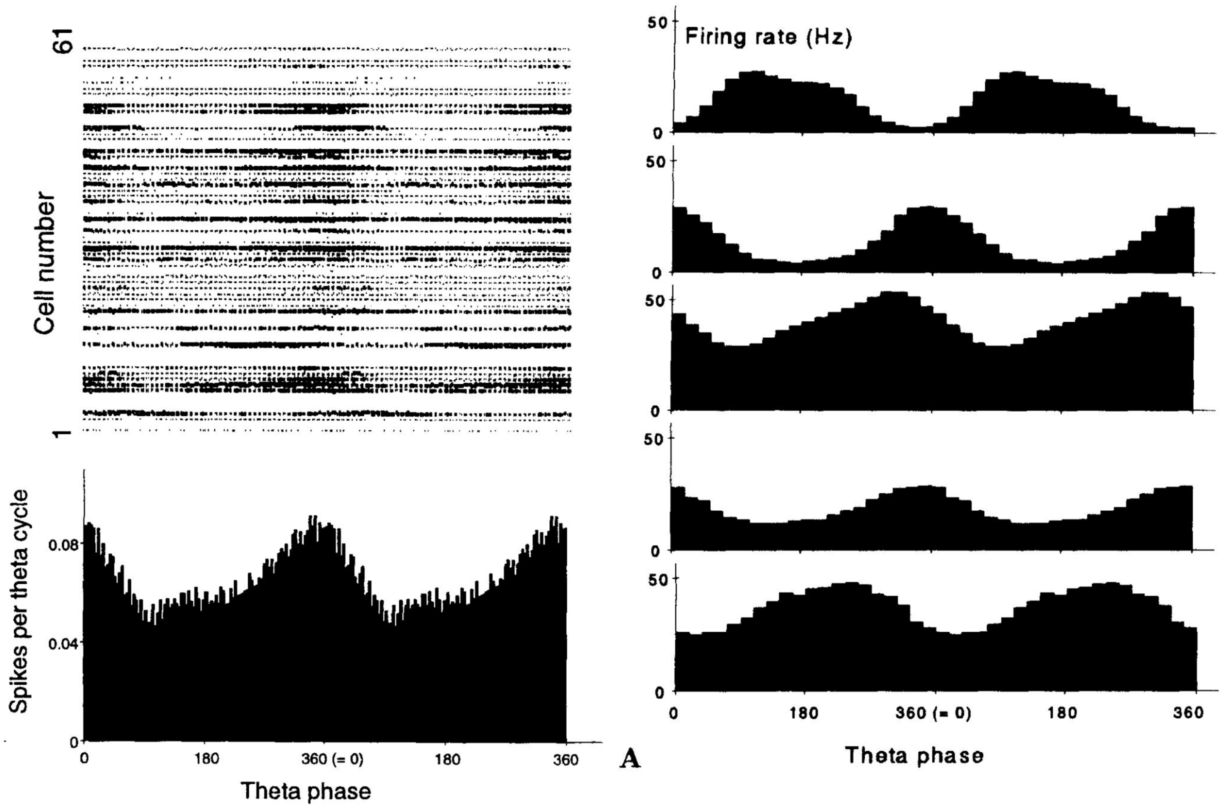
- **weighted phase lag index** (Vinck et al. 2011) - weighted average of the phase lag index using the imaginary coherency magnitudes as weights
- **debiased squared phase lag index** (Vinck et al. 2011) - the square of the phase lag index corrected for the positive bias induced by using the magnitude of the complex cross-spectrum
- **pairwise phase consistency** (Vinck et al. 2010) - The square of the phase locking value corrected for the positive bias induced by using the magnitude of the complex cross-spectrum.
- **imaginary coherence** (Nolte et al. 2004) - Return the normalized imaginary component of the cross-spectrum

Spike-LFP relationships

How do we relate LFPs (continuous) to spike times (point processes)?

Most commonly done through oscillations.

Phase tuning curves



Steps:

1. Filter LFP in narrowband with bandpass filter
2. Extract instantaneous phase via Hilbert transform / analytic signal
3. Compute occupancy normalized histogram of rate by phase

Skaggs et al. (1996)

Phase tuning curve considerations

1. Which LFP do we choose?
2. Need narrowband for phase to be meaningful
3. Need power in band for phase to be meaningful
4. Phase near start/end can be unreliable
5. Spikes within bursts aren’t independent

Circular statistics - how do we statistically quantify phase tuning?

Preferred phase - *Which phase of the LFP is the neuron most likely to spike at?*

Tuning strength (effect size) - *How concentrated are spikes around that phase?*

Phase variance - *How spread out are the spikes around that phase?*

Significance - *How unlikely is this under uniform spiking across phases?*

Key point: phase lives on a circle

0 and 2π are the same angle → averages and regressions must be **circular**

Can’t use linear statistics

Preferred phase - computing the circular mean

1. At each spike time, find the instantaneous LFP phase.

2. Convert the phase to polar coordinates (Assume each has amplitude of 1 like in PLV)

$$z_k = e^{i\phi_k} = \cos(\phi_k) + i\sin(\phi_k)$$

3. Take the mean in polar coordinates (vector averaging)

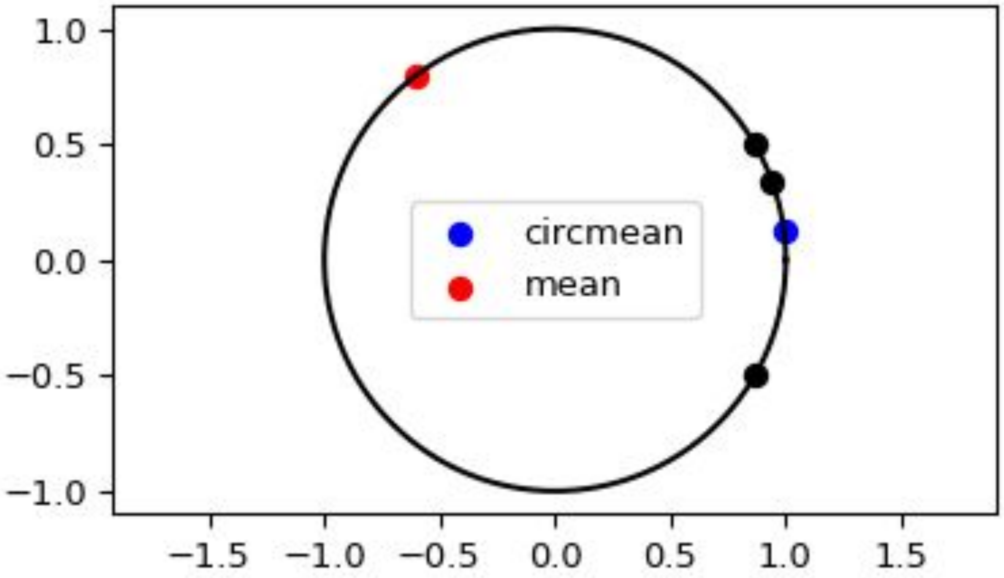
$$\bar{z} = \frac{1}{N}\sum_{k=1}^{N} z_k$$

4. The preferred phase is the angle of the mean vector (Arg)

$$\mu = \arg(\bar{z})$$

In python use: **scipy.stats.circmean** or **directional_stats**

Circular mean vs. arithmetic mean



Tuning strength (effect size) - mean resultant length

Same as preferred phase except compute the length of the mean vector

$$\bar{z} = \frac{1}{N} \sum_{k=1}^{N} z_k \qquad \bar{R} = |\bar{z}|$$

In python use: **directional_stats**

Circular variance

It turns out the variance is just 1 - the mean resultant length (what we computed last slide)

In python use: **scipy.stats.circvar**

$$\bar{R} = \left| \frac{1}{N} \sum_{k=1}^{N} e^{i\phi_k} \right| \qquad V = 1 - \bar{R}$$

Significance: Rayleigh test of circular uniformity

Question: Are spike phases clustered at a particular phase, or uniform across the cycle?

- **H0:** phases are independent and uniform on the circle $[0,2\pi)$ (no phase tuning)
- **H1:** phases are **unimodally** clustered (one preferred phase)

$$Z = n\bar{R}^2$$

Again use mean resultant length. Approx. exponentially distributed with rate 1

in python: **pycircstat.rayleigh**

Potential issues

Assumes samples are independent (spike bursts violate this assumption)

Assumes phases have unimodal phase preference (would miss biomodal with opposite phase preferences)

Non-parametric spike field coherence

So far, we have looked at phase preference **in a specific frequency band**

Instead of picking a band first and extracting phase, we treat:

- the **LFP** as a continuous signal
- the **spike train** as a point process

Then we ask:

At which frequencies does spiking consistently align with the LFP, across time?

Coherence: equations

Remember:

$$\kappa_{xy,\,j} = \frac{|< S_{xy,\,j} >|}{\sqrt{< S_{xx,\,j} >}\sqrt{< S_{yy,\,j} >}}$$

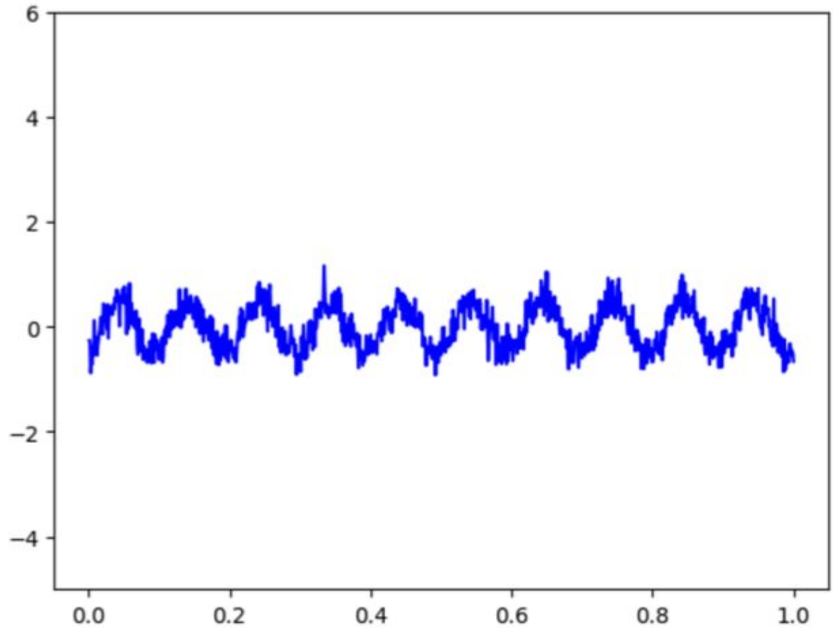
$S_{xy,j}$ = Cross-spectrum at frequency index j

$S_{xx,j}, S_{yy,j}$ = Auto-spectra at frequency index j

$< S >$ = Average of S over trials

Coherence: impact of scaling

Q. How does scaling x or y impact the coherence?



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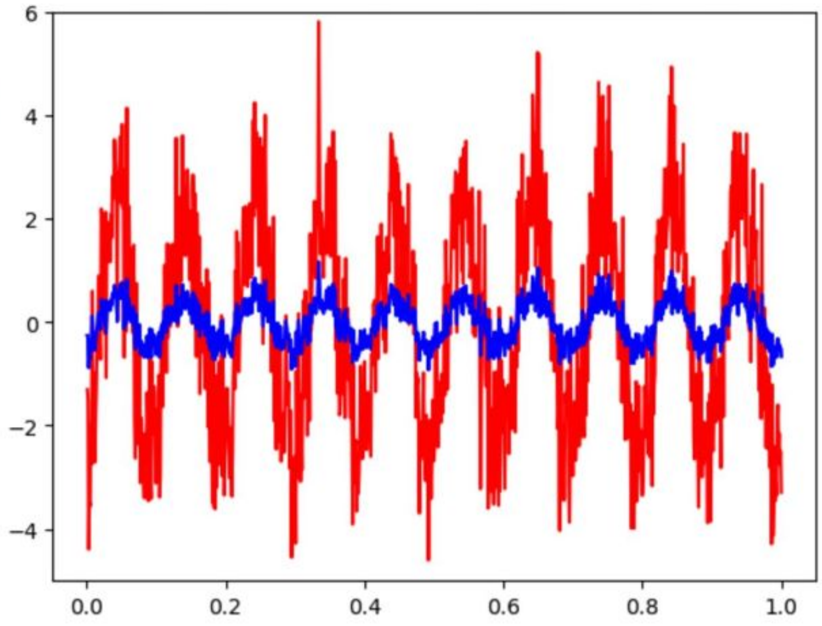
by
5



Q. Impact on coherence between x and y?

Coherence: impact of scaling

Scale: $A_{j,k} \rightarrow 5A_{j,k}$

$$\kappa_{xy,\,j} = \frac{\left|\sum_{k=1}^{K} 5A_{j,k} B_{j,k} \exp\left(i\Phi_{j,k}\right)\right|}{\sqrt{\sum_{k=1}^{K} (5A_{j,k})^2}\sqrt{\sum_{m=1}^{K} B_{j,m}^2}}$$

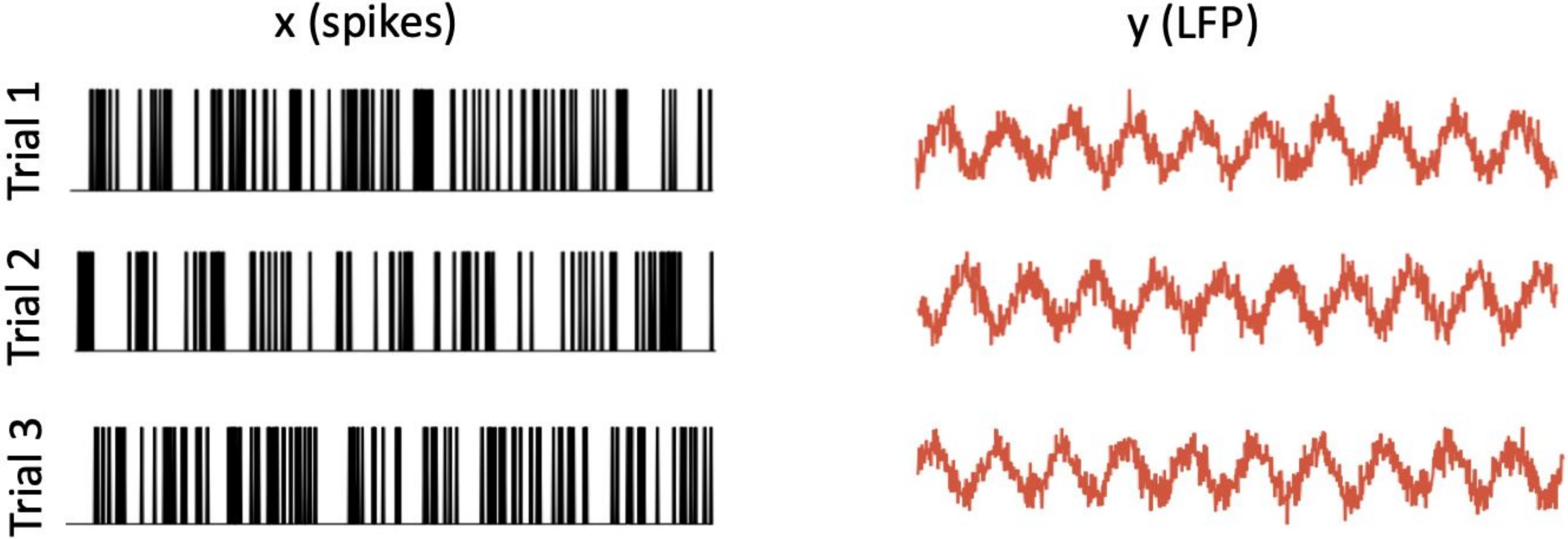
The 5's cancel ➔ no impact on coherence

Q. How does scaling x or y impact the coherence?

$\boxed{\textbf{A. } \text{It doesn't.}}$

Spike-field coherence: idea

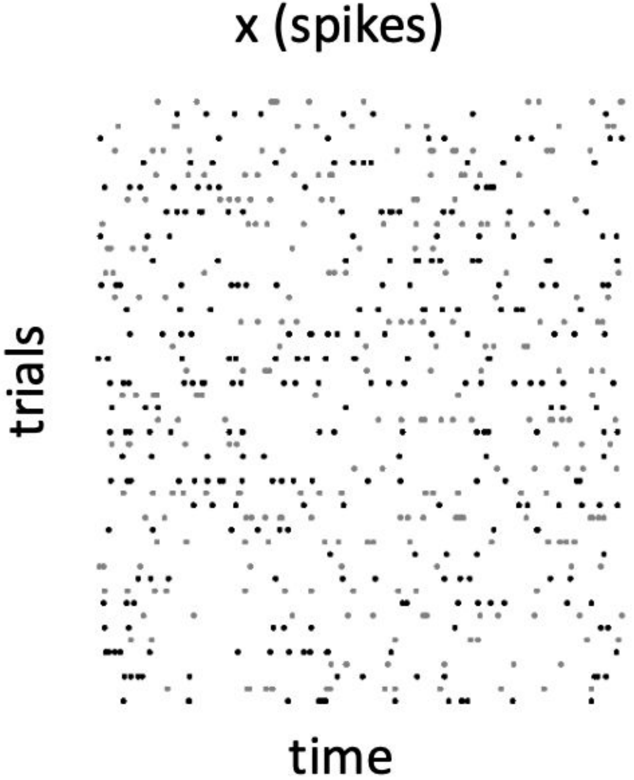
Example: Record data simultaneously from two sensors, across multiple trials

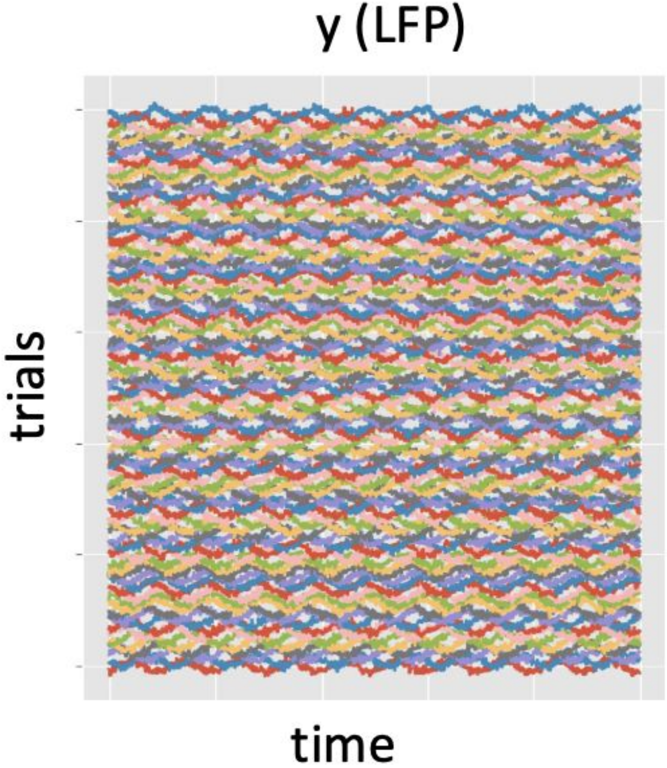


Is there a *constant phase relationship between x & y, at the same freq, across trials?*

Spike-field coherence

Consider the data:



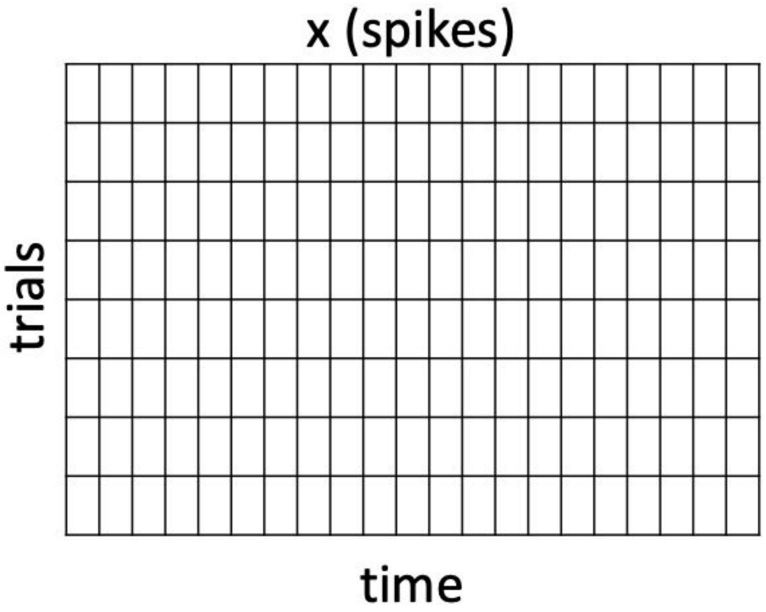


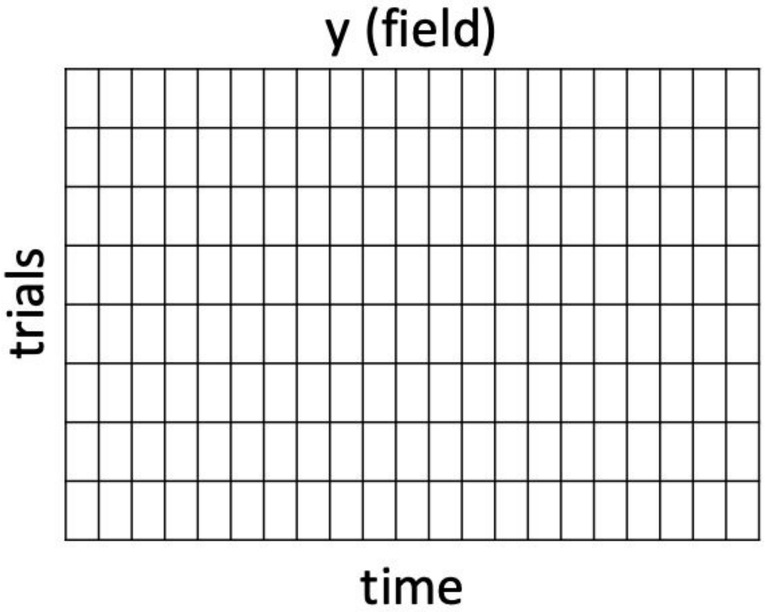
We want a measure of consistent neural spiking at a specific phase of the field ...

Spike-field coherence : idea

<u>Example</u>: Record data simultaneously from two sensors, across multiple trials

Organize the data ...





Each row is a trial, each column is a time point, organize data in matrices.

Spike-field coherence: equation

trial averaged cross spectrum

$$\kappa_{ny,\,j} = \frac{|< S_{ny,\,j} >|}{\sqrt{< S_{nn,\,j} >}\sqrt{< S_{yy,\,j} >}}$$

trial averaged spike spectrum

trial averaged field spectrum

y = field signal (e.g., EEG, MEG, LFP, ...)

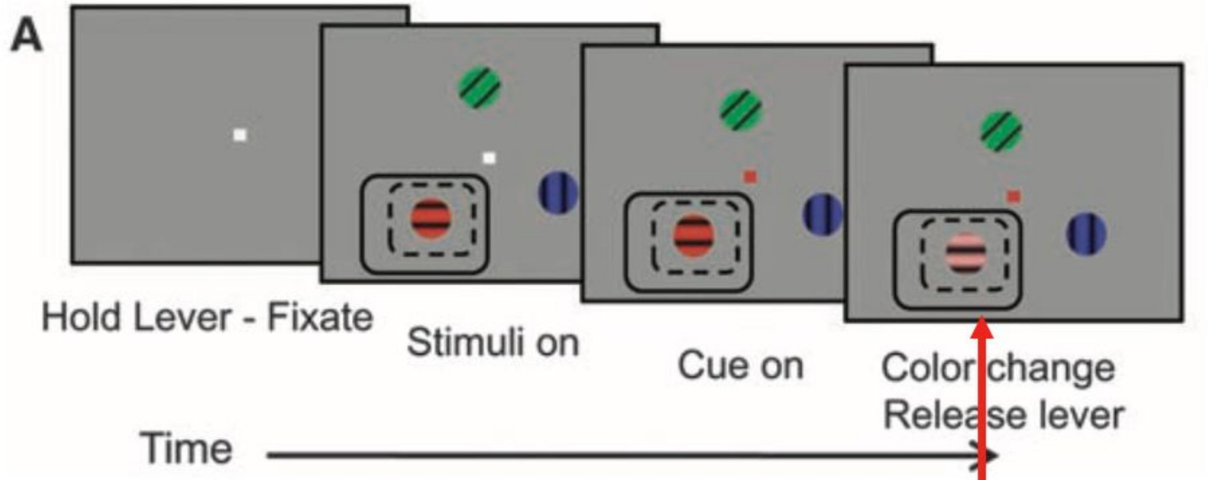
n = spike train (e.g., [0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 ...])

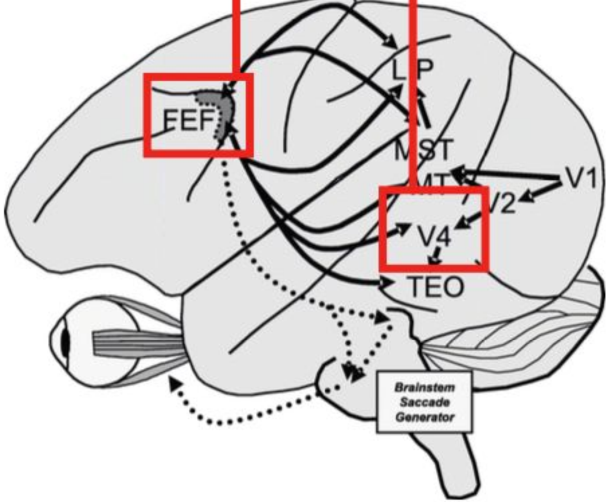
Same equations ... but new problems ...

Spike-field coherence: example

[Gregoriou et al., Science, 2009]

Record LFP and spikes



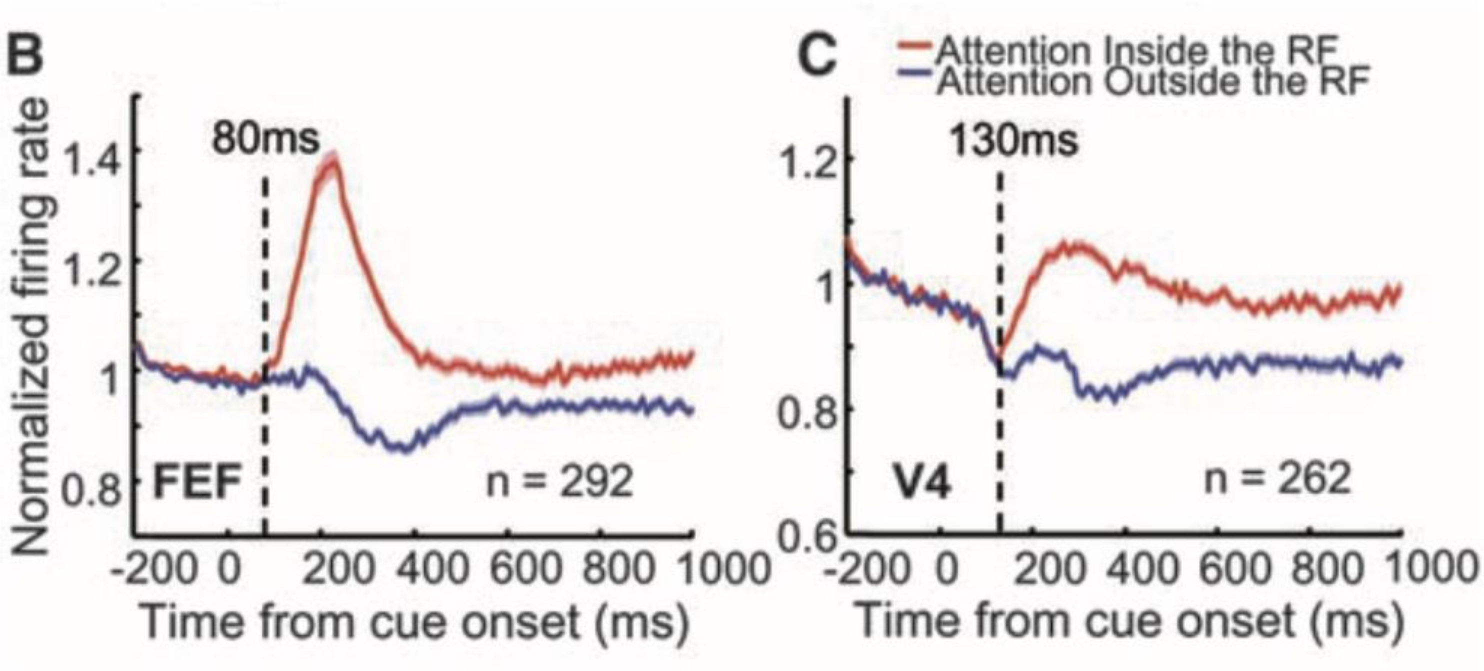


[Thompson & Bichot, Prog. Brain Res, 2005]

in the receptive field (RF) of FEF & V4

Spike-field coherence: example

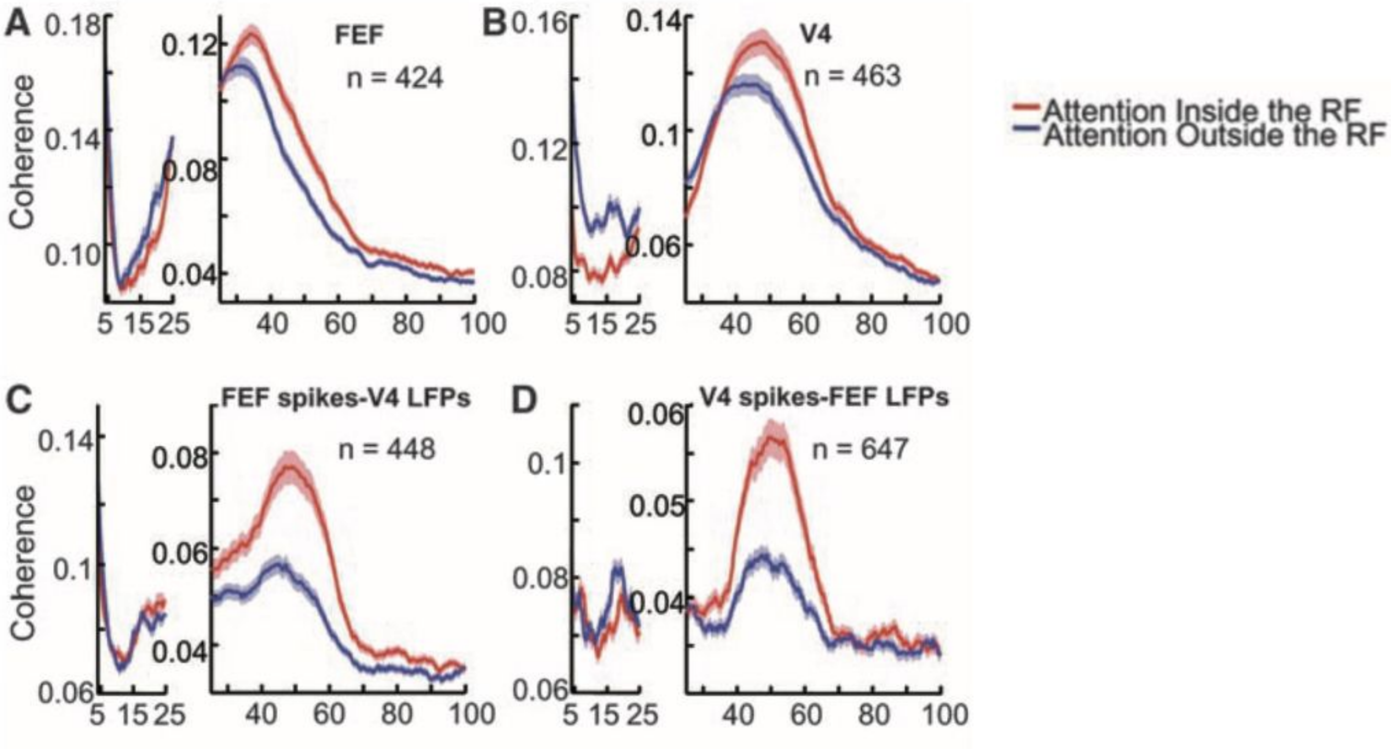
[Gregoriou et al., Science, 2009]



Firing rate <u>increases</u> when attending to stimulus in receptive field

Spike-field coherence: example

[Gregoriou et al., Science, 2009]



Spike field coherence <u>increases</u> when attending to stimulus in receptive field

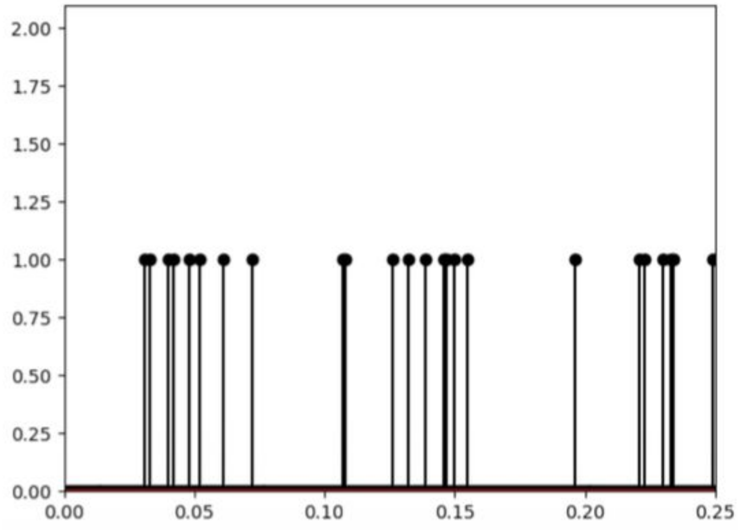
Spike-field coherence: dependence on rate

So, firing rate & spike-field coherence increase.

Q. Confounds?

Q. How does scaling the spikes (x) impact the spike-field coherence?

Q: How do you scale a spike train?



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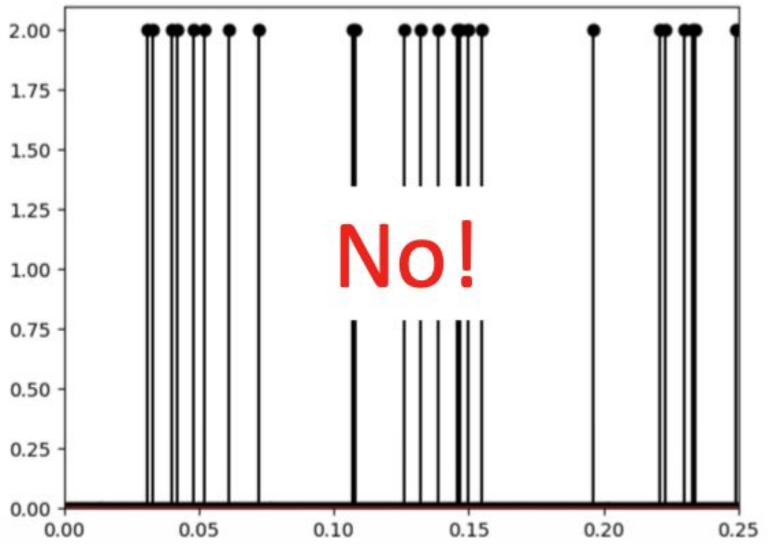
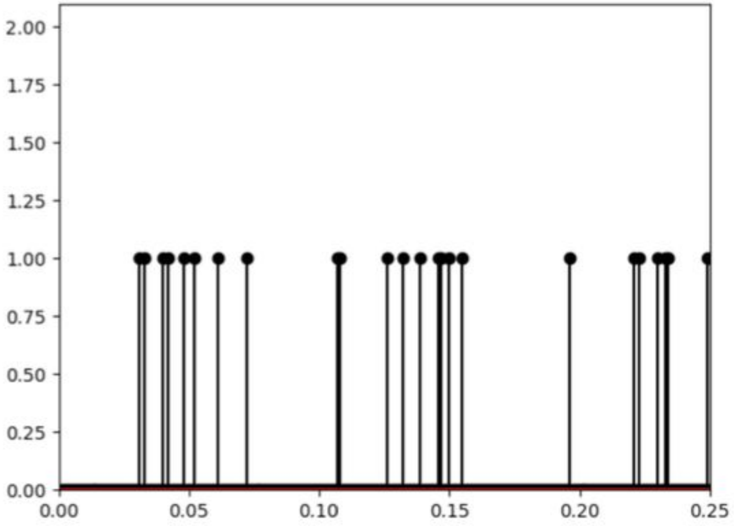


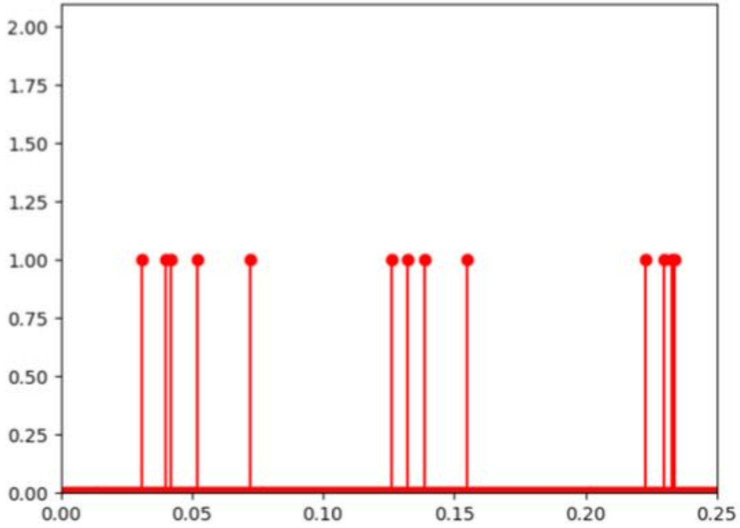
Spike-field coherence: dependence on rate

Q. How does scaling x or y impact the coherence?

Q: How do you <u>scale</u> a spike train?



thin
by
1/2

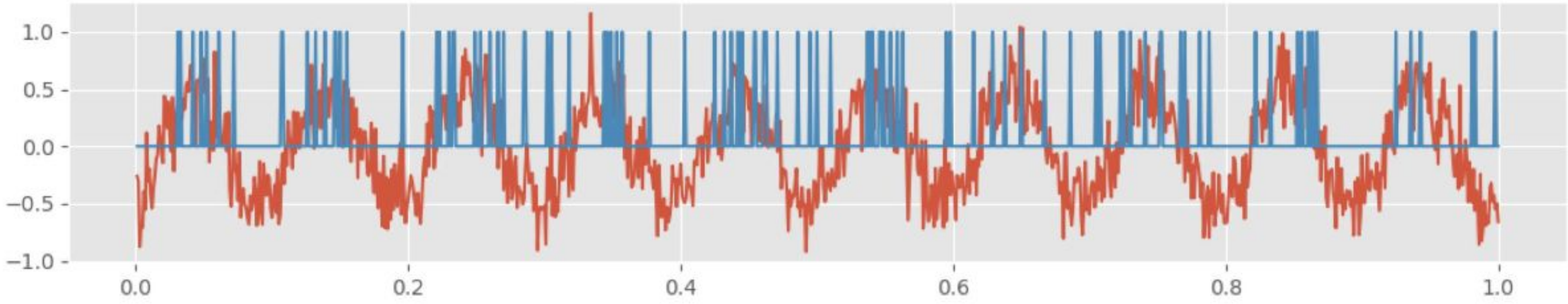


change the firing rate

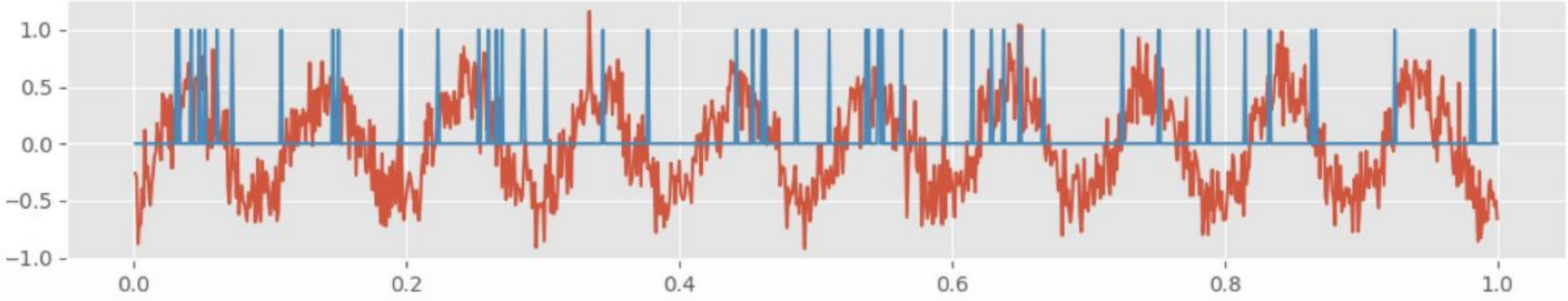
Spike-field coherence: dependence on rate

Q: Does the spike-field coherence depend on the firing rate of the neuron?

Original spike & field



Scale the spiking (remove 50% of spikes, chosen at random, “thinning”)



Spike-field coherence: dependence on rate

Q: Does the spike-field coherence depend on the firing rate of the neuron?

Observations:

greater thinning → fewer spikes → lower coherence

as the rate tends to 0, so does the spike-field coherence

The spike-field coherence reflects
(1) the relationship between spiking activity and the phase of field, and
(2) the mean firing rate.

Question: How can you compare the spike-field coherence of different neurons if they have different rates?

Harmonic Poisson regression

We want to measure spike-field coherence of a neuron while accounting for the firing rate of that neuron.

Remember, when we were doing Poisson regression, we could very easily account for the mean firing rate

How do we compute dependence on the phase of a continuous signal?

Recall: sine, cosine and instantaneous phase

We said before to represent phase we need both sine and cosine.

We can take the instantaneous phase of a bandpassed filtered signal.

How can we write this in a regression?

We can have coefficients for sine and cosine

$$\lambda(t) \;=\; \exp\big(\eta(t)\big)$$

$$\eta(t) \;=\; \beta_0 \;+\; \beta_1 \cos(\phi(t)) \;+\; \beta_2 \sin(\phi(t))$$

We can rewrite as a single cosine with a phase offset

$$\beta_1 \cos\phi + \beta_2 \sin\phi \;=\; \kappa \cos(\phi - \phi_0)$$

$$\kappa \;=\; \sqrt{\beta_1^2 + \beta_2^2}$$

$$\phi_0 \;=\; \mathrm{atan2}(\beta_2, \beta_1)$$

$$\lambda(t) \;=\; \exp(\beta_0)\, \exp\big(\kappa \cos(\phi(t) - \phi_0)\big)$$

We can interpret the combination of coefficients as modulation and phase preference

kappa = modulation

phi = preferred phase

$$\kappa = \sqrt{\beta_1^2 + \beta_2^2}$$

$$\phi_0 = \operatorname{atan2}(\beta_2, \beta_1)$$

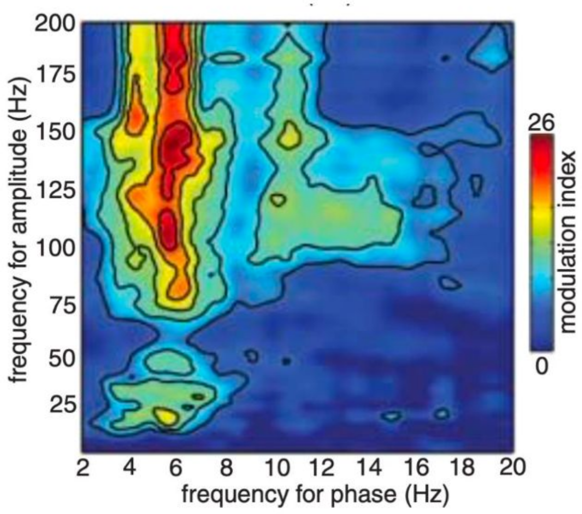
$$\lambda(t) = \exp(\beta_0)\,\exp\big(\kappa\cos(\phi(t) - \phi_0)\big)$$

Cross-frequency coupling

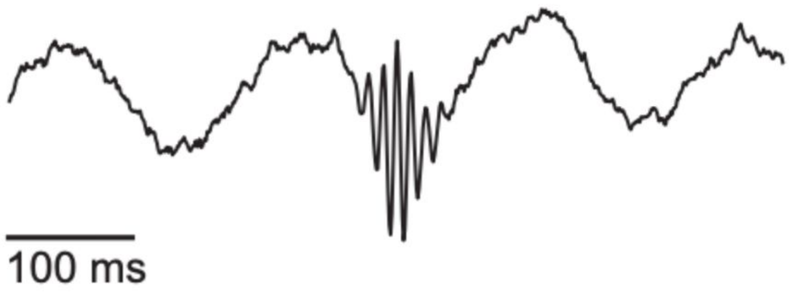
Coherence = constant linear phase relationship between two signals across trials at the same frequency

CFC = coupling between different frequencies (can be within a single signal or across signals)

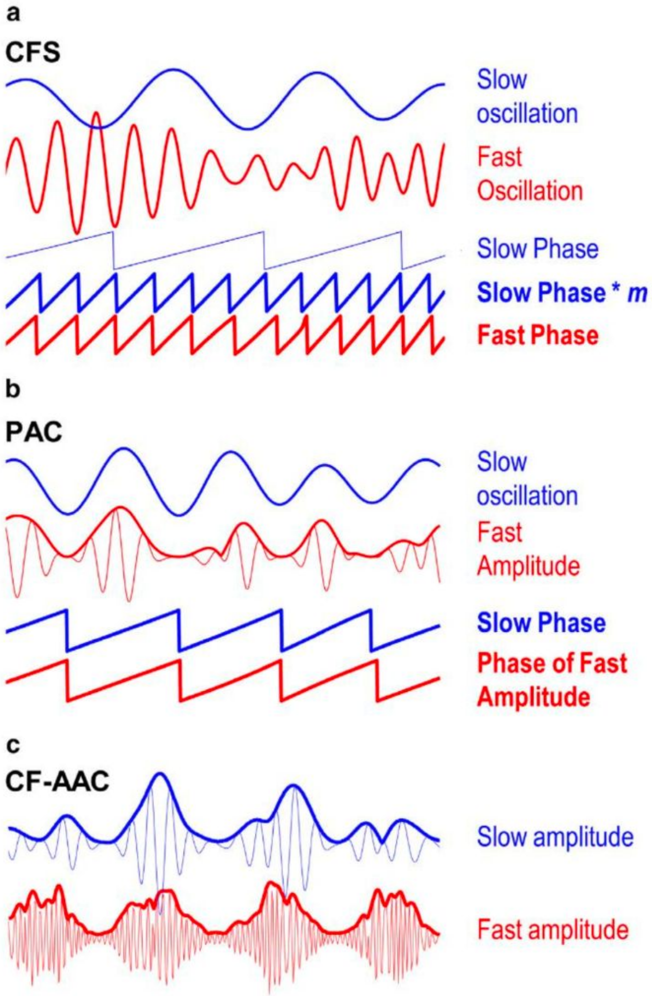
Examples



[Canolty et. al., Science, 2006]

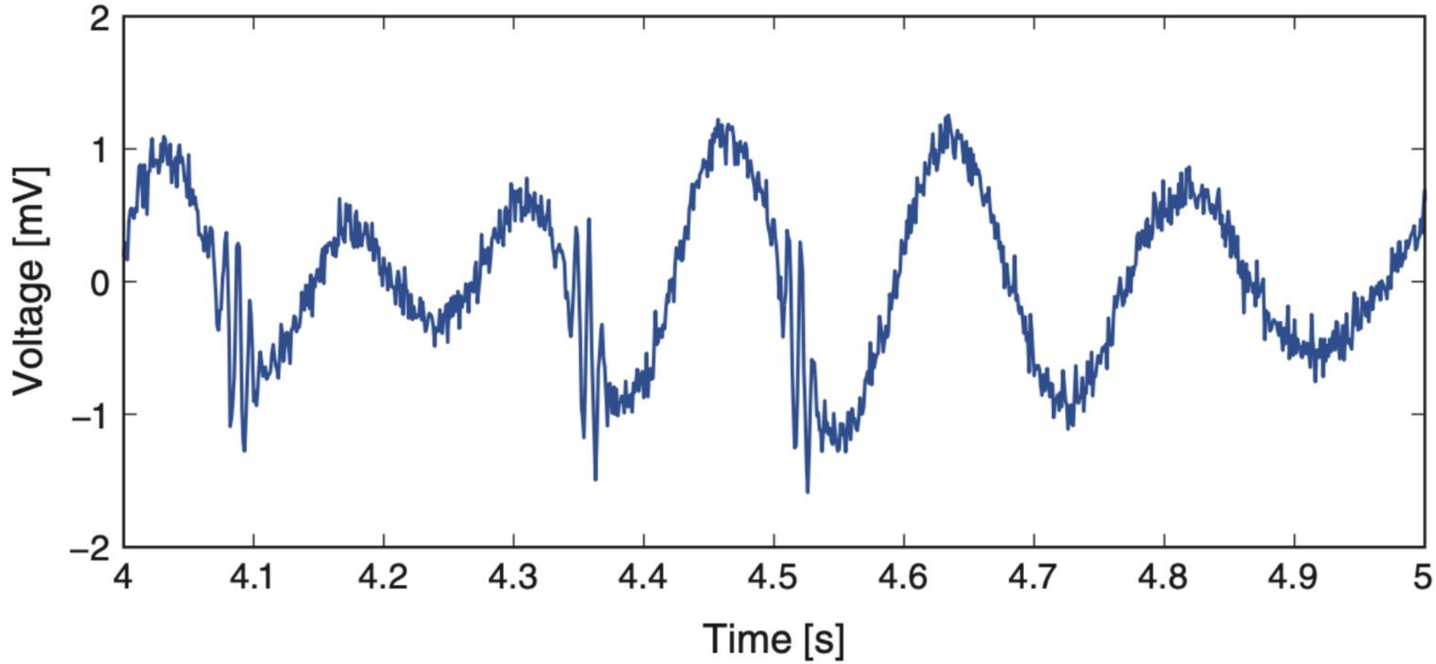


[Tort et. al., PNAS, 2008]



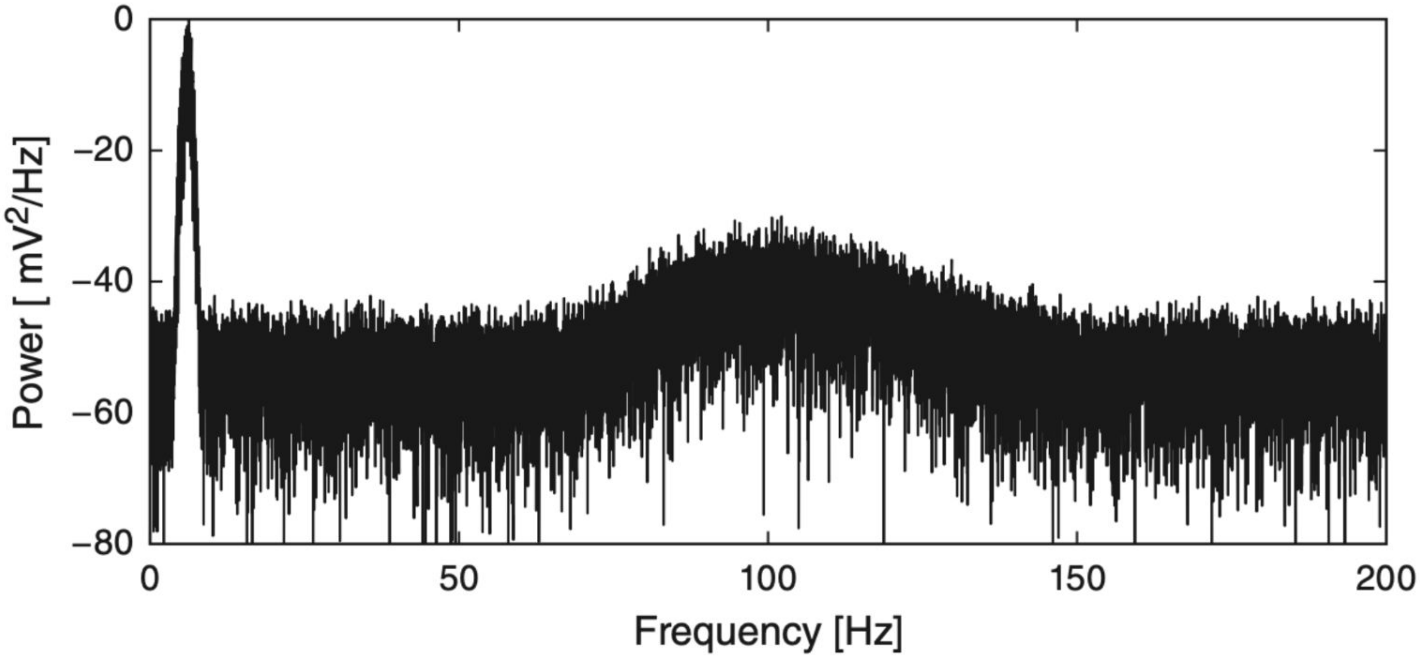
[Palva & Palva, EJN, 2018]

Data



Q. How to make sense of these data?

Spectrum



Q. What do you see?

CFC in three steps

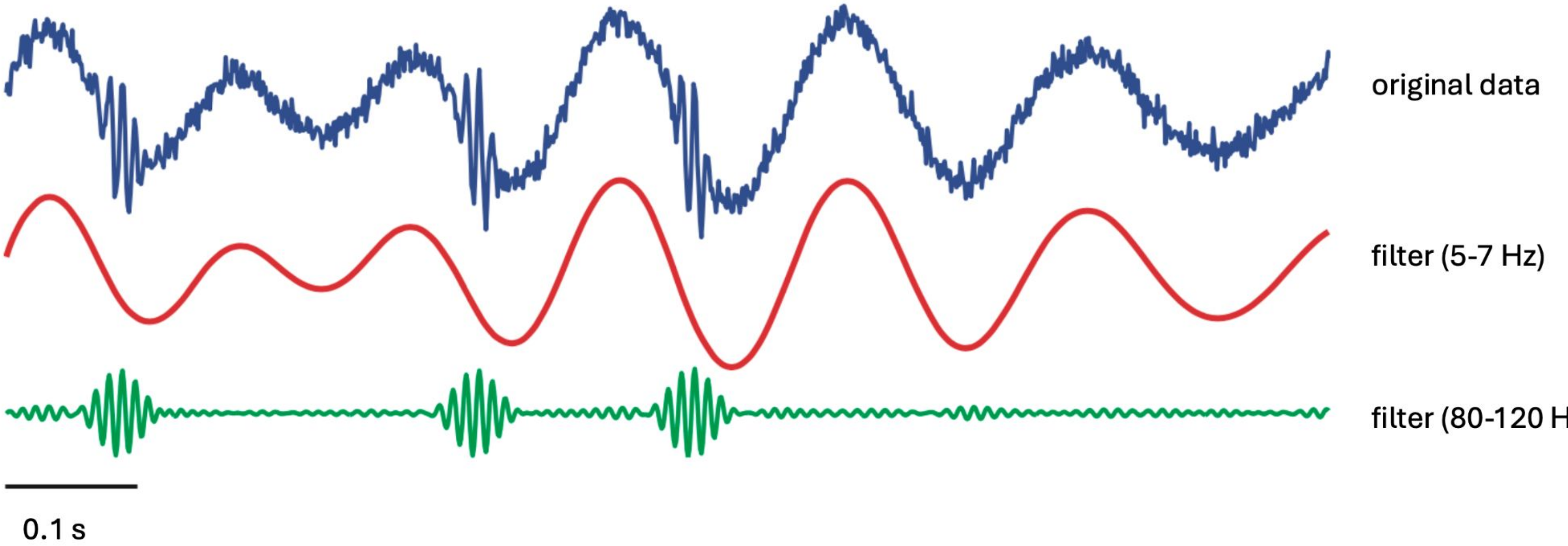
CFC analysis steps

1. Filter the data into high- and low-frequency bands.
2. Extract the amplitude and phase from the filtered signals.
3. Determine if the phase and amplitude are related.

Let's perform each step ...

CFC – Step 1

Filter the Data into High- and Low-Frequency Bands

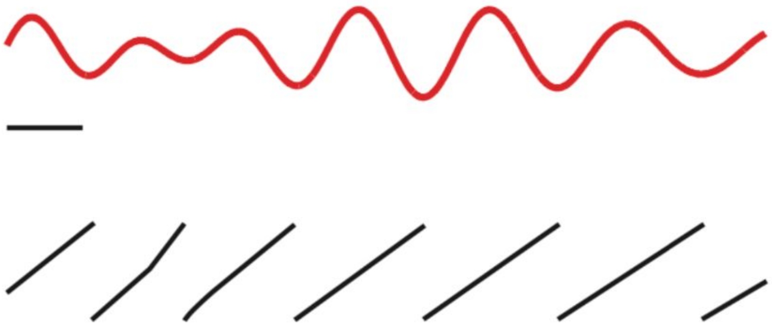


Q. Why did we filter in these bands?

CFC – Step 2

Extract the Amplitude and Phase from Filtered Signals

filter (5-7 Hz)



phase (of low frequency band)

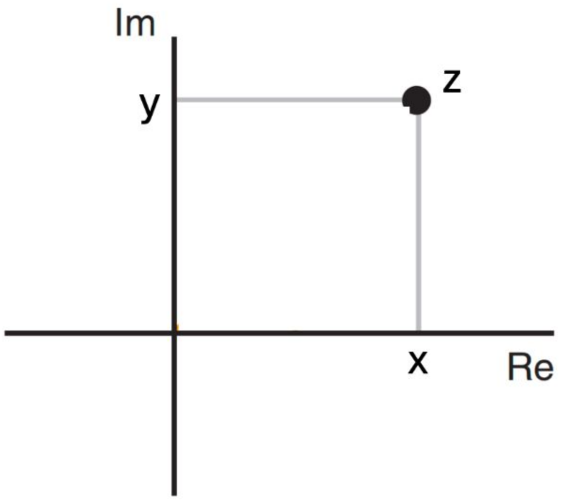
filter (80-120 Hz)

amplitude envelope (of high frequency band

Q. How?

Hilbert transform

<u>Analytic signal</u> $z = x + iy$ A point in the complex plane



$$z(t) = A(t)\, e^{i\,\phi(t)}$$

amplitude phase

Get the <u>**amplitude**</u> and <u>**phase**</u> from the analytic signal

<u>**Ex.**</u>

$z_0(t) = 2e^{i\omega_0 t}$ $A(t) = 2$ $\phi(t) = \omega_0\, t$

CFC in three steps

CFC analysis steps

1. Filter the data into high- and low-frequency bands.
2. Extract the amplitude and phase from the filtered signals.
3. Determine if the phase and amplitude are related.

CFC – Step 3

Determine if the Phase and Amplitude are Related

Define the two-column vector

$$\begin{pmatrix} \phi(1) & A(1) \\ \phi(2) & A(2) \\ \phi(3) & A(3) \\ \vdots & \vdots \end{pmatrix}$$

<u>phase</u> of low frequency band activity

<u>amplitude</u> of high frequency band activity

Make a histogram

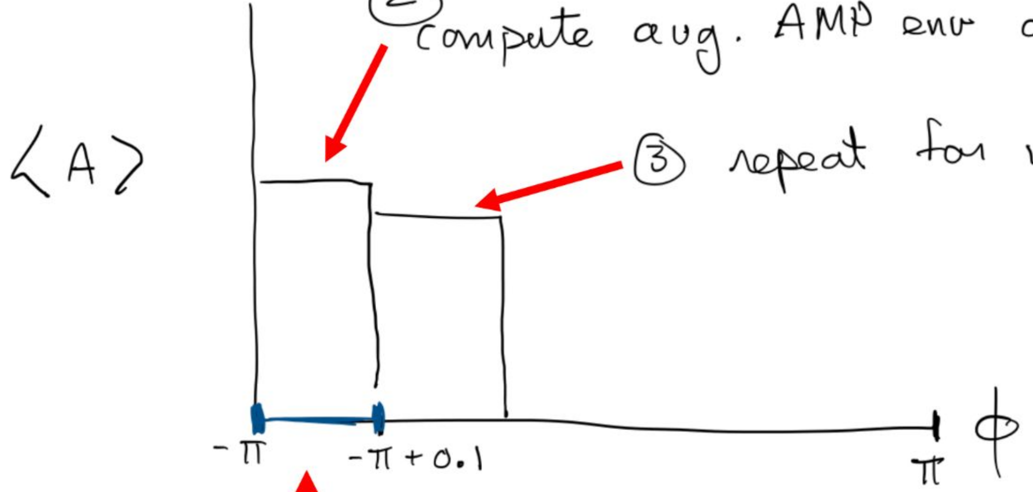
CFC – Step 3

Determine if the Phase and Amplitude are Related

Divide the phase into bins of size 0.1

(2) compute avg. AMP env at the indices in (1)

(3) repeat for next phase bin

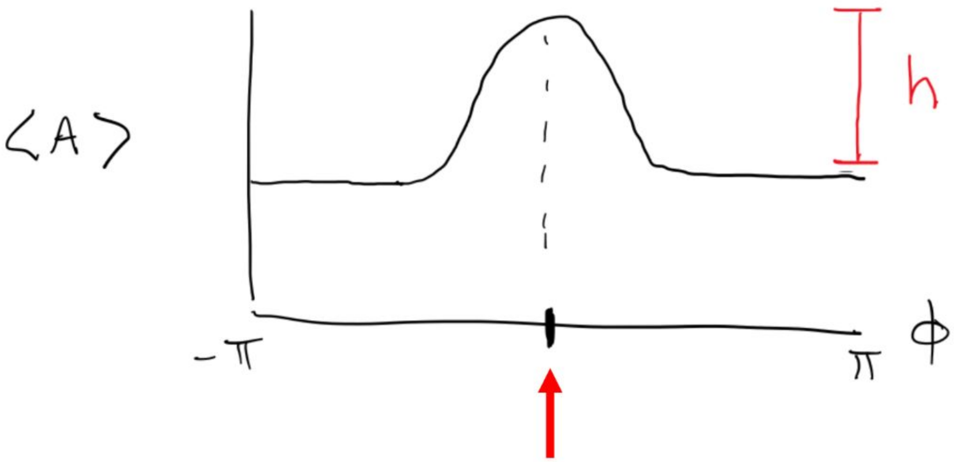


(1) Find all φ in this range [−π, −π + 0.1]
& get indices {1, 2, 3, 10, 11, 12, 41, 42, 43, ...}

CFC – Step 3

Determine if the Phase and Amplitude are Related

If phase modulate amplitude



summarize extent of modulation

Q. What does no phase-amplitude coupling look like in the plot?

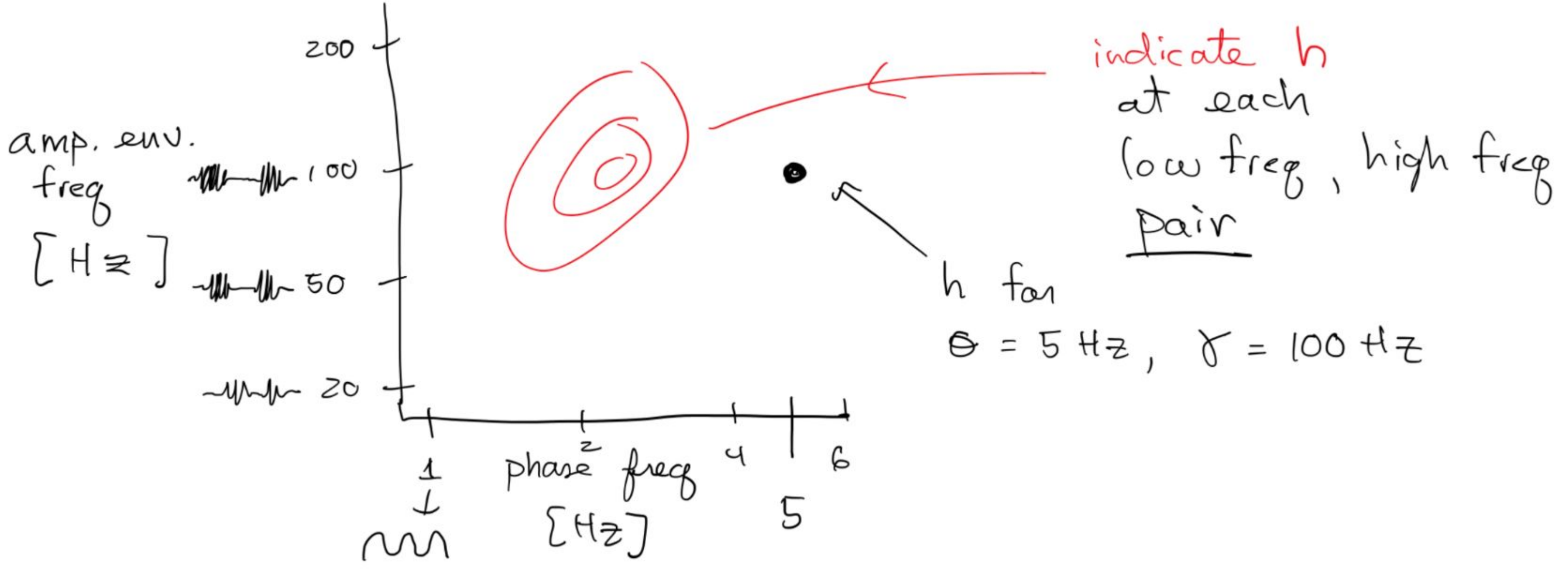
At this phase, amplitude envelope is big

➔ phase modulates amplitude

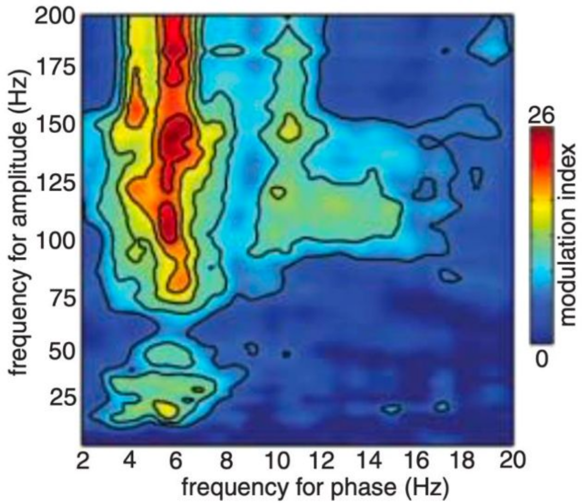
CFC – Step 4

(optional): Repeat for other frequencies.

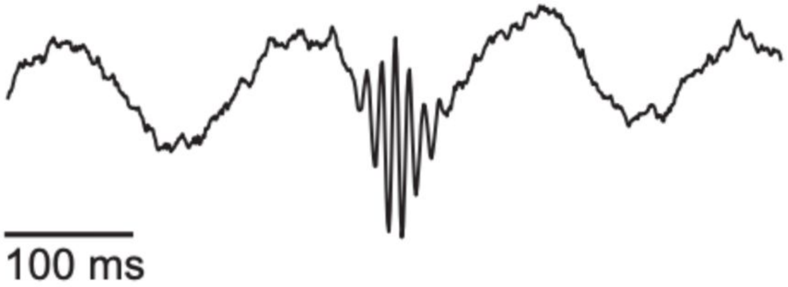
Summarize in a <u>comodulogram</u>



Examples



[Canolty et. al., Science, 2006]



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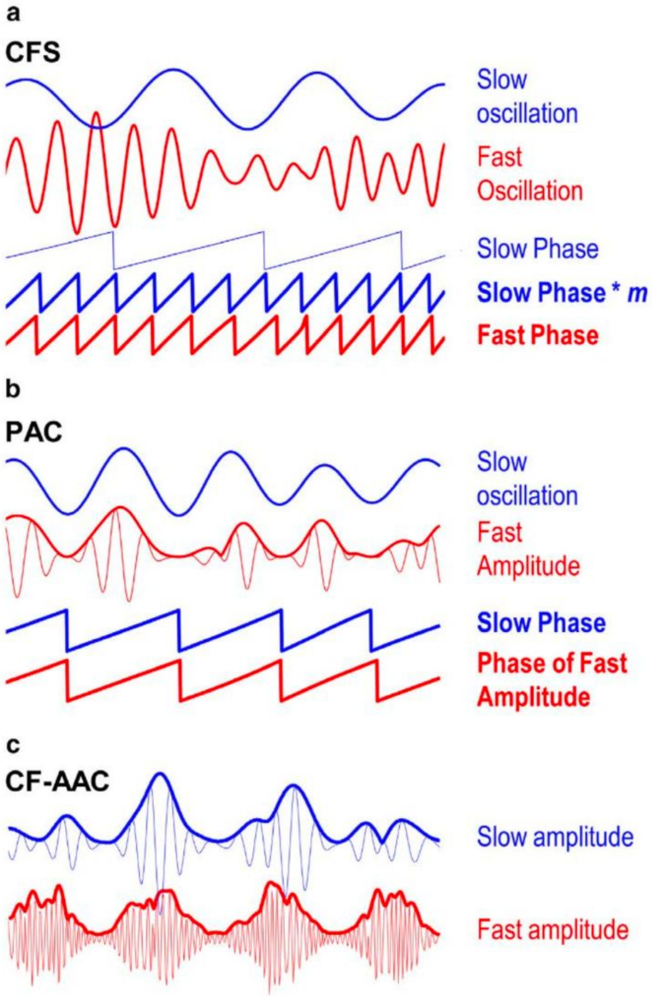

[Palva & Palva, EJN, 2018]

Summary: Analyzing LFP

- **Sampling:** continuous LFP sampled discretely → Nyquist, aliasing
- **Spectral representation:** DTFT/DFT decompose signals into complex sinusoids (frequency axis vs frequency resolution)
- **Time–frequency:** windows/tapers control leakage & variance; multitaper gives stable PSD/spectrograms
- **Filtering:** bandpass isolates bands; design tradeoffs (pass/stop specs & transition width ↔ order ↔ ringing/edge artifacts)
- **Analytic signal:** after narrowband filtering, Hilbert gives instantaneous phase and amplitude/power
- **Unifying constraint:** time-frequency tradeoff shows up in windows, tapers, filters, and spectrograms

Summary: LFP coupling, phase, and spikes

- **Field–field coupling:** coherence (frequency-specific linear coupling)
- **Phase-based coupling:** PLV and PLI (PLI downweights zero-lag coupling)
- **Spike–LFP phase locking (circular statistics):** preferred phase, tuning strength/variance; Rayleigh test
- **Spike–field coupling in frequency domain:** spike–field coherence (depends on firing rate/spike count)
- **Parametric spike–field coupling:** harmonic Poisson regression (rate as a function of phase; add covariates)
- **Cross-frequency coupling:** PAC/CFC