Neural Signal and Neural Noise in Primary Auditory Cortex

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Introduction

- Information is represented in neurons by sequences of action potentials (spikes).
- The response of a neuron to a given stimulus exhibits variability.
- Standard model: an underlying time-varying *probability function* governs the firing of spikes, usually modeled as a non-stationary point process.
- We measure the response of cell to broadband sounds and derived Spectro-Temporal Receptive Fields (STRF), a linear, quantitative descriptor of how a cell responds to dynamic sounds.
- When predicting responses to a new sound, there is a difference between the response predicted by the STRF and the actual response. How much difference is due to non-linearity, and how much is expected from neural variability, such as a Poisson processes?

Summary

- We previously modeled cells in Primary Auditory Cortex (AI) of ferrets as responding linearly to the low-passed envelope of incoming sounds.
- We model the response of a cell by a linear convolution between an STRF and the envelope of the sound.
- There is typically a difference between the predicted response and the actual response. How much can be attributed to intrinsic variability in the neural firings, and how much to non-linear effects?
- We conclude that most of the difference is attributable to the intrinsic variability ("noise") of the neurons, as manifested by the (non-homogeneous) Poisson statistics of the firings

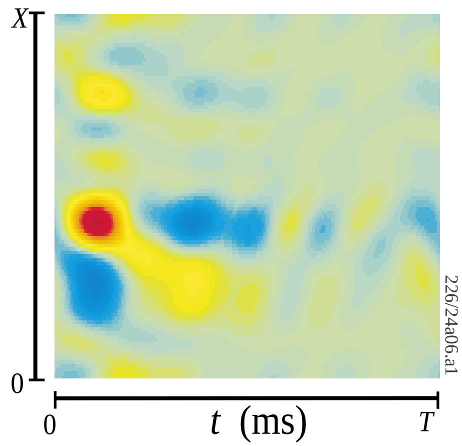
STRFs in AI

Cells are characterized their Spectro-Temporal Response Field (STRF)...

... or by the (Fourier domain) ripple transfer function (TF).

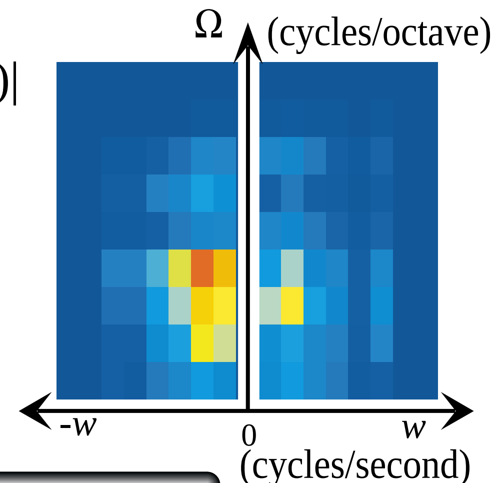
$STRF(t,x)$

$x = \log_2 f/fo$ (octaves)

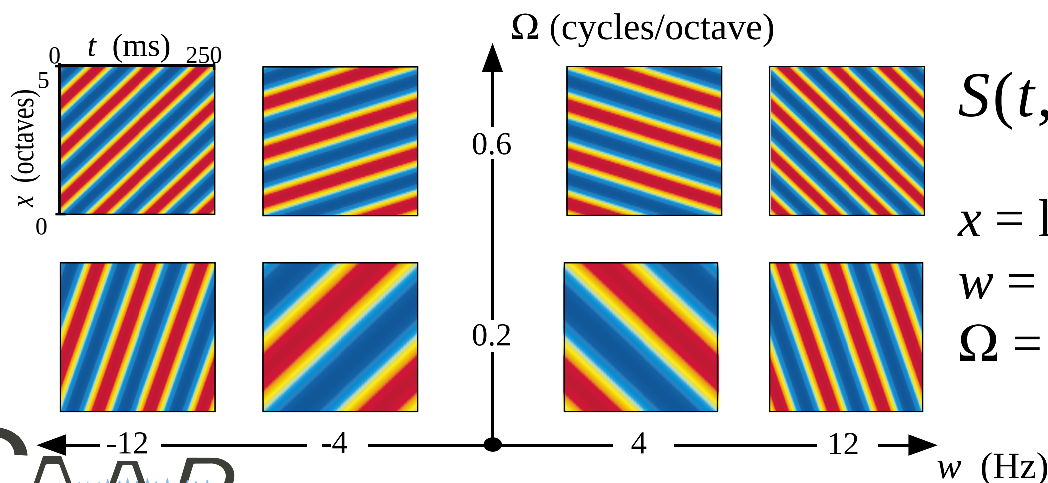


$|\mathcal{F}\{\ \}|$ $\longleftrightarrow$

$|TF(w,\Omega)|$



Moving ripples form the basis for the Fourier domain description of dynamic spectra. At time ***t*** and frequency ***x***, the amplitude ***S(t,x)*** is given by:



$$S(t,x) = \sin(2\pi wt + 2\pi\Omega x + \Phi)$$

$x = \log_2[f / f_0]$
w = ripple velocity, modulation rate
Ω = ripple frequency, spectral density

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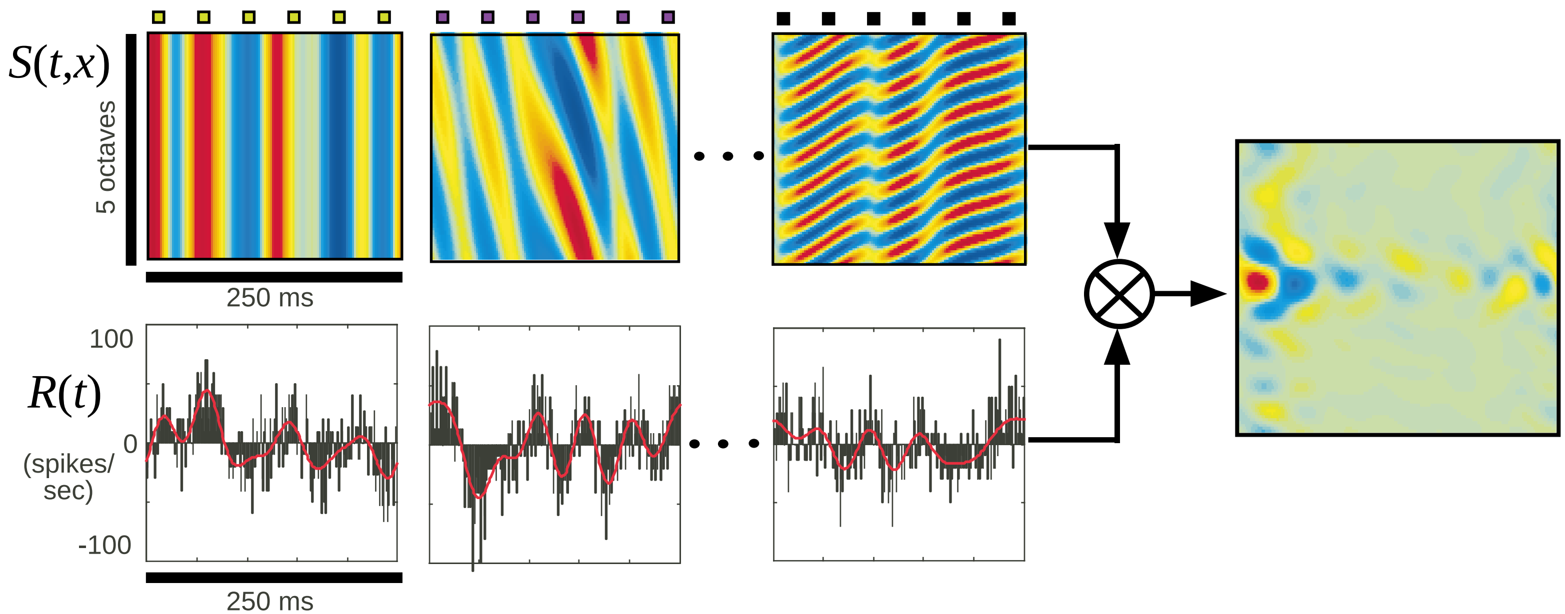
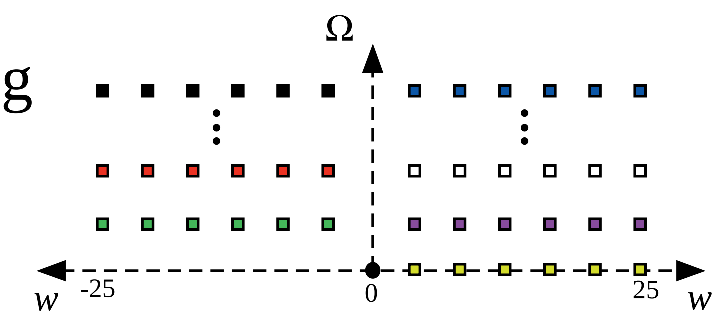
Temporally Orthogonal Ripple Combinations

- STRF measured by reverse-correlating with dynamic spectrum of a broad-band stimulus.
- Temporally Orthogonal Ripple Combinations composed of ripples with different modulation rates.
- Allow clean STRF estimates in relatively short time.



The stimuli shown contain ripples covering the same range of ripple velocities, but at different ripple frequencies.



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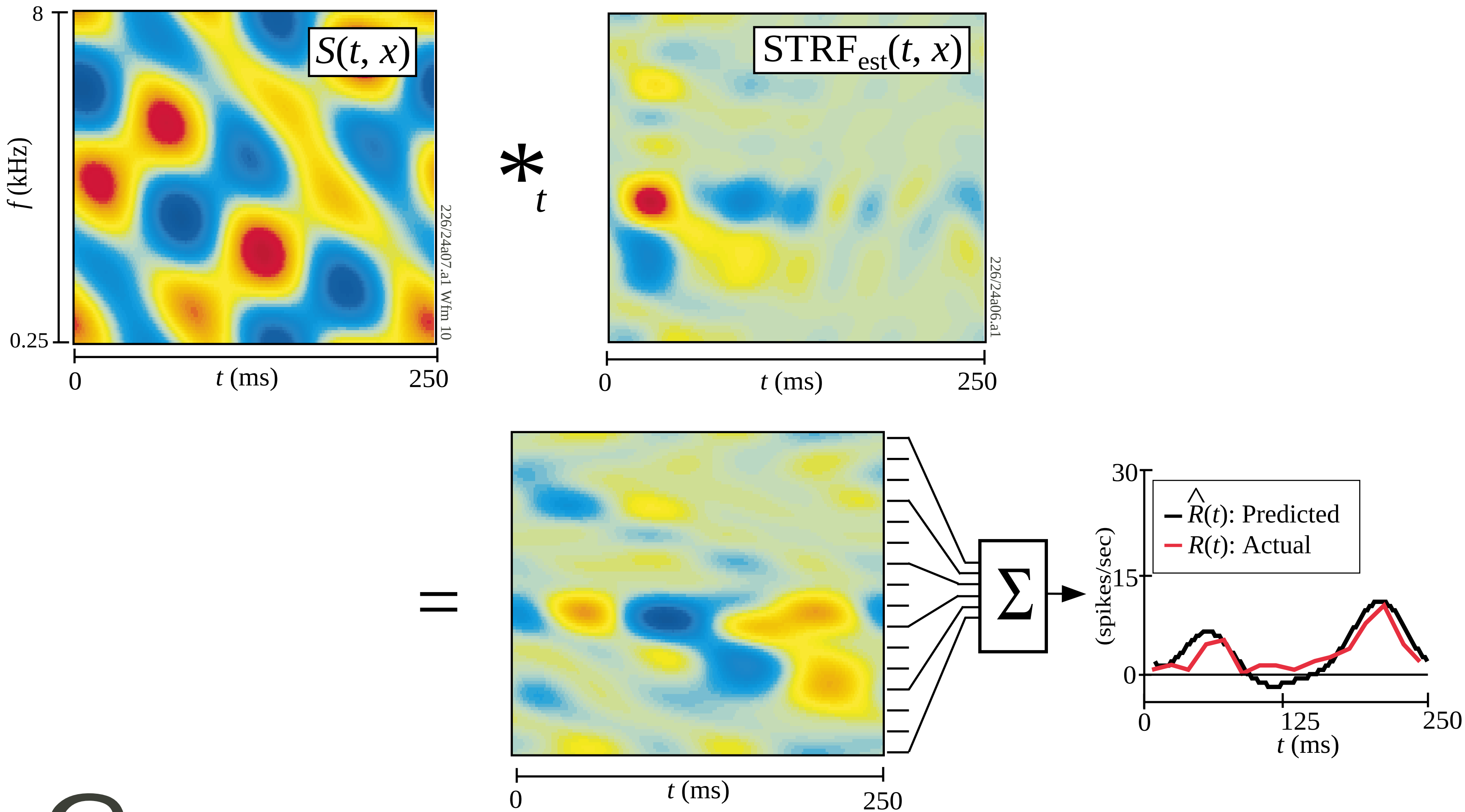
Predicting Responses from STRF

The response to an arbitrary sound is predicted by the convolution of the STRF with the stimulus' spectro-temporal envelope (plus a constant).

$$\hat{R}(t) = \frac{1}{X}\sum_{x}\{\mathrm{STRF}_{est}(t, x) *_t S(t, x)\} + \mathrm{E}\{R(t)\}$$



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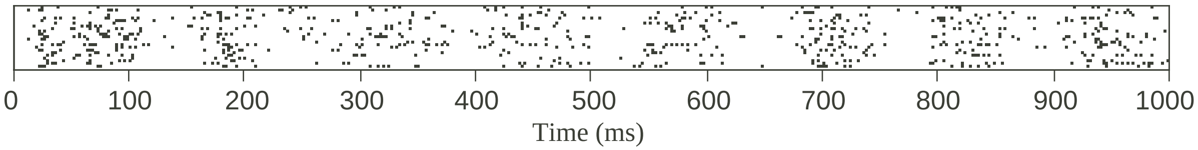
Bootstrap Technique

- From presentation to presentation, there is **variability** or "noise".
- We use **resamples** of data to estimate variability.
- Resamples are of same size as original samples: *N* samples of bootstrap data are drawn *with replacement* from the *N* original samples.
- Repeat procedure many times to create a population of bootstrap resamples whose probability distribution is a good estimator of the probability distribution from which the original data was drawn.
- Mean, variance, and higher order moments of bootstrap population are good, unbiased, estimators of those same moments of the true distribution.
- Related to "Jackknife" technique.

Bootstrap Example

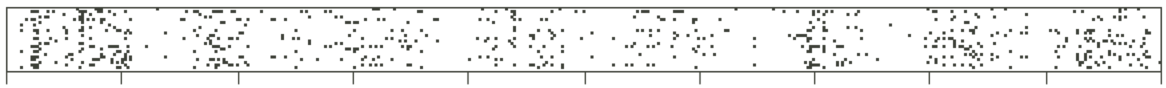
Raster Data 30 sweeps



Mean firing rate: 25.0 spikes/s
Percentage ISI = 40 ms: 0.23%

Resample 1

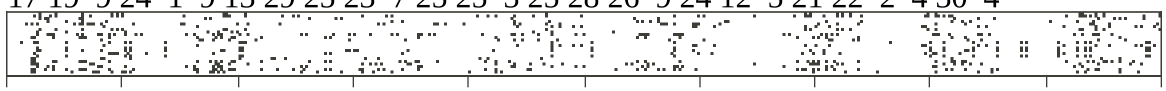
14 5 1 4 17 29 25 6 14 7 23 1 2 13 30 5 27 25 22 14 20 28 7 21 29 2 20 24 9 16



23.1 spikes/s
0.40%

Resample 2

17 19 9 24 1 9 13 29 25 23 7 25 25 3 25 28 26 9 24 12 5 21 22 2 4 30 4

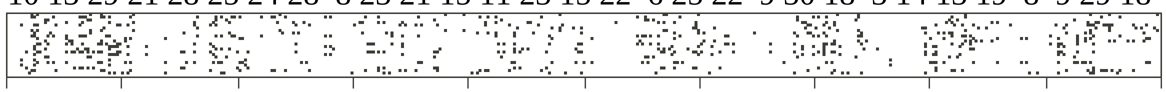


25.4 spikes/s
0.09%

⋮

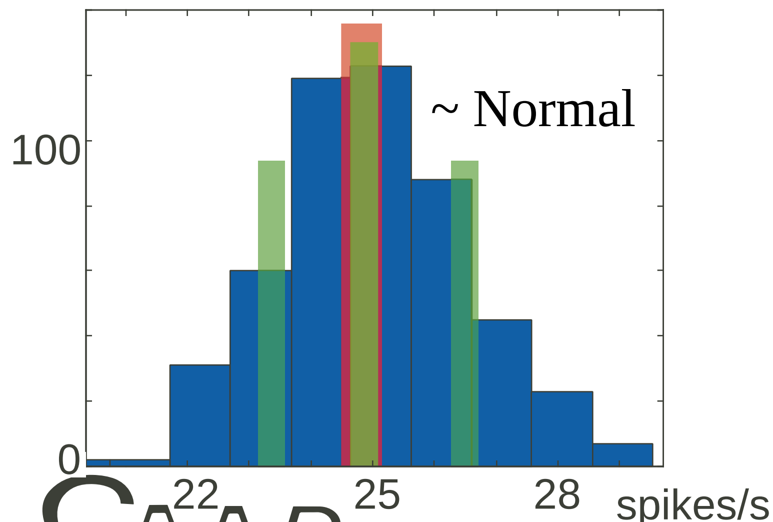
Resample *N*

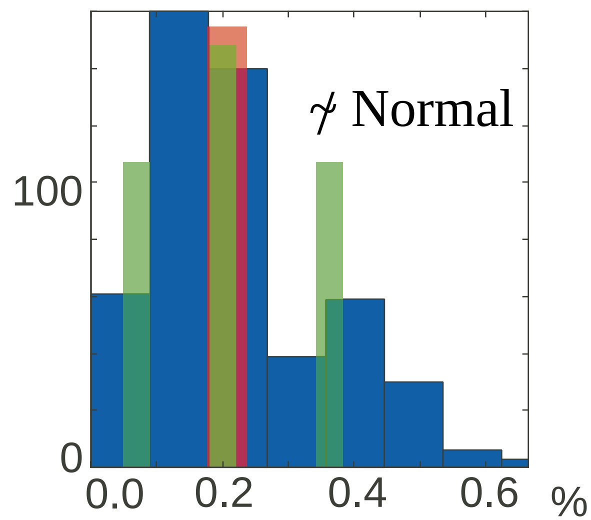
10 13 29 21 28 25 24 28 8 23 21 15 11 23 15 22 6 25 22 9 30 18 3 14 13 19 8 9 29 18



23.6 spikes/s
0.23%

Bootstrap distributions





Best Estimate

Bootstrap mean and standard deviations

N = 500

226/20a04.m2-spk 8 Hz, -0.4 cyc/oct, 65 dB

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Poisson Statistics

- The measured observable is the spike train, which we model as a Poisson random variable.
- Assume underlying, deterministic, probability density for firing, $\boldsymbol{r(t)}$
- # of measurements (stimulus presentations) = $\boldsymbol{n}$
- probability of measuring N spikes between $\boldsymbol{t}$ and $\boldsymbol{\Delta t}$: $\boldsymbol{p(N(t;\Delta t)) = r(t)\,\Delta t}$
- Expectation values for mean, $\boldsymbol{\eta}$, and variance, $\boldsymbol{\sigma}$, of $\boldsymbol{N}$:

$$\eta_N(t;\Delta t) := E\{N(t;\Delta t)\} = n\, r(t)\, \Delta t$$

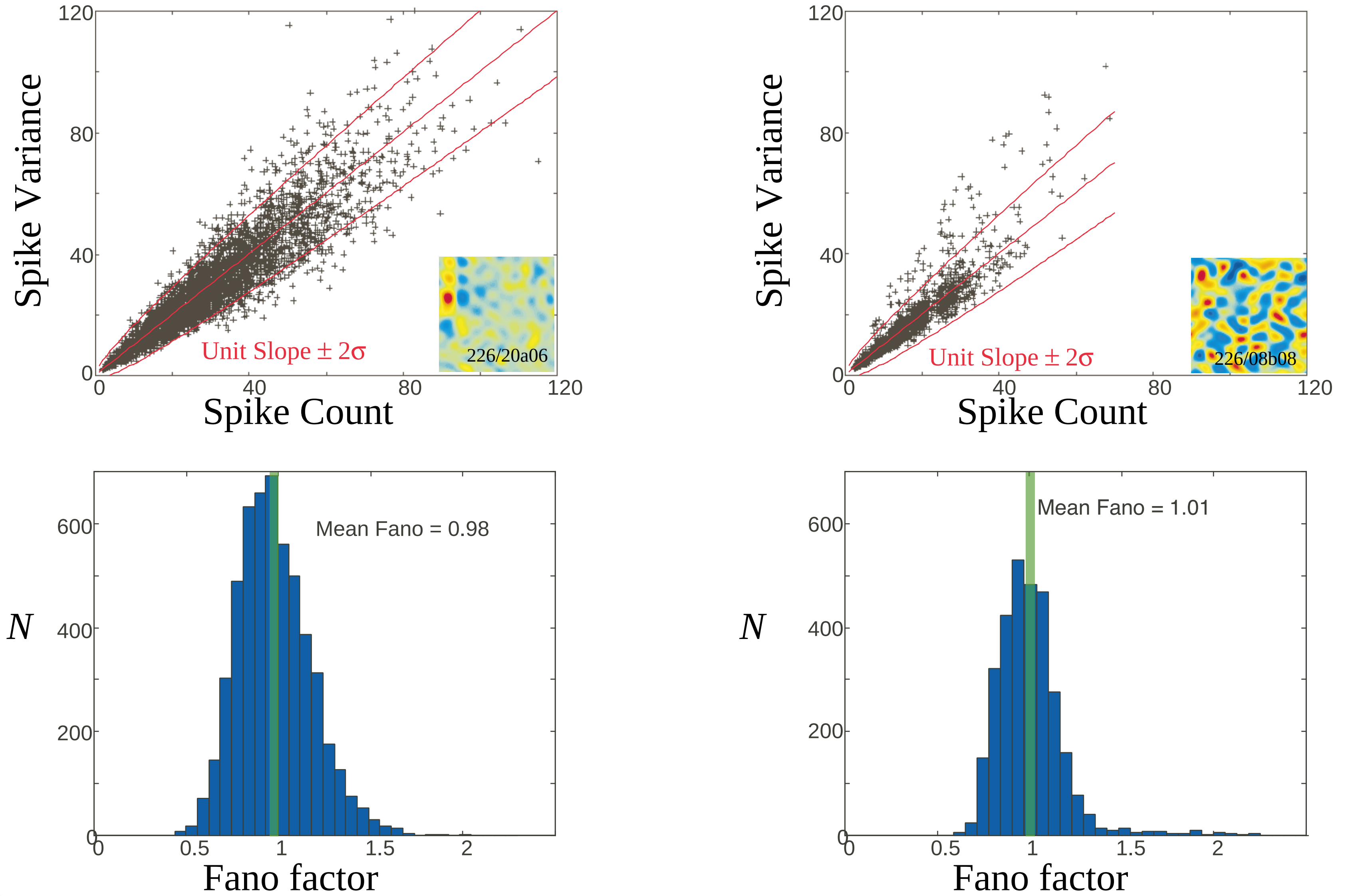
$$\sigma_N^2(t;\Delta t) := E\{(N[t;\Delta t)]^2\} - [\eta_N(t;\Delta t)]^2 = \eta_N(t;\Delta t) = n\, r(t)\, \Delta t$$

- Thus a prediction for the Fano factor:

$$\phi_N(t;\Delta t) := \eta_N(t;\Delta t)/\sigma_N^2(t;\Delta t) = 1$$

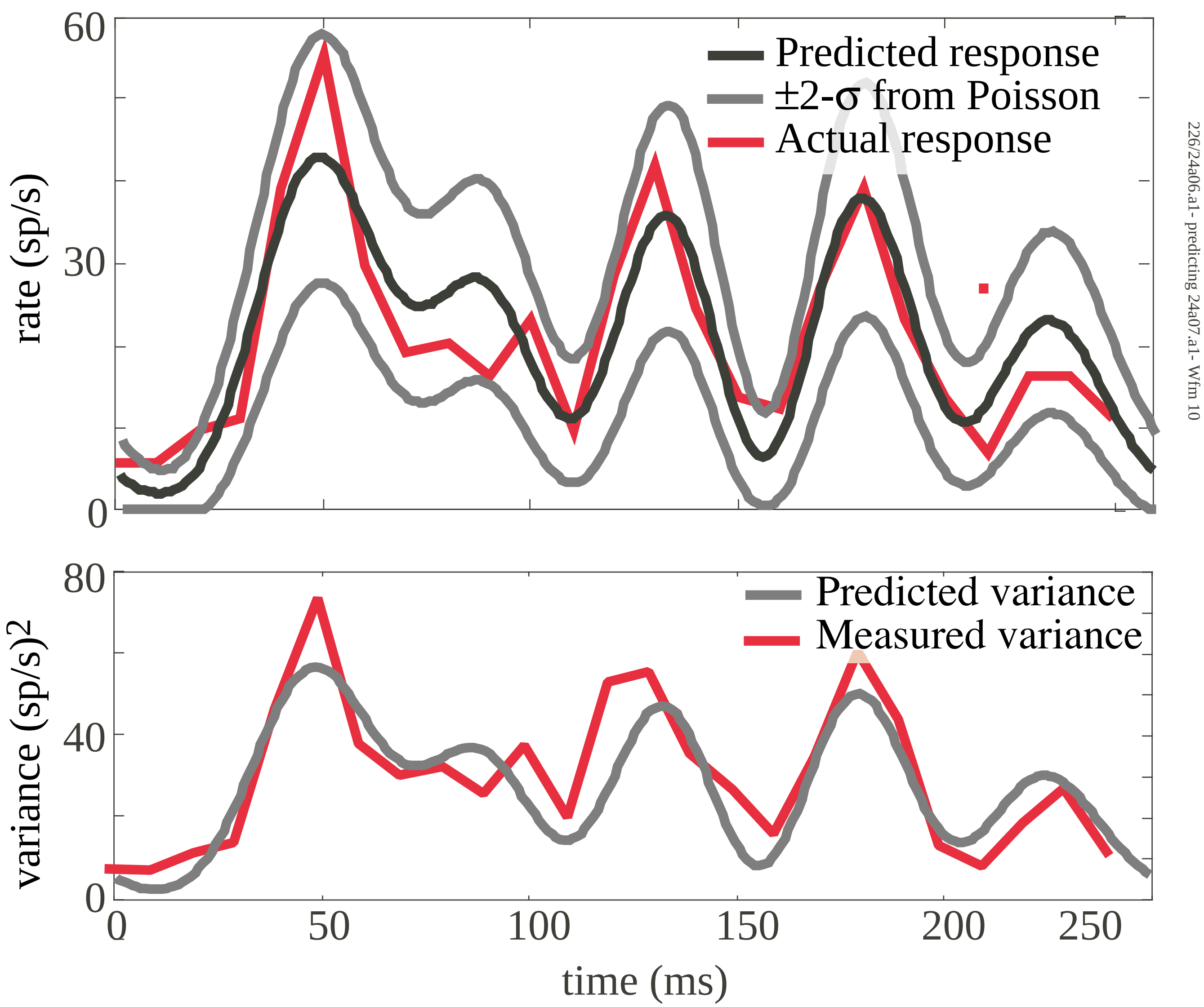
Poisson Variance Examples

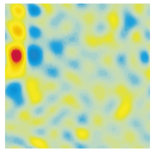
- Examples of the computation of the Fano factor for two cells, one "clean" and the other very noisy.



Examples Continued

- The actual response lies nicely within the variability predicted by Poisson noise.
- The variance in the measured response corresponds nicely to the predicted variance.





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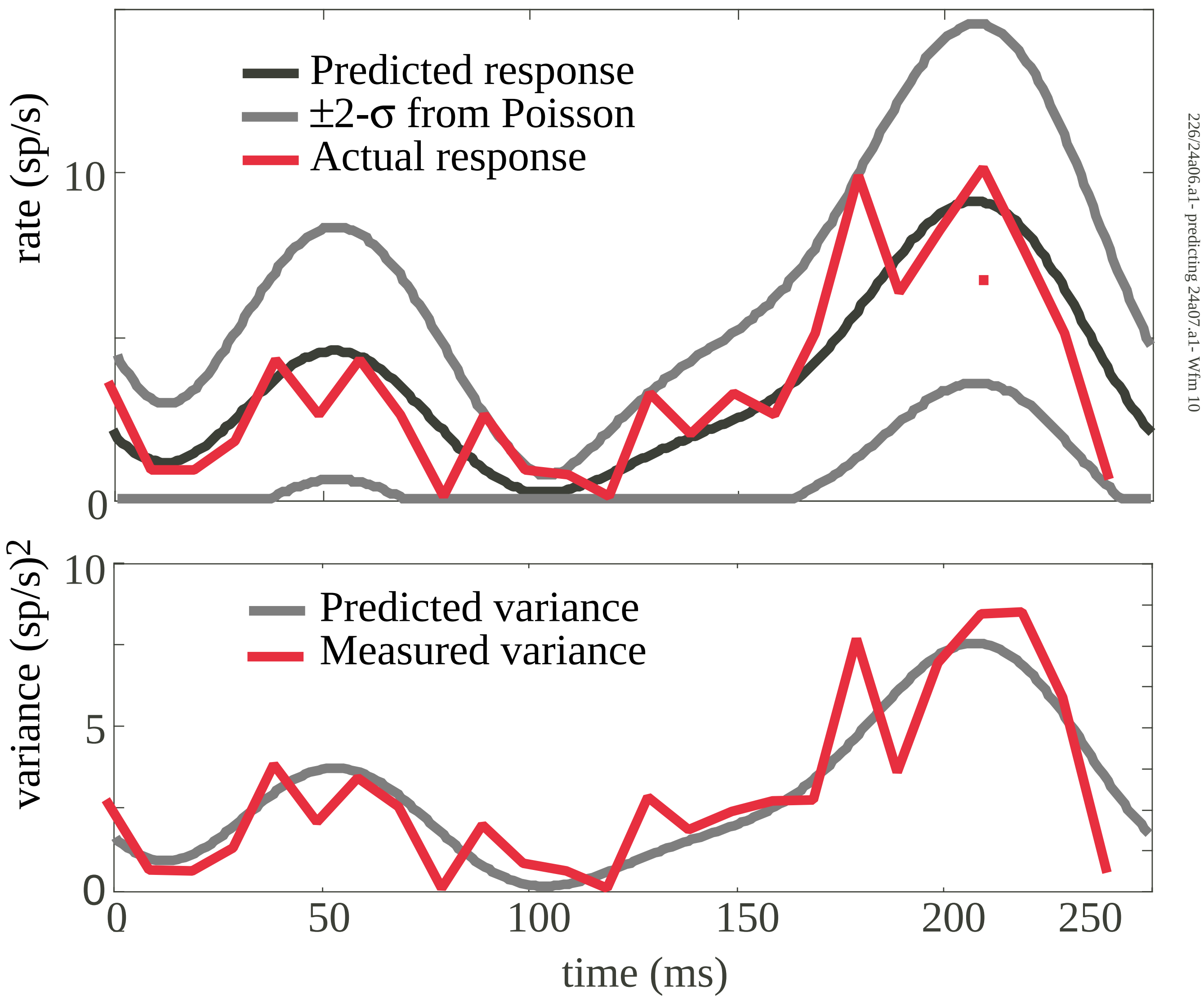
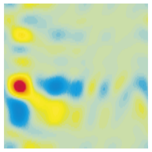
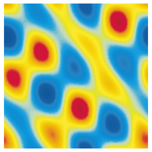
Predictions with Variability

- The actual response lies nicely within the variability predicted by Poisson noise.
- The variance in the measured response corresponds nicely to the predicted variance.







Signal to Noise Theory

- Define observed firing rate: $\boldsymbol{R(t;\Delta t) = (1/n)\, N(t,\Delta t)/\Delta t}$
- $\boldsymbol{\eta_R(t,\Delta t) := E\{R(t;\Delta t)\} = r(t)}$

  $\boldsymbol{\sigma_R^2(t;\Delta t) := E\{[R(t;\Delta t)]^2\} - [\eta_R(t;\Delta t)]^2 = r(t)/(n\,\Delta t)}$
- Signal & Variance ("Noise") Power:

$$\boldsymbol{P := \sum_t [r(t)]^2 \qquad P_\sigma := \sum_t \sigma_R^2(t;\Delta t)}$$

- Signal to Noise Ratio:

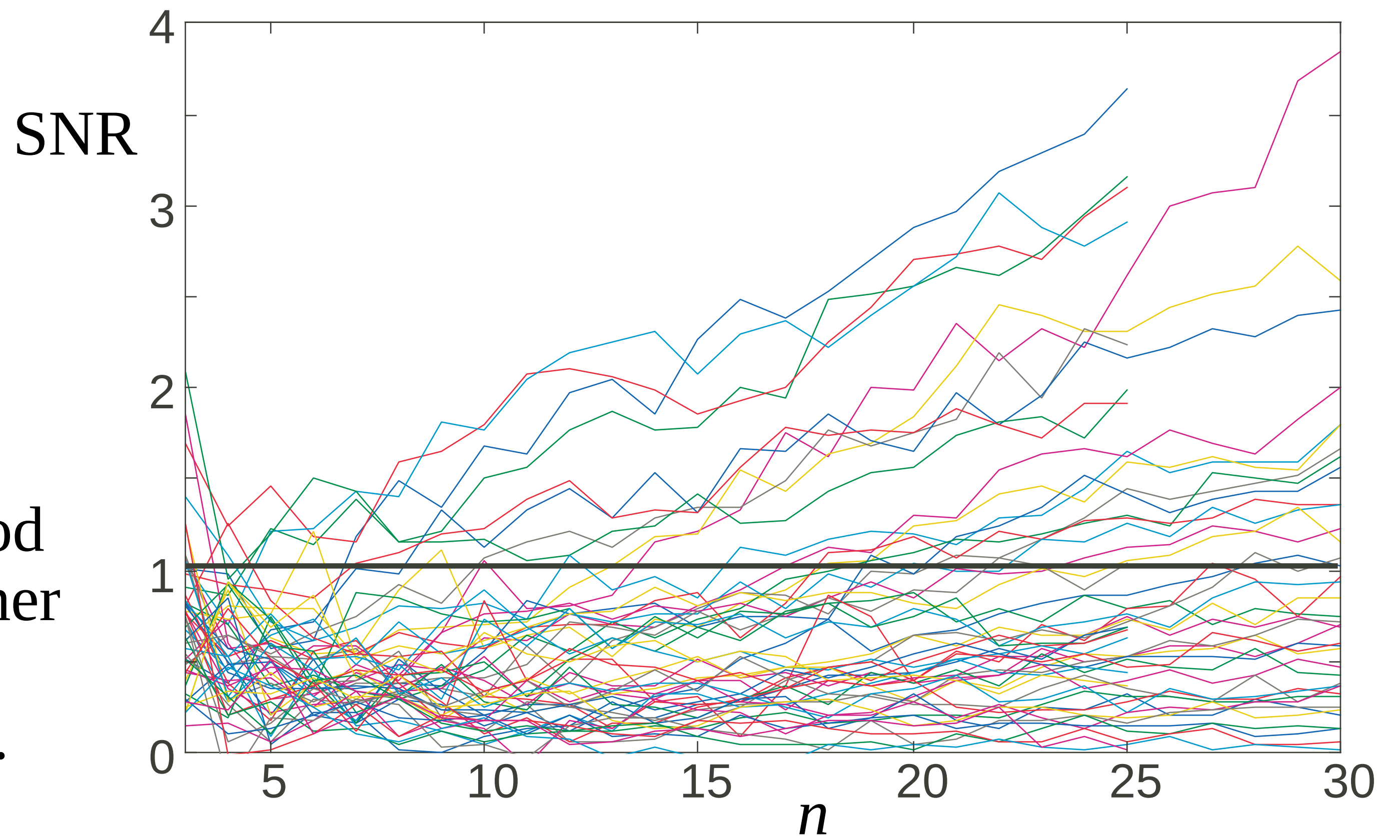
$$\boldsymbol{\mathrm{SNR} := P/P_\sigma = n\,\Delta t \left(\sum_t [r(t)]^2\right) / \left(\sum_t r(t)\right)}$$

- SNR grows with rate
- SNR proportional to number of repetitions (more general than Poisson).

Signal to Noise in Practice

- Variability analysis distinguishes high SNR (> 1) from low SNR

- SNR for good cells increased (linear with steep slope) with # of sweeps *n*.



- SNR for linear component of good cells is much higher than that for non-linear component.

Increasing the SNR

- Frequency domain:
  - $\Pi_\sigma(\omega) = \mathcal{F}\{P_\sigma(t)\}$ is constant for all ω.
  - In practice, $\Pi(\omega) = \mathcal{F}\{P(t)\}$ is band-limited, so

$$\sum^{\infty} \Pi(\omega) = \sum^{\omega^{crit}} \Pi(\omega).$$

  - We can increase the SNR by using

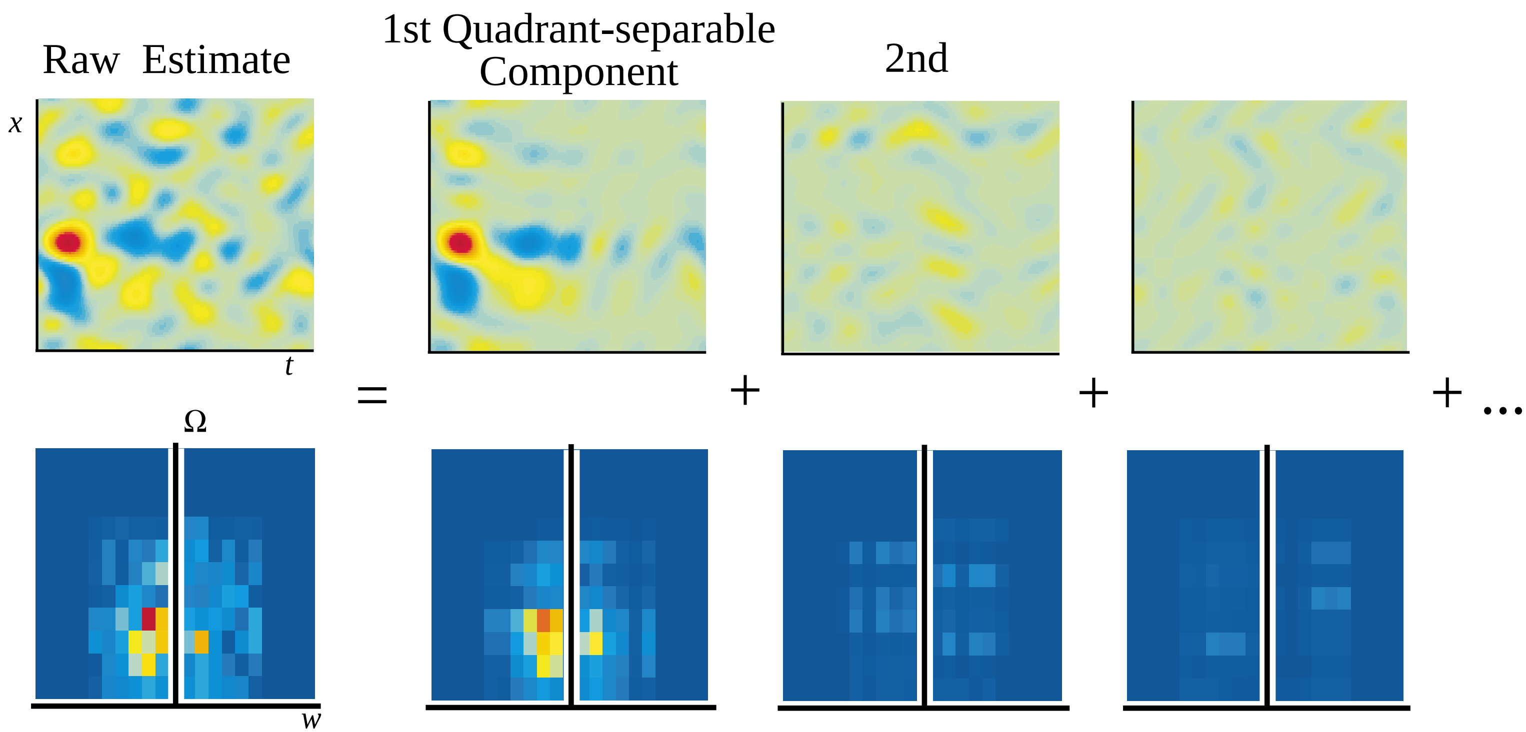
$$\mathrm{SNR}^{incr} := P^{incr}/P_\sigma^{incr} = \left(\sum^{\omega^{crit}} \Pi(\omega)\right) / \left(\sum^{\omega^{crit}} \Pi_\sigma(\omega)\right)$$

  - This is done implicitly by binning or, when deriving the STRF, using low-passed frequency envelopes.

Singular Value Decomposition

- Singular Value Decomposition (SVD) can be used to estimate the rank of a matrix corrupted by noise. It decomposes the matrix into a sum of rank one matrices, ordered by magnitude. The first *k* components sum to a matrix of rank *k* which minimizes the power of the remaining components.

- We apply SVD to each quadrant of the transfer function. Below, an STRF and the three most significant quadrant-separable components, derived from SVD, are shown.



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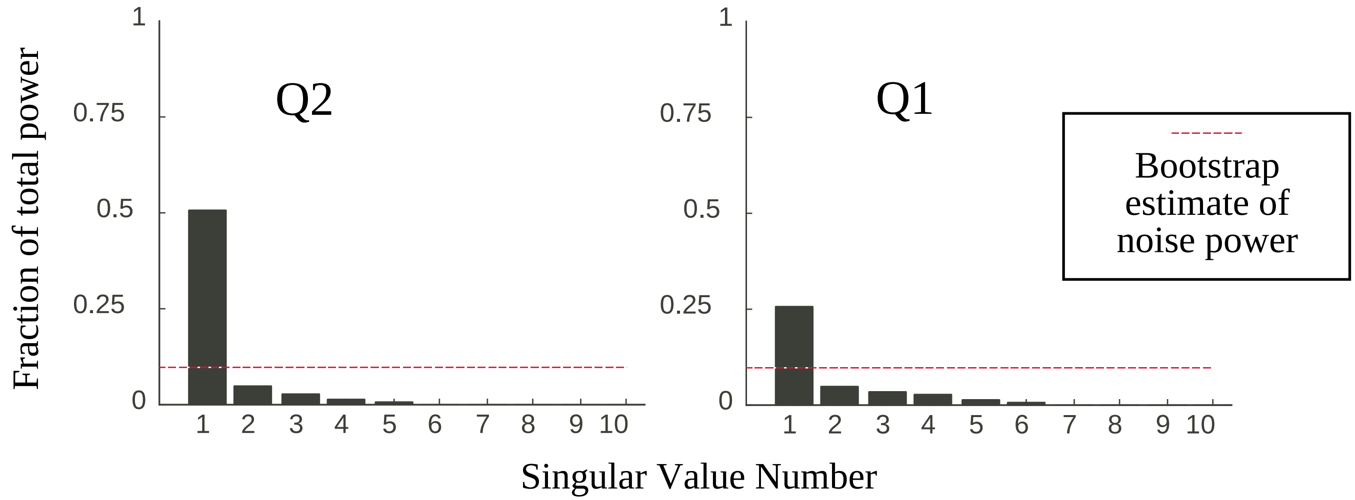
Singular Value Decomposition Example



- SVD naturally picks out high SNR components of a matrix.
- Large jumps in the singular values.
- Jumps straddle bootstrap estimate of noise.
- Noise can be removed by discarding lower-magnitude components.

Selected References

Spectro-Temporal Correlation Methods

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Poisson models, Fano factors, information theory and all that

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