A tutorial on spike-field methods made for Vanderbilt neuroscientists

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Learning goals

- 1) What are the main kinds of spike-field analyses?
- 2) What are the strengths and limitations of different methods?
- 3) How do we practically implement these analyses?

Recommended background literature

Review Article | Published: 25 June 2018

Investigating large-scale brain dynamics using field potential recordings: analysis and interpretation

Bijan Pesaran, Martin Vinck, Gaute T. Einevoll, Anton Sirota, Pascal Fries, Markus Siegel, Wilson Truccolo, Charles E. Schroeder & Ramesh Srinivasan

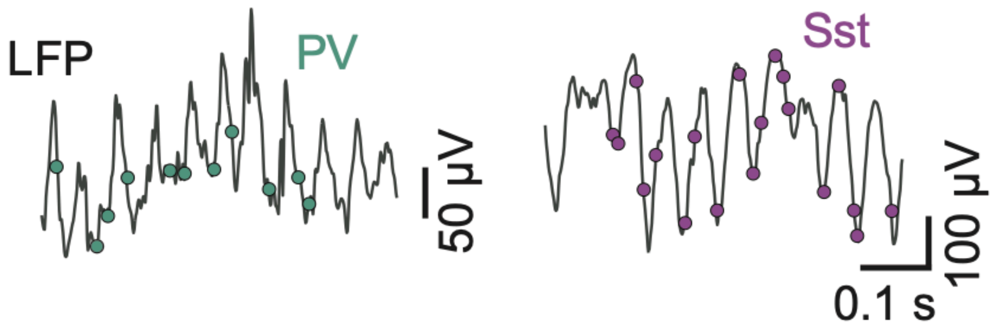
Nature Neuroscience **21**, 903–919 (2018) | Cite this article

17k Accesses | **180** Citations | **58** Altmetric | Metrics

Motivation

- Widely used method to study mechanisms and function of neural synchronization
- Highly sensitive method to quantify rhythmicity of different cell types to network activity
- LFP allows to immediately assign a “phase” for every spike relative to network activity
    - LFP picks up activity of about 10^5 neurons in vicinity electrode

Example Mouse V1

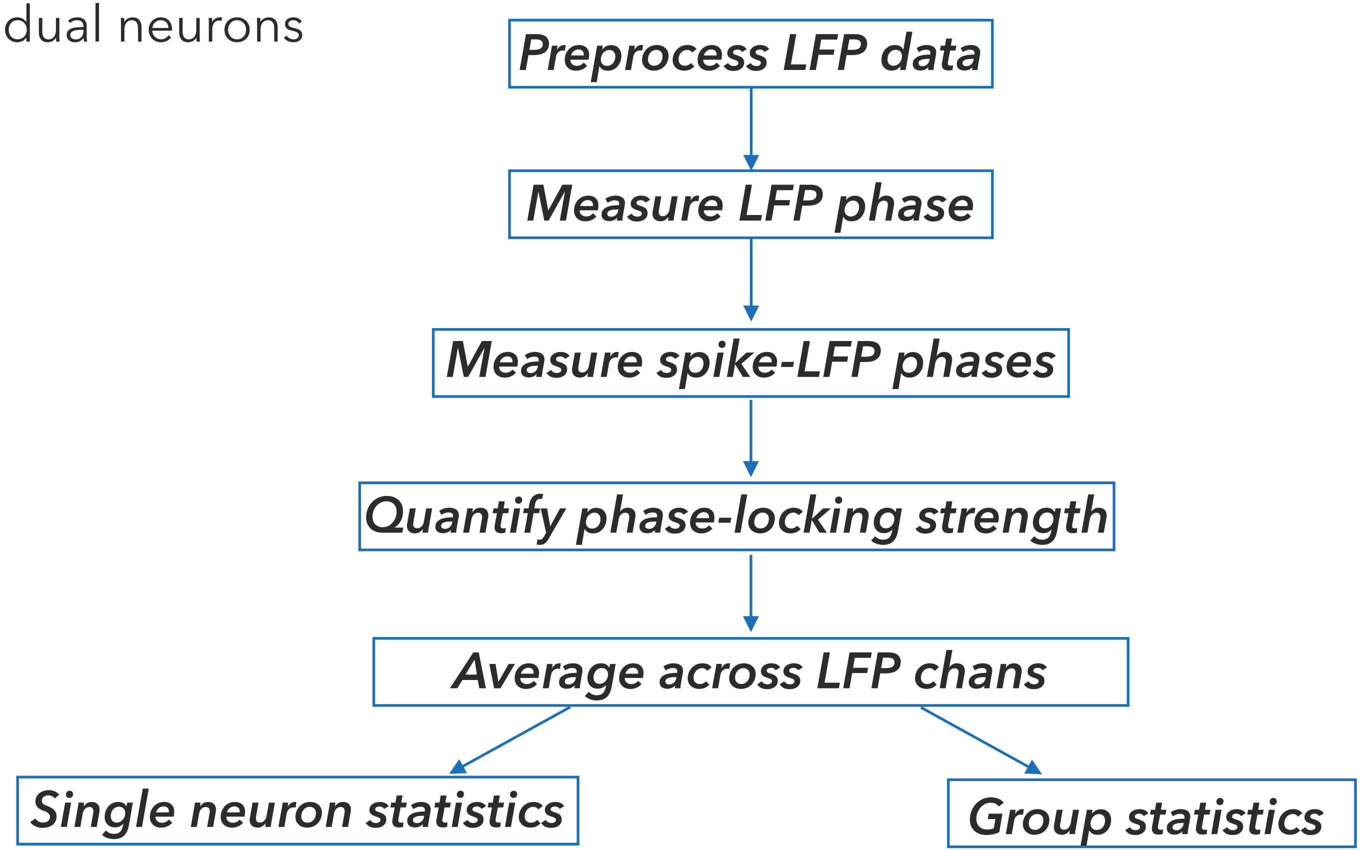


Onorato, …, Vinck, 2023

Live Drawing

Pipeline

- 1) Measure phase
- 2) Quantify phase locking
- 3) Statistics on phase locking for individual neurons
- 4) Statistics for groups of neurons



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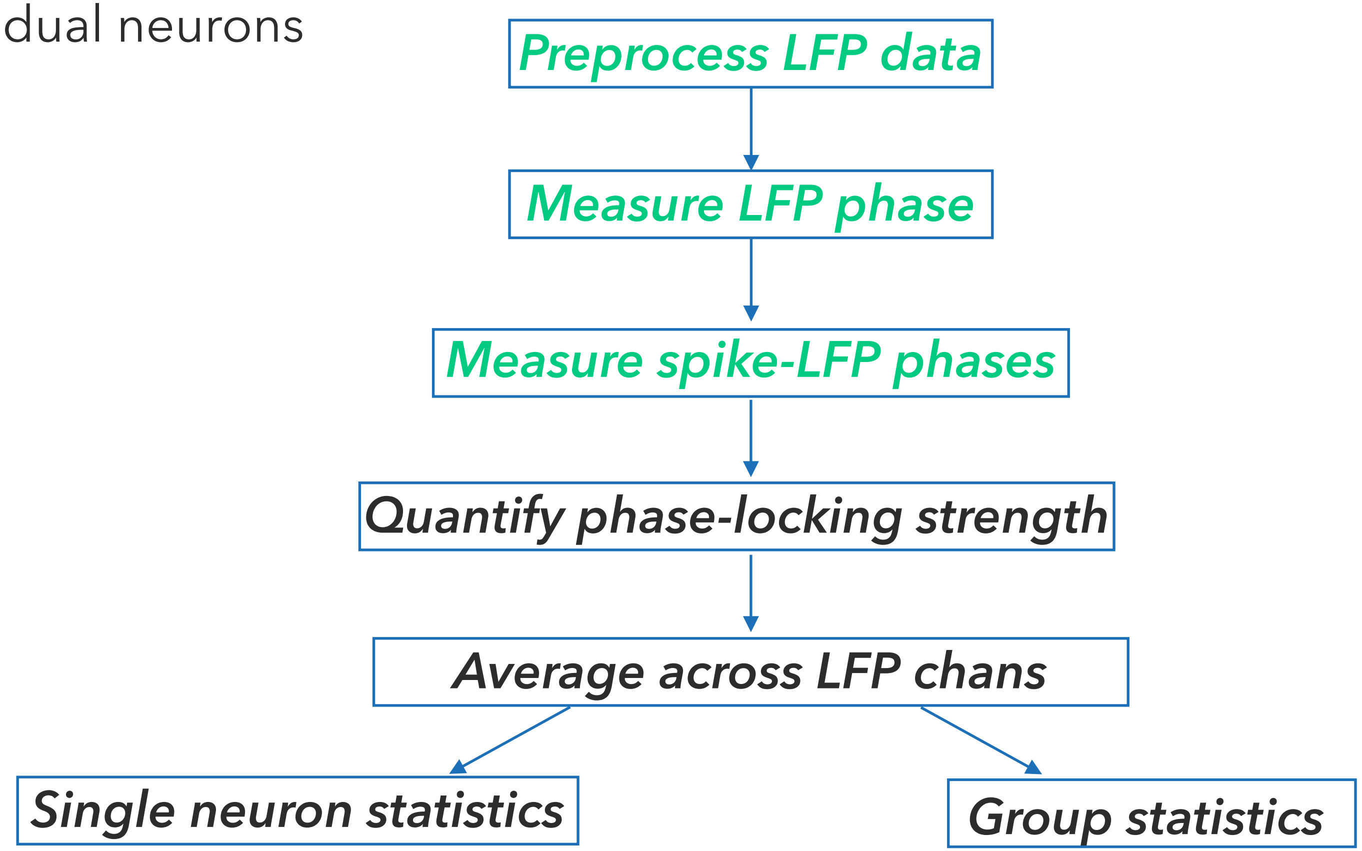
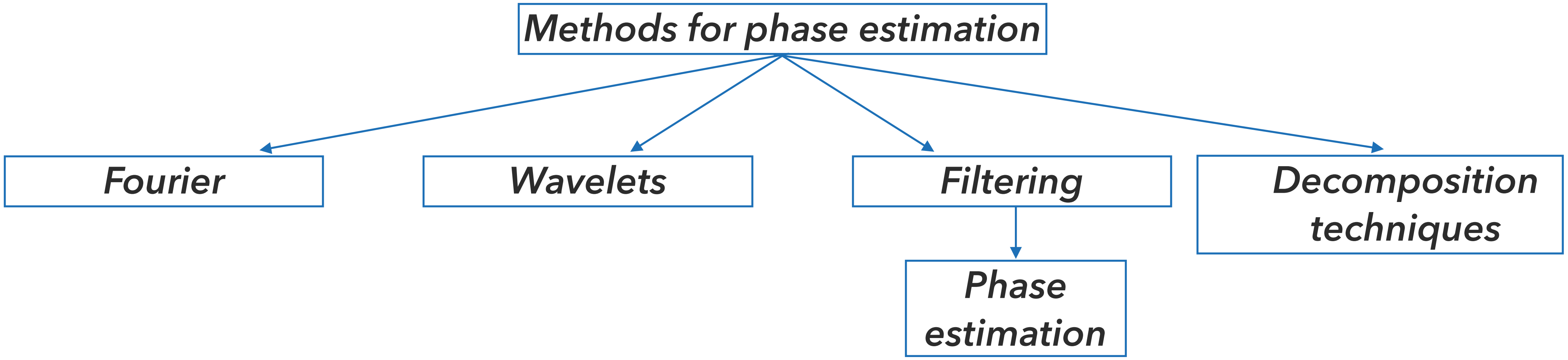


Methods to estimate phase

- 1) **Short-term Fourier** with fixed window centered on each spike - slow for many neurons
- 2) **Wavelets** (fixed numbers of cycles per frequency) (see Vinck et al., 2013, Neuron)
- 3) **Filtering** -> Hilbert or other forms of phase estimation (see Onorato, …, Vinck, 2020, Neuron)
- 4) **Other decomposition techniques,** e.g. ICA, empirical mode decomposition

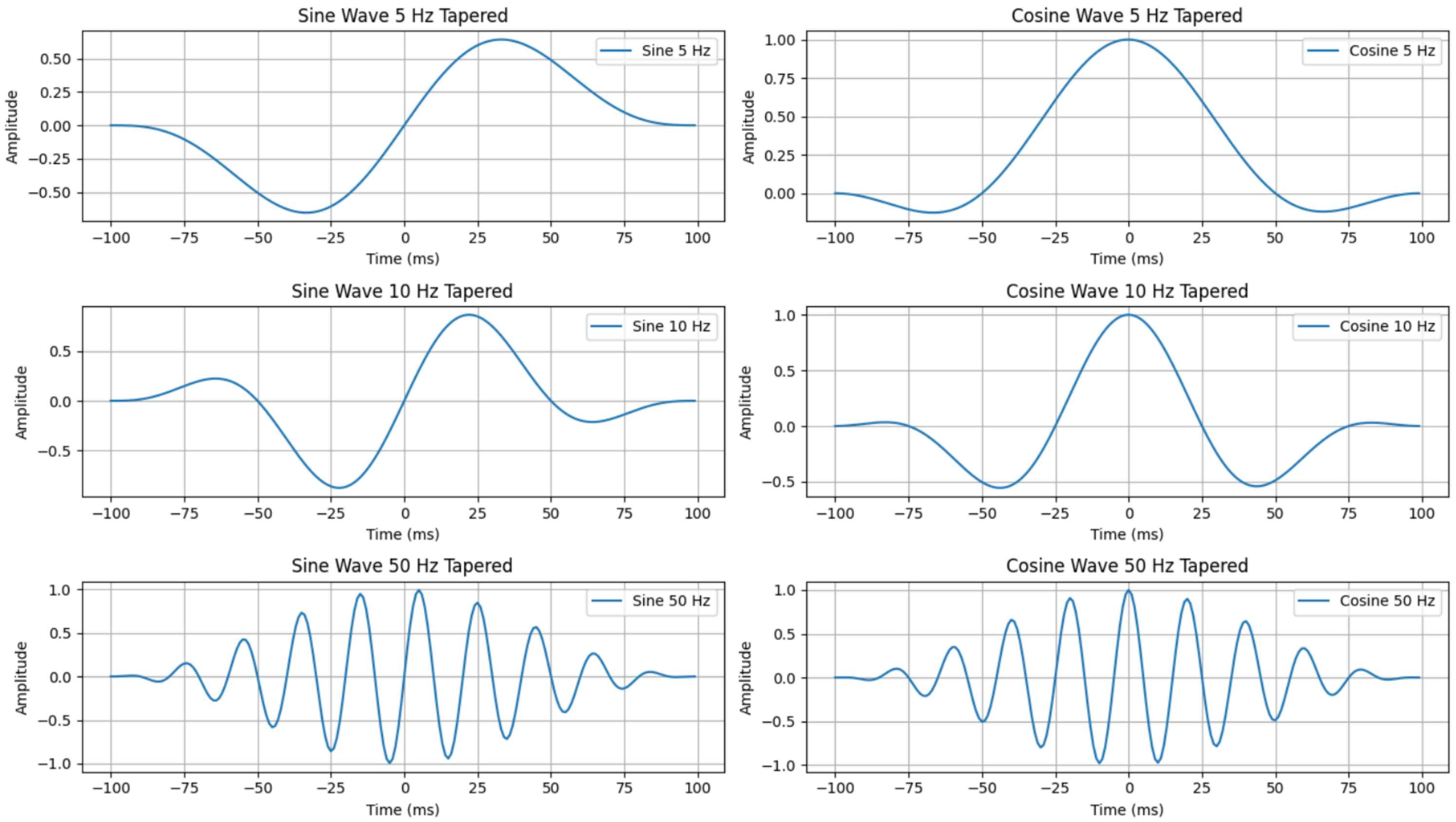


Live Drawing

Live Drawing

Spiketriggeredspectrum with fft

- **Short term Fourier** of LFP centered around each individual spike
  - **Speed trade-off:** Slow if many units and spikes, fast if few and sparse neurons
- **Disadvantage**: The chosen window length is likely only optimal for a narrow frequency range

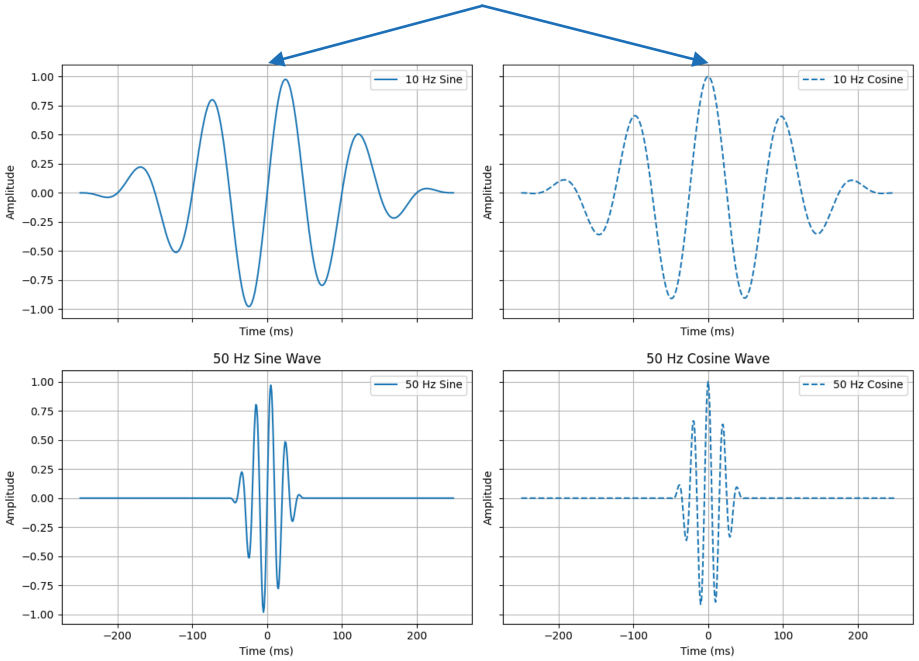


Live Drawing

Spiketriggeredspectrum with “convol”

- **Wavelet decomposition** with fixed number of cycles per frequency - computed for all t
  - Fast method when data has many units and spikes
- **How to choose number of cycles?**
  - Using too many cycles can underestimate phase locking if oscillation is not narrow-band
  - Using too few cycles brings risk of leakage

Centered on each spike



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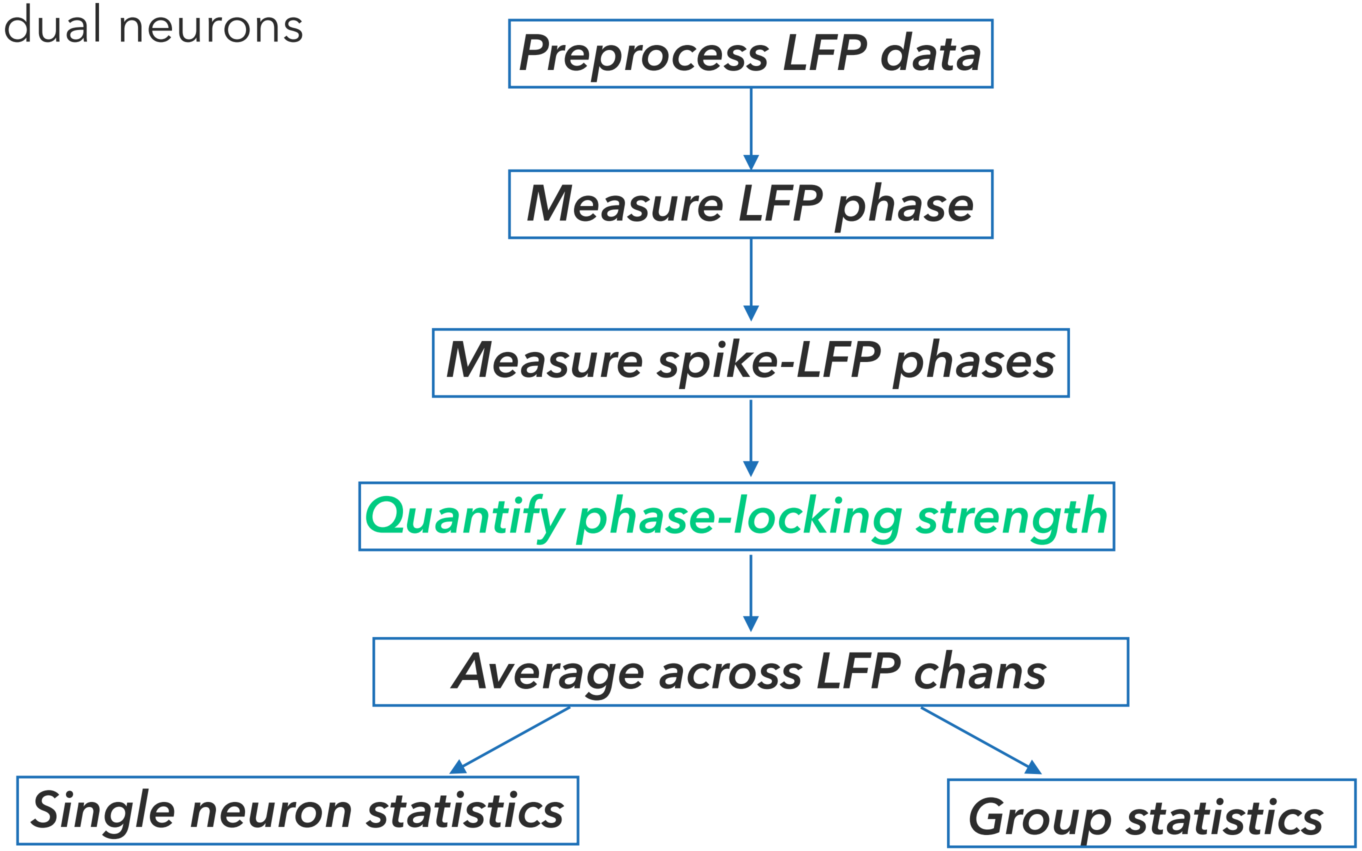
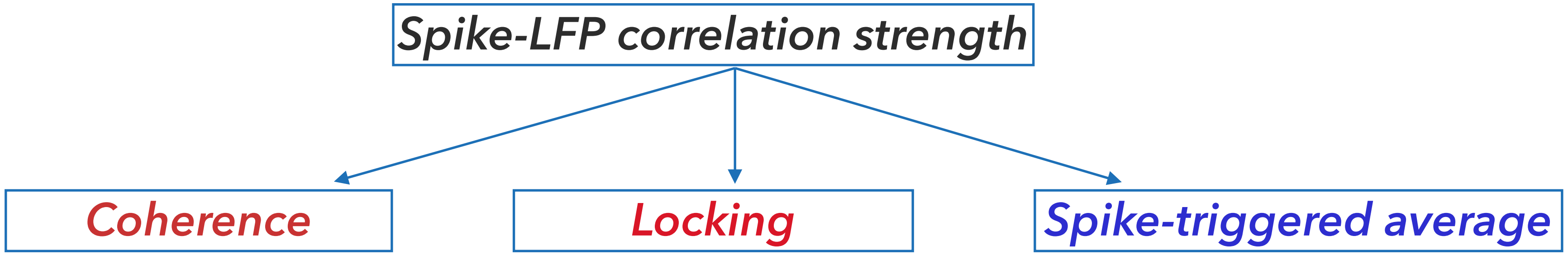


Methods to assess spike-field locking

- **Frequency resolved**
  - Spike-field locking
    - Quantify consistency of locking based on set of spike-field phases
  - Spike-field coherence
    - Linear correlation between spike trains and LFPs in the frequency domain
- **Time resolved**
  - Spike-triggered average



Spike-triggered average (STA)

- **STA:**
  - Take each spike and compute the average LFP around the spike.

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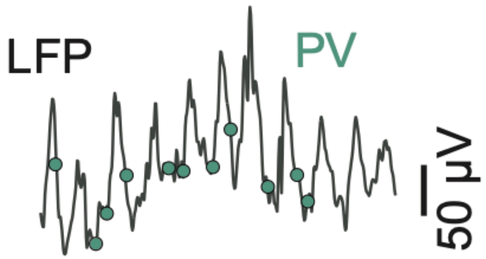
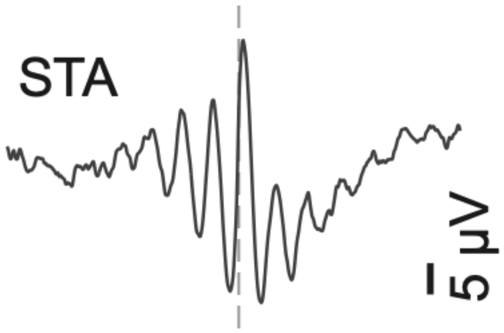
- **STA:**
  - Take each spike and compute the average LFP around the spike.
- **Properties:**
  - STA is not normalized for power - dominated by frequencies with more LFP power
  - The STA gives an indication of rhythmicity (side-lobes)
    - Rhythmic side lobes are a property of the LFP signal, not of the spike train



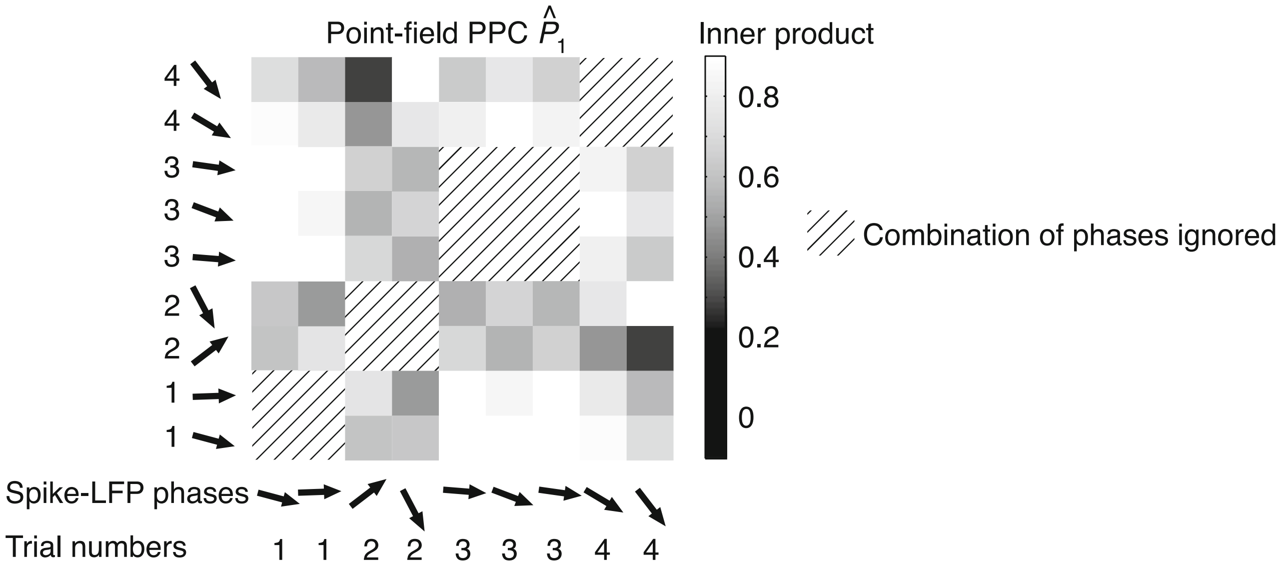


Pairwise phase consistency

- **Phase-locking value** - **resultant vector length**
  - Biased by spike counts
  - Biased by spiking history effects (refractory period, bursting)

Pairwise phase consistency

- **PPC1**: **Pairwise phase consistency** (Vinck et al., 2012, J Comp Neuro**)**
  - Compares pairs of spike phases across trials - like "spin model"
  - Avoids history effect
  - Unbiased by spike count



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Spike-field coherence

- **Standard coherence expression** see (Bastos' tutorial)
  - Explained variance for linear prediction at each individual frequency

Spike-field coherence

- **Standard coherence expression** see (Bastos' tutorial)
  - Explained variance for linear prediction at each individual frequency
- **Advantage:**
  - Fast to compute
  - Can deal better with edges of trial periods than spike-centered methods
- **Disadvantages:**
  - Spike-field coherence is a strictly linear measure
    - Not adequate to measure locking to oscillator in broad frequency band
  - Strongly positively biased by firing rates
    - Subsampling approaches are computationally expensive and lose information

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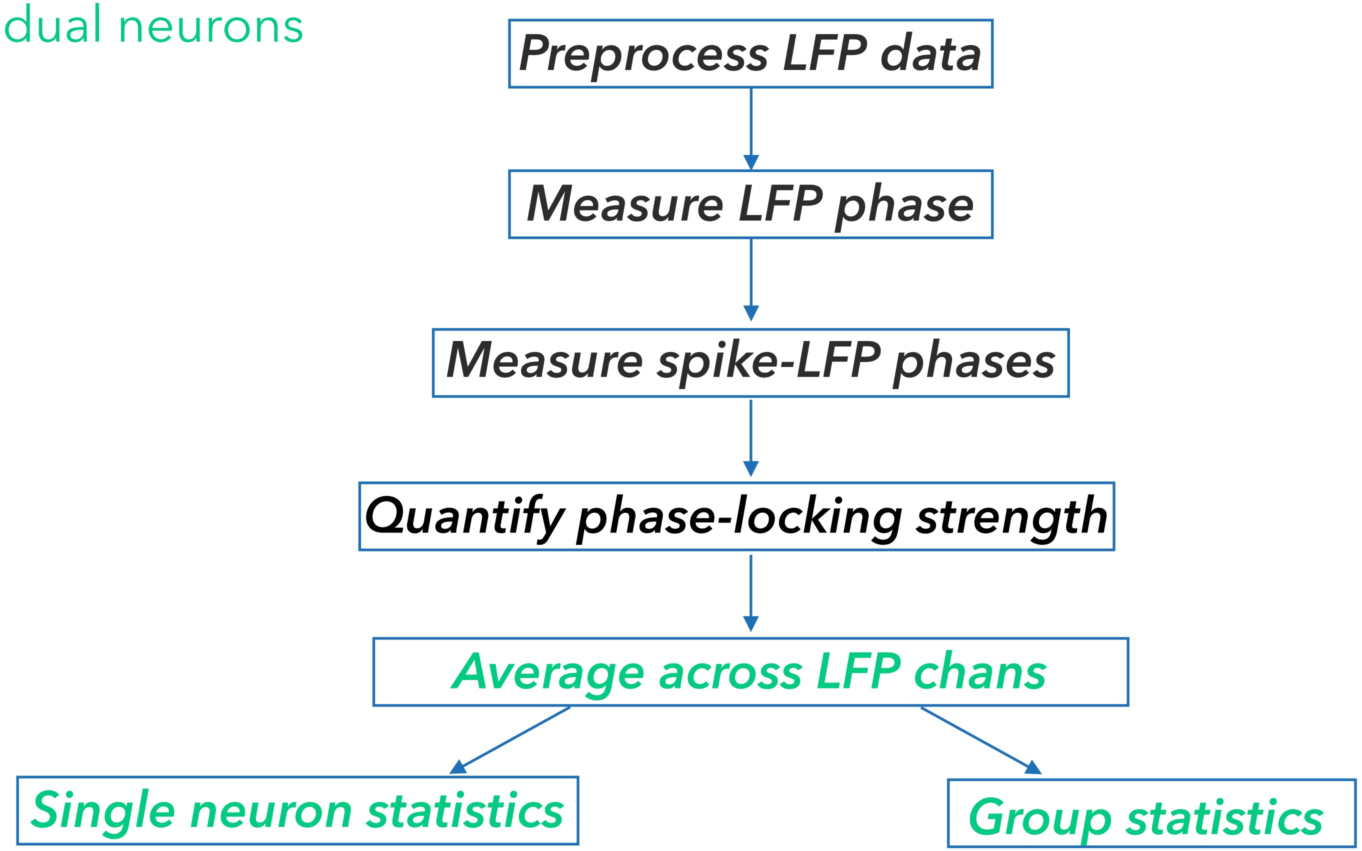

Single-site statistics

- **Rayleigh test**
  - Circular statistics test for significance individual neurons
  - Does not adequately deal with history effects in spike trains

Single-site statistics

- **Permutation test**
    - Preferred statistical testing, permuting spikes and fields across trials
    - Can be combined with multiple comparisons

Descriptive group statistics

- Reliability of measurements depends on the number of spikes per neuron

Descriptive group statistics: solutions

- **Unweighted PPC**
  - Can be strongly driven by variance in neurons with few spikes
- **Threshold >50 spikes**
  - Works well in practice, but the threshold is arbitrary
- **Weighted PPC** (Vinck et al., 2013, Spyropoulos et al., 2024, Neuron)
  - Assumes identical distribution of neurons independent of spike count
- **Questionable procedures:**
  - Select neurons with positive PPC values (recreates bias)
  - Select only significantly locked neurons (recreates bias)

Software

- **SPIKE toolbox for Matlab:**
  - Main developer *Martin Vinck*
- **Tutorial using Matlab:**
  - Simple example of synthetic dataset of spike trains locked to synthetic modulation signal
  - Signal is generated as a damped harmonic oscillator driven by noise (Spyropoulos et al.)
- **Optimized Python code** performing similar analyses will be released within ~1 year

Spike structure

- ***spike.time***: {1x#Neurons} cell array
  - Each cell contains a 1x#spikes vector: spike times relative to some event
    - `spike.time{1} = [0.4360 0.2360 0.7720 0.2520 0.9920 0.1920 0.8000]`
- ***spike.trial***: {1x#Neurons} cell array
  - Each cell contains a 1x#spikes vector: the trial in which the spike occurred
    - `spike.trial{1} = [3 8 13 16 20 24 24 28 28 28]`
- ***spike.trialtime***: [nTrials x 2] array
  - Each row contains the beginning and end of each trial relative to the event
    - `spike.trialtime(2,:) = [0 0.9960]`

Spike structure in Matlab

- Working with spike times is much more memory efficient than binary (continuous) format
- For some analyses it is necessary to convert to binary format
  - e.g. Spike-field coherence
- Can convert spike structure to continuous data structure in FieldTrip, and back
- **Important:**
  - Match number of trials and time axis in trial definition of spikes and LFPs

```
>> spike = ft_checkdata(dataspike,'datatype', 'spike', 'feedback', 'yes');
the input is raw data with 50 channels and 100 trials
converting raw data into spike data
```

Spiketriggeredspectrum with fft

- Example using SPIKE toolbox:
  - `cfg.timwin = [-0.1 0.1]`
  - `cfg.taper = 'hann'`
  - `sts = ft_spiketriggeredspectrum(cfg,data,spike)`
- Output added:
  - `sts.fourierspctrm = {1x#Neurons} cell array`
- Each cell contains a
  - `#spikes x #lfpchans x #freq array`

Spiketriggeredspectrum with convol

- Example using SPIKE toolbox with 5 cycles for each frequency and a Hann taper:
  - `cfg.foi = [10 : 1 : 100]`
  - `cfg.taper = ‘hann’`
  - `cfg.t_ftimwin = 5 . / cfg.foi;`
  - `sts = ft_spiketriggeredspectrum_convol(cfg,data,spike)`
- Output added:
  - `sts.fourierspctrm = {1x#Neurons} cell array`
- Each cell contains a
  - `#spikes x #lfpchans x #freq array`

Spike-triggered average (STA)

- Example using SPIKE toolbox:
  - `cfg.timwin = [-0.1 0.1]`
  - `sta = ft_spiketriggeredaverage(cfg,data)`
    - Here data contains both lfp and spiking data in continuous format
- Output added:
  - `sta.avg = #Neurons x #time_points array`
  - `sta.time = 1x#time_points array`