Spectro-Temporal Processing of Dynamic Broadband Sounds In Auditory Cortex

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Outline

- Introductory Material
- Stimulus Types
- Spectro-Temporal Response Fields
- Predicting Responses to Novel Stimuli
- Non-Linearities

- **Introductory Material**
- Stimulus Types
- Spectro-Temporal Response Fields
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Motivation

- **The Big Quest**
  Teasing out “function” of Primary Auditory Cortex (AI)

$$\text{function} \approx \begin{cases} \text{which sounds/features evoke responses?} \\ \text{how are they encoded into spike trains?} \end{cases}$$

- **Broadband and dynamic sounds**
  - Evoke strong, sustained, dynamic responses in AI
  - Many natural sounds
    e.g. speech, vocalizations, backgrounds

- **Reasonable quest**
  Quantitative measure of how spikes encode sound features
  - Quantitative descriptor
  - Quantitative predictor
  - Visual tool—*a la* Spectral Response Field/Tuning Curve

- **Compromise** from quantitative necessity
  - Restrict broadband and dynamic sounds to mathematically simple subset:
  - **Noise**—strongly modulated in **spectrum** and **time**
  - not a severe compromise

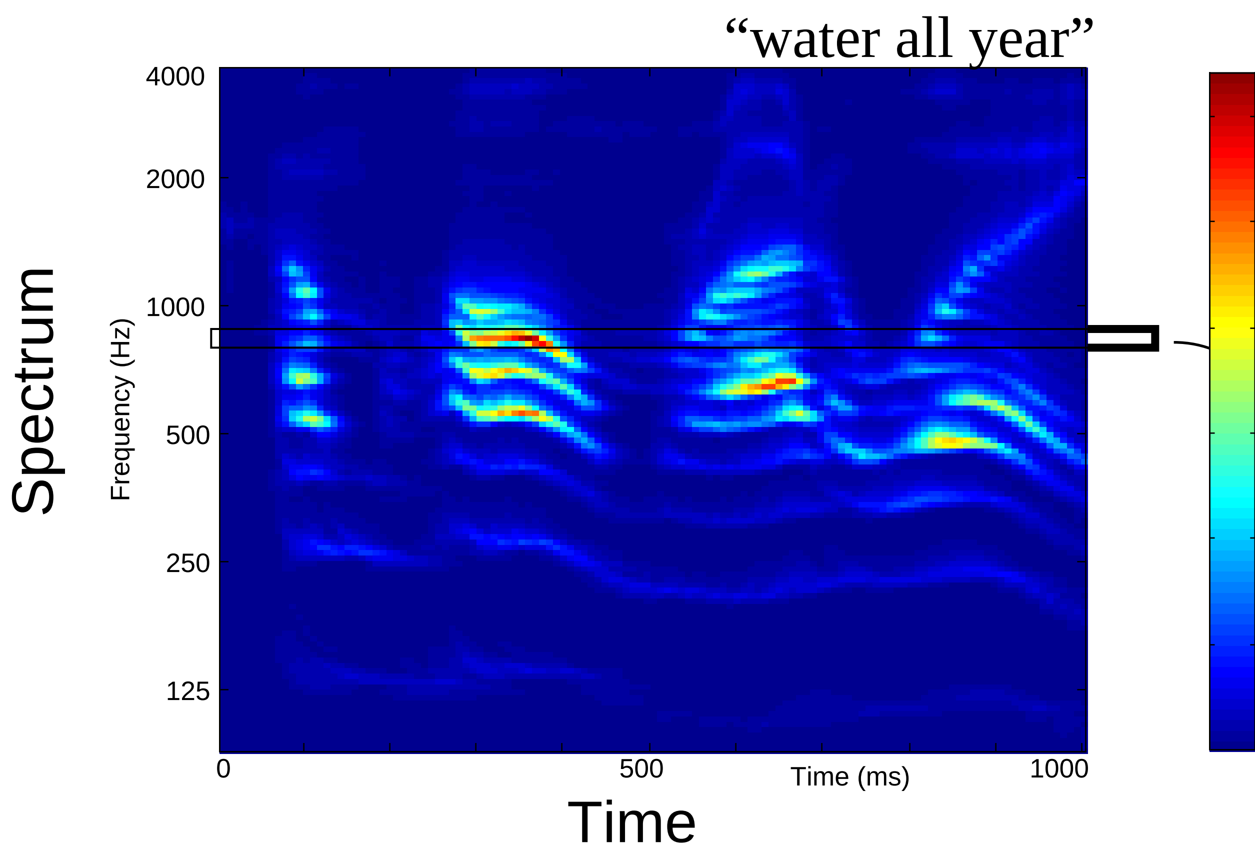
- **Spectro-Temporal Receptive Field (STRF)** meets criteria:
  - Quantitative descriptor
  - Quantitative predictor
  - Visual Tool

Sound Features

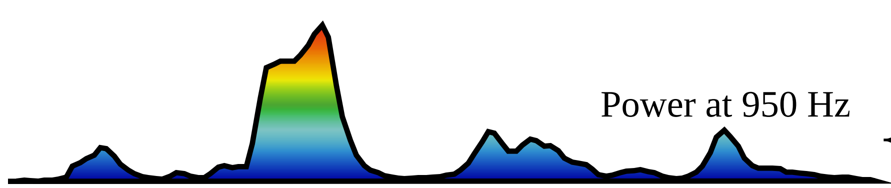
- **Spectro-Temporal Features of Any Sound**

- Spectral content of sound as a function of time.

  Which spectral frequency bands have enhanced power?
  Which spectral frequency bands have diminished power?
  How do these change as a function of time?



- log (f) ≈ linear cochlear distance

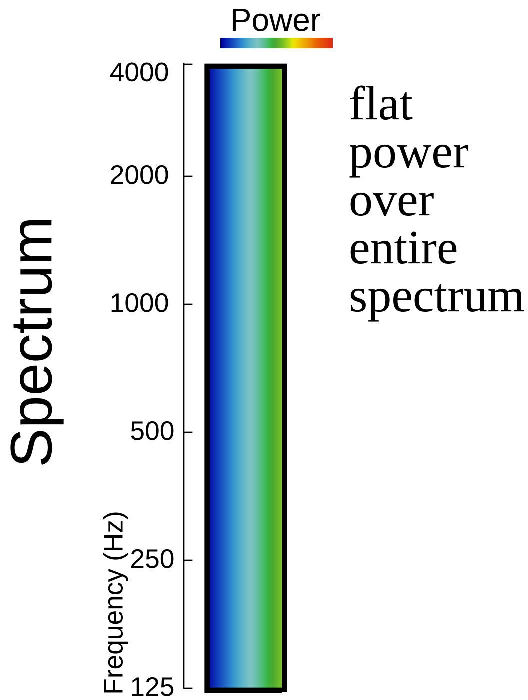


- Characterization from cross-section is limited

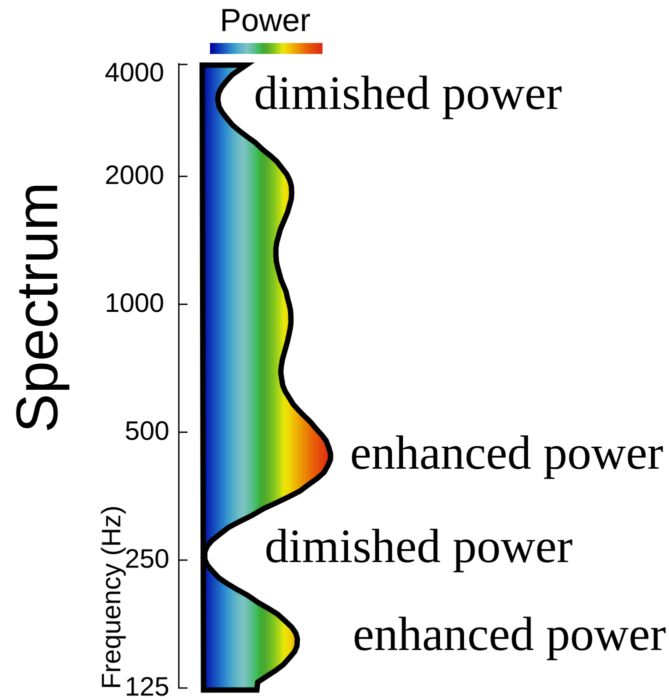
Stimulus Construction

- Pink Noise = flat power density in octaves [log (*f*)]
  not white

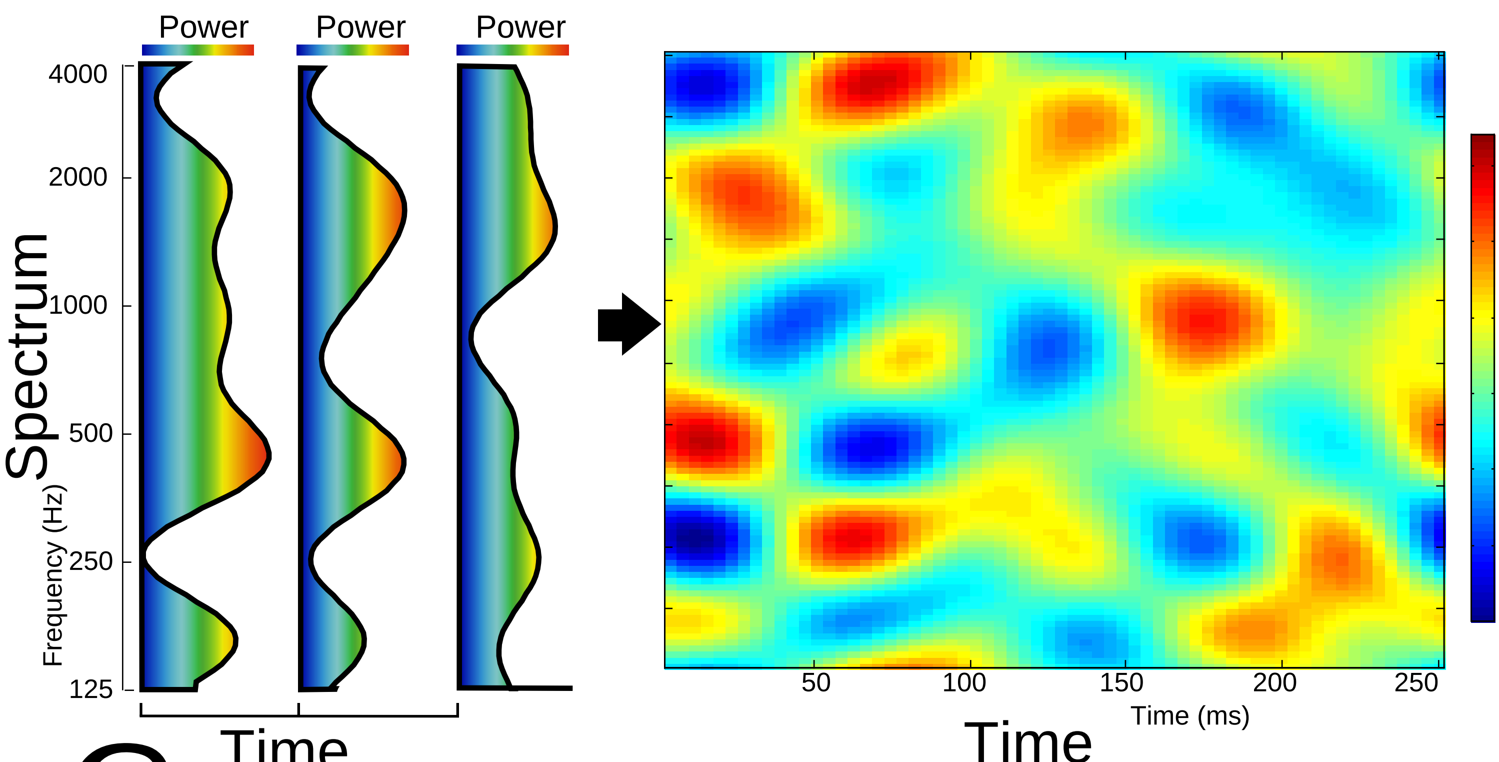
- ***Unmodulated noise** (flat)*



- ***Spectrally modulated noise***



- ***Spectro-Temporally modulated noise***



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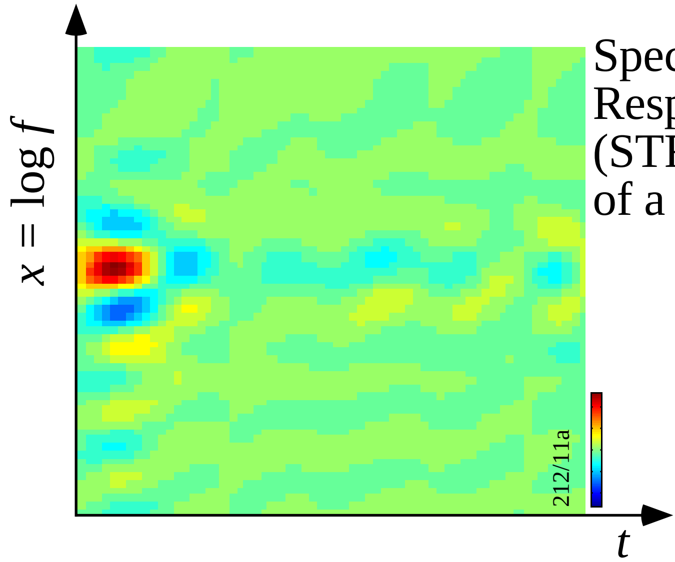
Spectro-Temporal Response Field (STRF)

- Spectro-temporal response field of neuron is the standard response field, made time-dependent.
- Frequencies mapped along cochlea on log frequency axis



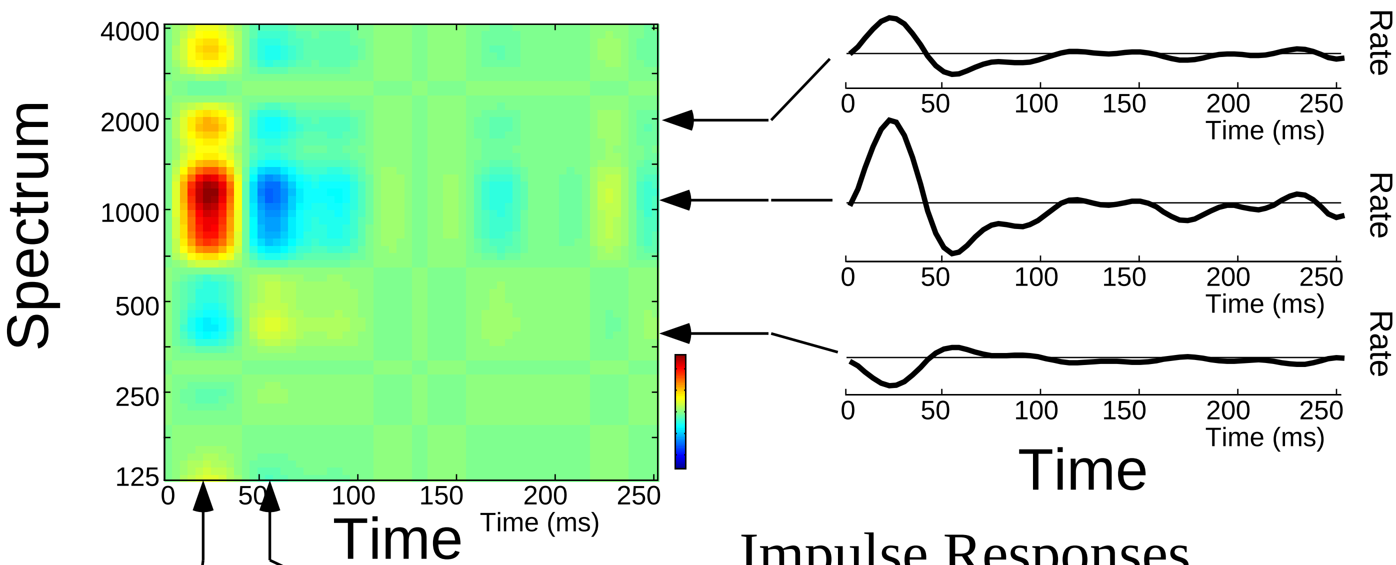
Spectro-Temporal Response Function (STRF) of a neuron

Interpreting STRFs

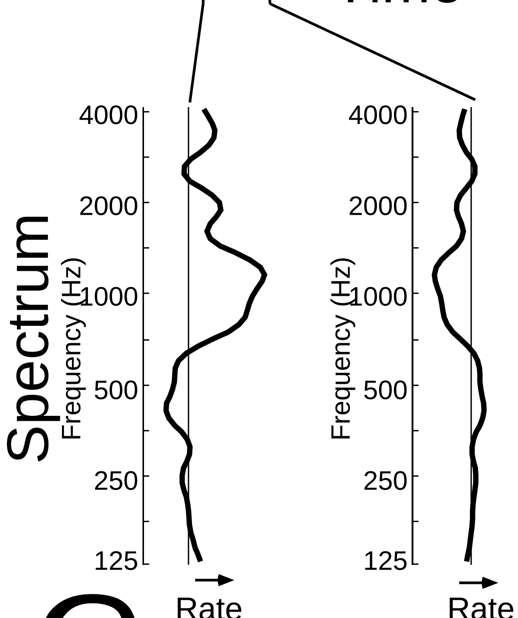
Stimulus Effect on Rate

STRF region	Stimulus Power	Spike rate contribution
Excitatory	Enhanced	Faster
Inhibitory	Enhanced	Slower
Excitatory	Diminished	Slower
Inhibitory	Diminished	Faster (!)

Cross-section interpretations



Impulse Responses,
parametrized by spectral band



Spectral Response Fields,
evolving in time

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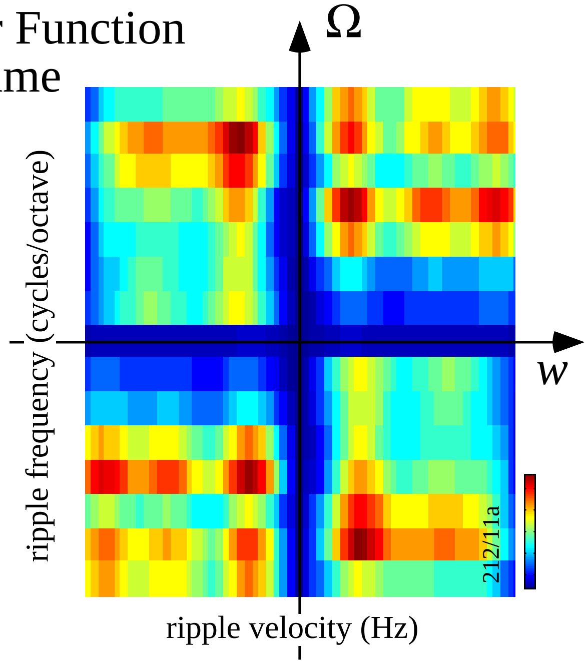
Spectro-Temporal Response Field (STRF) & its Transfer Function

2 Dimensional Fourier Transform

$$\int [.] \exp(\pm 2\pi j \Omega x \pm 2\pi j w t)$$

Inverse Transform

2 Dimensional Transfer Function of the same neuron



- Its Fourier transform is the transfer function.
- Analysis is often conceptually simpler in the Fourier domain.
- Either can be used to predict the linear response to *any* broadband dynamic sound.

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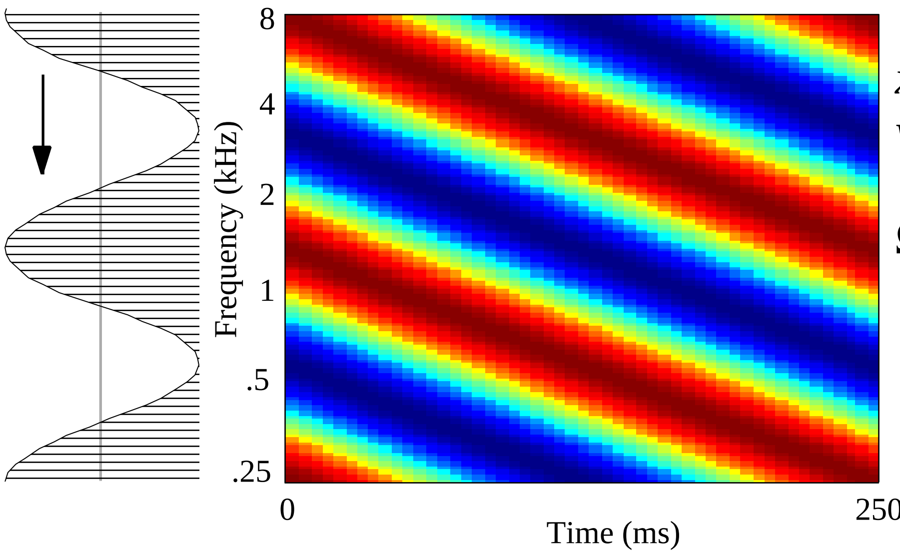
Single Moving Ripple

Single Ripple in Spectro-Temporal Space (*Spectrogram*)

Ripples are auditory "gratings" whose spectral envelope is a sinusoid along the log(*f*) axis. At any time *t* and any 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,

e.g. 4 Hz = 4 cycles/s

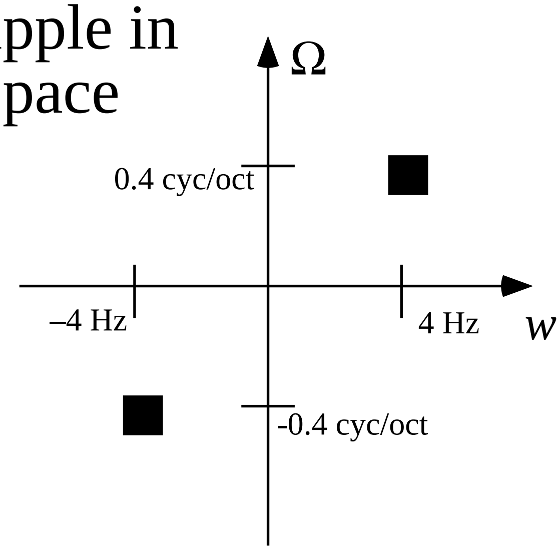
Ω = ripple density,

e.g. 0.4 cycles/octave

= 2 cycles/5 octaves

$$\int [.] \exp(\pm 2\pi j\Omega x \pm 2\pi jwt)$$

Single Ripple in Fourier Space



The Fourier transform of a single moving sinusoid has support only on a single point (and its complex conjugate).

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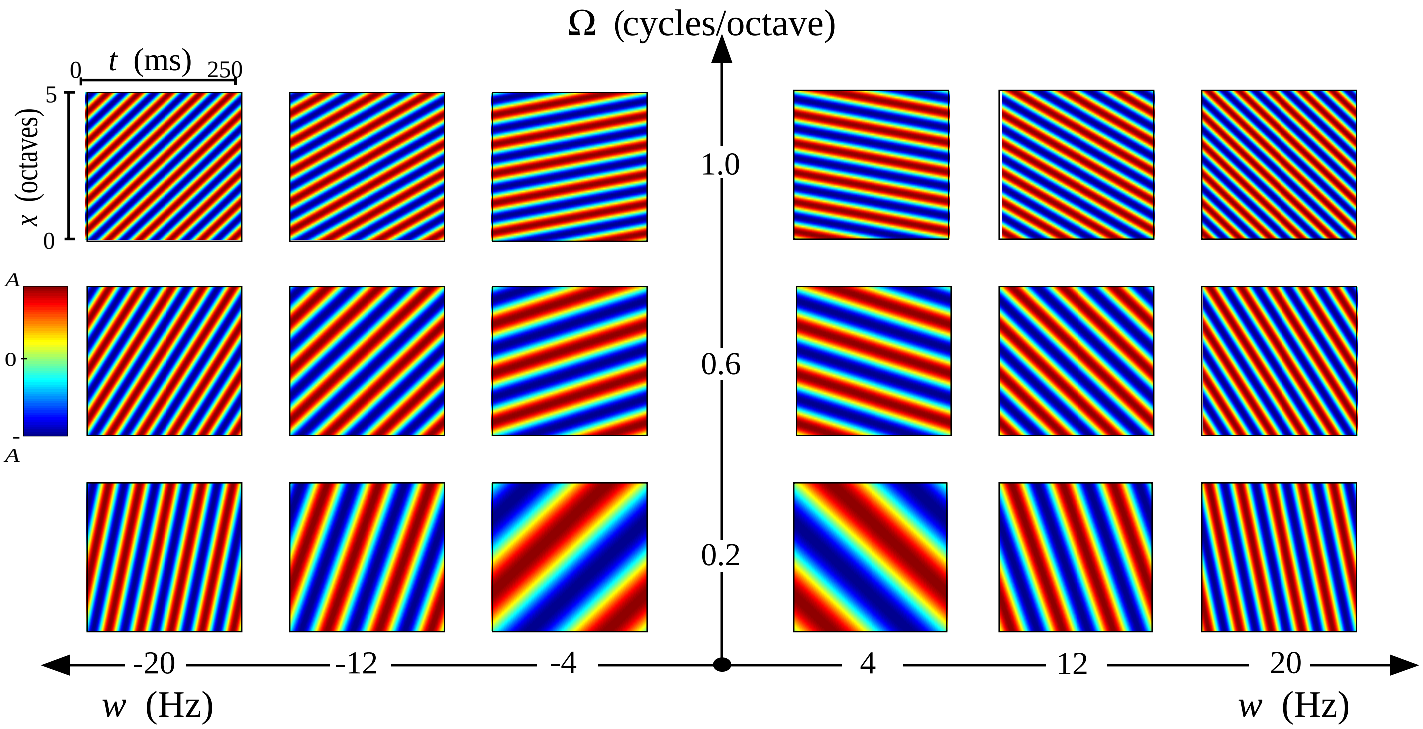
Multiple Individual Ripples

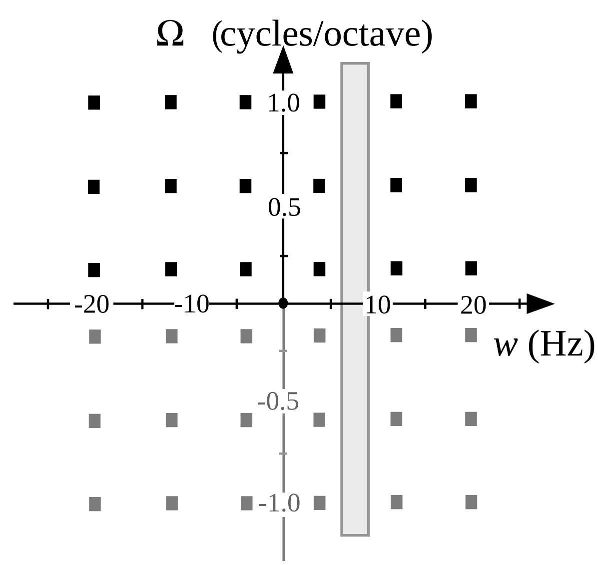
$S(t,x) = \sin[2\pi w t + 2\pi \Omega x + \phi]$ — w = ripple velocity

$x = \log_2[f / f_0]$ — Ω = ripple density

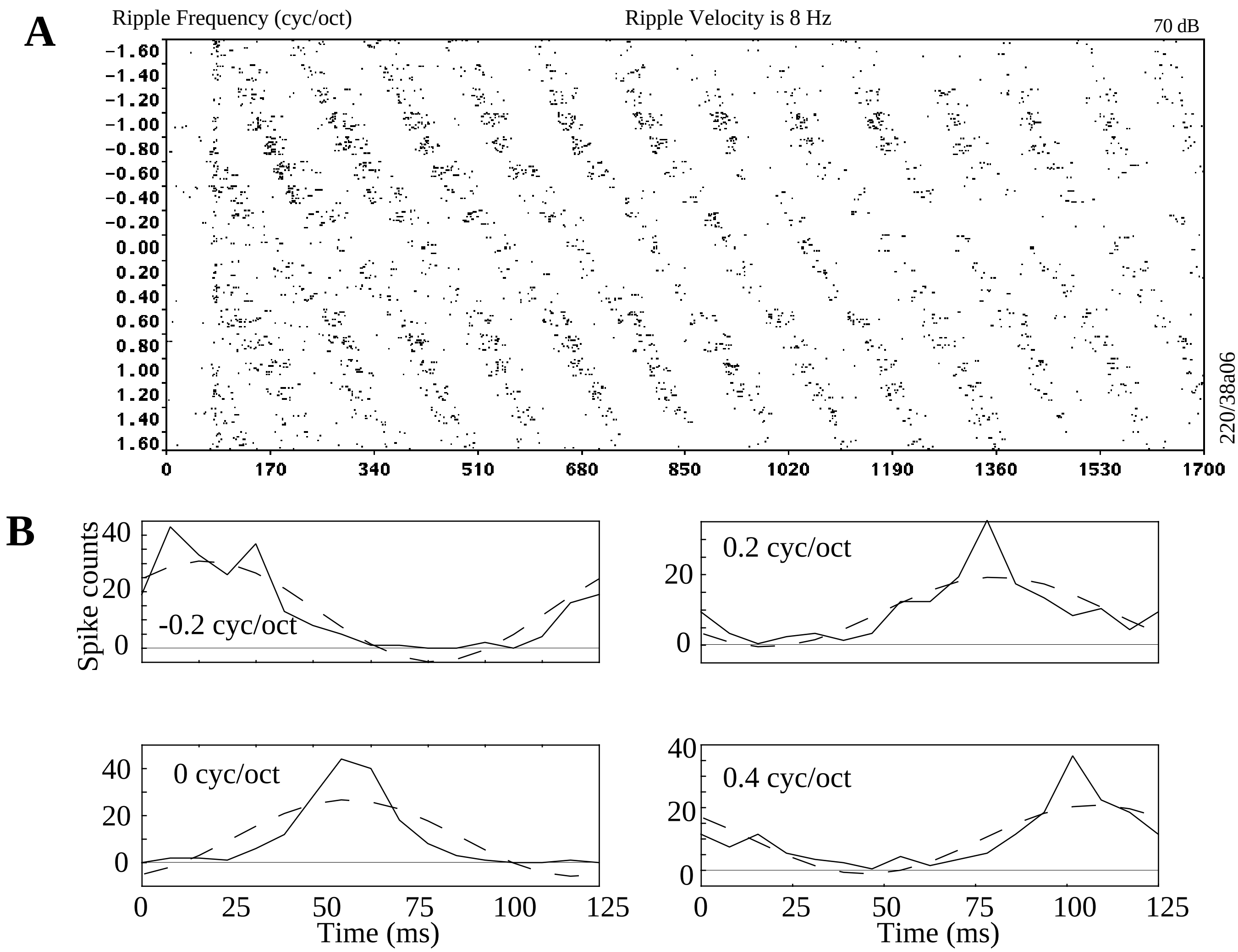


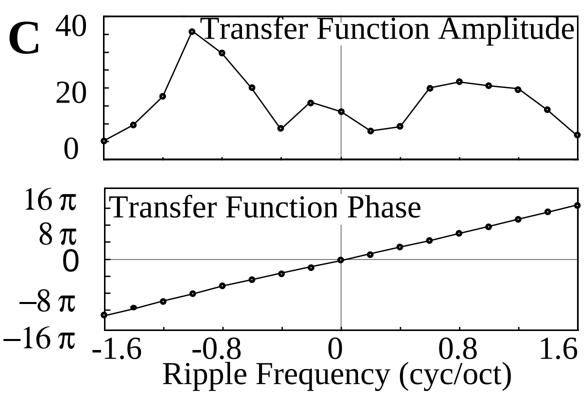
The Fourier space of the spectrograms. We probe a cell at different velocities w and different densities Ω, and quantify the response for up and down-moving sounds.

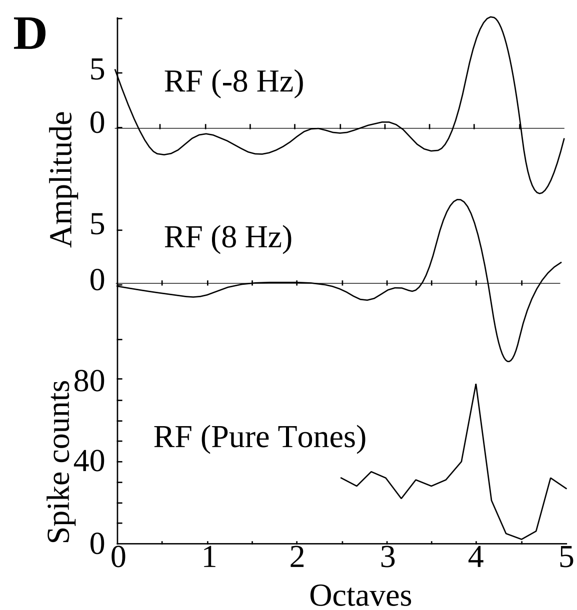
Any ripple in the lower half-plane is equivalent to a ripple in the upper-half plane.



Spike Train Measurements





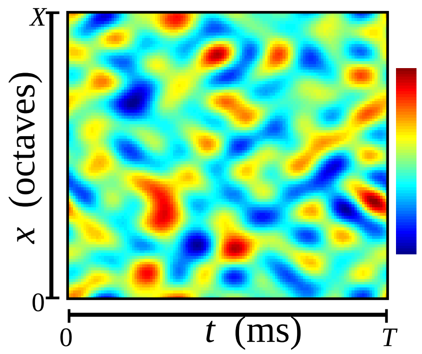


Spike events in (**A**) are turned into period histograms in (**B**). The amplitudes and phases give the transfer function in (**C**), which can be inverse Fourier transformed to give Response Fields in (**D**).

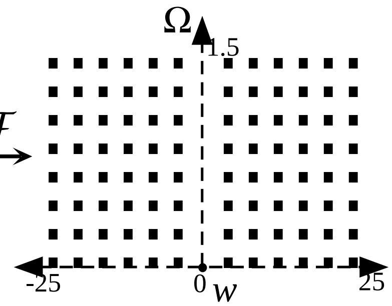
Spectro-Temporal Noise

To speed up the characterization of a cell's response, we use combinations of ripples of *all* velocities w and densities Ω, with random phases.

$$S^{noise}(t,x) = \sum_j \sum_k \sin[2\pi w_j t + 2\pi \Omega_k x + \phi_{j,k}]$$



$\mathcal{F}$

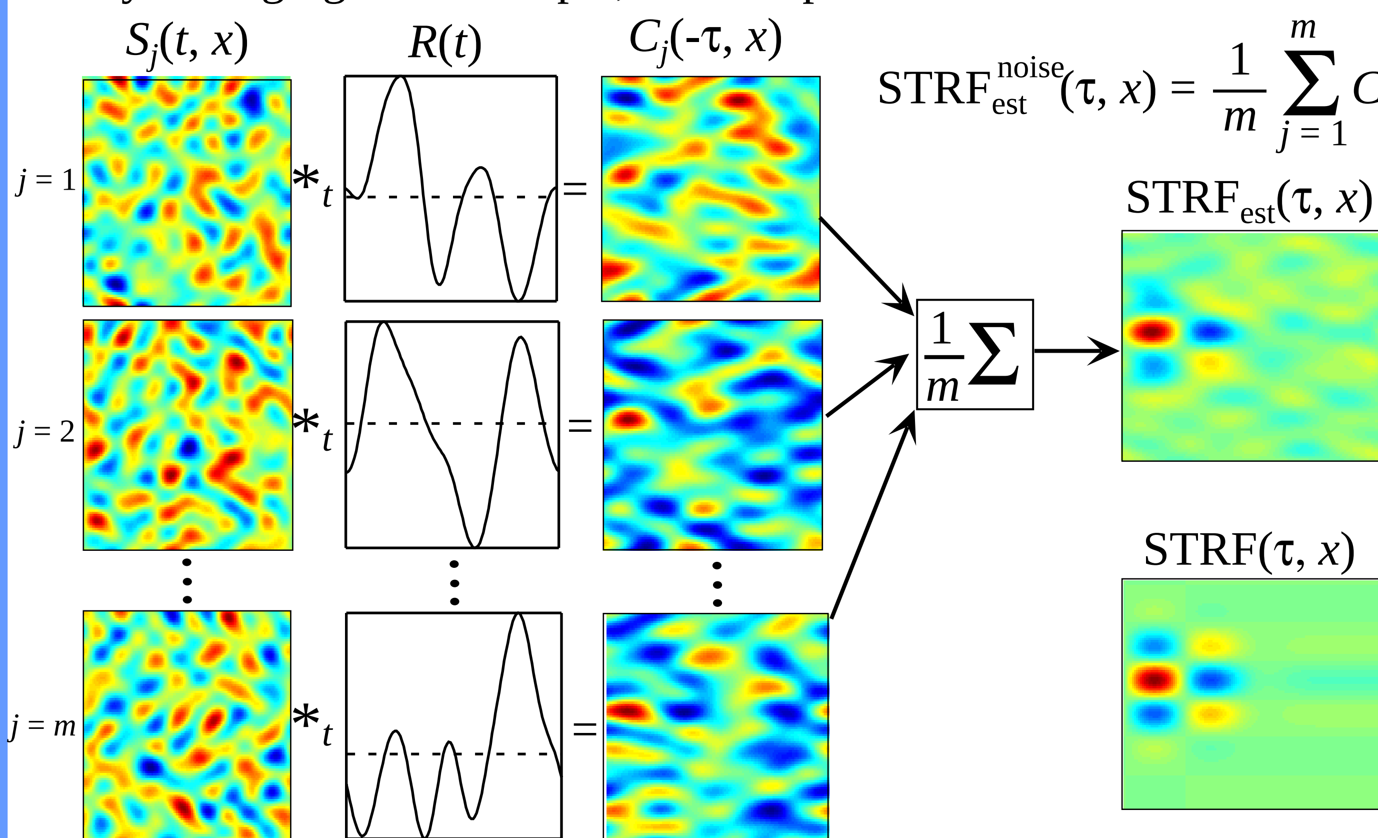


Spectro-Temporal generalization of white noise

$$\text{Cross-Correlation: } C(\tau, x) = \frac{1}{T}\int_0^T S(t,x)R(t-\tau)dt = \frac{1}{T}\underbrace{\sum_k S(t_k-\tau, x)}_{=\ \text{Spike-Triggered Average}}$$

- $C(\tau, x)$ contains cross terms
- Cross terms have random phase and can be attenuated by averaging over multiple, random-phase stimuli.

$$\mathrm{STRF}_{est}^{noise}(\tau, x) = \frac{1}{m}\sum_{j=1}^{m} C_j(-\tau, x)$$



Simulation

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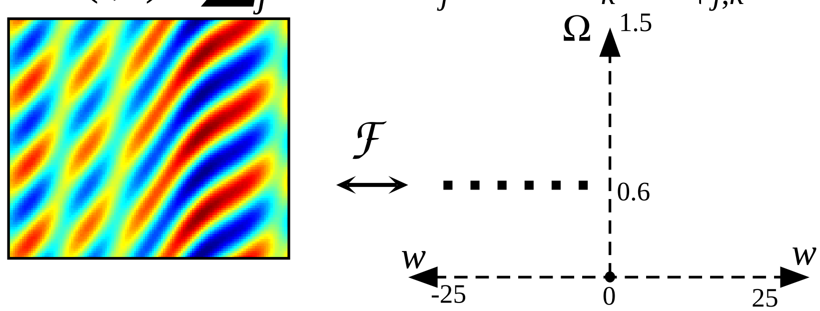
Temporally Orthogonal Ripple Combinations (TORCs)

To eliminate interference from cross-terms, we use specific combinations of ripples with differing velocities *w* and random phases.

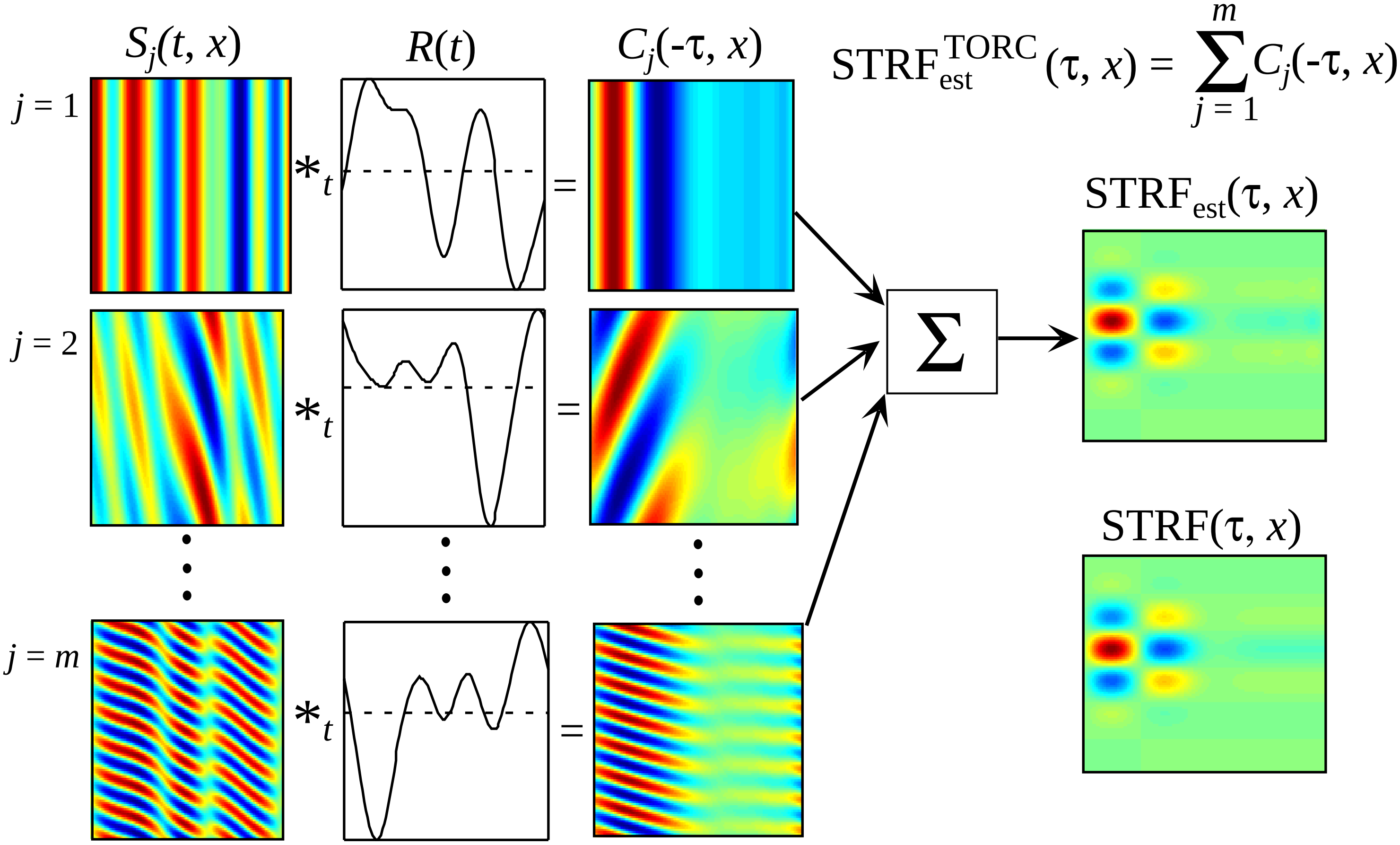
- Stimuli are composed only of ripples with different ripple velocities.
- Each stimulus contains ripples which cover the same range of ripple velocities, but at different ripple frequencies.
- Multiple stimuli are still needed to present a complete set of ripples.

$$S^{\mathrm{TORC}}(t,x) = \sum_j \sin[2\pi w_j t + 2\pi\Omega_k x + \phi_{j,k}]$$



TORCs are better suited for temporal cross-correlation because there are no cross terms. The resulting estimates are robust, use short-duration stimuli, and are quickly computed.

$$\mathrm{STRF}_{\mathrm{est}}^{\mathrm{TORC}}(\tau, x) = \sum_{j=1}^{m} C_j(-\tau, x)$$



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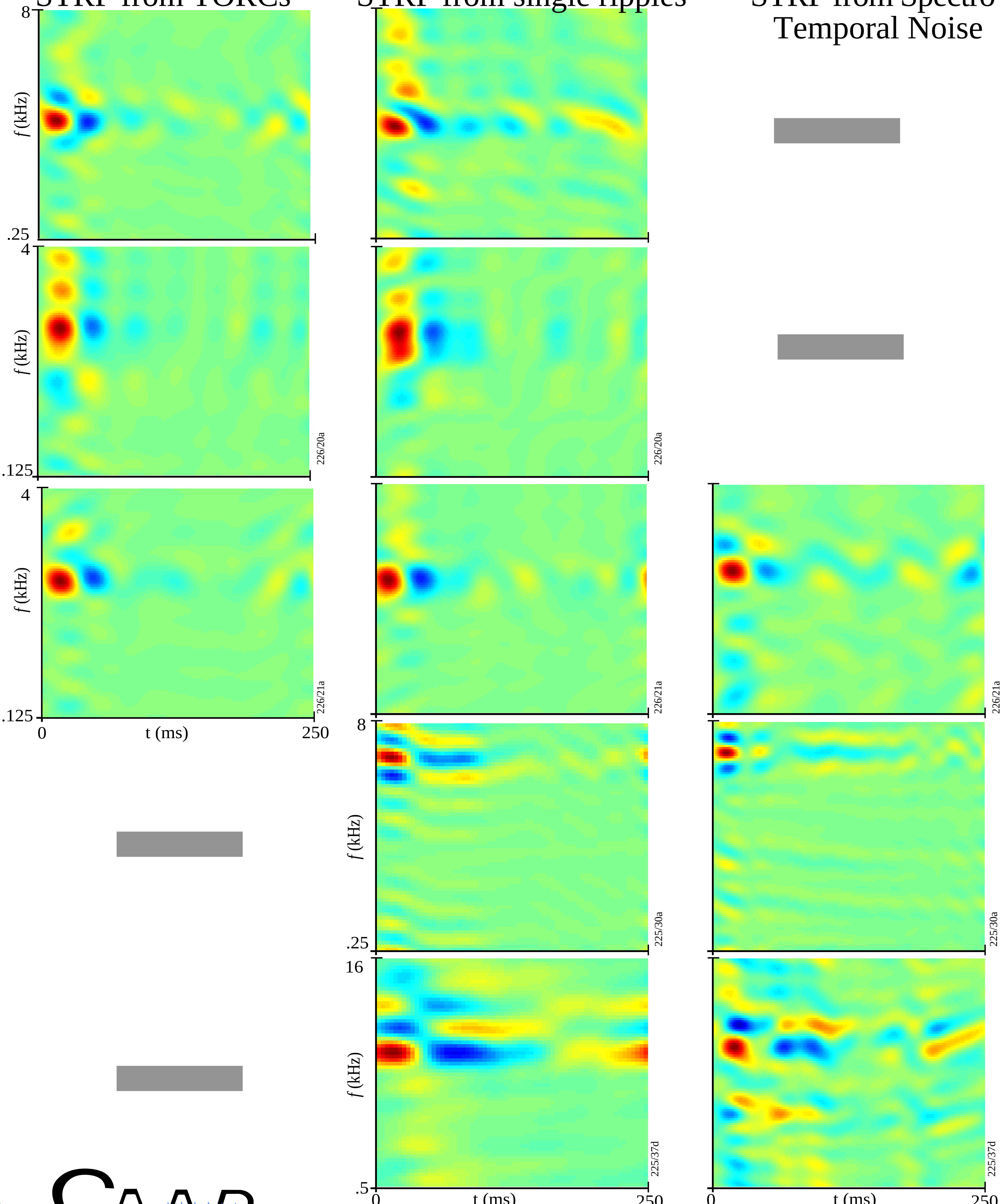
STRFs Compared



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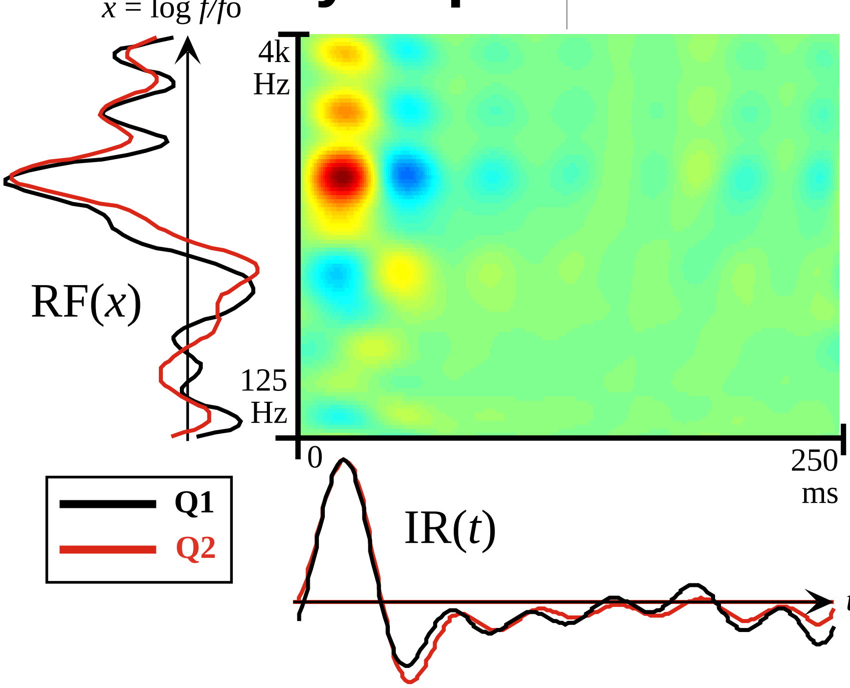
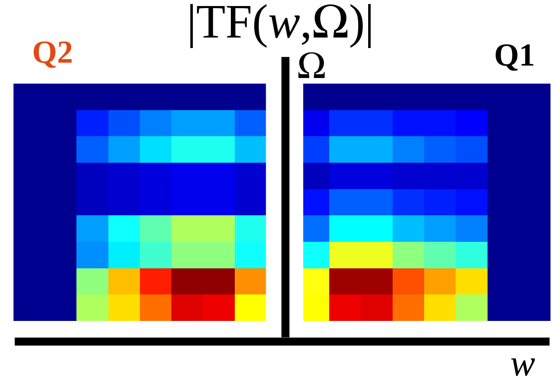
Separability

Fully Separable STRF

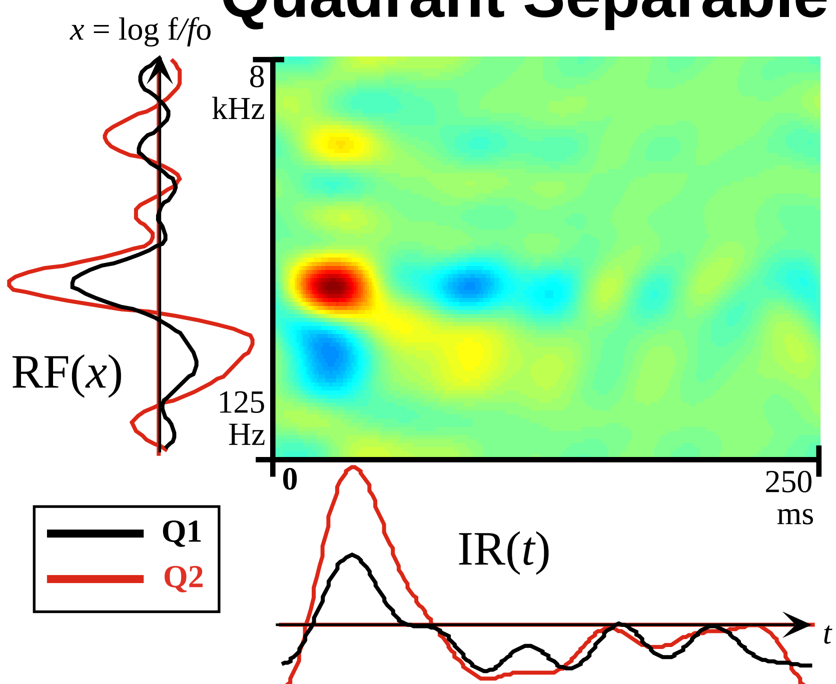


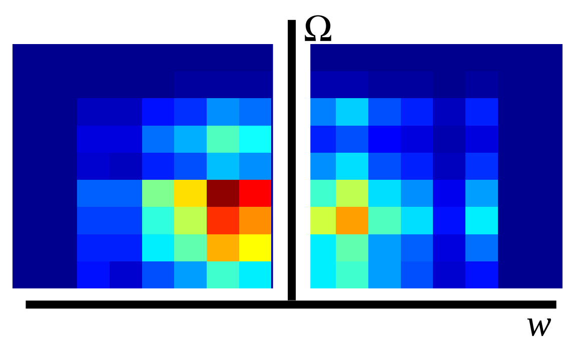


The STRF and TF are a product of a single spectral response function with a single temporal response function.

Shown above are the impulse responses (IR) and receptive fields (RF) derived from quadrant 1 (black) and quadrant 2 (red) of the transfer function by inverse Fourier transformation.

Quadrant Separable STRF





The STRF is not separable, but each quadrant of the transfer function is, i.e., there are different spectral and temporal responses for upwards and downwards frequency modulation.

This neuron responded twice as strongly to rising frequencies as it did to falling frequencies.

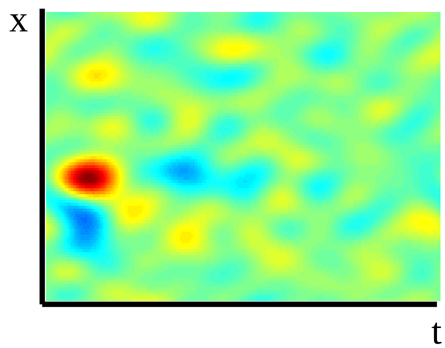
Singular Value Decomposition (SVD)

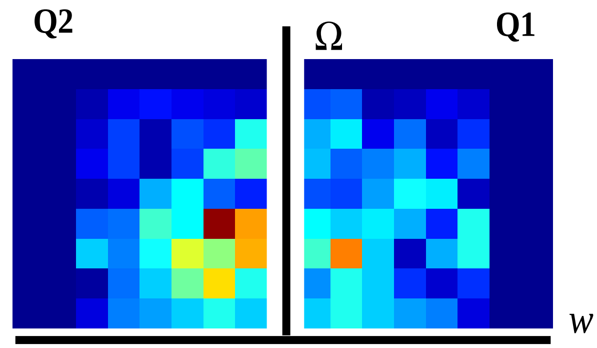
- Evaluation of Separability
- Noise Reduction

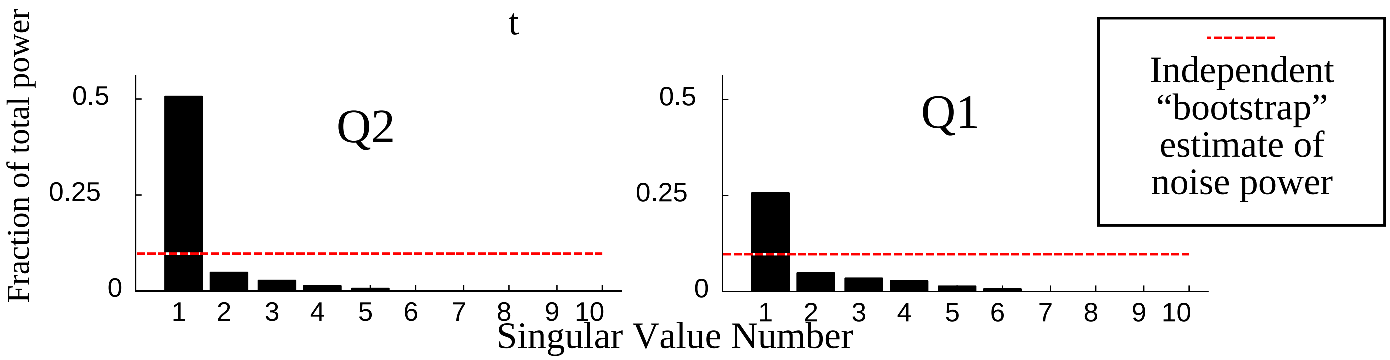
Singular Value Decomposition (SVD) decomposes the matrix into a sum of separable matrices, ordered by their overall magnitudes. The first *k* components sum to a matrix which minimizes the power of the remaining components.

We apply SVD to each quadrant of the transfer function.

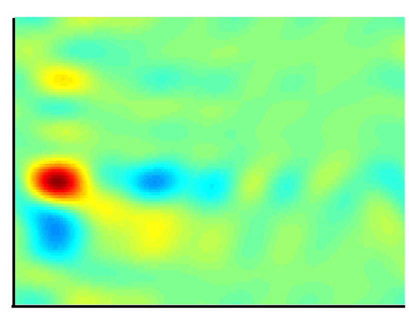
Raw STRF estimate







SVD naturally separates the signal and noise components of a matrix. Typically, large jumps in the singular values indicate where the separation occurs. Noise is removed by discarding the lower-magnitude components.



Without prior assumptions, SVD indicates that a large majority of STRFs in AI are quadrant separable.

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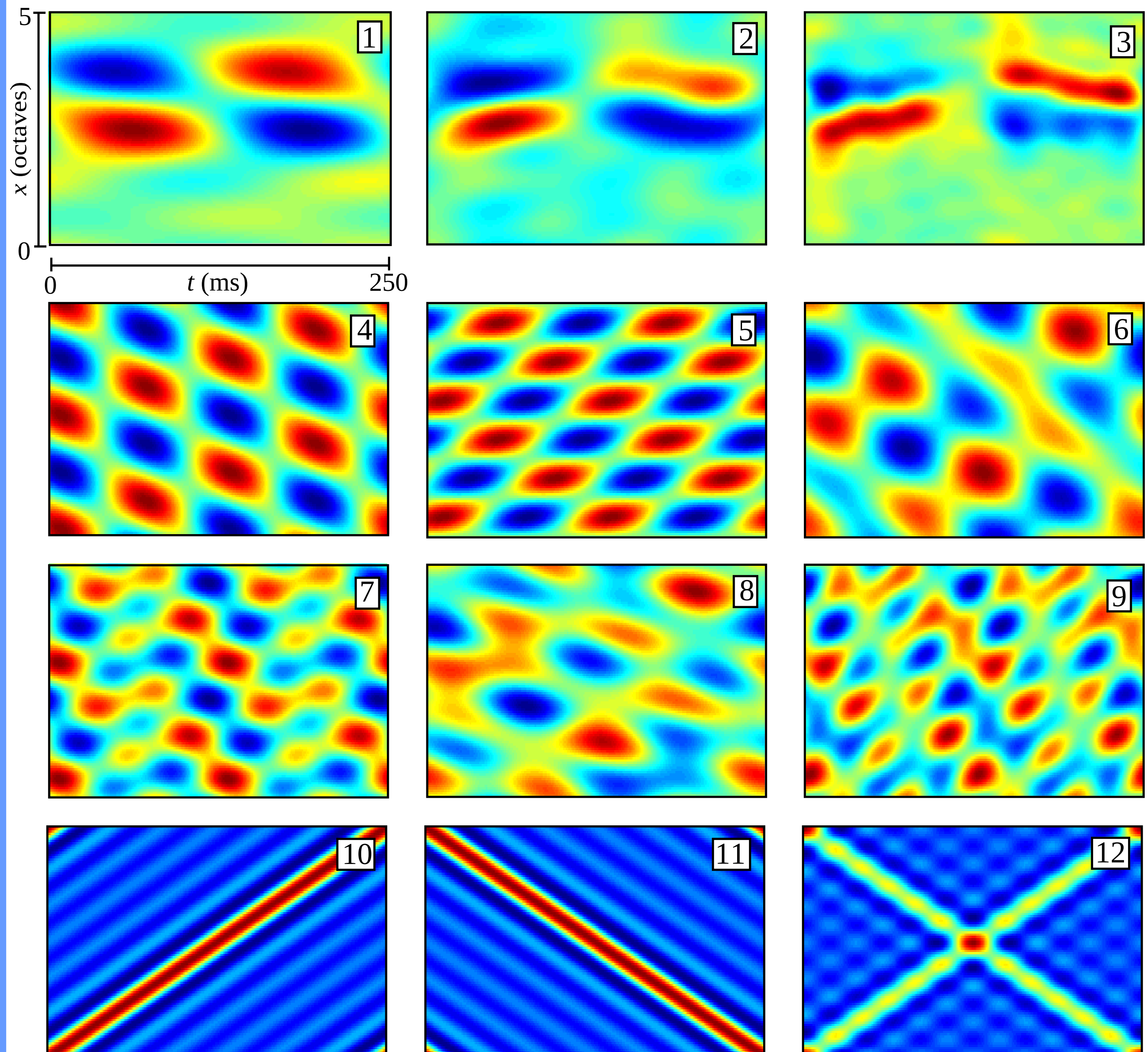
Predicting Responses

- **Predictions of Responses to Novel Stimuli**

  Good test of linearity

Stimuli Used for Predictions



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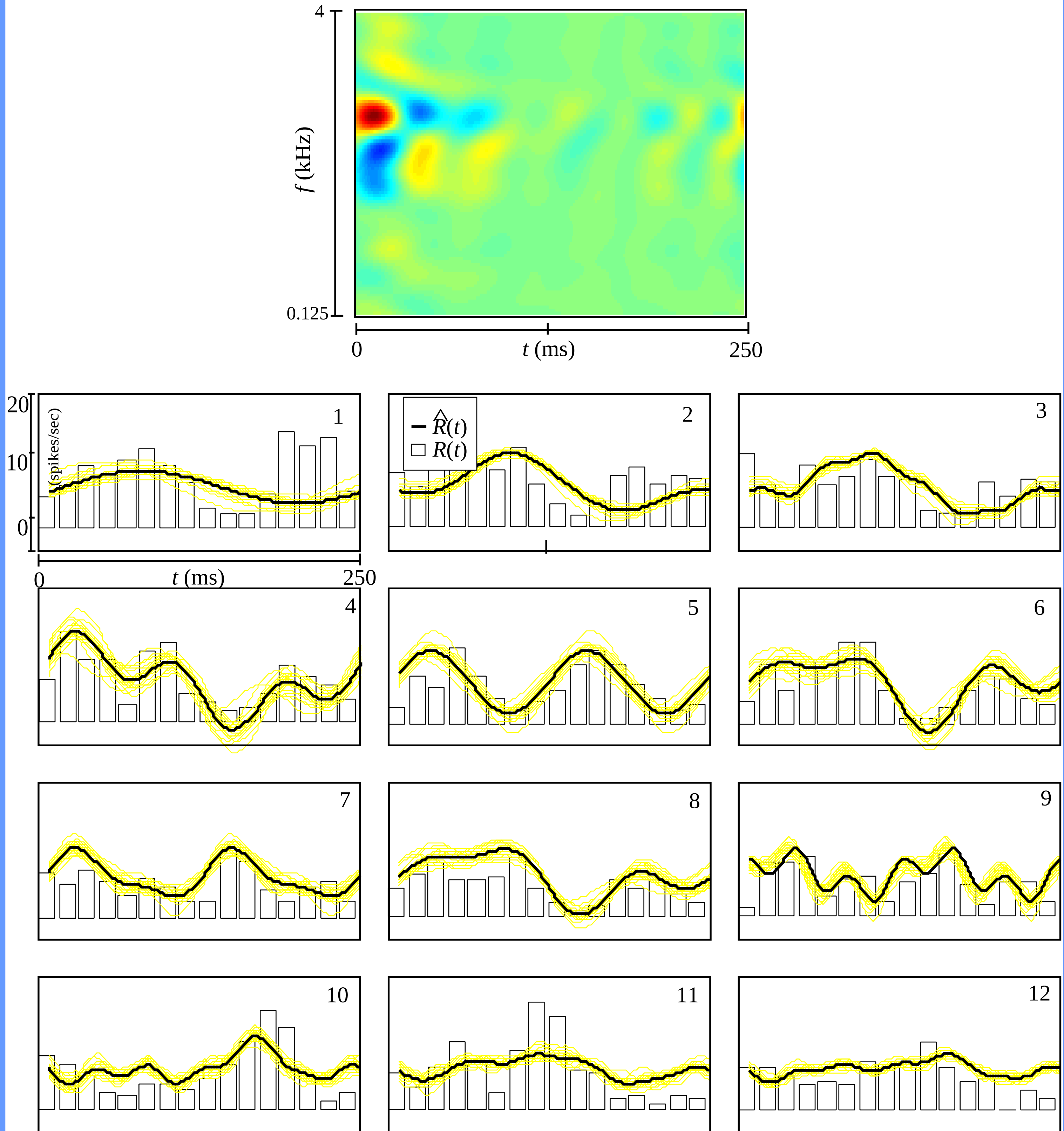
Predictions and Responses

The STRF estimates often predict the magnitude and dynamics of the response well.



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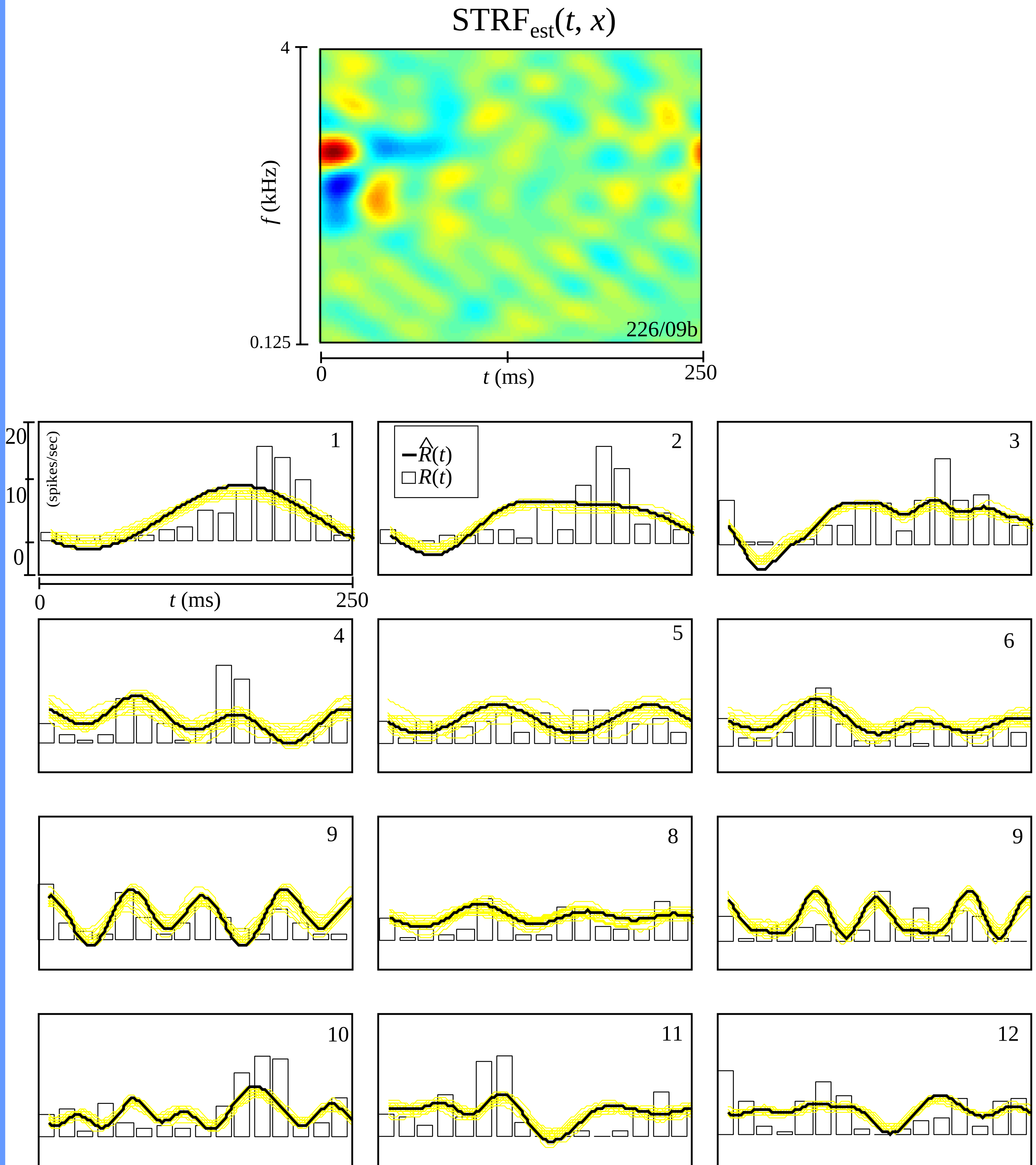
Predictions and Responses II



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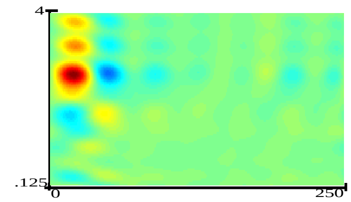
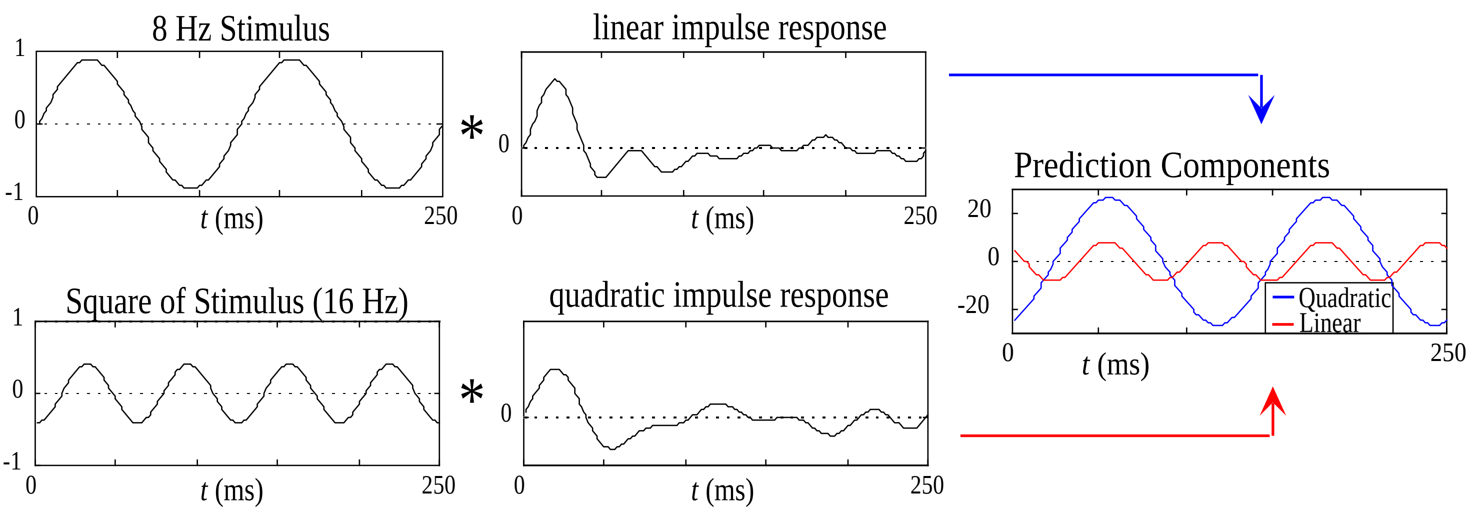
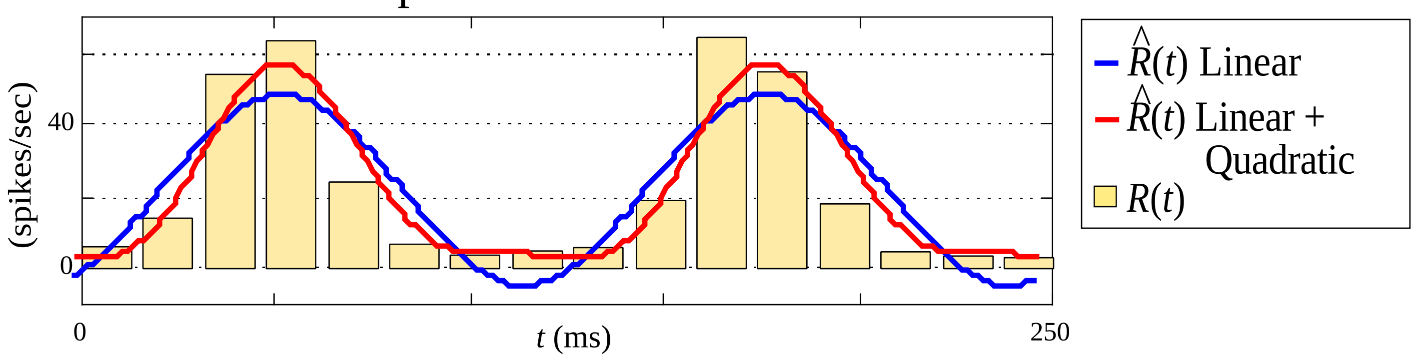
Non-Linearity—Predictions

- Preliminary results indicate that the non-linear predictions fit the responses more accurately than the linear predictions, although the differences between the two are typically subtle.

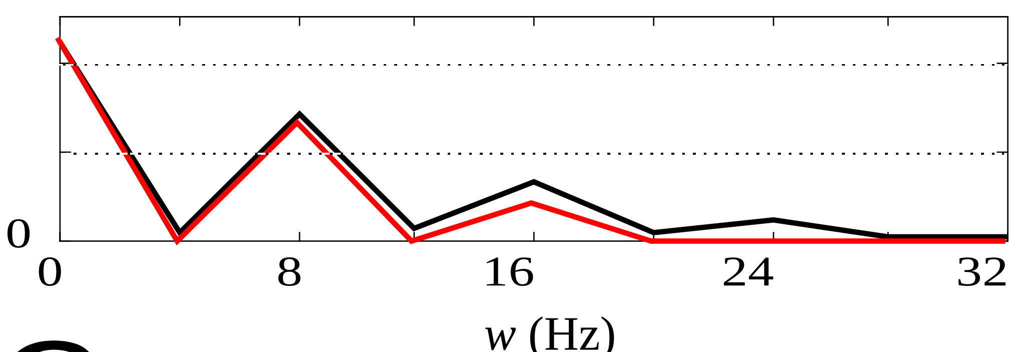




Response and Predictions



Response and Prediction Spectra



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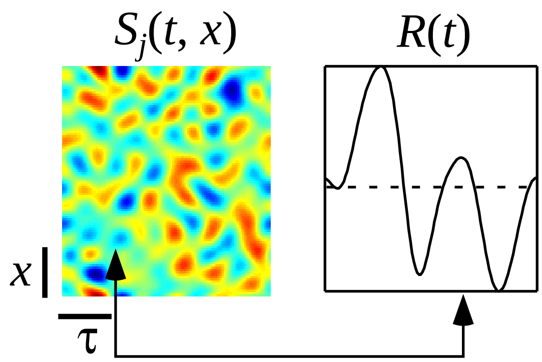
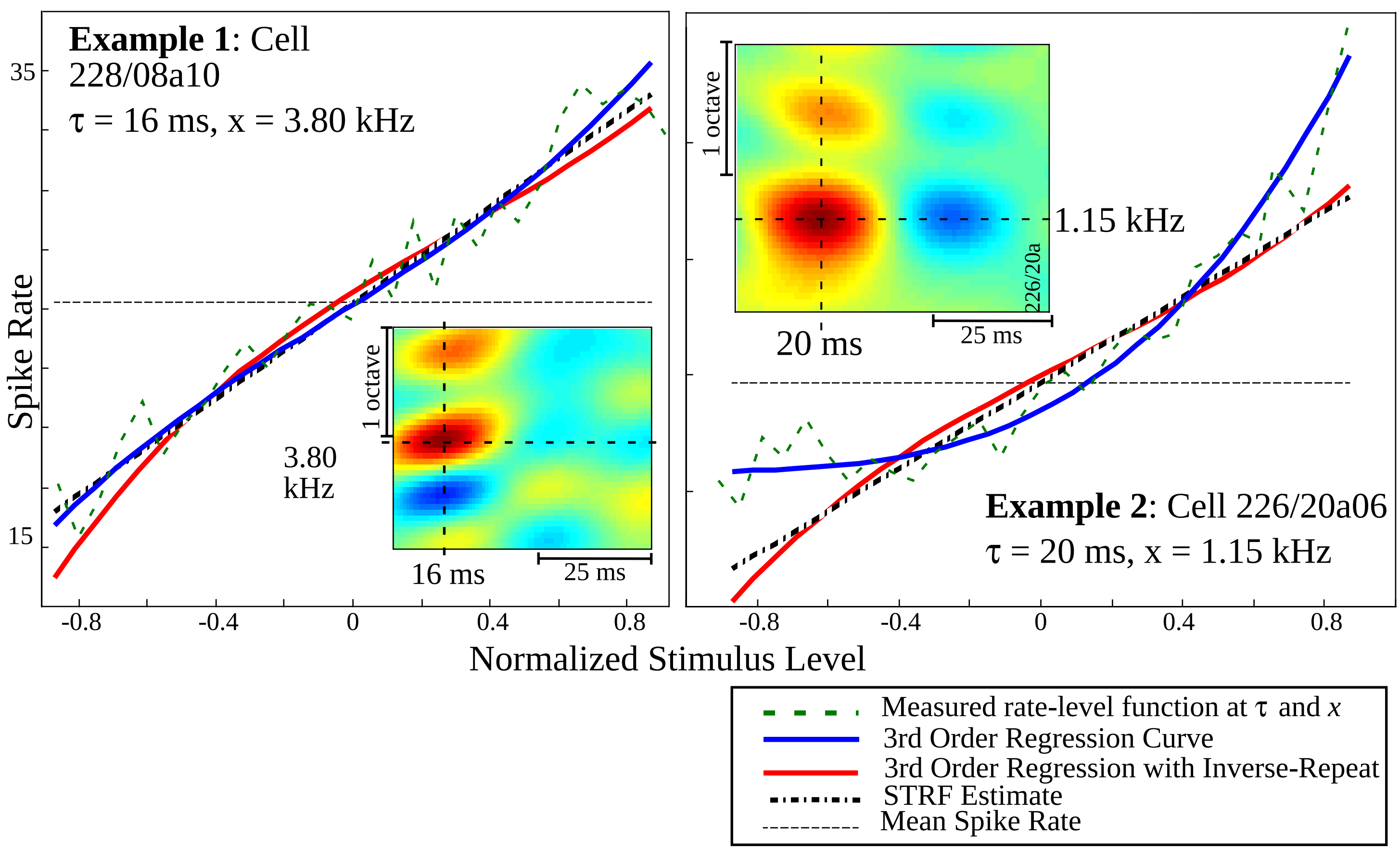
Non-Linearity—Theory

- The value of the STRF at each point (τ, x) is the slope of a linear rate-level function: $R_{\tau,x}(t) = [\mathrm{STRF}(\tau, x)] \cdot S(t-\tau, x)$.
- Polynomial rate-level curves measured at every (τ, x) improve the description. These are potentially non-linear functions.





- **Using cubic polynomials, we have shown that either the non-linearities are absent, or they are dominantly second order.**
- **Subtraction of the response to the inverted envelope gives a nearly linear polynomial fit. This would be expected, for example, from a purely even order (e.g., rectifying non-linearity).**

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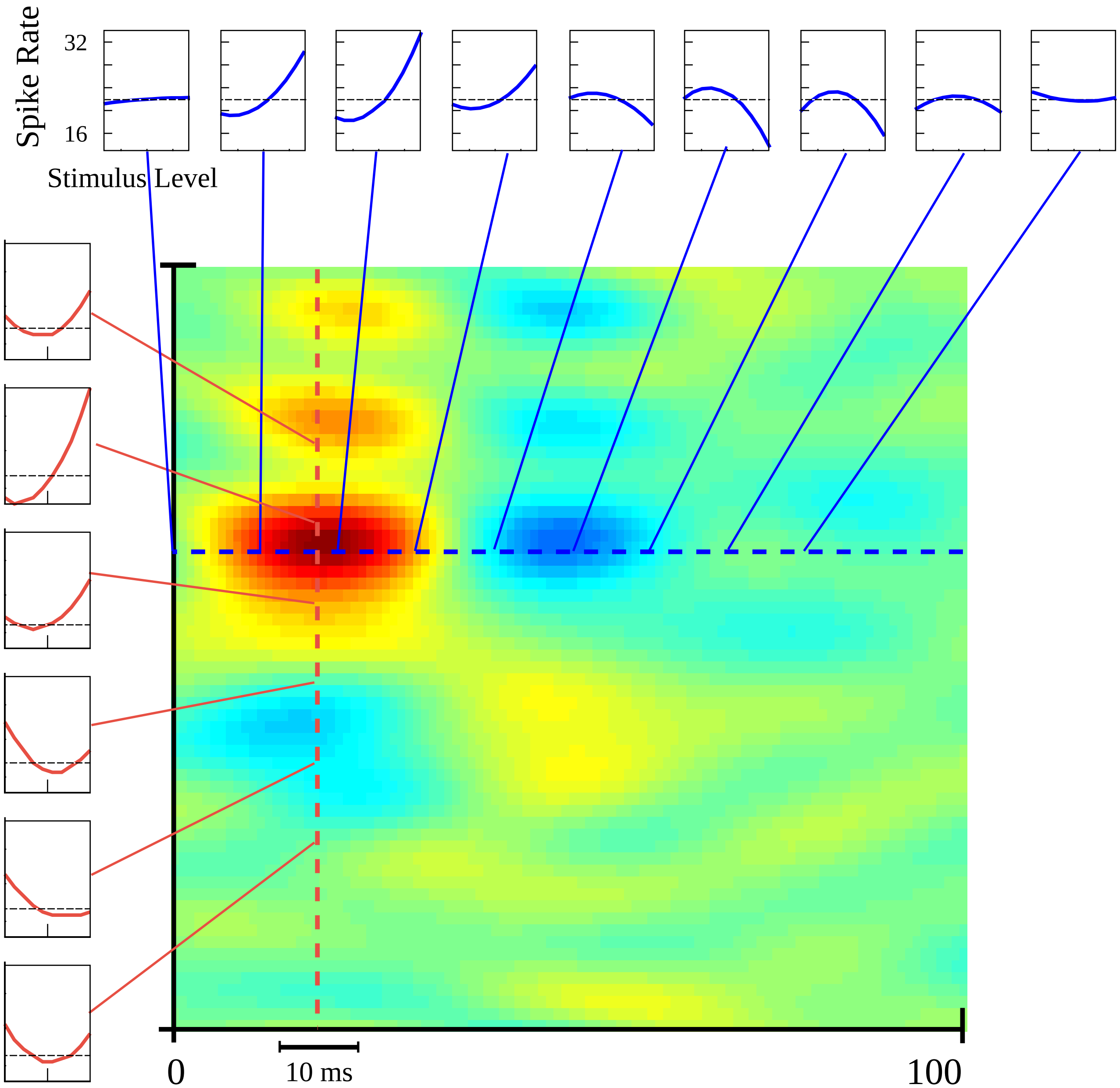
Spectro-Temporal Rate-Level Functions

Rate-level functions change with τ and x.



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Summary

- **The function of AI**
  To encode spectro-temporal features of sounds
  spectrally: up to ~ 1 cycles/octave (rarely up to 4 c/o)
  temporally: ~ 2 to ~ 20 Hz (rarely up to 100 Hz)
  (in ferret)
  plus, of course, to encode other sound features not addressed here

- **Spectro-Temporal Response Field (STRF)**
  - **Descriptor** of spike rate for broadband dynamic stimuli
  - **Predictor** of spike train for stimuli of dynamic, spectral modulations of noise
    - STRFs agree despite measurement method
    - Predictions of responses to novel stimuli

  - **Visual Tool** demonstrates spectro-temporal regions of excitation and inhibition

- **Physiological Constraints (e.g. Separability)** constrain possible network dynamics

- **Non-linear corrections/generalizations**
  realizable and work in progress

Selected References

Moving Ripple / STRF / Ripple Transfer Function

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