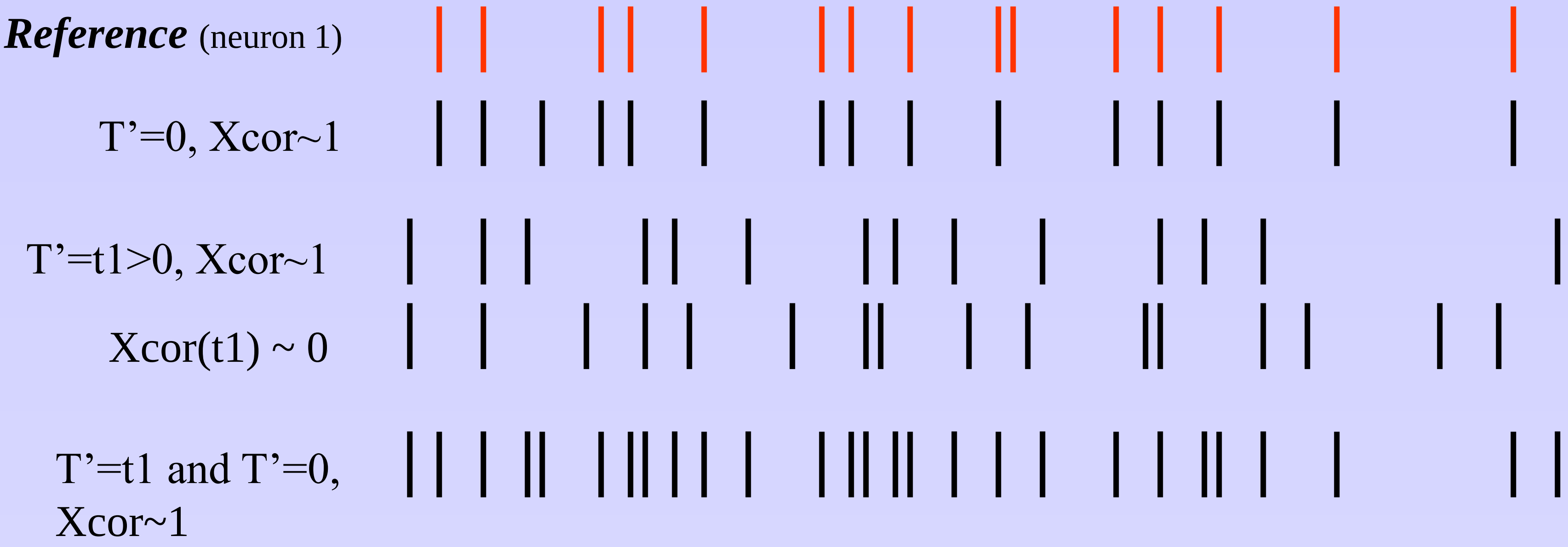
Class 12

Cross-Correlation
JPSTH-Coherence

Cross-correlation

- Autocorrelation: Is one spike of a spike train correlated with another spike of the same spike train (t’ sec later/sooner)?
- Cross-correlation: Is one spike of **neuron1** correlated with another spike of **neuron2** (t’ sec sooner or later)?



Reference (neuron 1)

T’=0, Xcor~1

T’=t1>0, Xcor~1

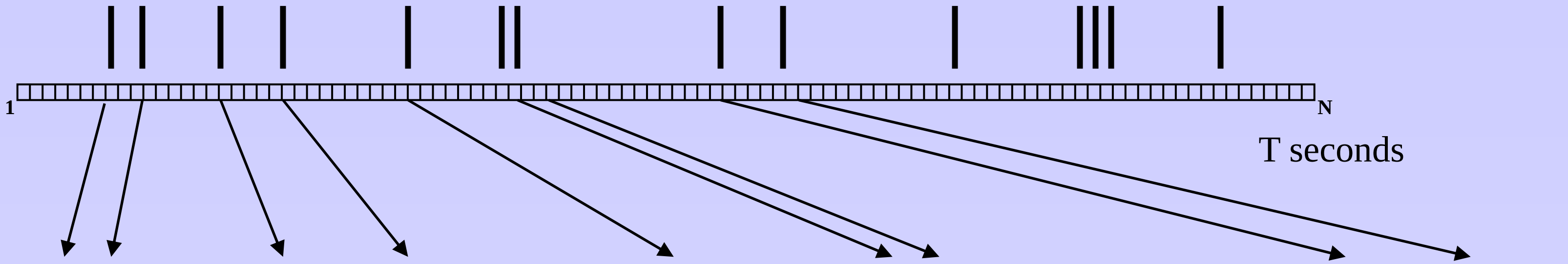
Xcor(t1) ~ 0

T’=t1 and T’=0, Xcor~1

→ Need: reference neuron **and** common time scale (simultaneous recordings, or stimulus locking) **and** time bin.

Cross-correlation

- Cross-correlation function (a.k.a. cross-correlogram)



x(t) 000000010100000010000100000000010000000011000000000000000100001…

$$C_{1,2}(t') = \left\langle \frac{1}{T}\int_0^T x_1(t)\,x_2(t+t')\,dt \right\rangle_{trials}$$

Absolute spike-spike correlation. Problem if mean firing rates are very different

Cross-covariance

- Cross-covariance: How deviation from mean firing rate in **neuron1** is correlated with deviation from mean firing rate in **neuron2**.

$$Cov_{1,2}(t') = \left\langle \frac{1}{T}\int_0^T (x_1(t)-\mu_1(t))(x_2(t+t')-\mu_2(t+t'))dt \right\rangle_{trials}$$

Time varying mean rate (across trials)

$$Cov_{1,2}(t') = \frac{1}{T}\int_0^T < x_1(t)(x_2(t+t') > dt - \frac{1}{T}\int_0^T \mu_1(t)\mu_2(t+t')dt$$

Problem: the variation of firing within a trial may be very different between **neurons1** and **neuron2**.

Cross-correlation

- Cross correlation **coefficients**

$$h(t') = \frac{Cov_{1,2}(t')}{\sigma_1 \sigma_2}$$

$$\sigma_1{}^2 = \left\langle \frac{1}{T} \int_0^T (x_1(t) - \mu_1(t))^2 \, dt \right\rangle$$

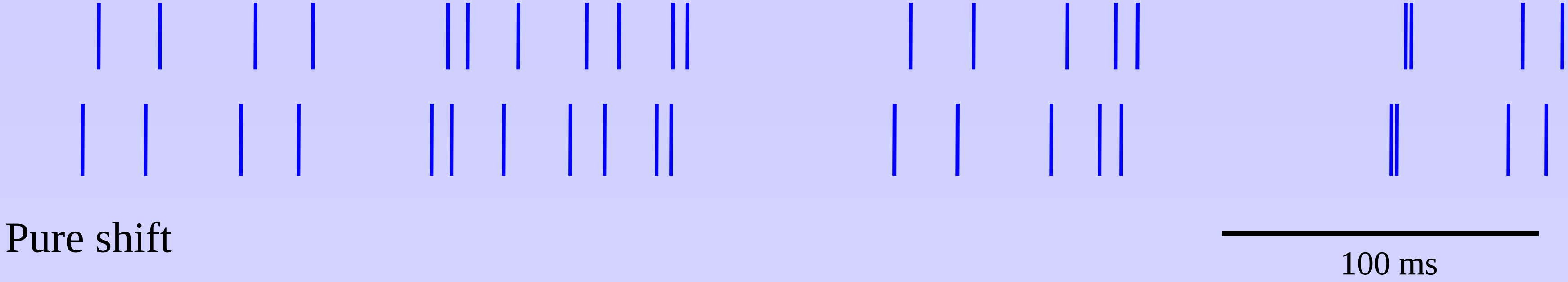
h(t) is the firing ‘probability’ of 2, given that 1 has fired. In [-1 1].

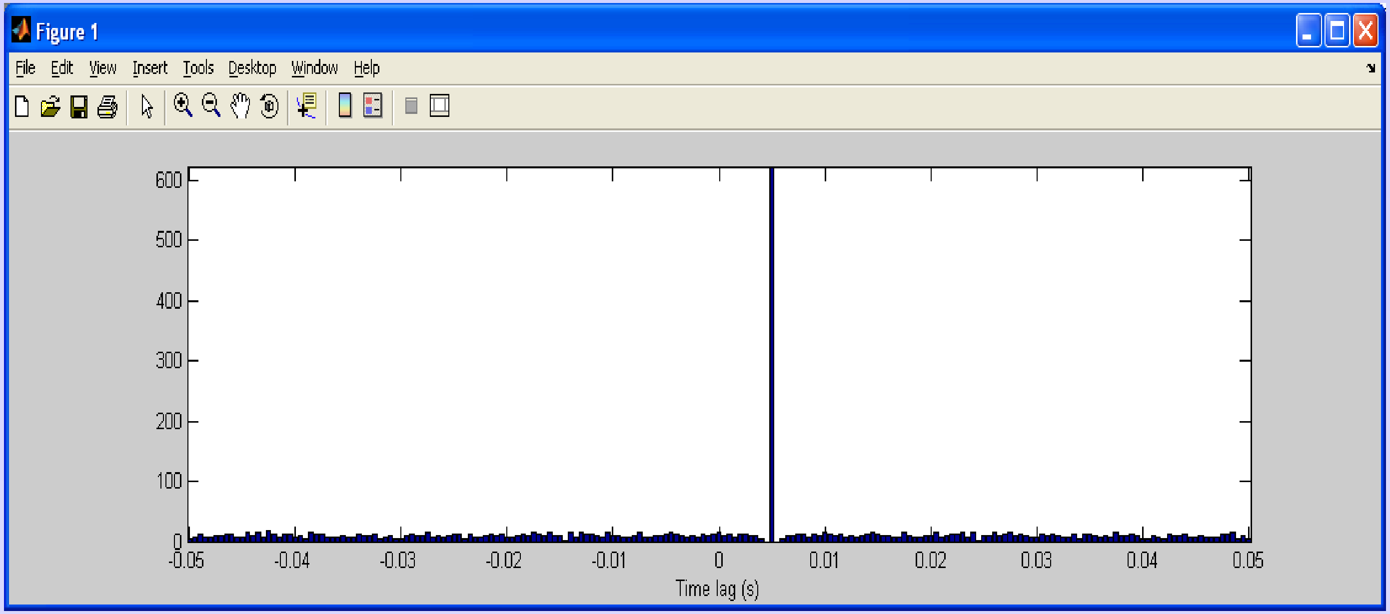
- problem: time varying mean firing rate needs to be estimated

$$Cov_{1,2}(t') = \frac{1}{T} \int_0^T < x_1(t)(x_2(t+t') > dt - \boxed{\frac{1}{T} \int_0^T \mu_1(t) \mu_2(t+t') dt}$$

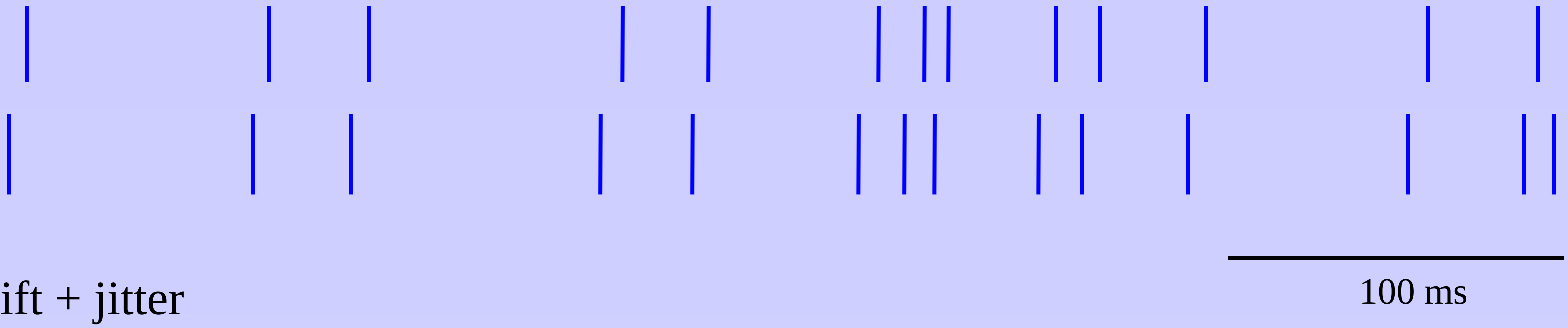
Cross-Correlation – in practice

- Measure the inter-spike-interval between any two spikes in the two spike trains.
- Build a histogram of these values between –TimeLag and +TimeLag.
- ➔ Cross-correlogram

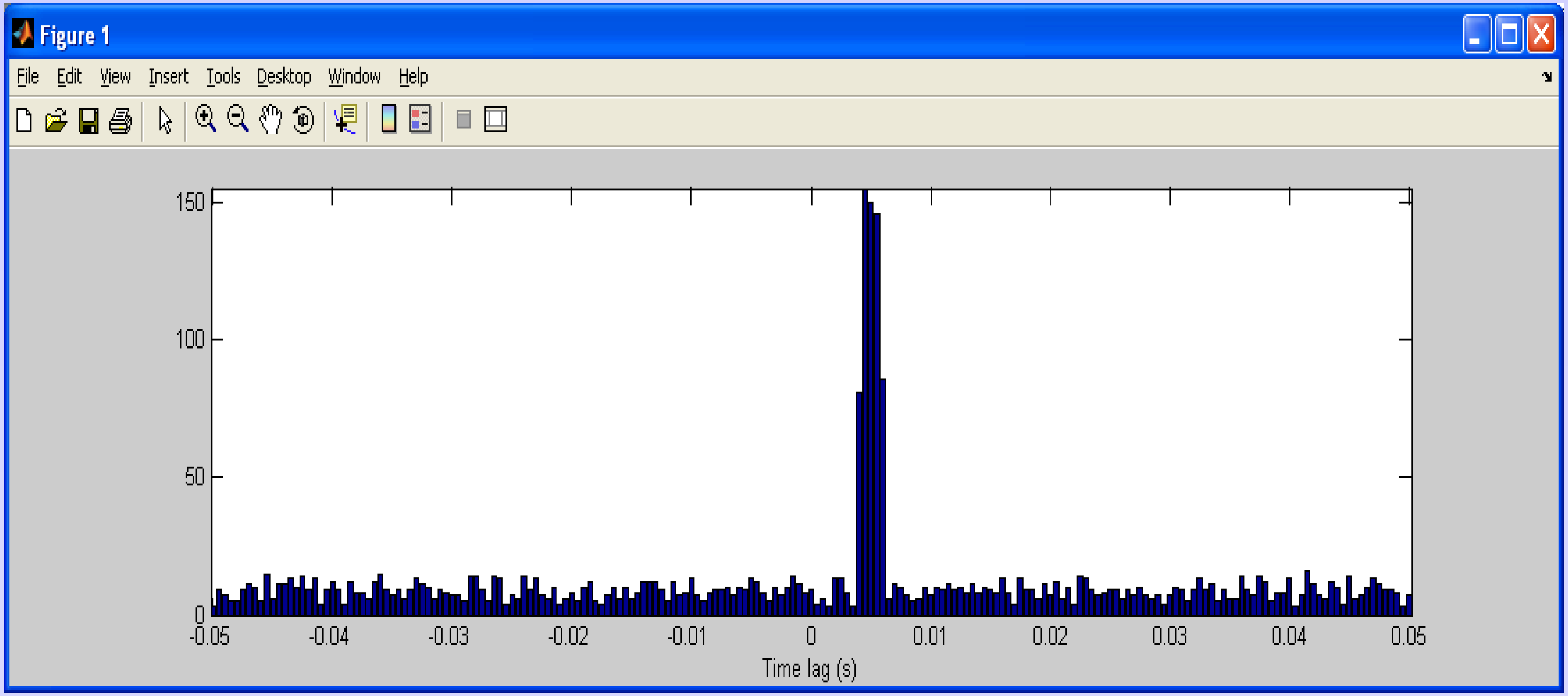




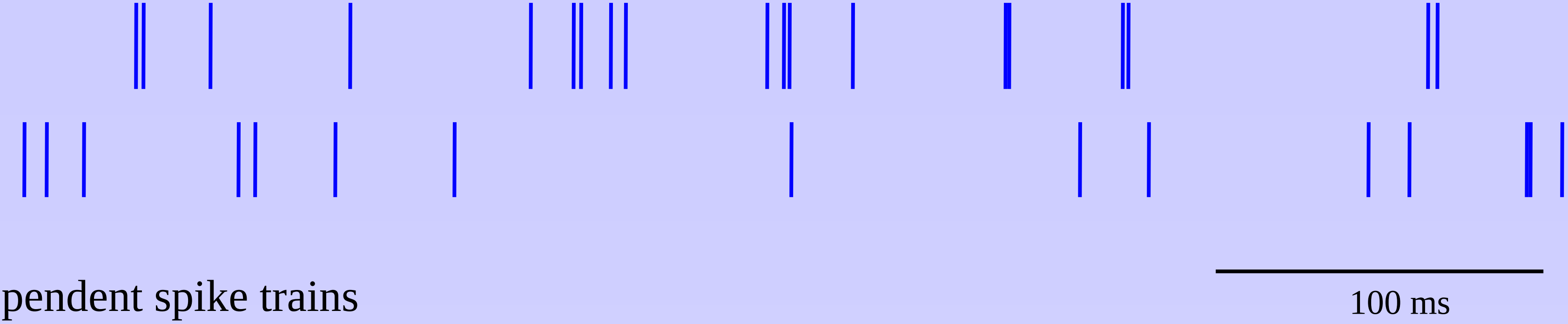
Cross-correlation



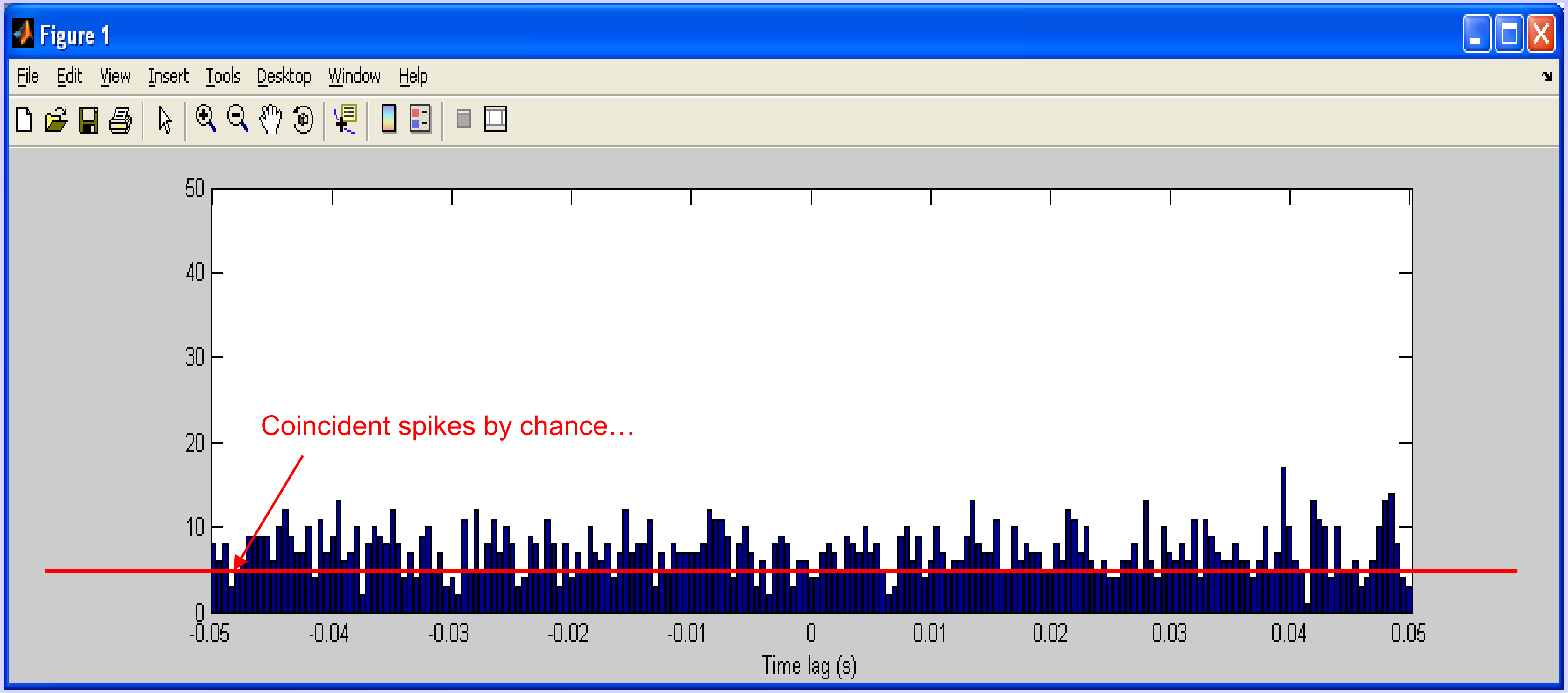
Pure shift + jitter



Cross-correlation



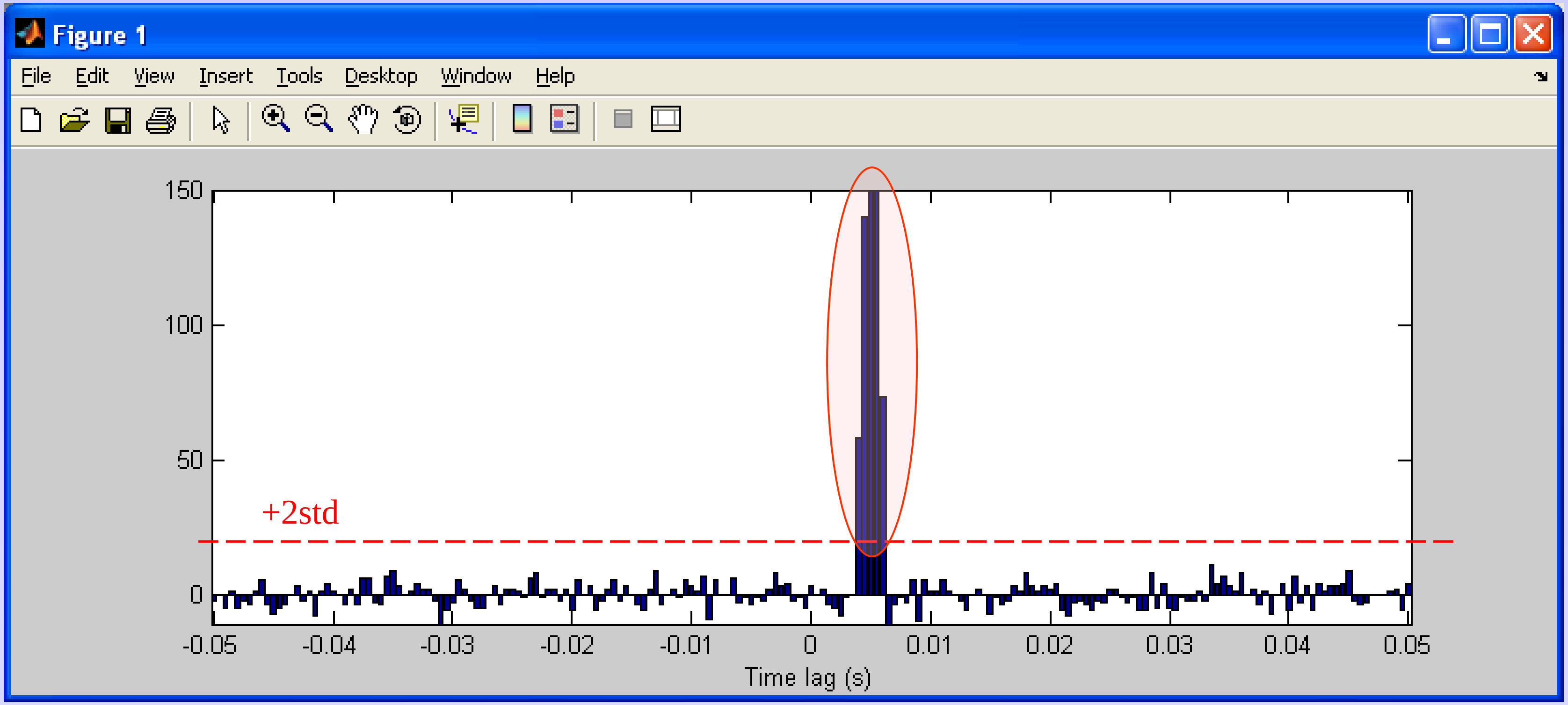
Independent spike trains



Coincident spikes by chance…

Cross-correlation: Corrections and significance

- Correction for random correlations:
  1- Compare with 2 Poisson trains with same mean firing rate.
  2- Shuffle the ISIs of the original trains.
    Compute the (shuffled) cross-correlation.
    Subtract from original cross-correlation.

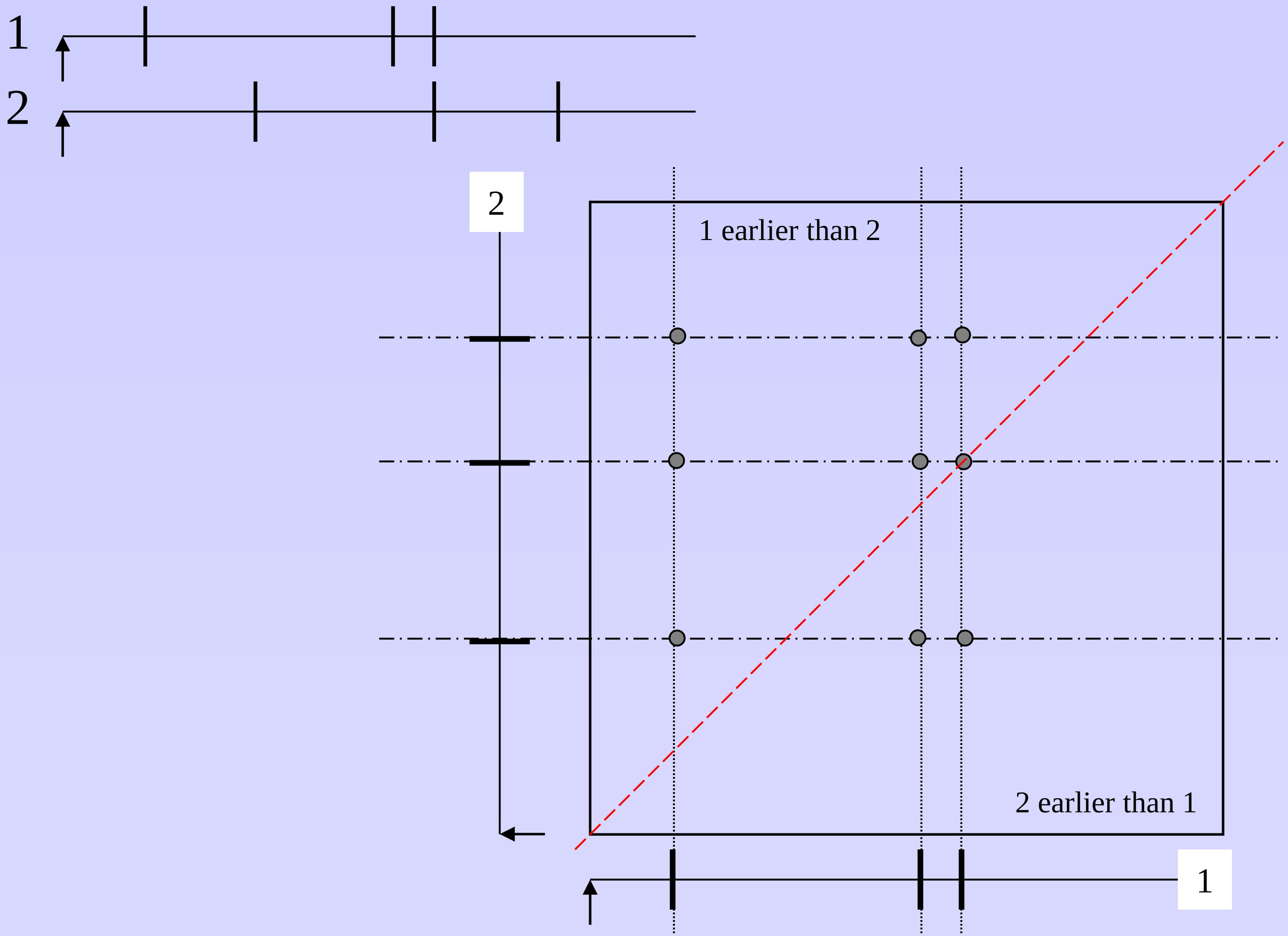


- Scale correction: Divide each bin by binSize (→ Hz)

Joint Peristimulus Time Histogram

- Cross correlation uses the time average of all correlations. What if the correlations are not stationary? Are there fluctuations in ‘effective connectivity’?

➔ Joint peristimulus (spike) time scatter diagram:

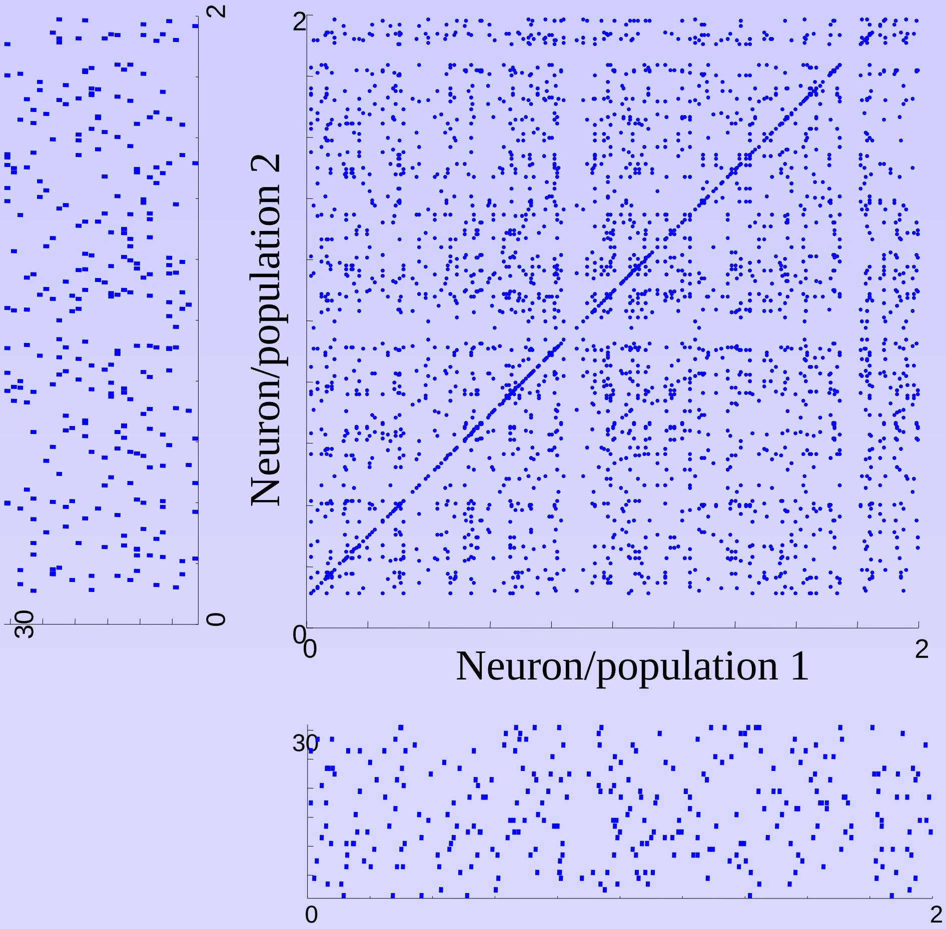


Joint Peristimulus Time Histogram

Multiple trials for neurons 1 and neurons 2

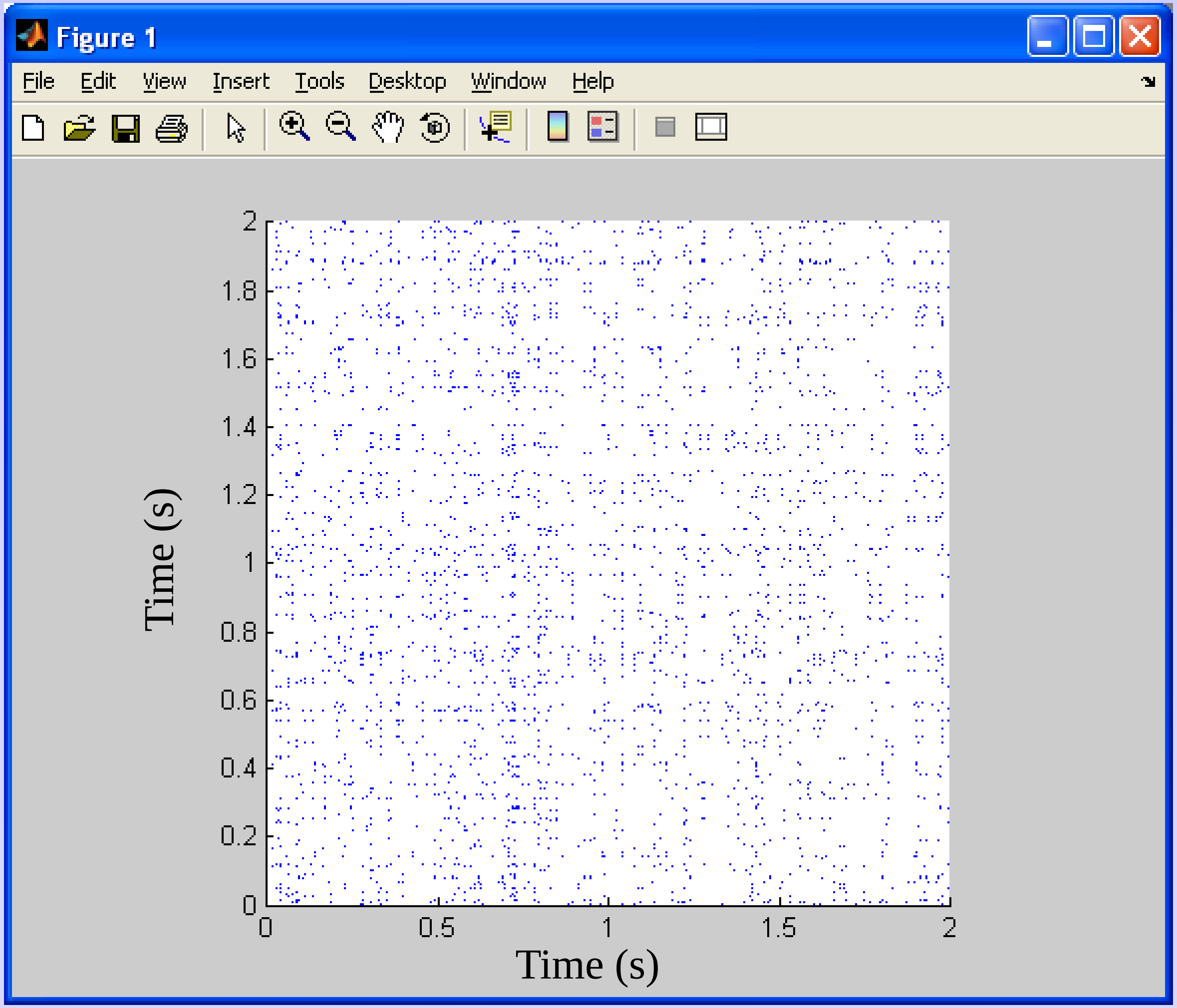
OR

2 simultaneous recordings of 2 neuronal populations



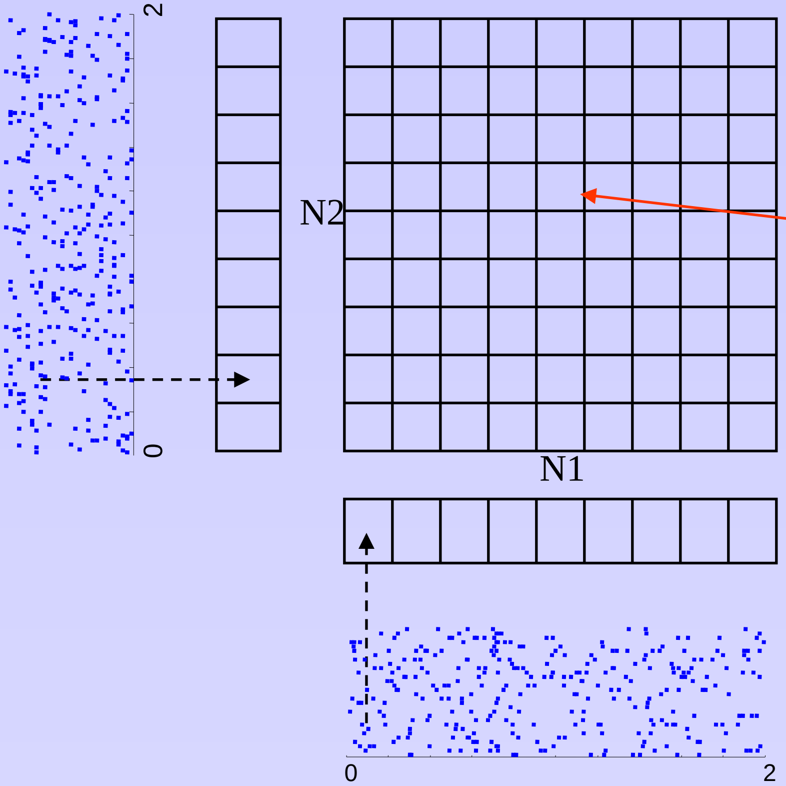
Joint Peristimulus Time Histogram

- 2 independent neurons/populations



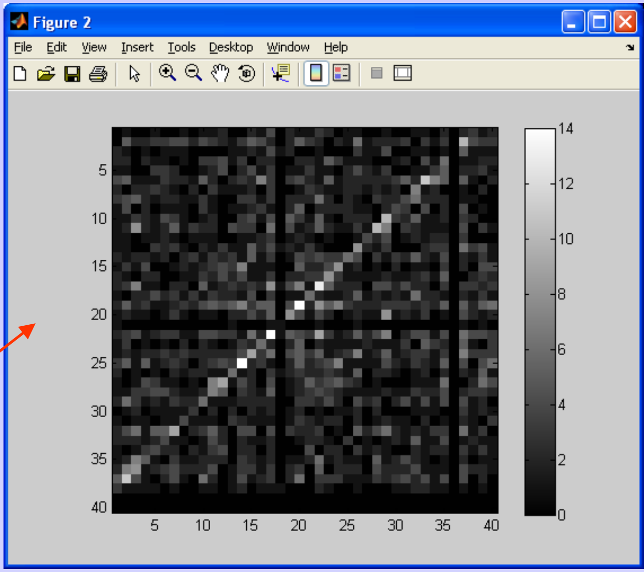
Joint Peristimulus Time Histogram

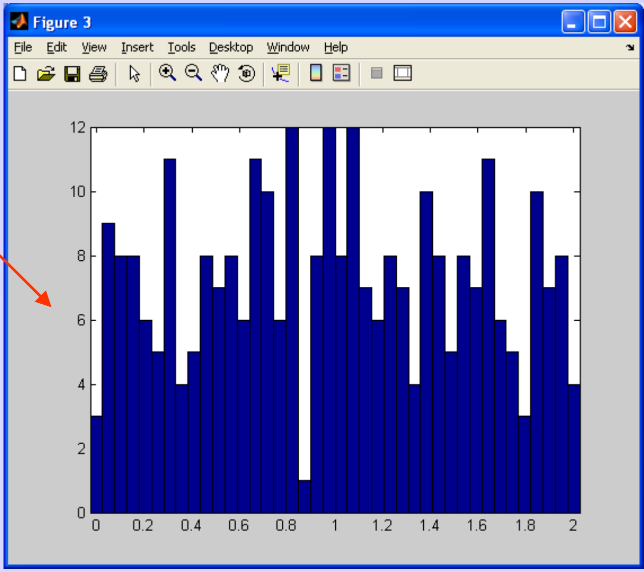
- From scatter plots to histograms: JPSTH.
Bin the scatterplot.



Joint Peristimulus Time Histogram

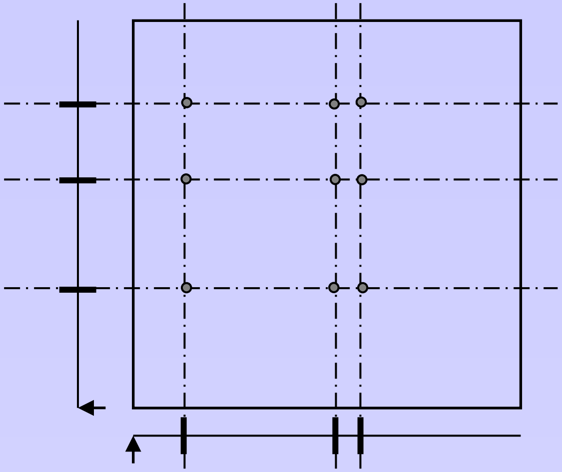
Hist1

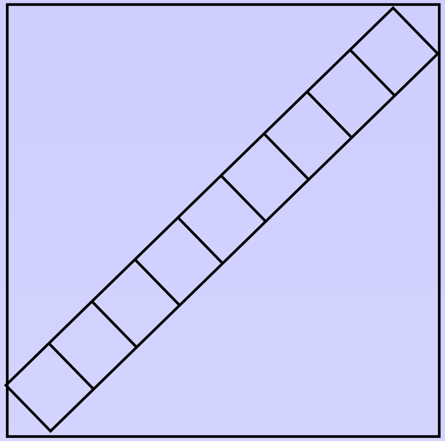


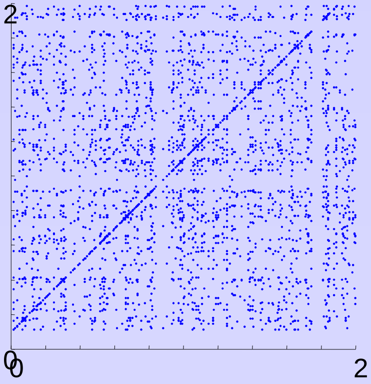


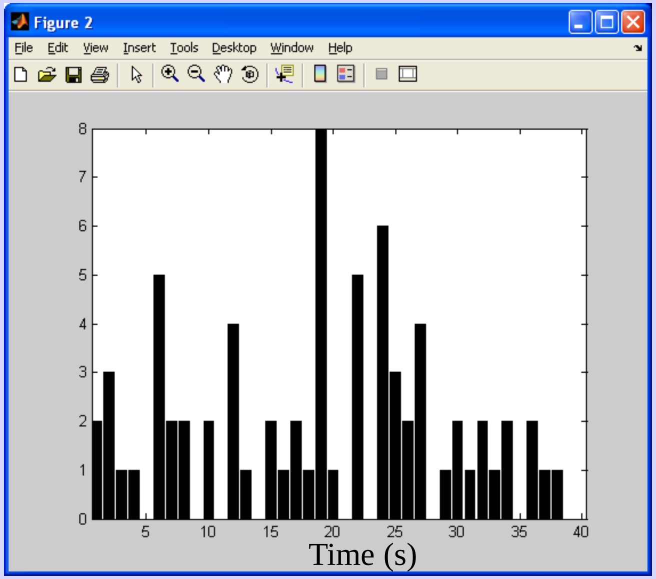
Joint Peristimulus Time Histogram

- From scatter plots to histograms: *Near coincidence Histogram*



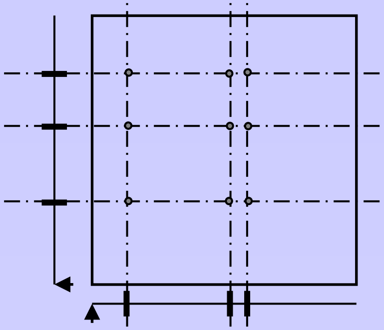


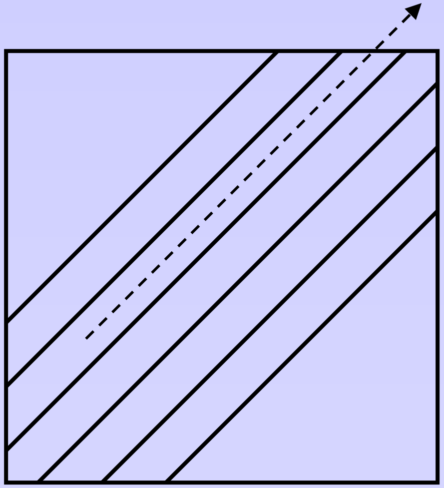




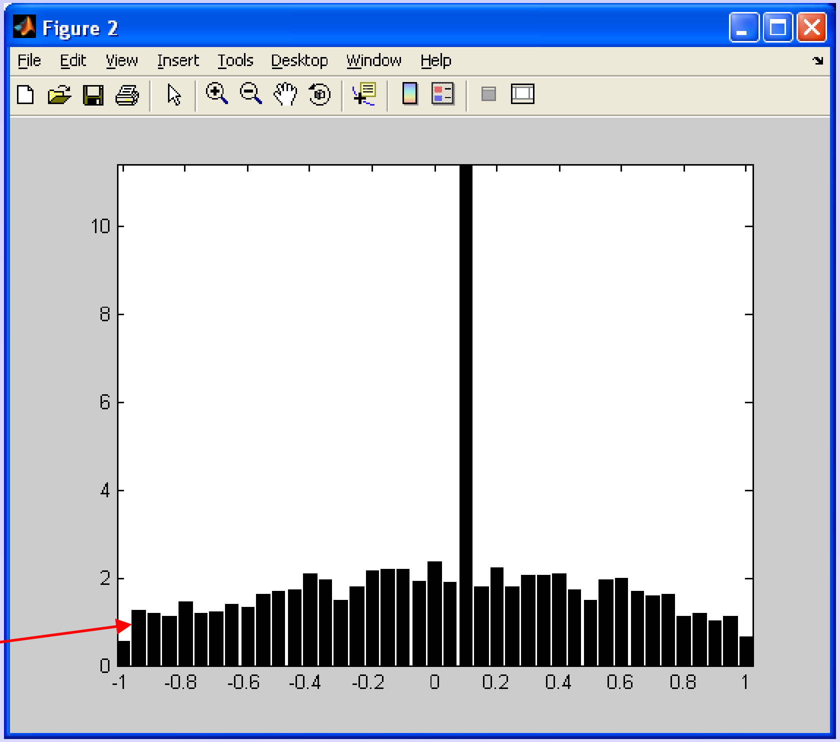
Joint Peristimulus Time Histogram

- From scatter plots to histograms: Cross-correlation





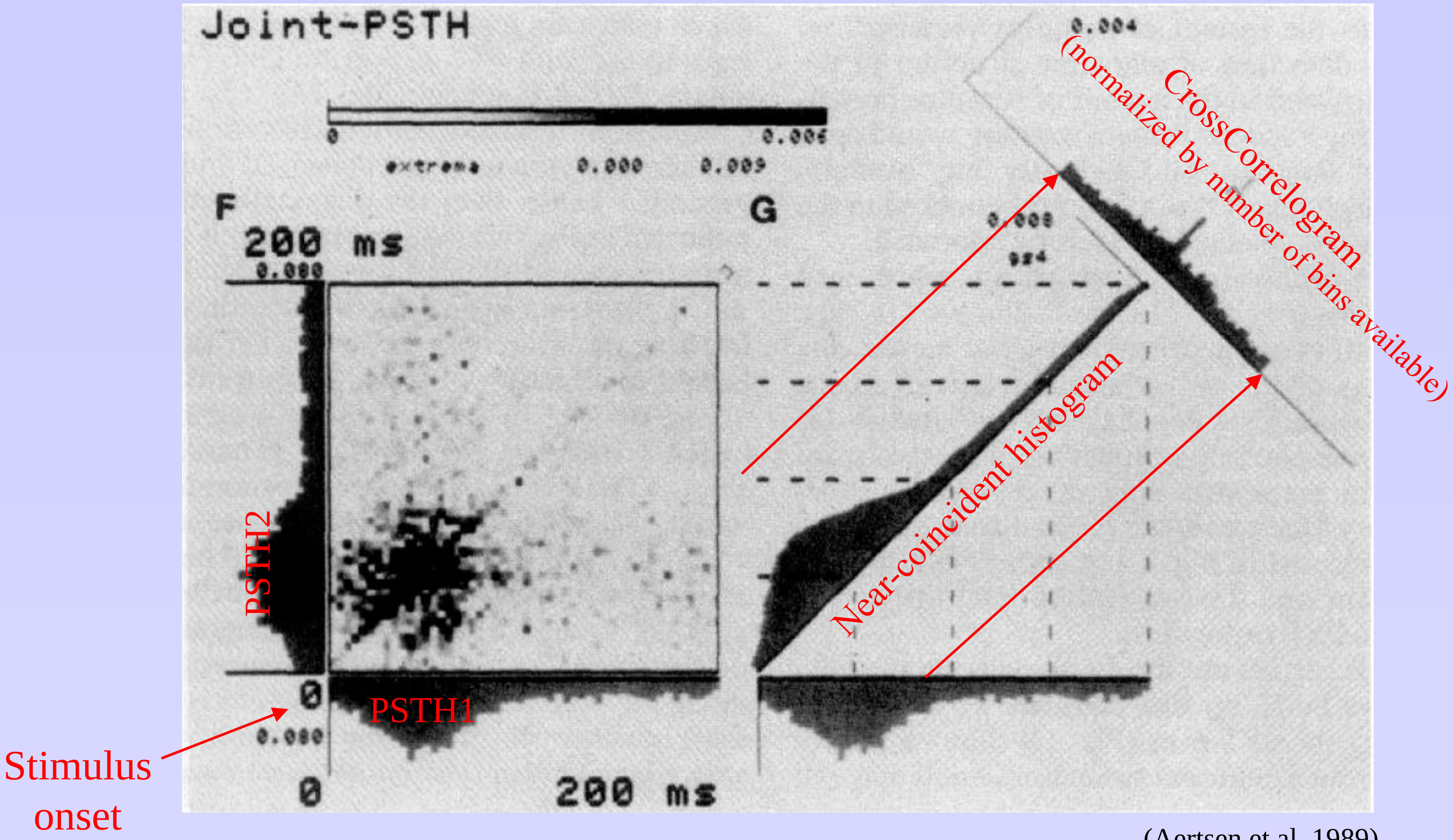
(uncorrected)



- Warning: Unbalanced binning occupancy
- ➔ divide by nb bins

Joint Peristimulus Time Histogram

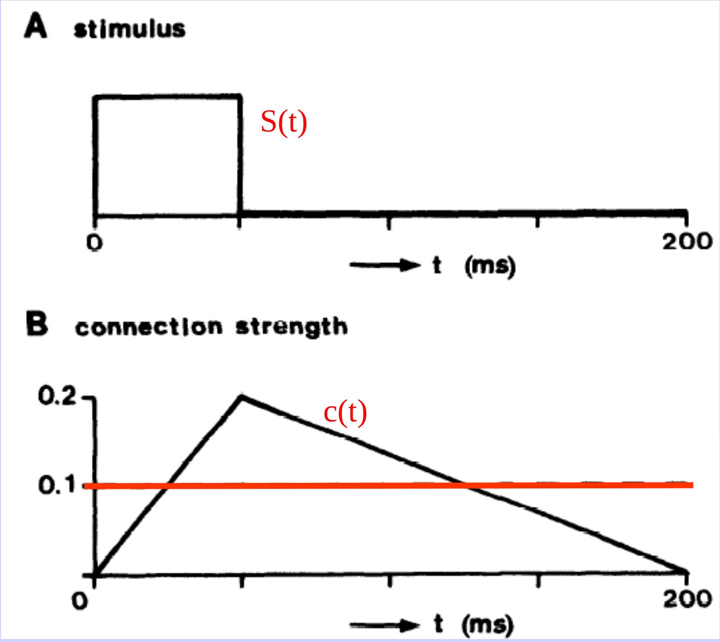
- Building the JPSTH, PSTHs and Cross-correlogram



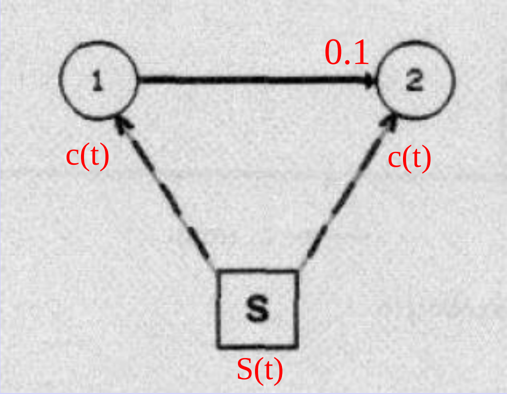
(Aertsen et al. 1989)

JPSTH: contains mixture of stimulus and neuron interaction effects

Joint Peristimulus Time Histogram

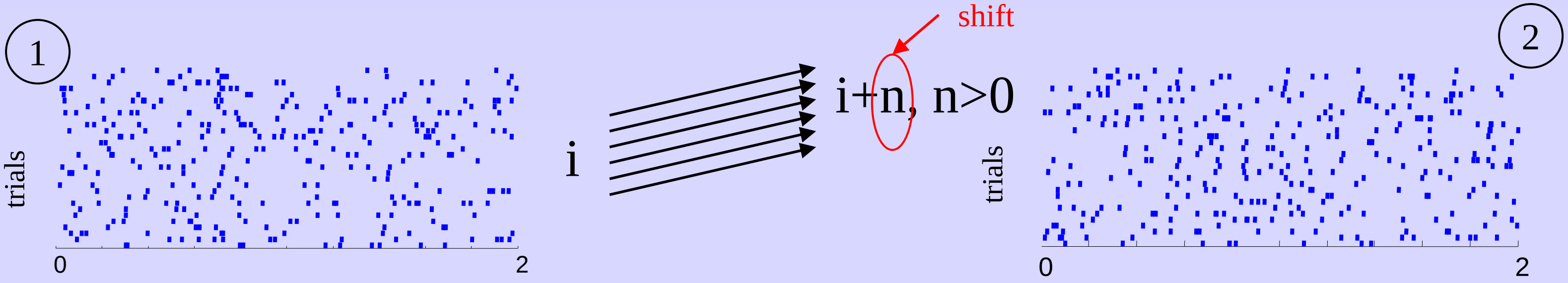


Computational model



(Aertsen et al. 1989)

- Separating the stimulus effect from the neural interaction effects: Shift predictor



Preserve stimulus effects, cancels out neural interactions

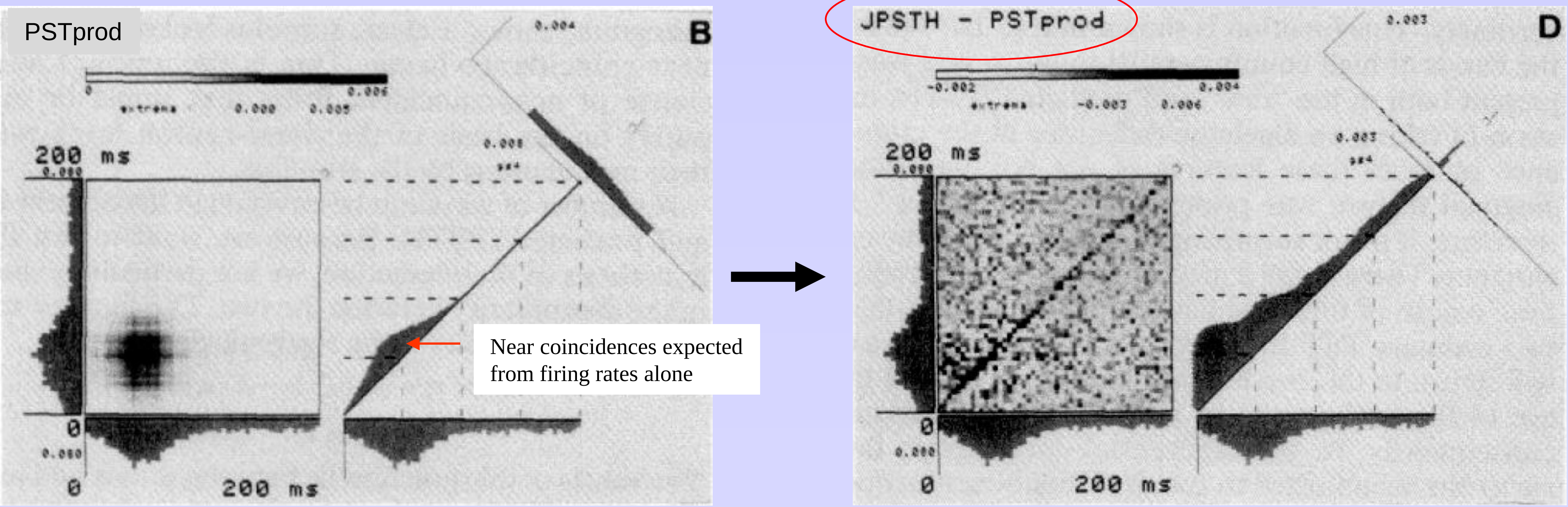
Joint Peristimulus Time Histogram

- Averaging across all shifts ⇔ Cross-products of PSTHs (PSTprod).
  Estimate of:

$$\frac{1}{T}\int_0^T \mu_1(t)\mu_2(t+t')dt$$

(i.e. assuming no interactions between neurons)

Cross-covariance function



Near coincidences expected from firing rates alone

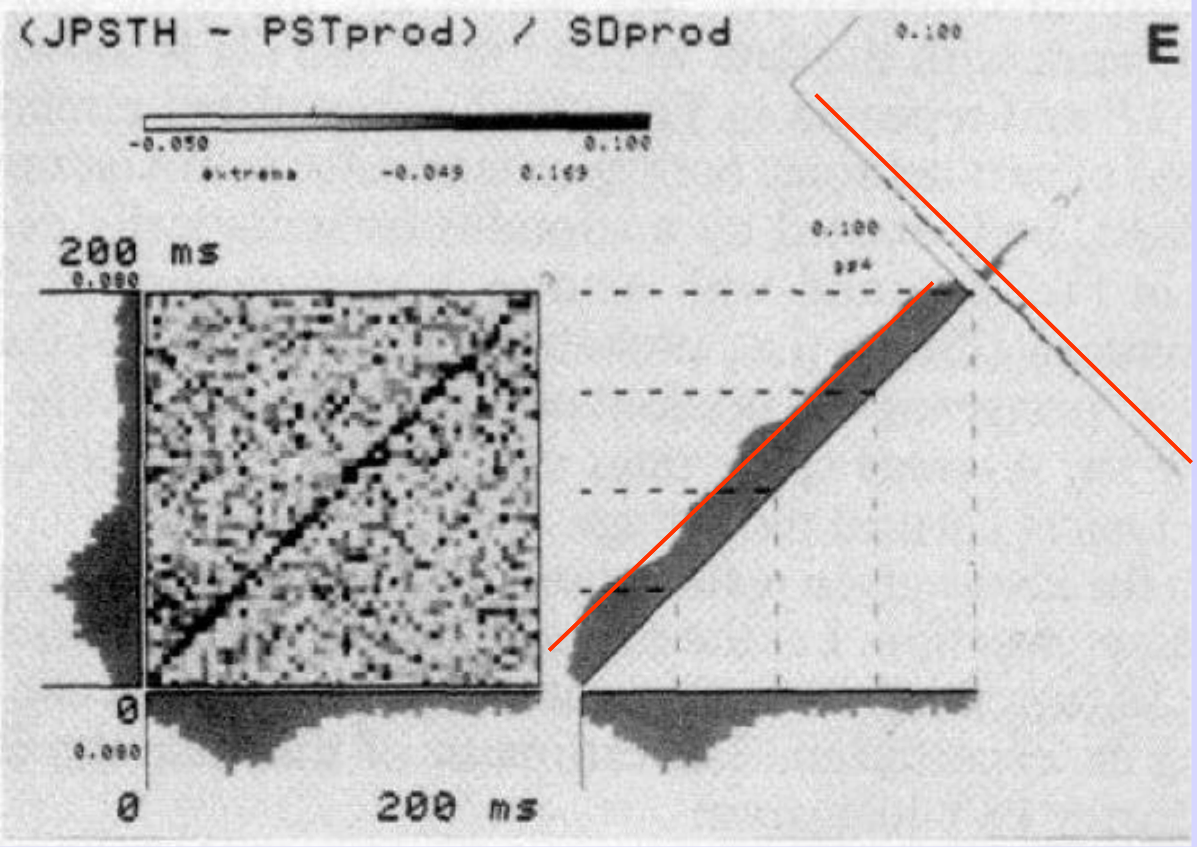
(Aertsen et al. 1989)

- problem: Firing rate modulations (due to the stimulus) may not be stationary

Joint Peristimulus Time Histogram

- Normalization (due to chance)

  → Divide by the standard deviation of the shift predictor:



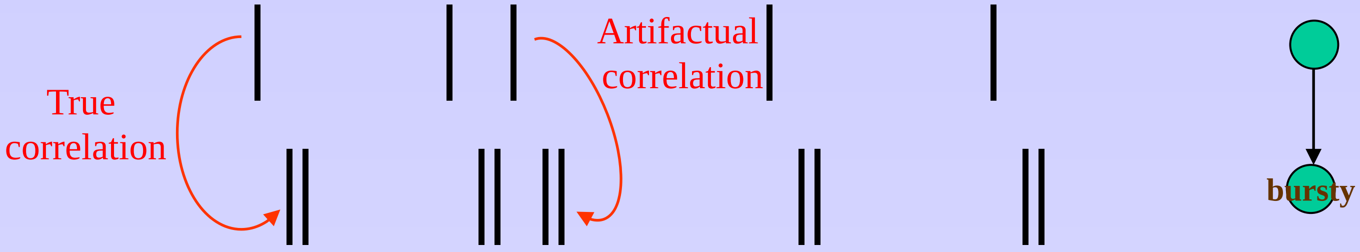
(Aertsen et al. 1989)

Conclusion: Effective/significant neural interactions dynamics

Coherence / Coherency

Cross-correlation coefficients: $$h(t') = \frac{Cov_{1,2}(t')}{\sigma_1 \sigma_2}$$

- problem: What if there are intrinsic correlations within each spike train?



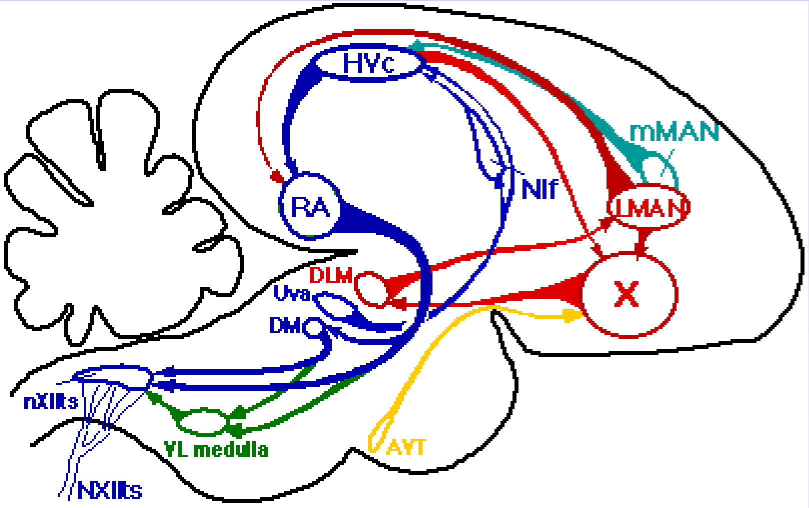
➔ Coherence, Coherency

$$\gamma(w) = \frac{fft(Cov_{1,2}(t'))}{\sqrt{fft(Cov_{1,1}(t')\, fft(Cov_{2,2}(t')}} = \frac{XPower_{1,2}(w)}{\sqrt{PS_1(w) PS_2(w)}}$$

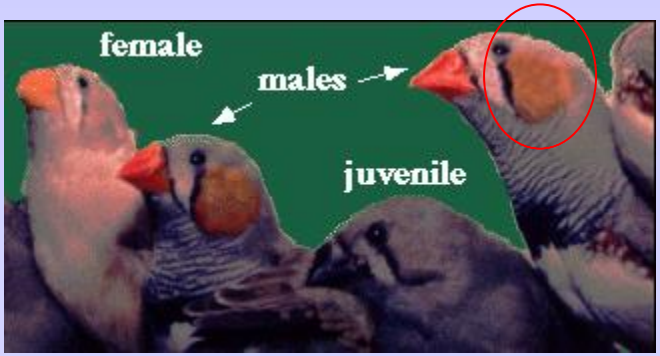
‘removes’ contribution of internal spike train structure (e.g. bursts)

Zebra Finch

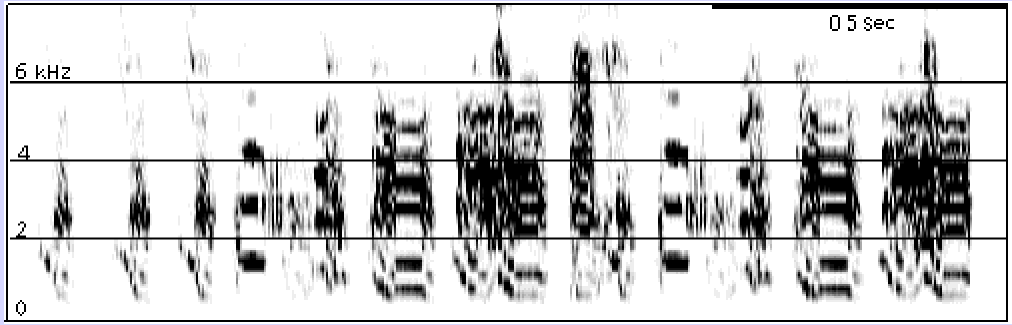
- Social animals - monogamous
- Males learn specific songs
- Songs elicit very precise firing (away from sensory neurons)



Song learning and production circuit

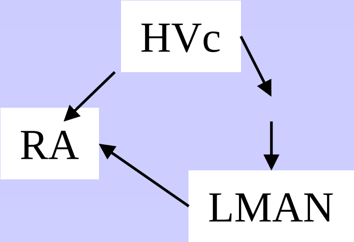


Song spectrogram

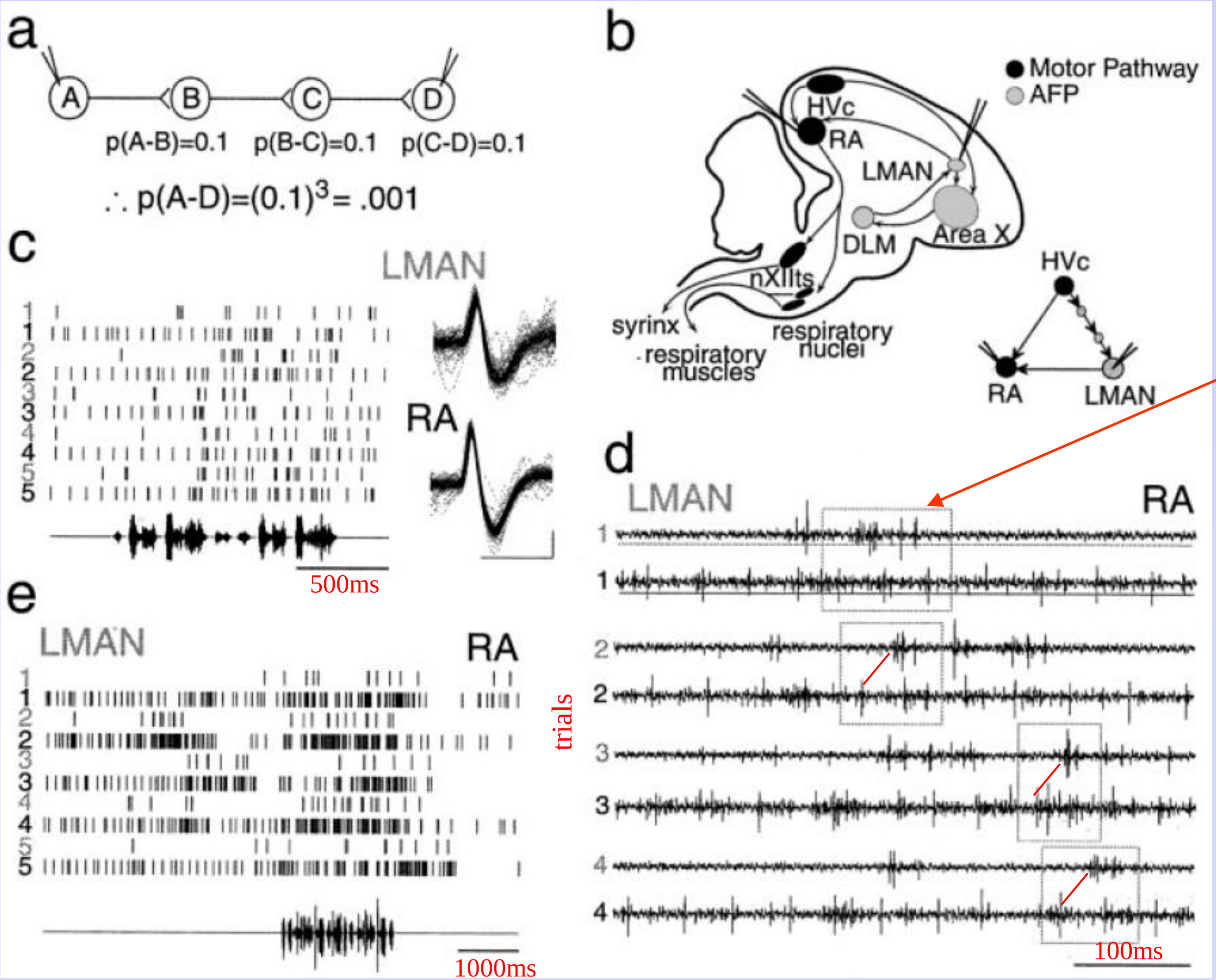


Coherency

- Simultaneous recordings in LMAN and RA


HVc
RA
LMAN

Single units
(5 trials)



Multiunit

Multiunit:
RA before LMAN

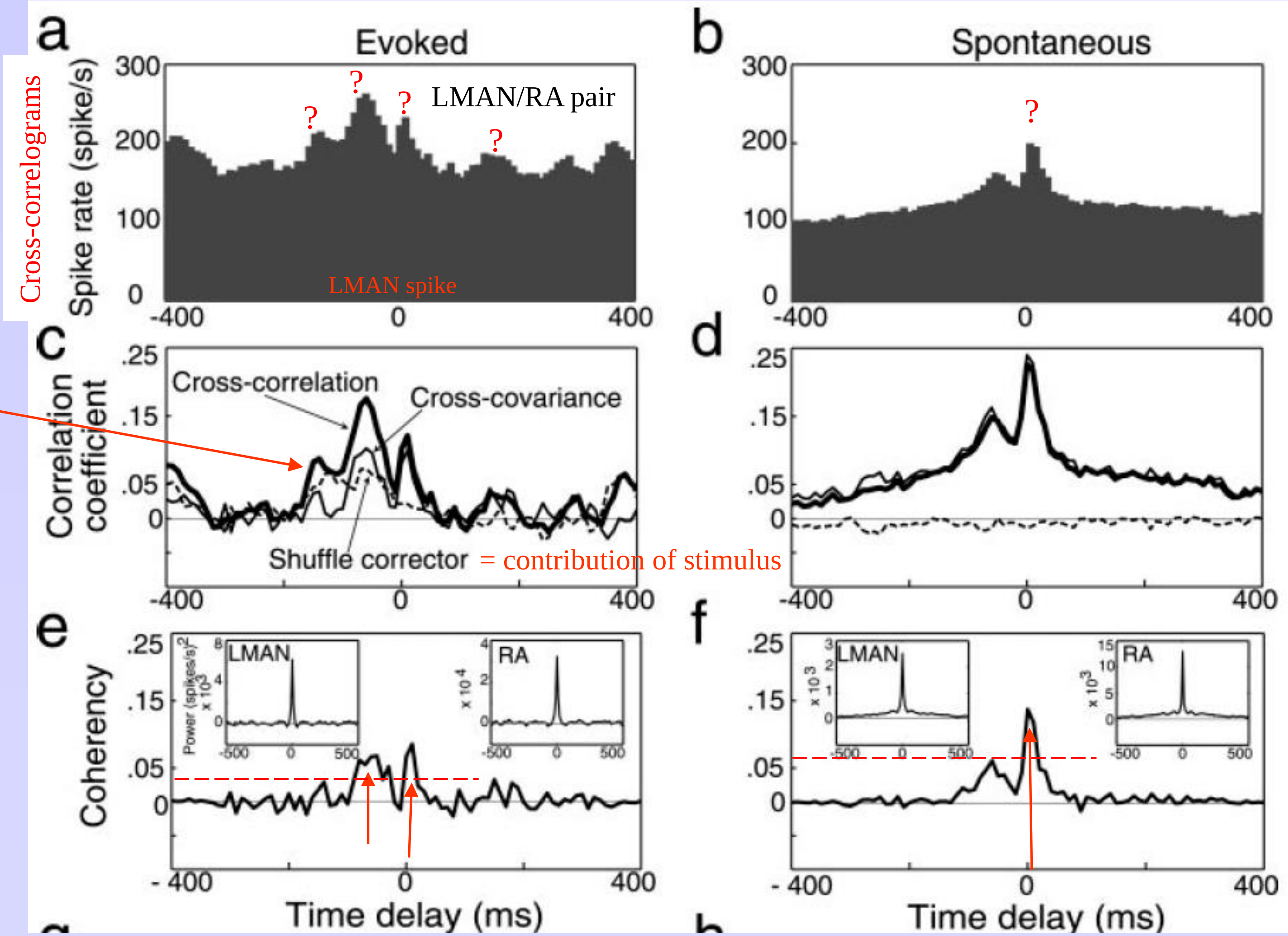
Spont.

Evoked

(Kimpo et al, 2003)

Coherency

- Extracting ‘true’, stimulus-independent, correlations



Cross-correlograms

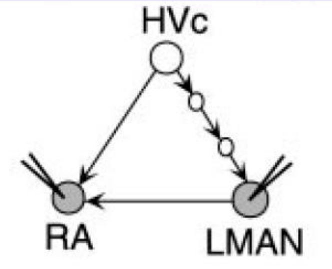
LMAN/RA pair

? ? ? ? ?

LMAN spike

Correlation?

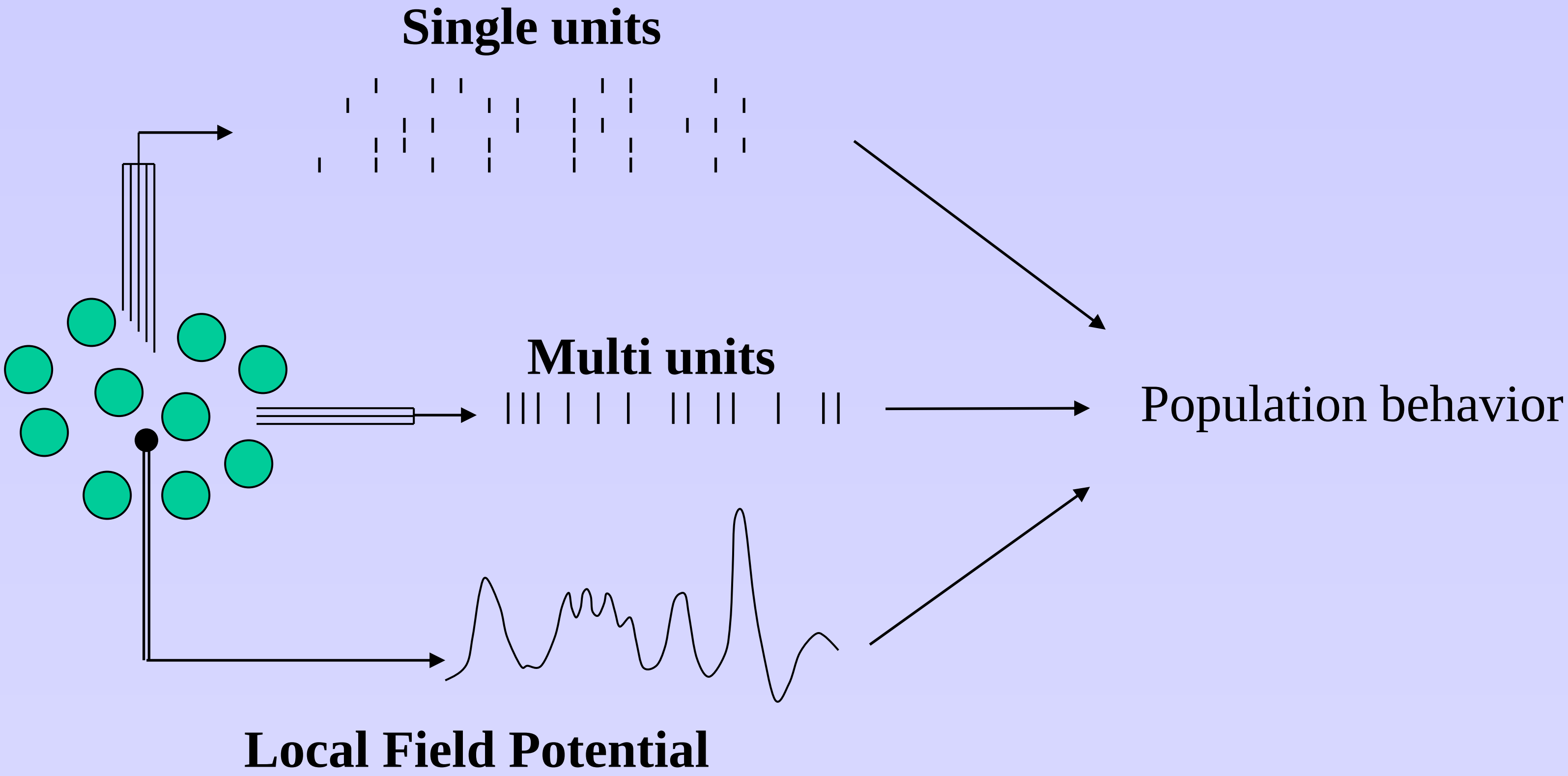
= contribution of stimulus



(Kimpo et al, 2003)

Spike-Field coherence

- Different ways to measure population behavior



Single units

Multi units

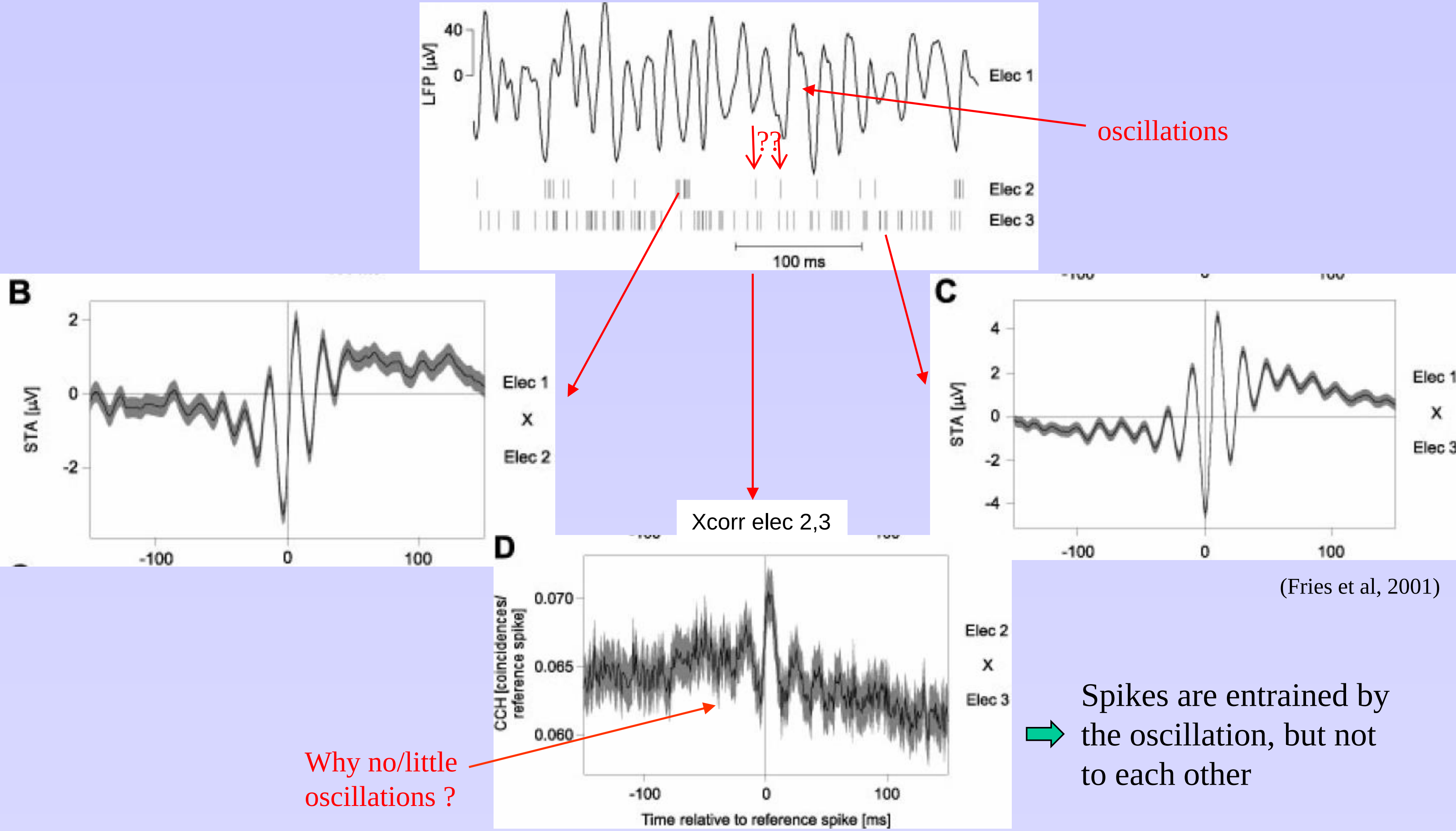
Population behavior

Local Field Potential

Typically: filtered 1-200 Hz

Spike-Field coherence

- Measuring relationships between 1 cell and 1 population: STA of the LFP



oscillations

??

Xcorr elec 2,3

Why no/little oscillations ?

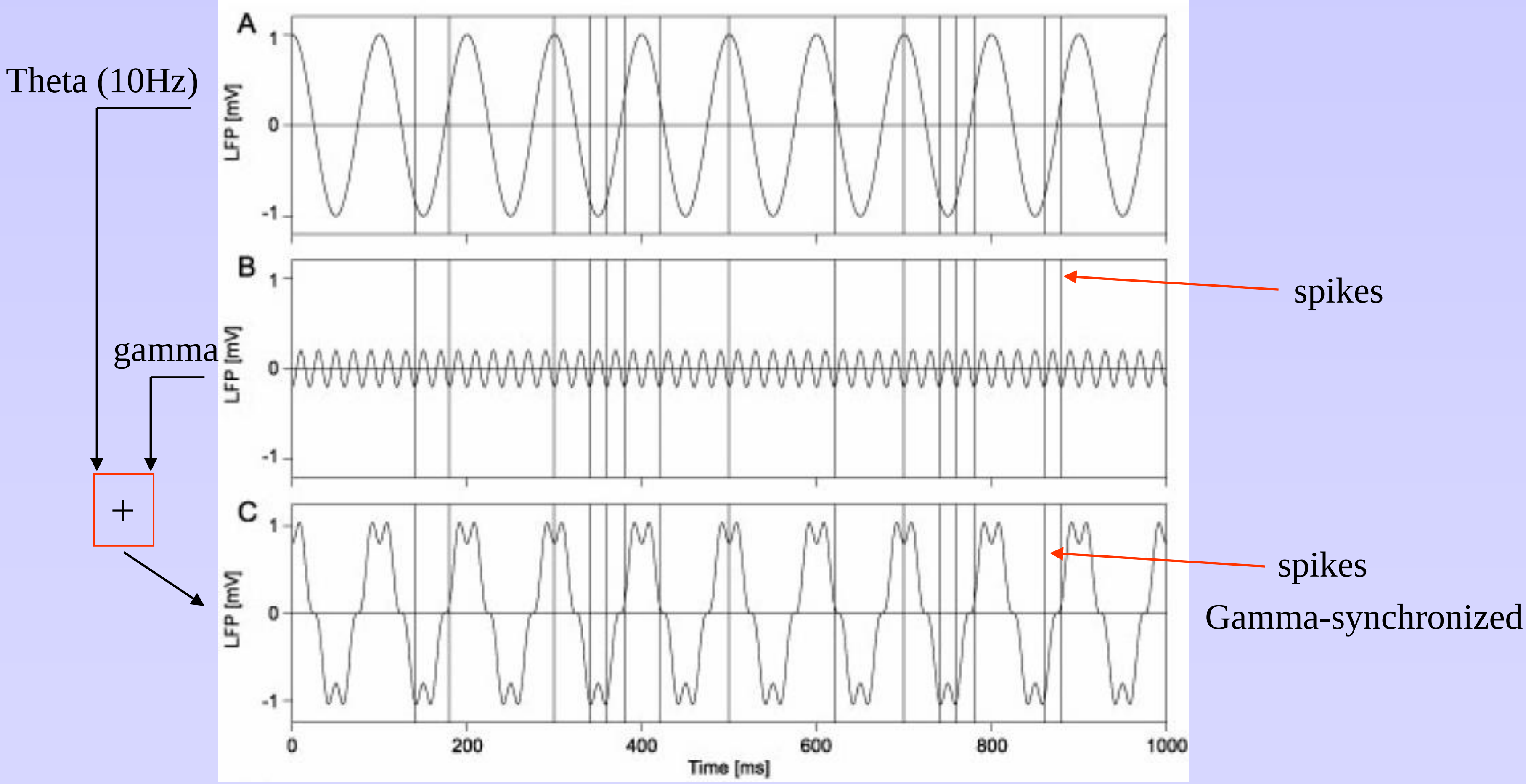
(Fries et al, 2001)

⇨ Spikes are entrained by the oscillation, but not to each other

Problem: what if the LFP’s frequency is non-stationary or non-unimodal?

Spike-Field coherence

- Understanding Spike-Field Coherence: Toy example



Theta (10Hz)

gamma

+

spikes

spikes

Gamma-synchronized

(Fries et al, 2001)

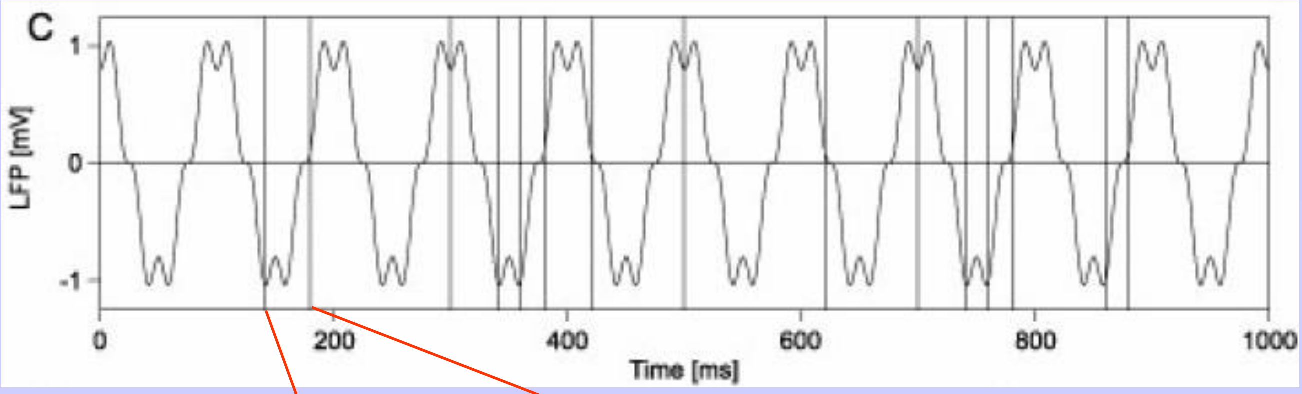
→ Can one ‘recover’ the gamma-synchronization?

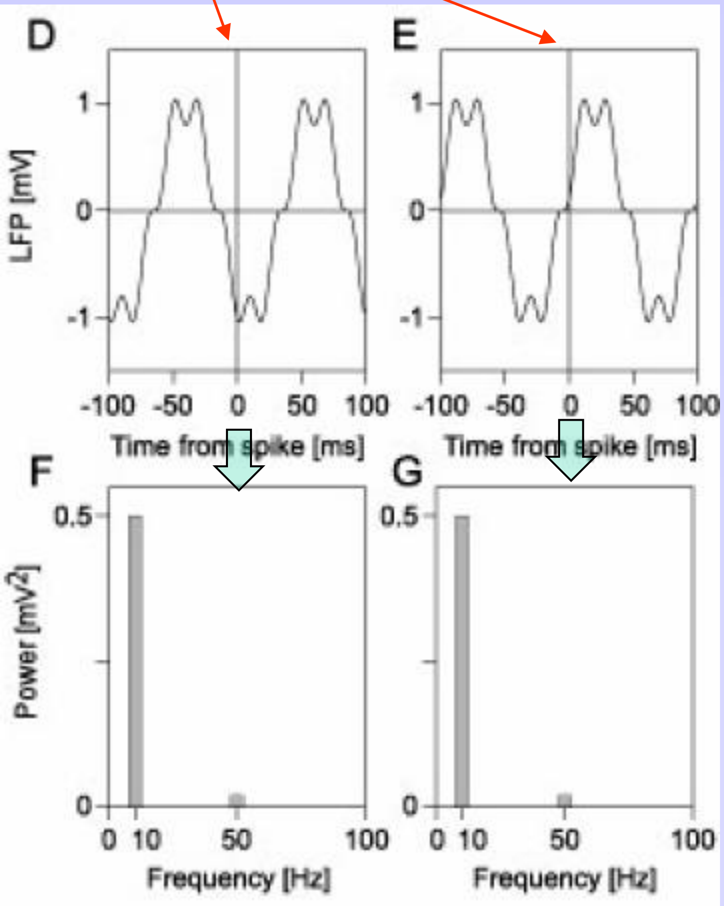
Spike-Field coherence

- Step 1

Spike-triggered LFPs

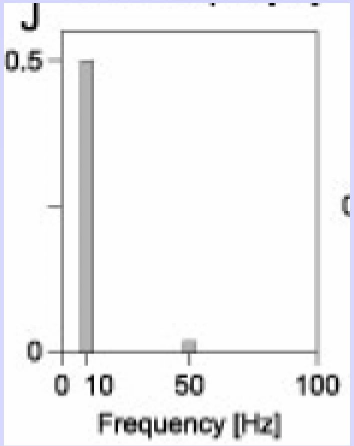
Power spectrum





~average amount of frequency around spikes (irrespective of phase)

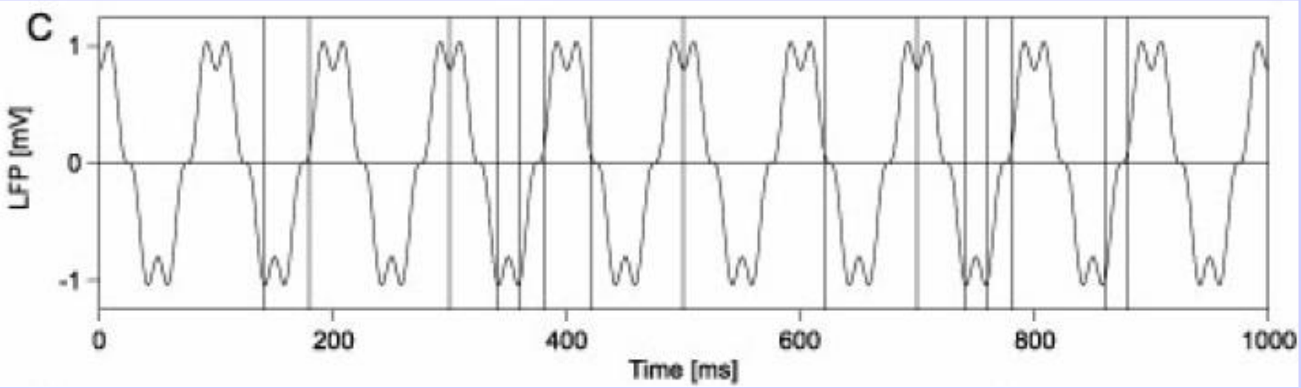
Average Power spectrum N= n spikes



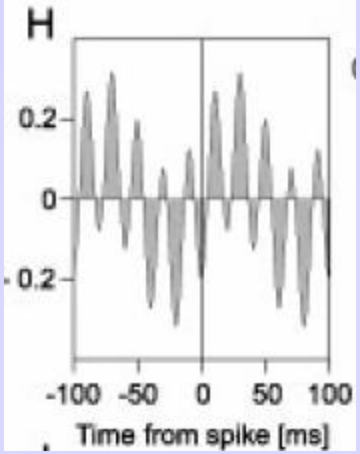
(Fries et al, 2001)

Spike-Field coherence

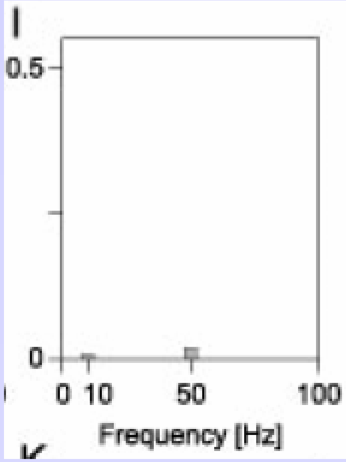
- Step 2



Spike-triggered average



Power spectrum of STA

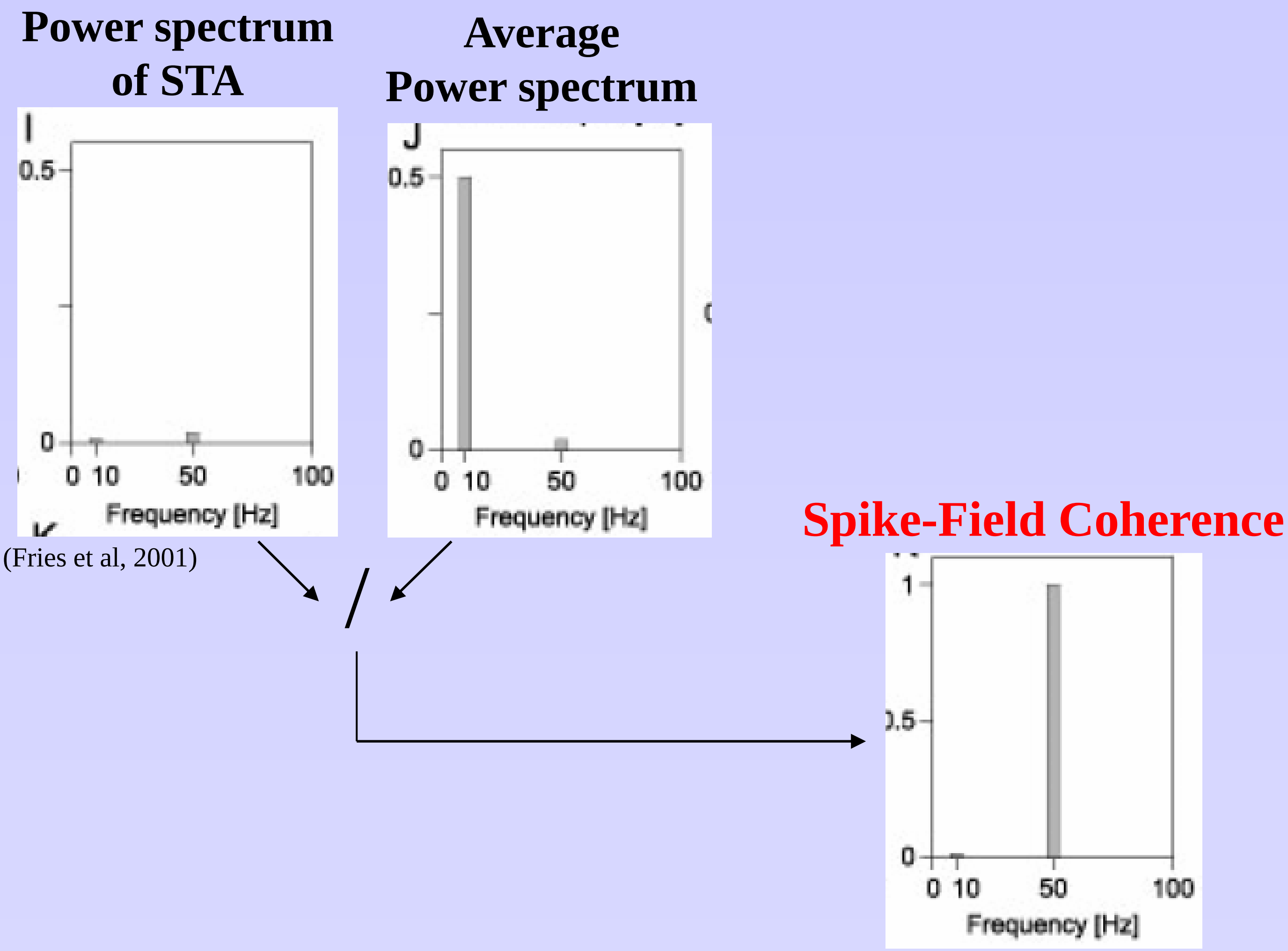


~amount of frequency around average phase-locked LFP

(Fries et al, 2001)

Spike-Field coherence

- Step 3



Power spectrum of STA

Average Power spectrum

(Fries et al, 2001)

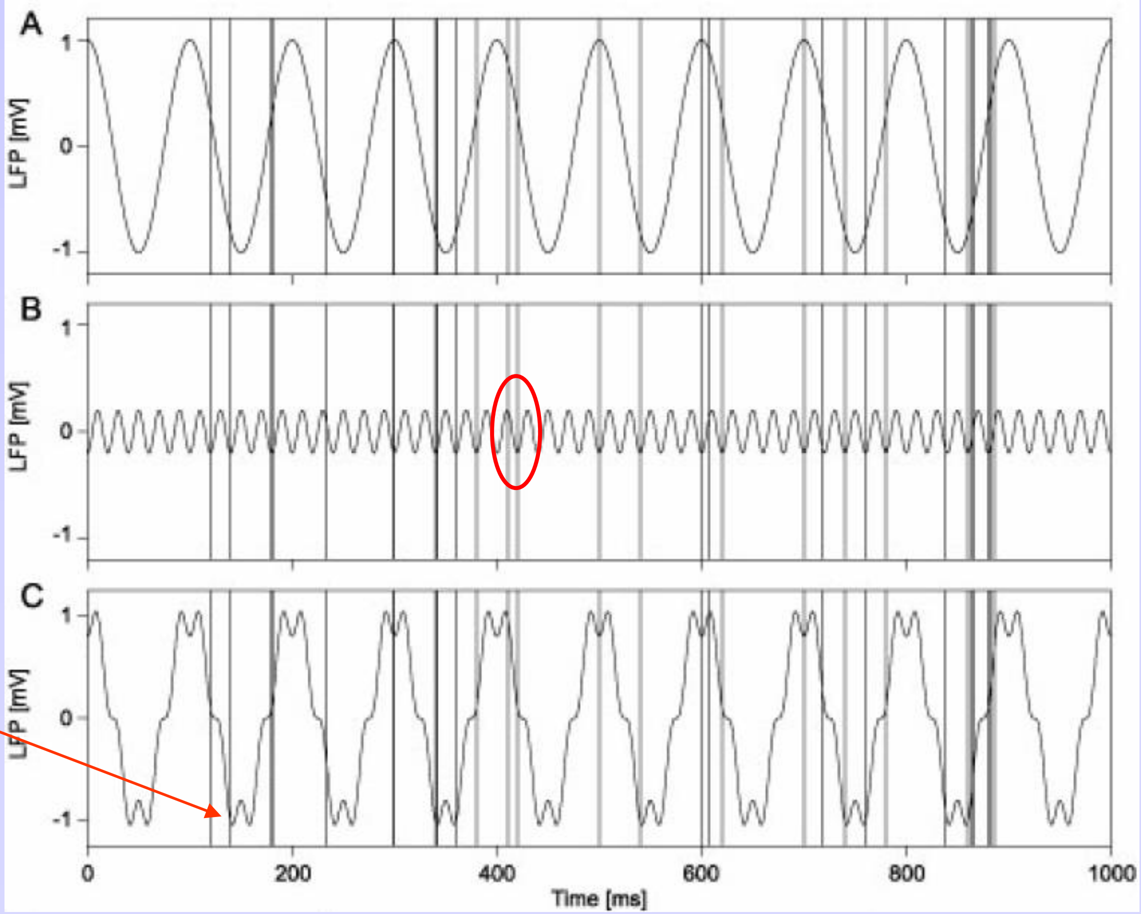
/

Spike-Field Coherence

Spike-Field Coherence: amount of synchrony at each particular frequency

Spike-Field coherence

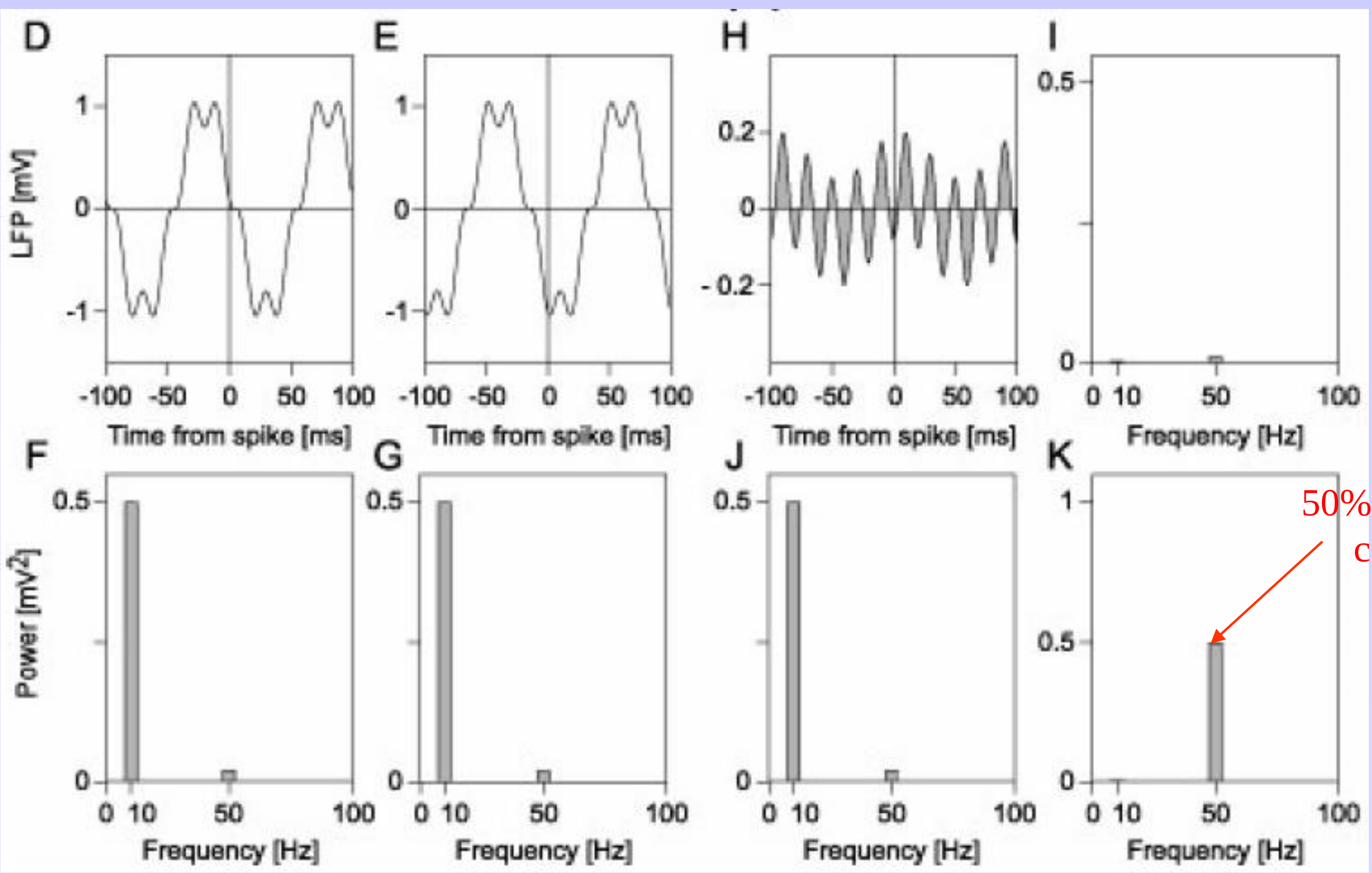
- Spike Field coherence is a linear measure of synchrony



50% gamma synchrony

(Fries et al, 2001)

Spike-Field coherence



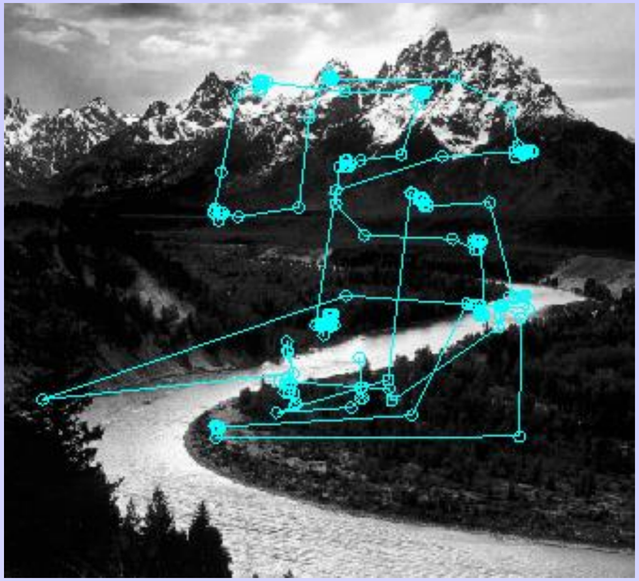
50% Spike-field coherence

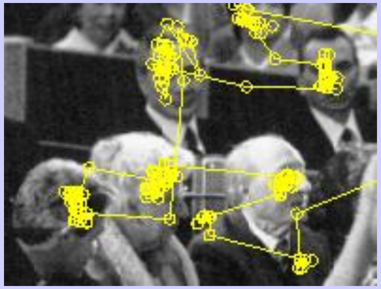
(Fries et al, 2001)

Linear measure of spike-LFP synchrony

Spike-Field coherence

- Visual attention: Directing visual processing toward particular visual objects





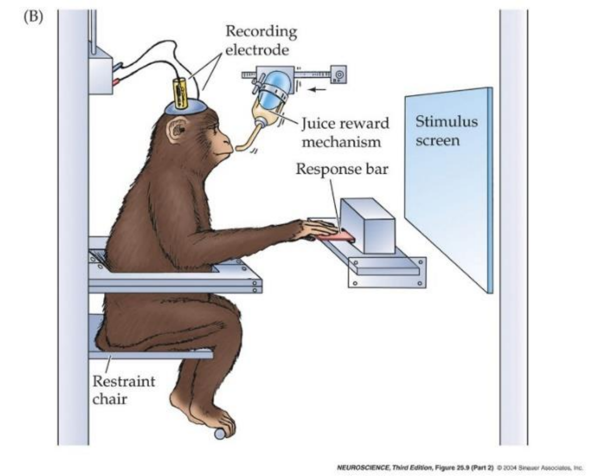
Eye Movements
of Reading

Viewing a Face

- What happens to visually-responsive cells during attention ?

Spike-Field coherence

- Experimental setup



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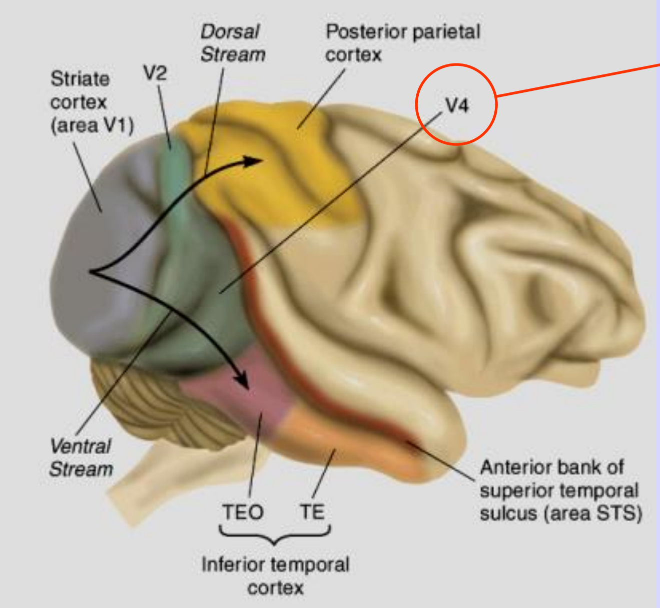
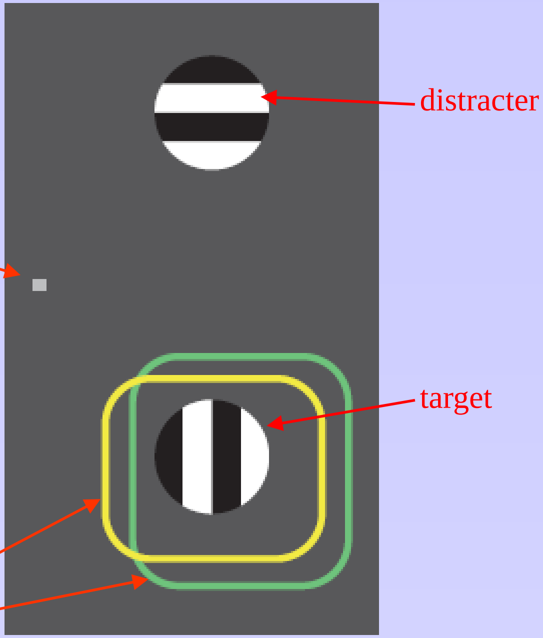




Fixation

Receptive Fields

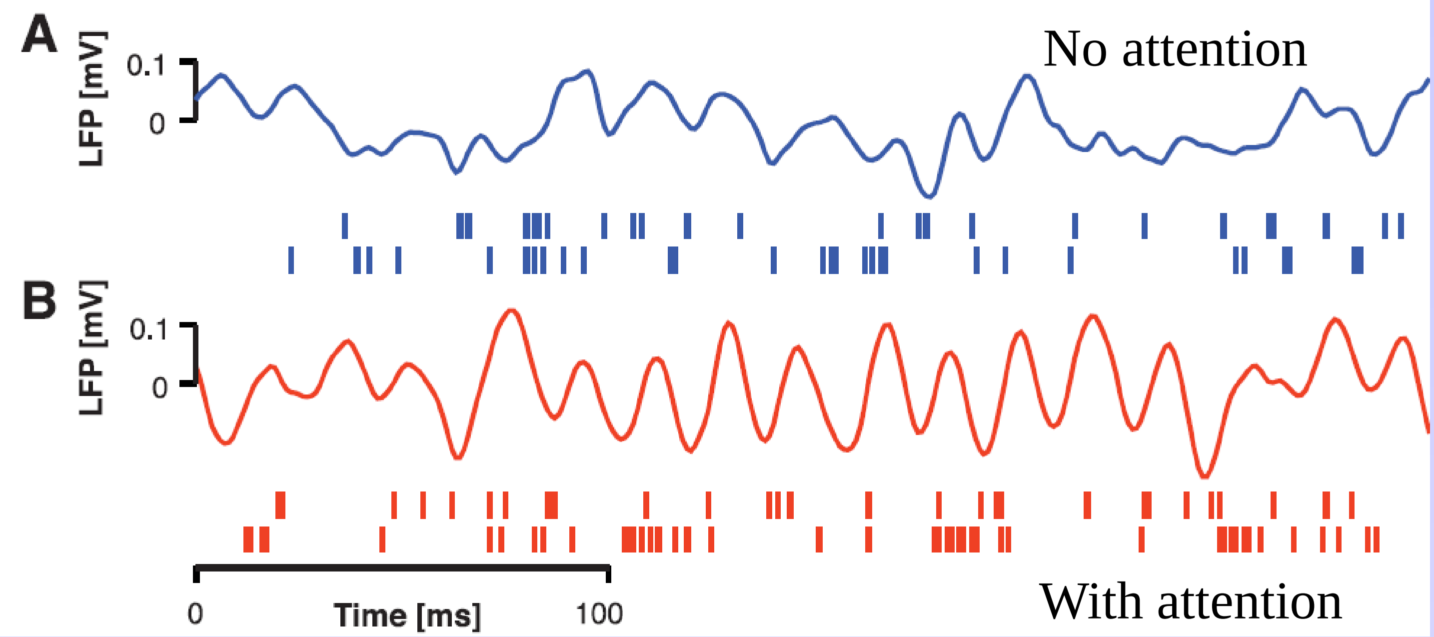
(Fries et al, 2001)

Delay   Stimulus on   Response

2 conditions: with/without attention in RF (attention cue=fixation spot color)

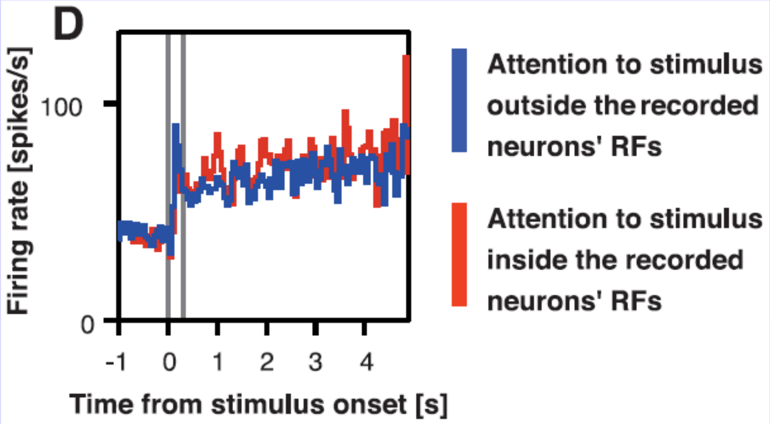
Spike-Field coherence

- Data



No attention

With attention

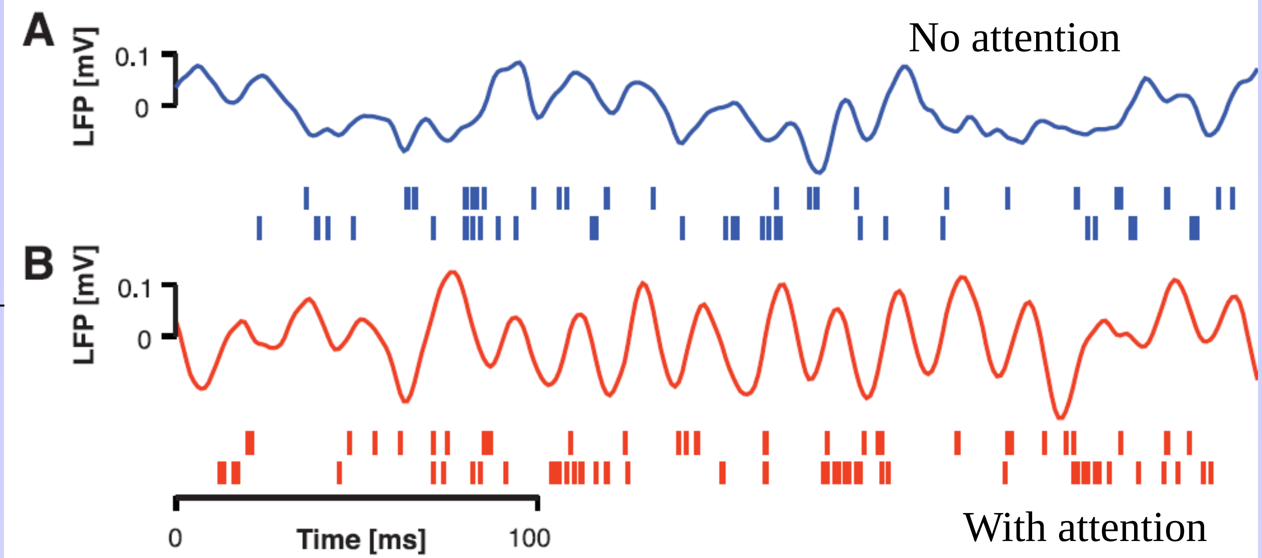


→ No difference in firing rates

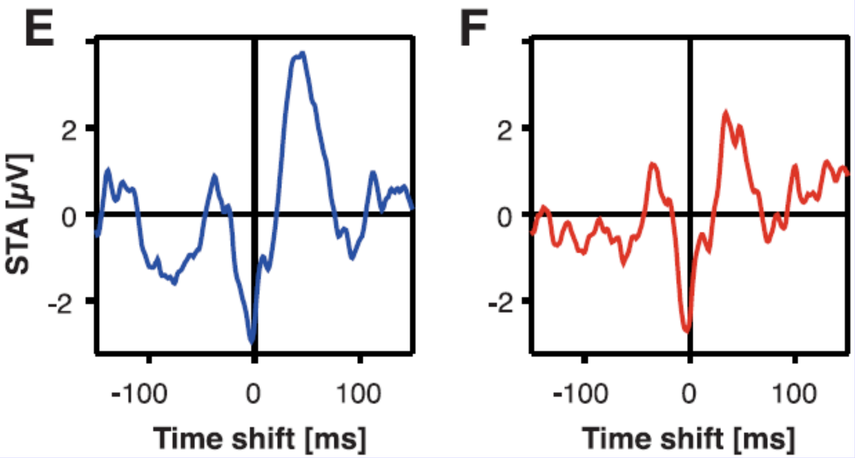
(Fries et al, 2001)

Spike-Field coherence

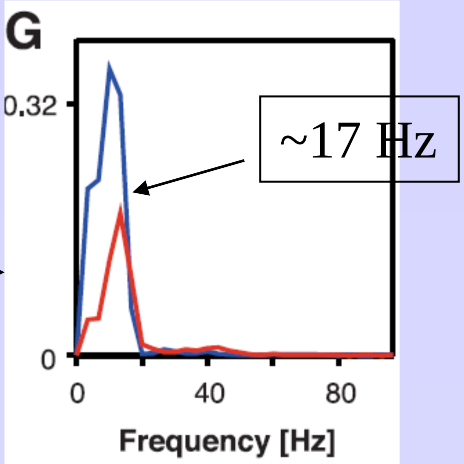
- Delay period



STA of LFP



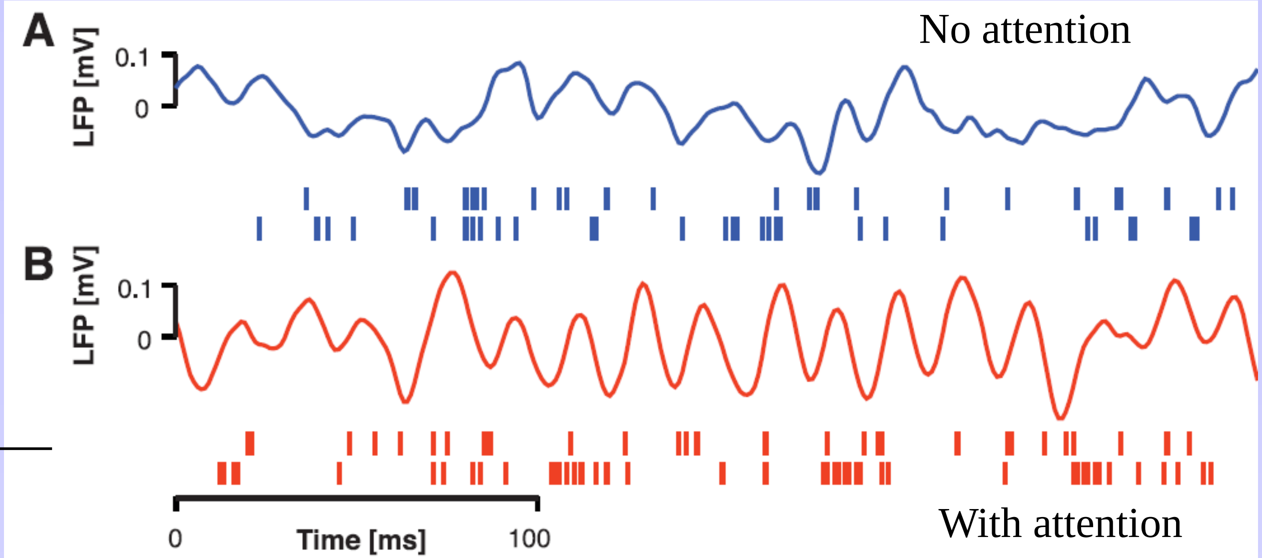
Average Power Spectrum



(Fries et al, 2001)

Spike-Field Coherence

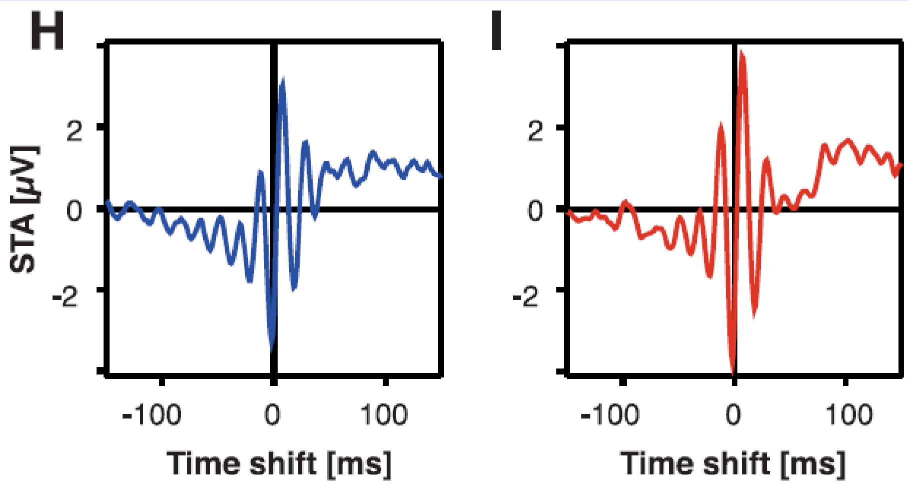
- Stimulus Period



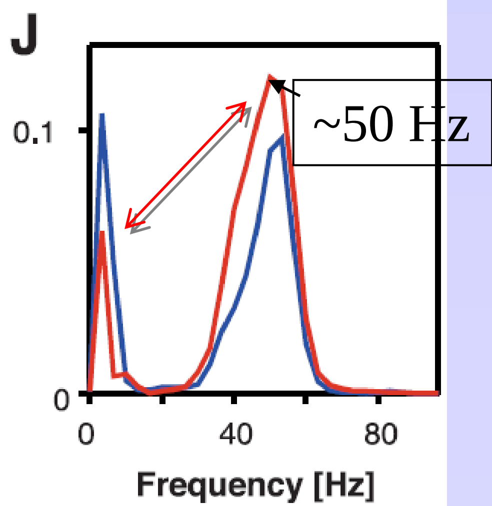
No attention

With attention

Spike triggered average



Power spectrum of STA



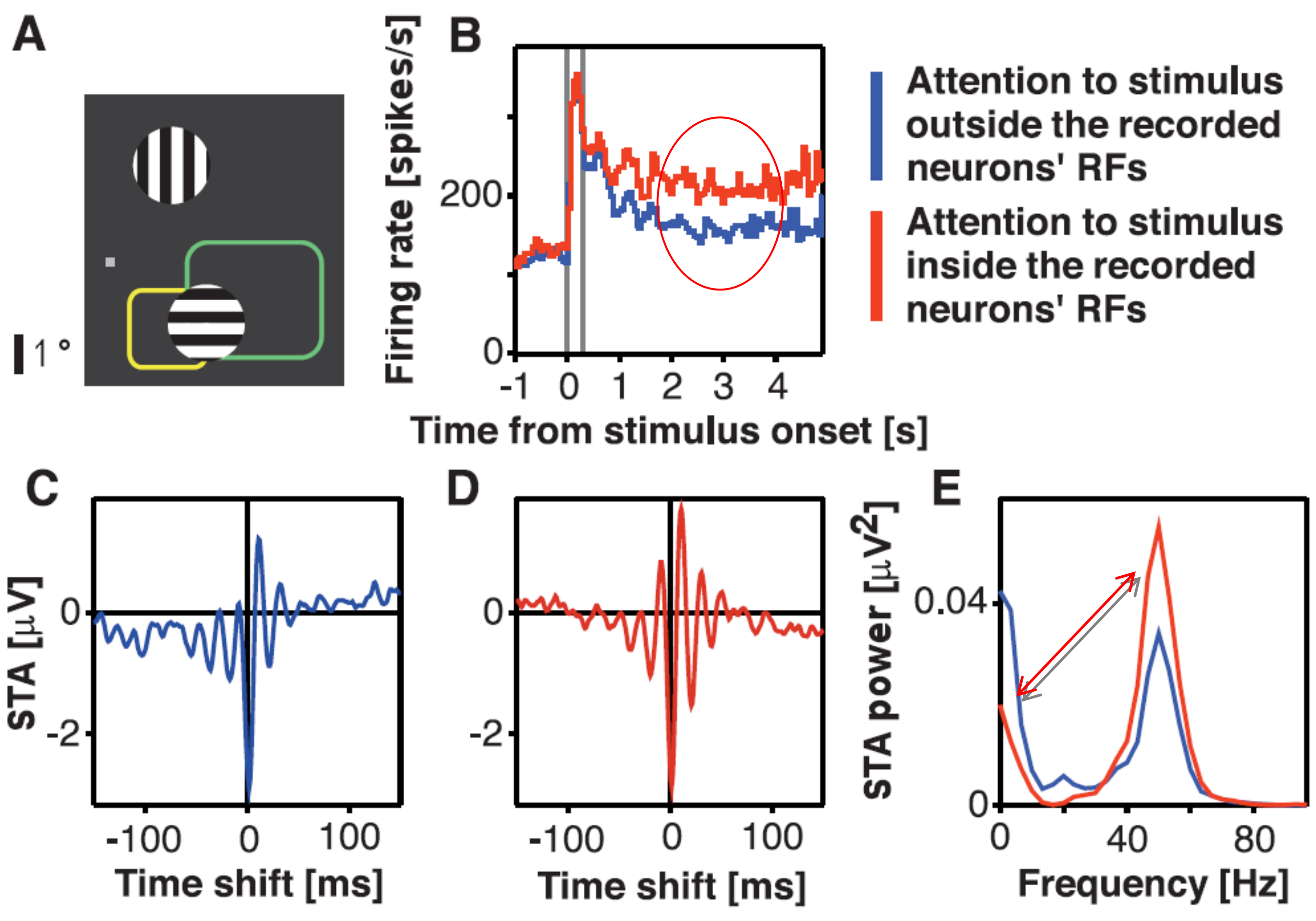
~50 Hz

➔ More gamma synchrony during stim presentation, if attended

(Fries et al, 2001)

Spike-Field coherence

- Distracter close to the receptive fields: Same effects and suppression of firing rate when attention is just outside the RF → Attention is competitive.



(Fries et al, 2001)

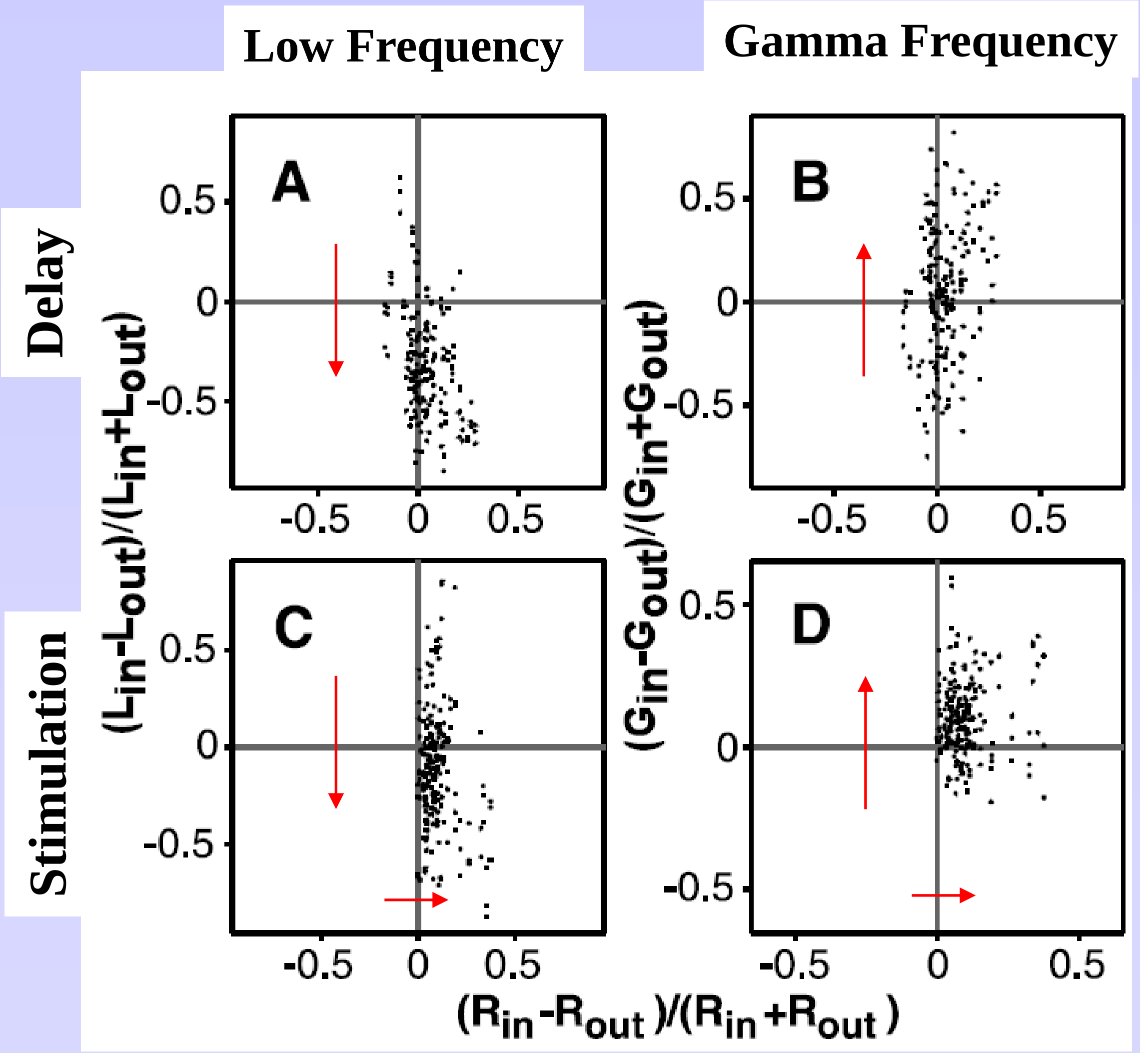
Spike-Field coherence

- Attention-mediated changes of height of peak in SFC for (L)ow frequency, (G)amma frequency, Vs. Firing (R)ate change

Effect of Attention:

Delay: decrease SFC at low freq., increase SFC at gamma freq.

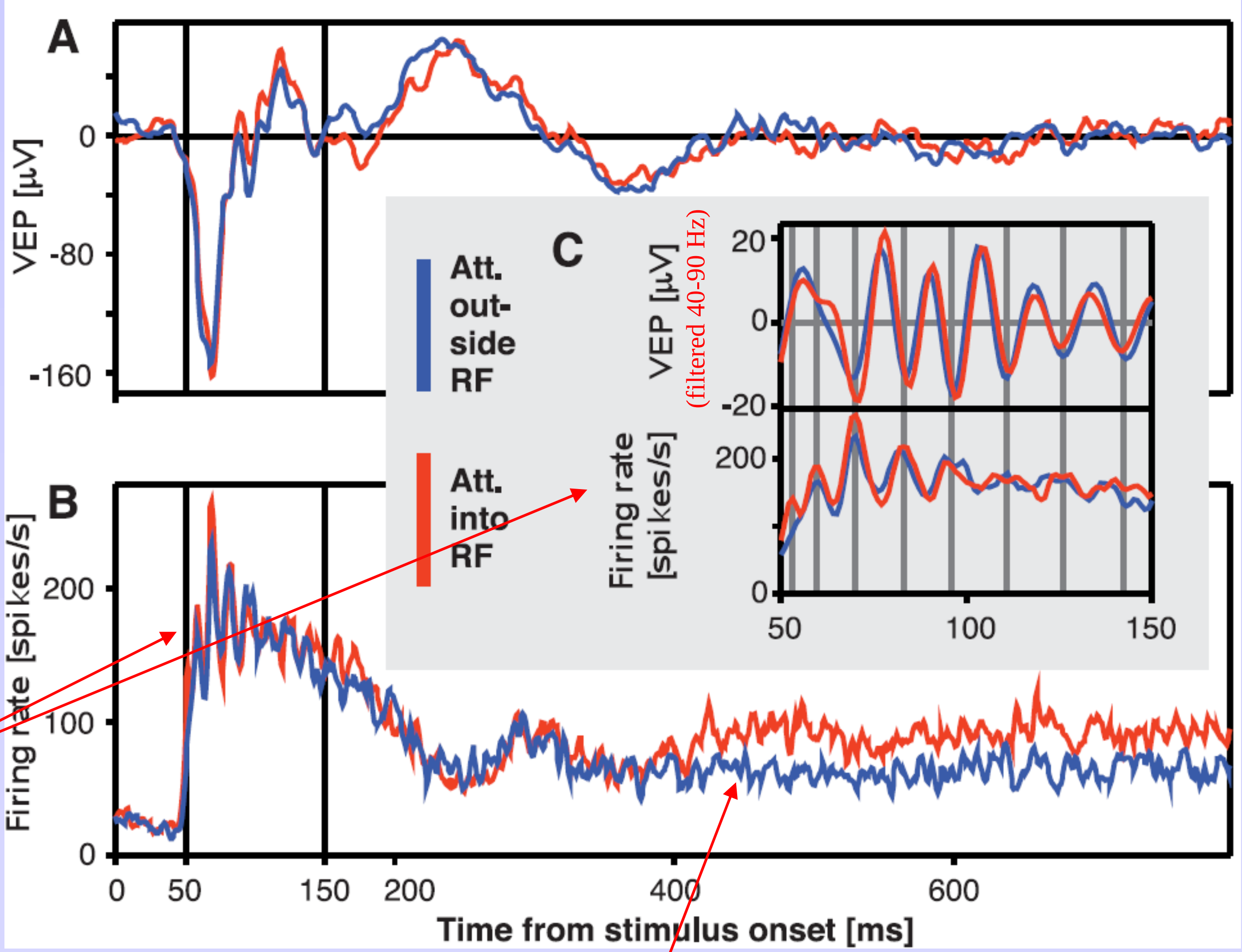
Stim: same, plus increase in Firing Rate



(Fries et al, 2001)

Spike-Field coherence

- Poststimulus Firing rate and LFP (Visual Evoked Potentials)



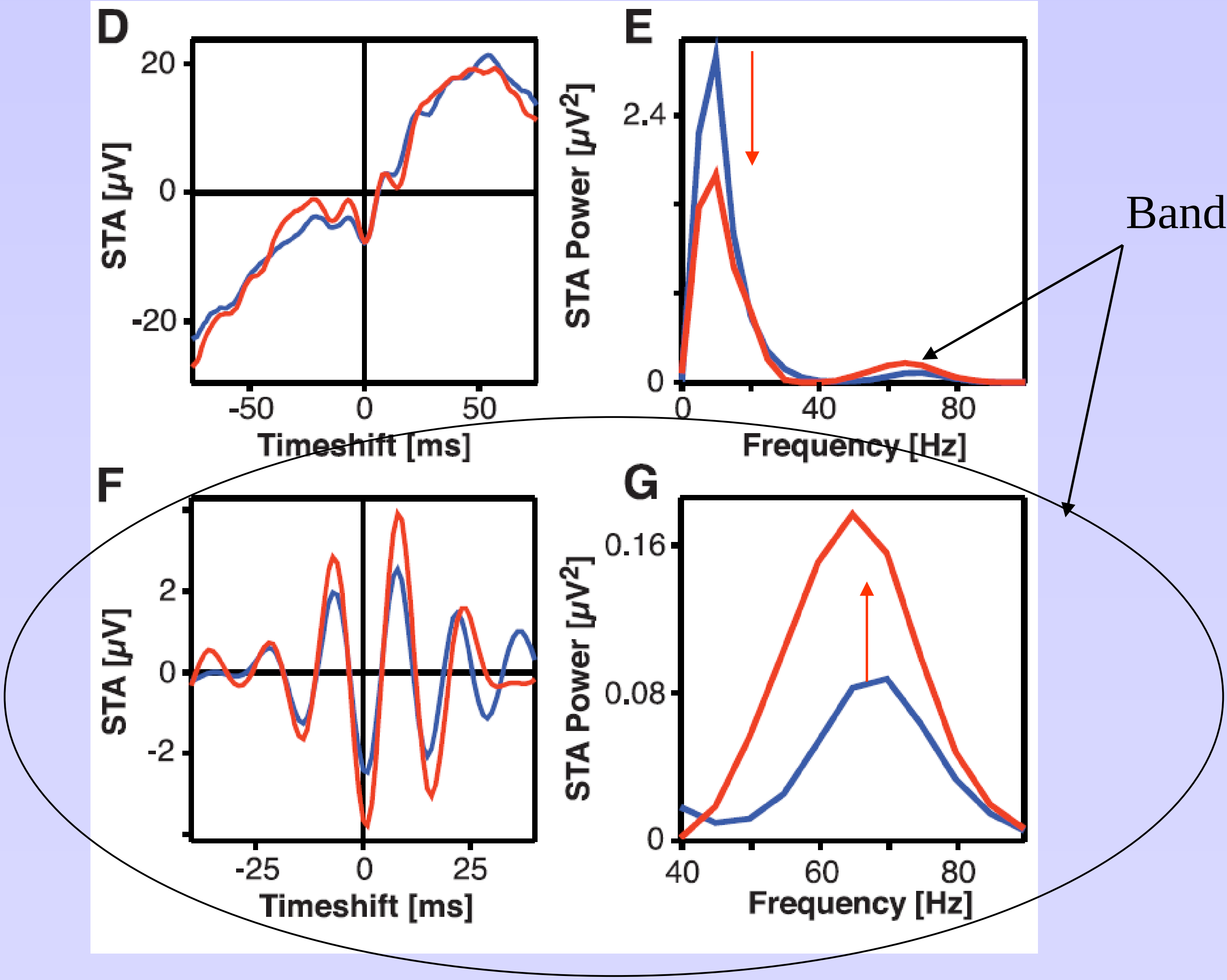
Stimulus-locked
Gamma (50-100 ms)

Late firing rate difference onset

(Fries et al, 2001)

Spike-Field coherence

- First 100 ms after stimulus onset: gamma synchrony is modulated by attention



Bandpass at gamma

(Fries et al, 2001)