Spectro-Temporal Processing In Primary Auditory Cortex: *Simplicity & Linearity*

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Outline

- Introduction to Auditory Spectro-Temporal Processing
- Stimuli—Dynamic & Broadband: Ripples, Ripple Combinations
- Examples & Properties of Spectro-Temporal Response Fields
- Constraints on Neural Connectivity

- **Introduction to Auditory Spectro-Temporal Processing**
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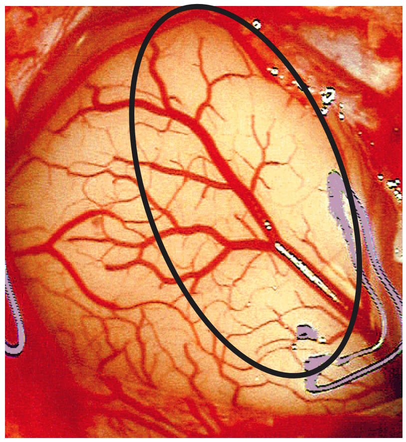
Basics

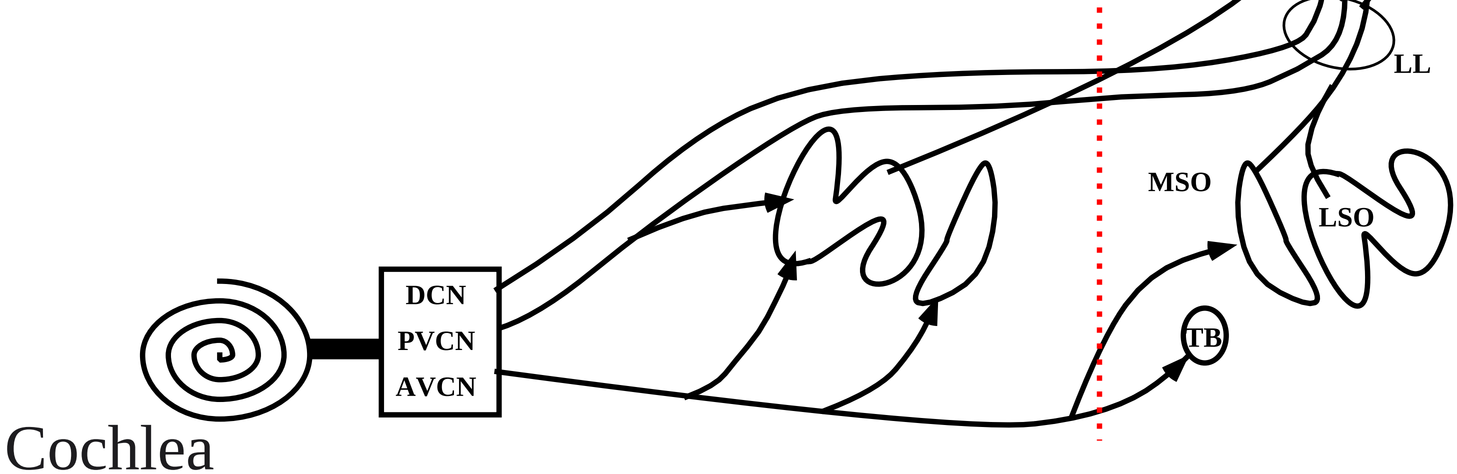
- **Most important auditory cues are acoustically non-trivial**
  - e.g. speech, speaker ID, emotional content, pitch, timbre, sound location, and many, many others
- **Enormous parallel and serial neural processing in multiple stages** from auditory nerve to cortex
- **Neural code is essentially unknown** for almost all auditory features
  - Especially in cortex
  - Much progress in coding near periphery, especially coding of sound location

Auditory Pathway
(oversimplified)

Primary Auditory Cortex (AI)



Phase-locks to envelope of acoustic waveform up to ~20 Hz



Linear distance ~ log *f*

Phase-locks to acoustic waveform itself up to ~2 kHz

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Motivation

- **The Quest**

  Teasing out "function" of Primary Auditory Cortex (AI)

  $\approx \left\{ \begin{array}{l} \text{which sounds/features evoke responses?} \\ \text{how are they encoded into spike trains?} \end{array} \right.$

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

- **Reasonable quest:** Quantitative measure of how spikes encode sound features
  - Quantitative descriptor (and predictor)
  - Qualitative descriptor/Visual tool

The Path

- **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)** succeeds:
  - Quantitative descriptor (and predictor)
  - Qualitative descriptor/Visual Tool

- **Bonus**
  - Constraints on Neural Connectivity

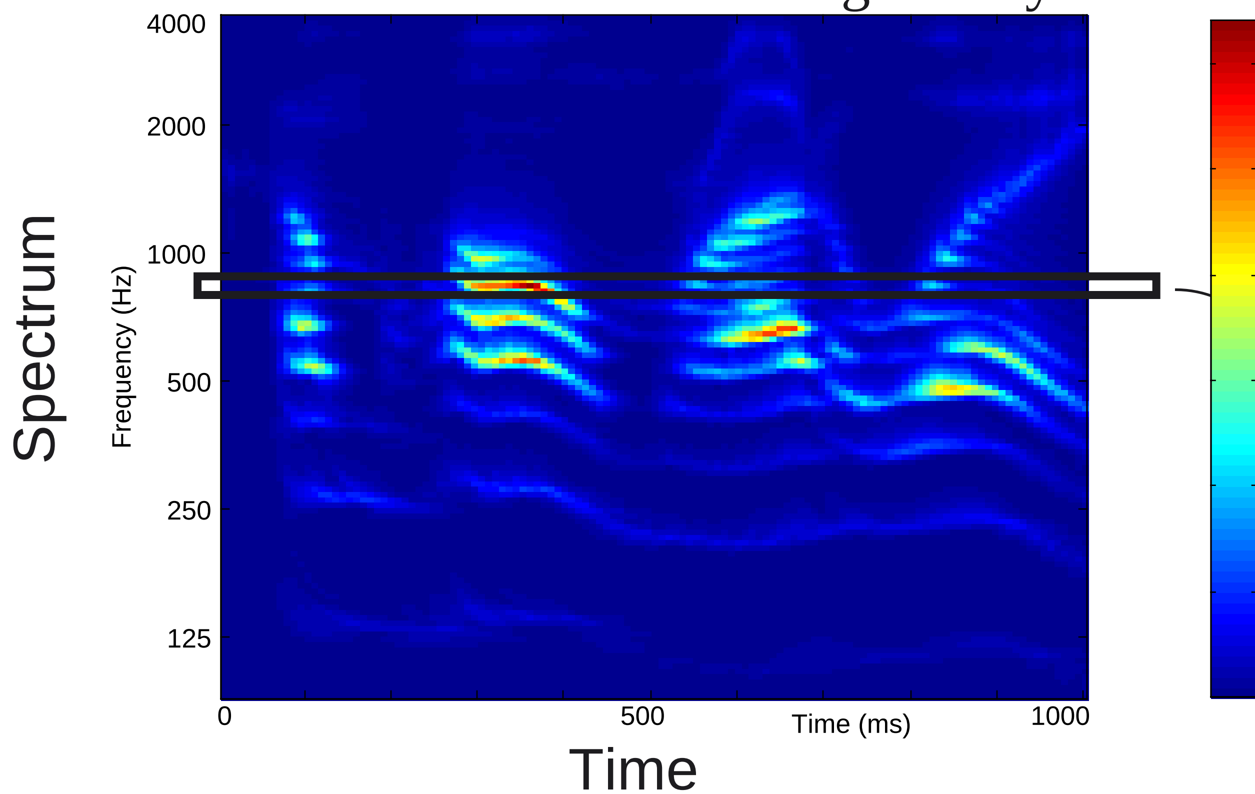
Sound Features

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

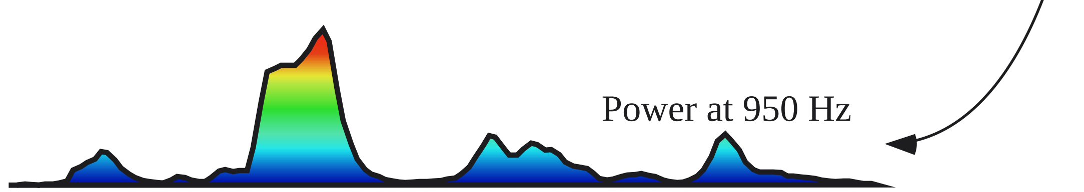
- Spectral content of sound as a function of time.

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

“Come home right away.”



- log $f \approx$ linear cochlear distance



- Characterization from cross-section is limited

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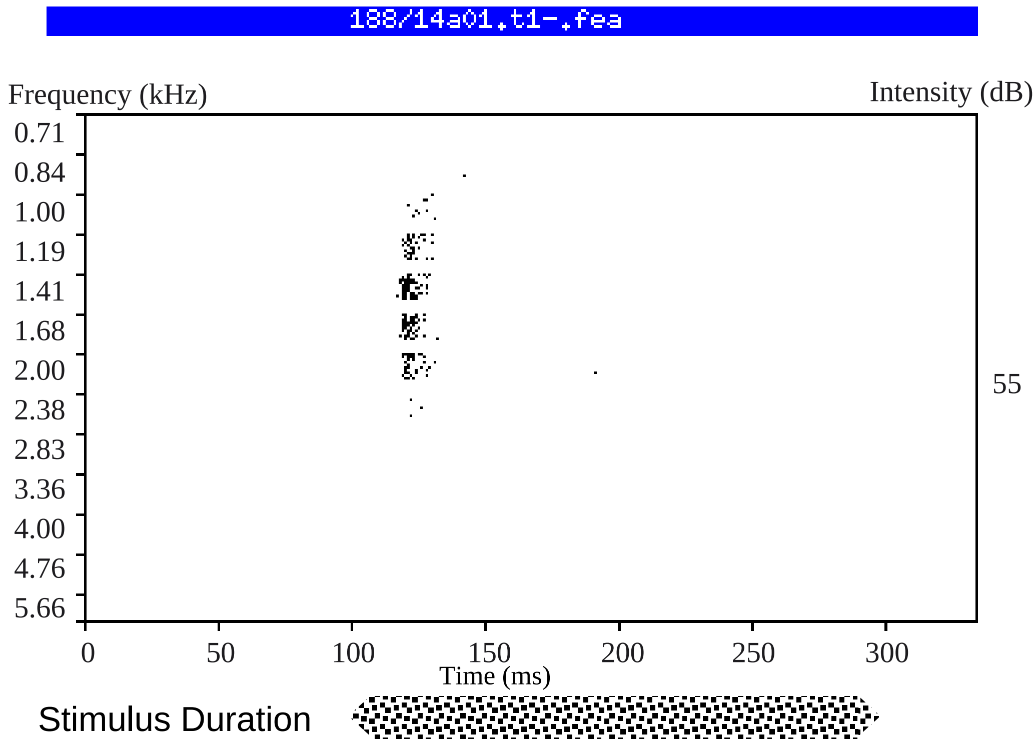
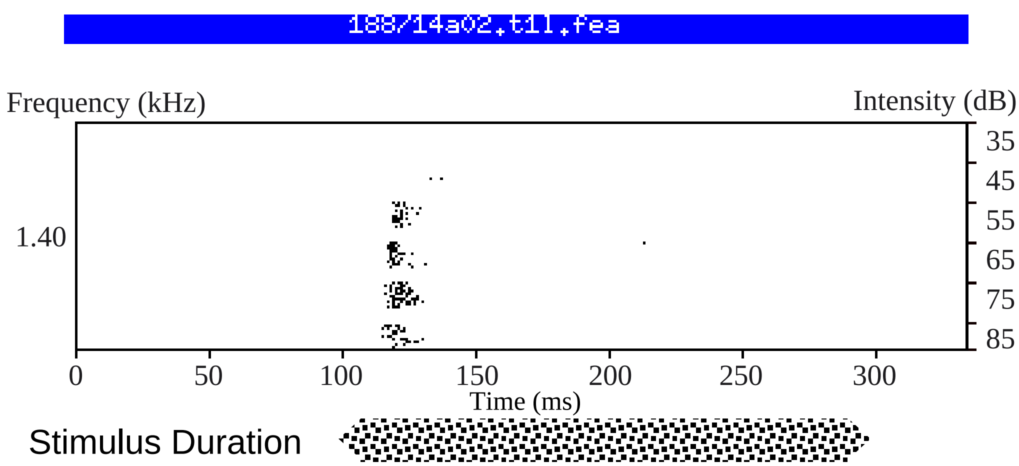
Response to Pure Tones





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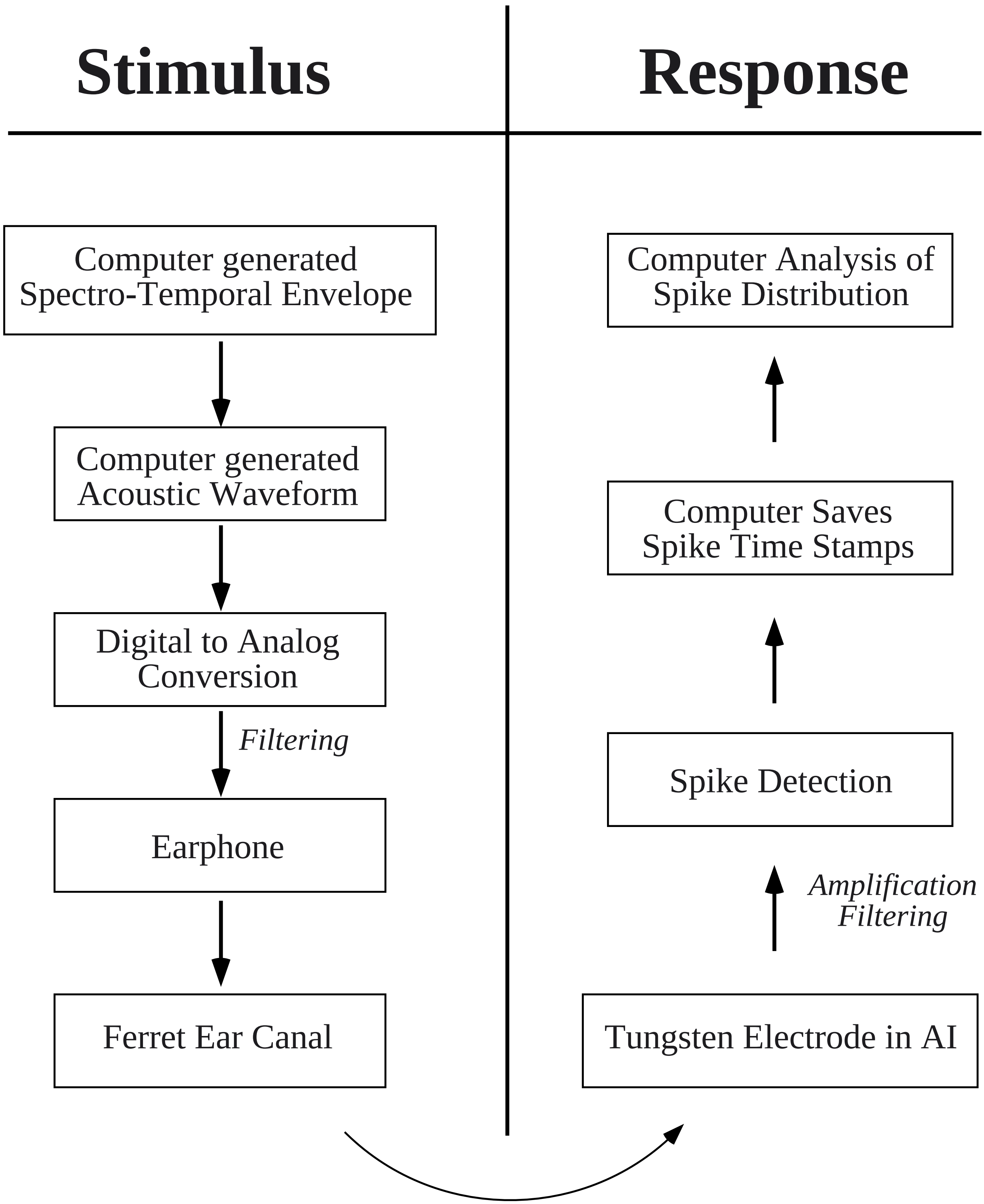
Experiment Design



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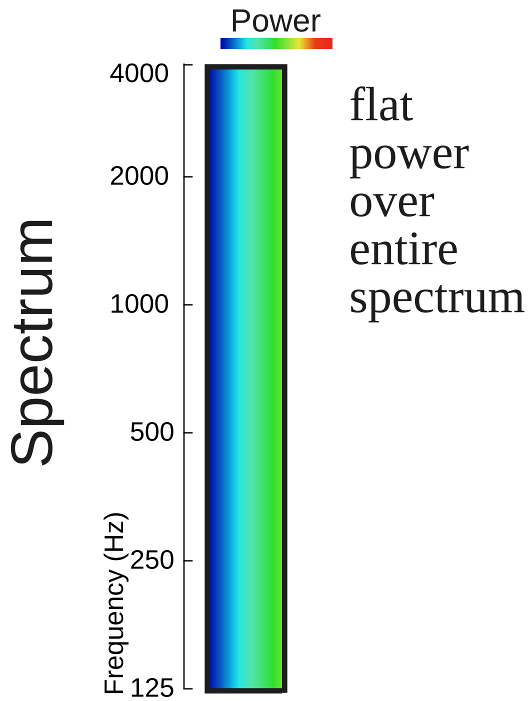
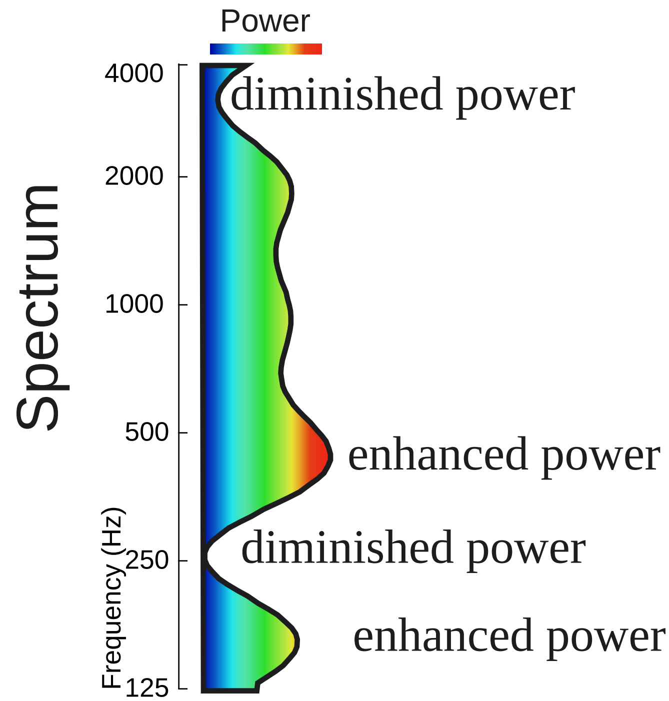
Stimulus Construction

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

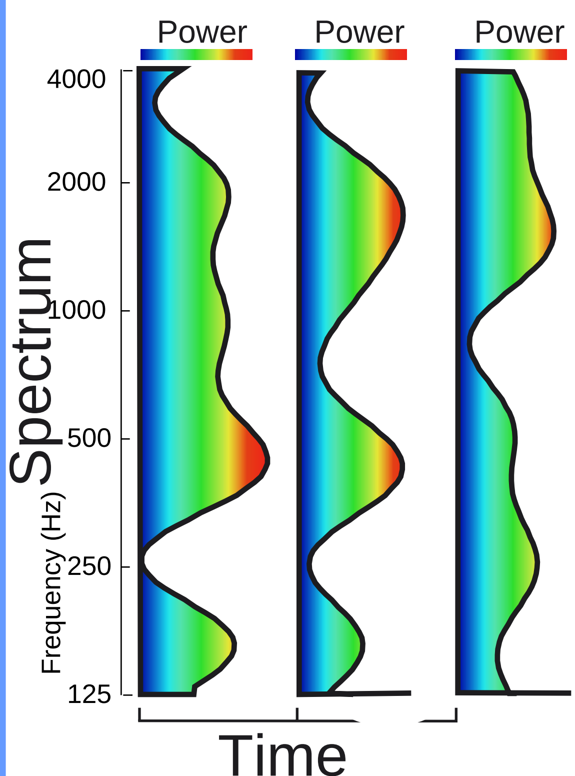
- ***Unmodulated noise*** *(flat)*



- ***Spectrally modulated noise***



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



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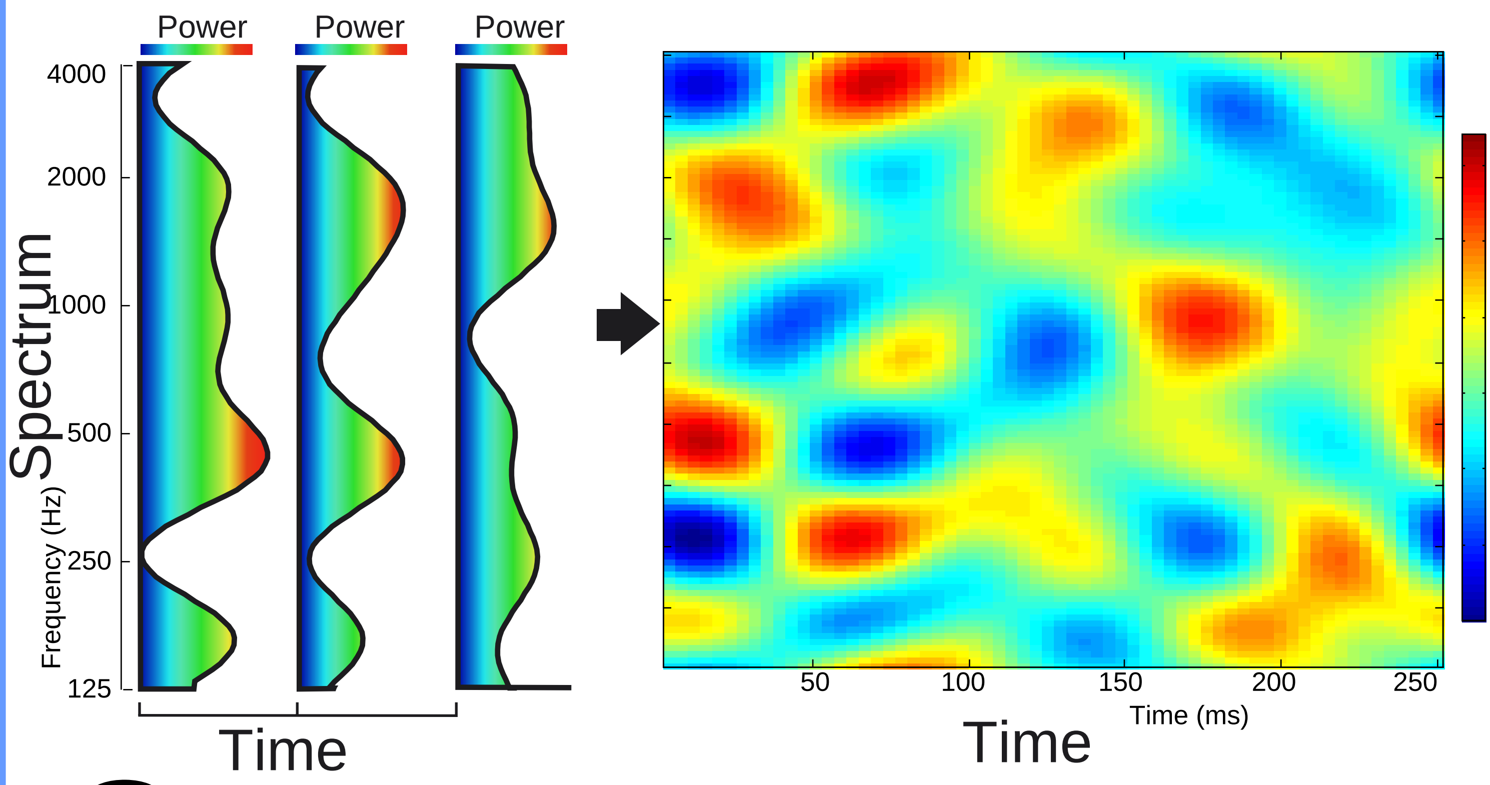
Stimulus Construction

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



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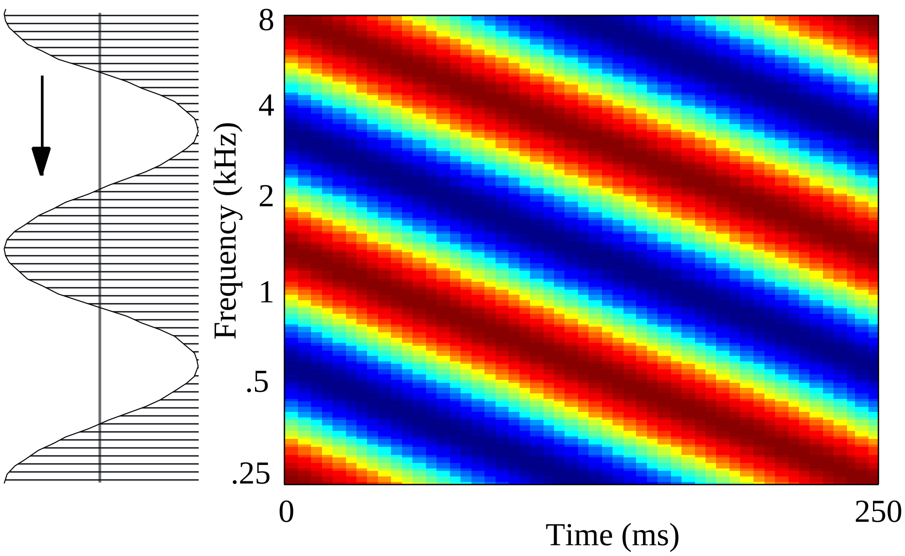
Single Moving Ripple

Simplest Dynamic Stimulus Used

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

$x = \log_2(f / f_0)$
w = ripple velocity,
e.g. 4 Hz = 4 cycles/s
Ω = ripple density,
e.g. 0.4 cycles/octave
= 2 cycles/5 octaves

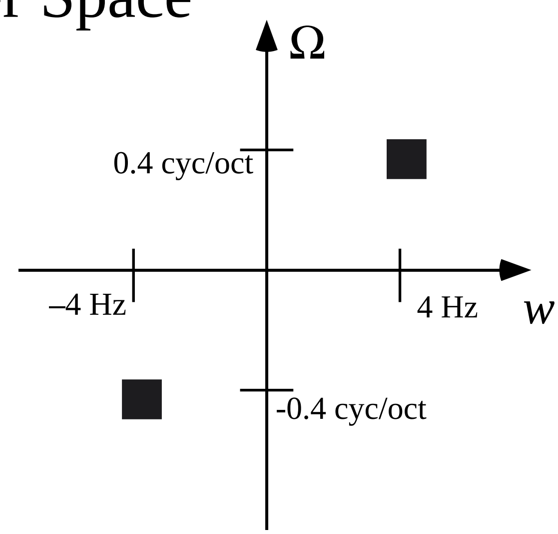
in Spectro-Temporal Space (*Spectrogram*)



c.f. visual contrast gratings

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

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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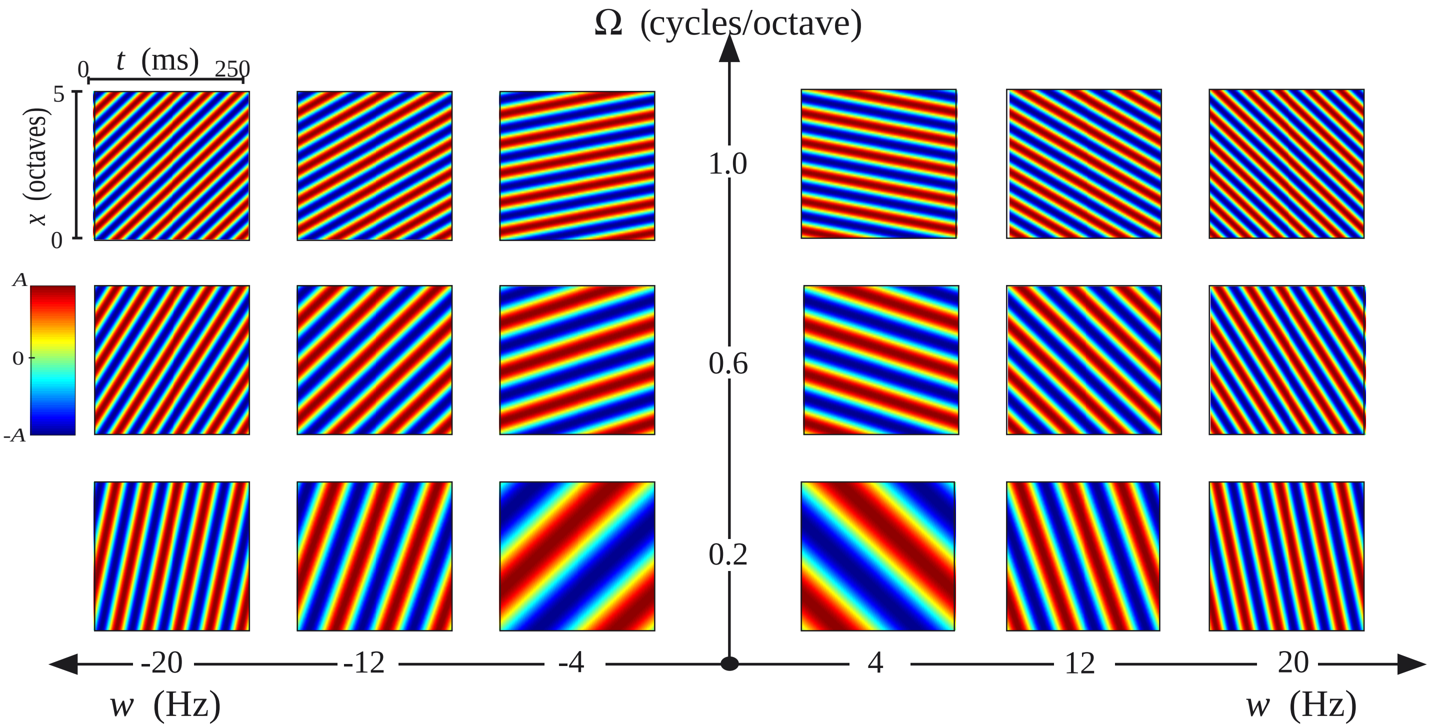
Multiple Individual Ripples

$S(t,x) = \sin(2\pi w t + 2\pi \Omega x + \phi)$

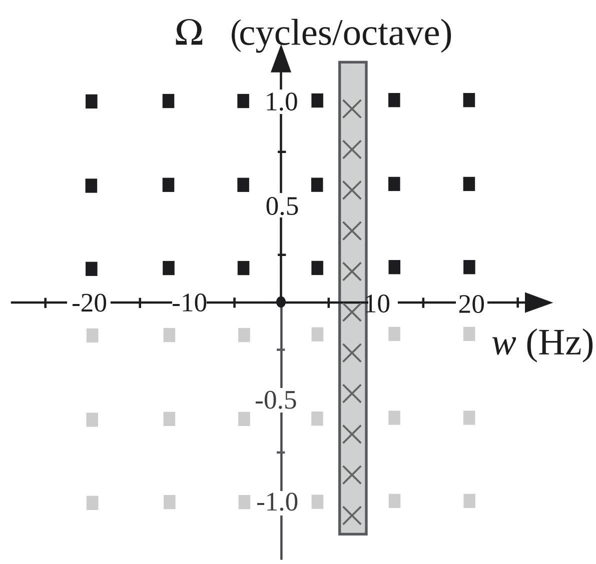
$x = \log_2(f / f_0)$

w = ripple velocity (Hz)

Ω = ripple density (cyc/oct)



The Transfer function can be obtained by measuring the amplitude and phase of the response to each single ripple.



Audio Demo

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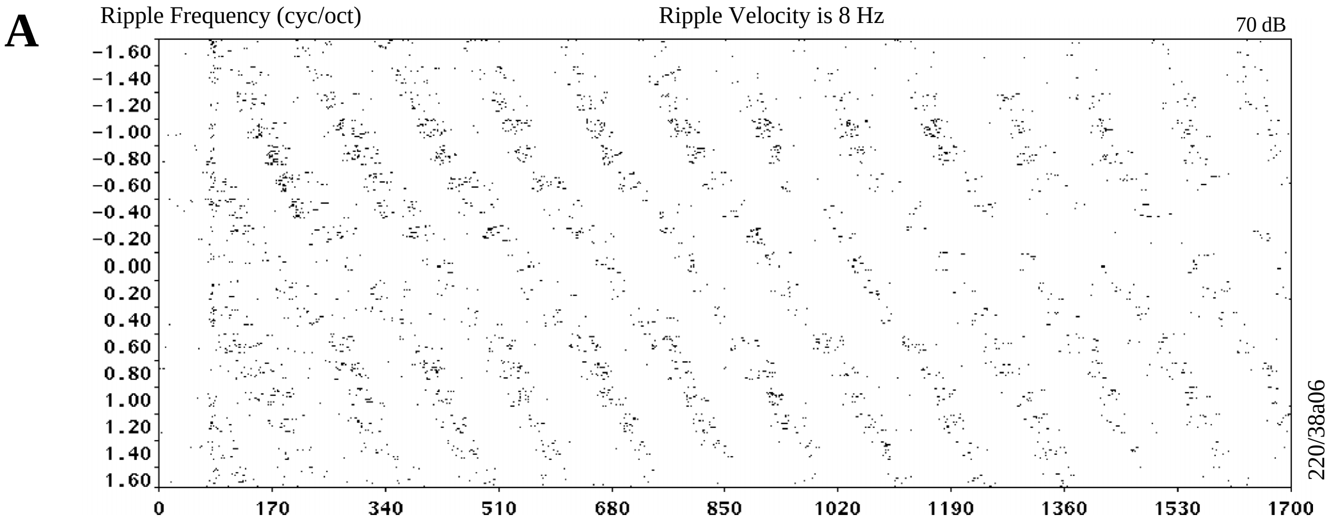
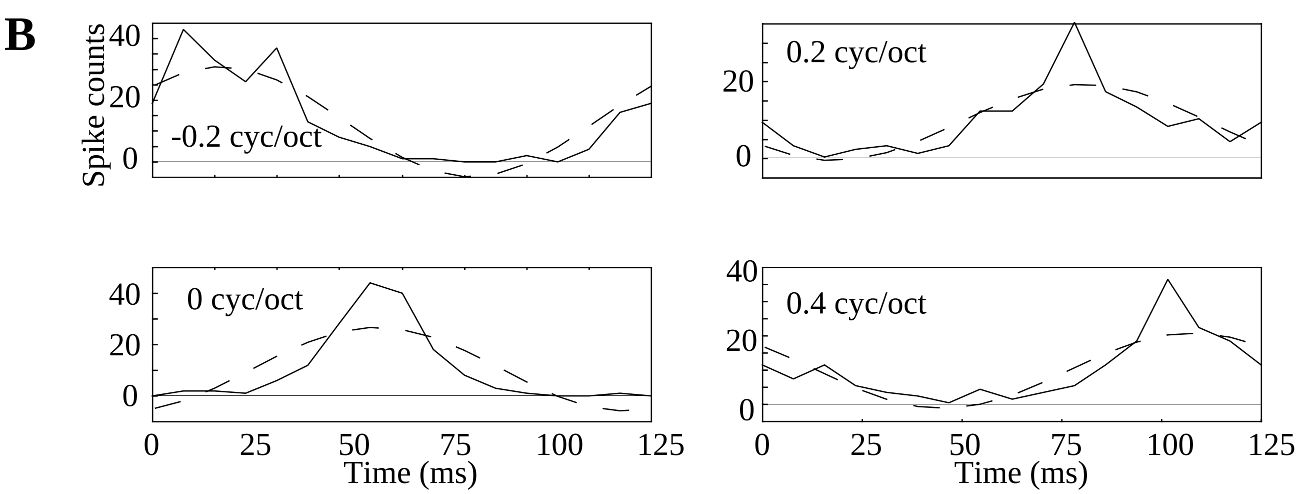
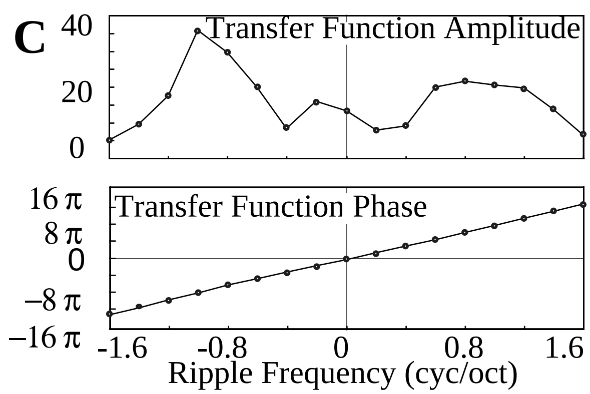
Spike Train Measurements







Spike events in (**A**) are turned into period histograms in (**B**).
The amplitudes and phases give the transfer function in (**C**).

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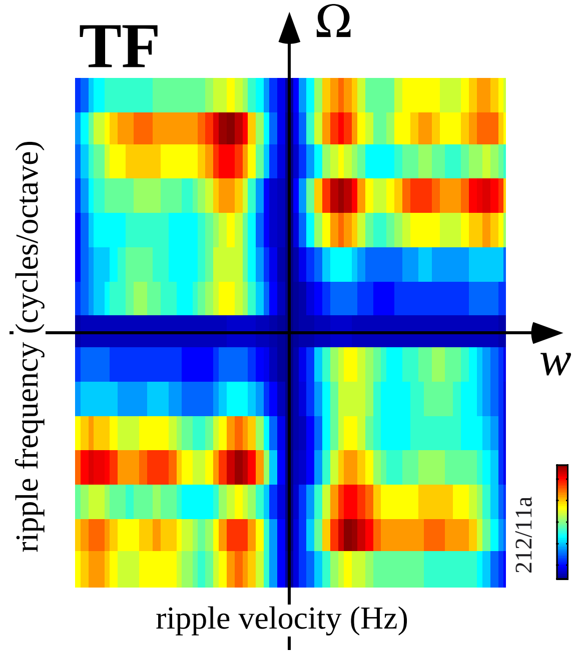
Spectro-Temporal Response Field (STRF)



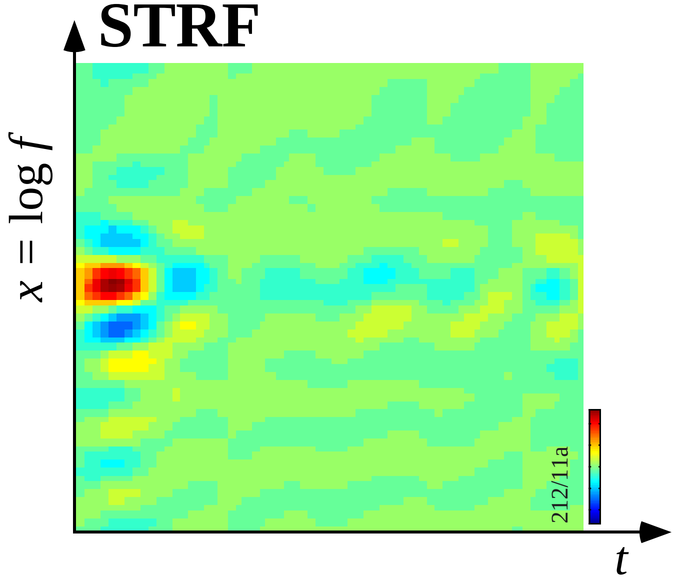
2 Dimensional Transfer Function

- Complex conjugate symmetric
- Spectral range: ~ 0 — ~ 2 cycle/octave
- Temporal range: ~ 2 — ~ 20 Hz

2 Dimensional Inverse Fourier Transform

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

2 Dimensional Fourier Transform



Spectro-Temporal Response Function of the same neuron

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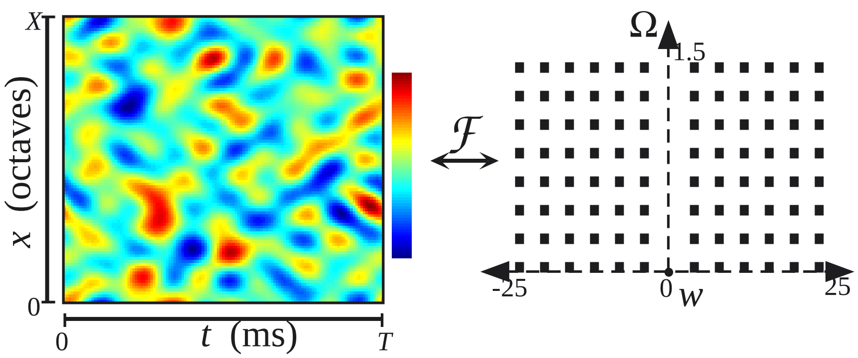
Spectro-Temporal Noise

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.

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



Spectro-Temporal generalization of white noise

$$\text{Cross-Correlation: } C(\tau, x) = \frac{1}{T}\int_0^T S(t, x)R(t-\tau)\mathrm{d}t = \frac{1}{T}\sum_k S(t_k-\tau, x)$$

= 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 S_j

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

- Cross terms give noisy estimates without many random-phase stimuli

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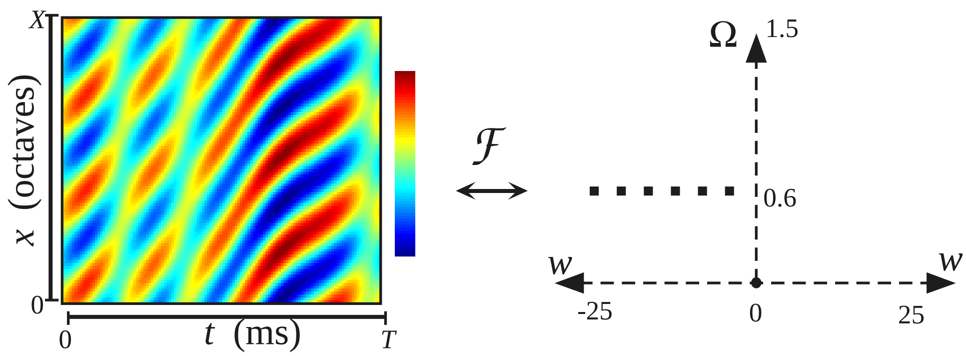
Temporally Orthogonal Ripple Combinations (TORCs)

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

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



- Stimuli have unique instances of each ripple velocity.
- Multiple stimuli are still needed to present a complete set of ripples.

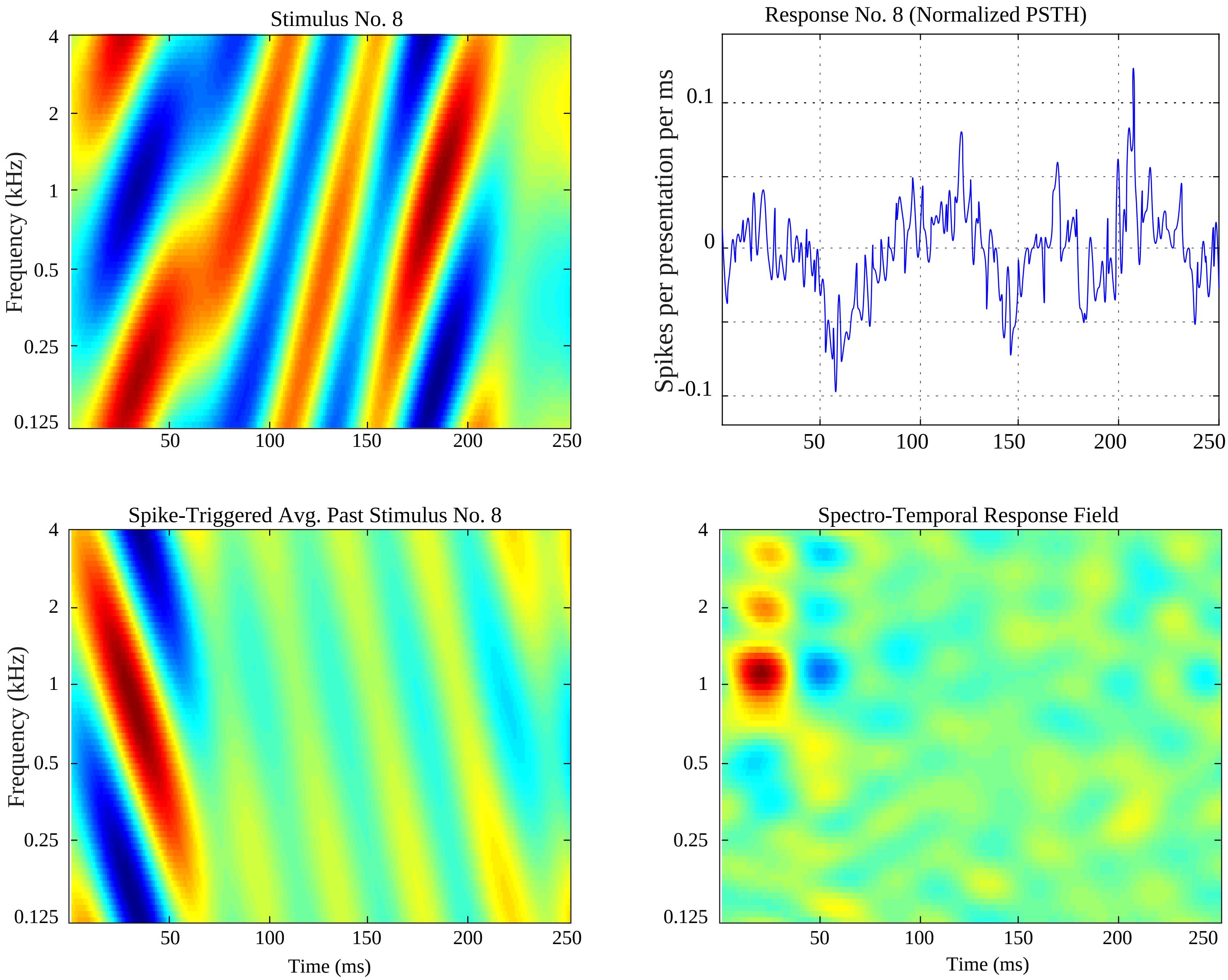
Cross-Correlation: $C(\tau, x) = \frac{1}{T}\int_0^T S(t, x)R(t-\tau)\mathrm{d}t = \frac{1}{T}\sum_k S(t_k-\tau, x)$

= Spike-Triggered Average

- $C(\tau, x)$ contains no cross terms

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

Spike Averaged Data



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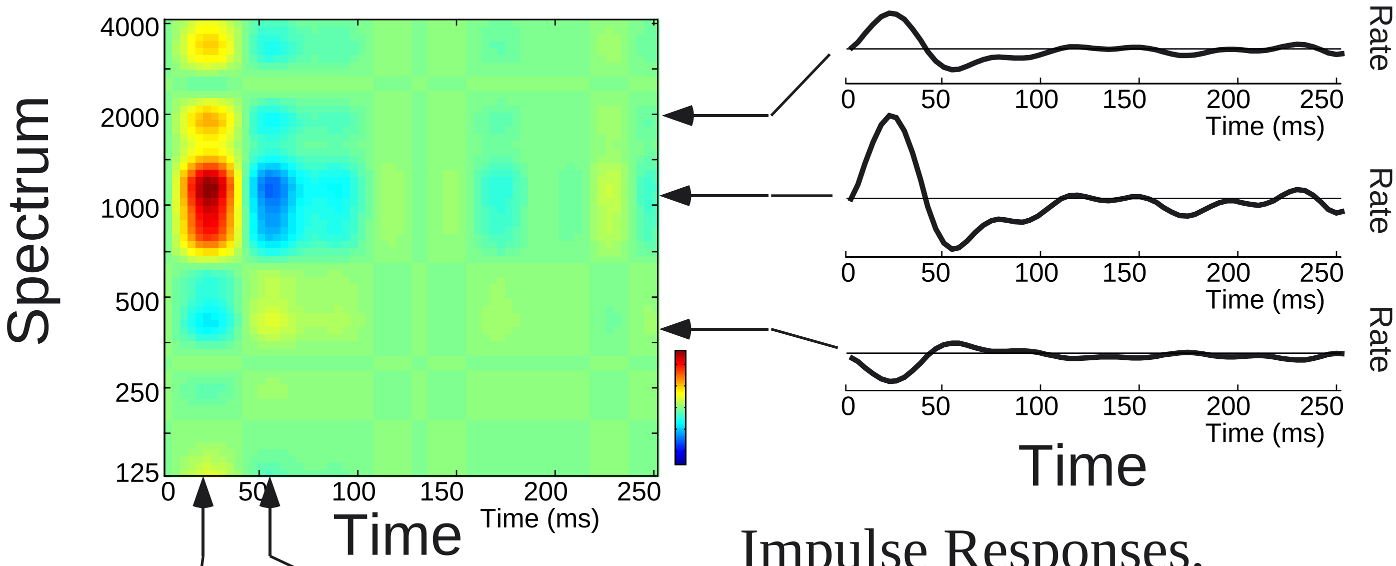
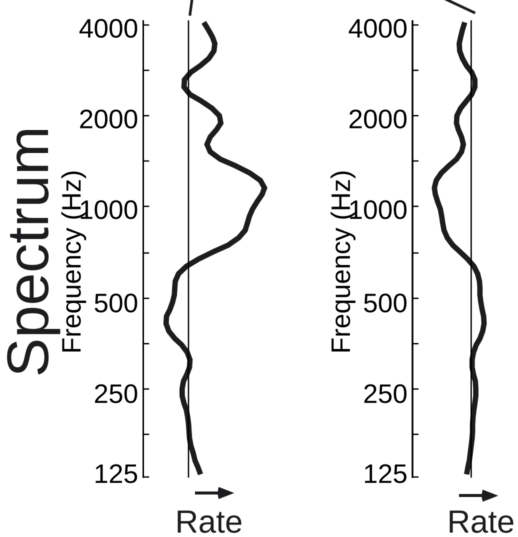
Interpreting STRFs

Cross-section interpretations

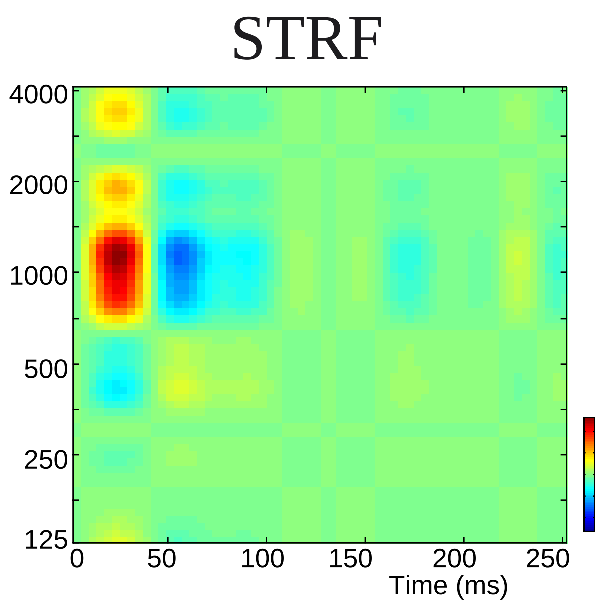


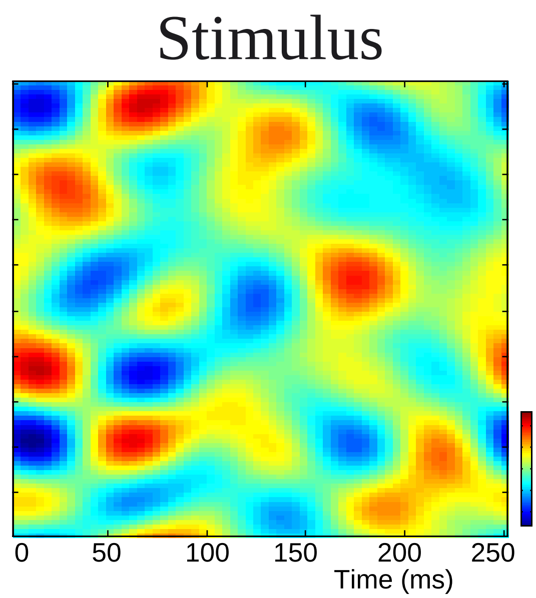
Impulse Responses,
parametrized by spectral band



Spectral Response Fields,
evolving in time

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 (!)

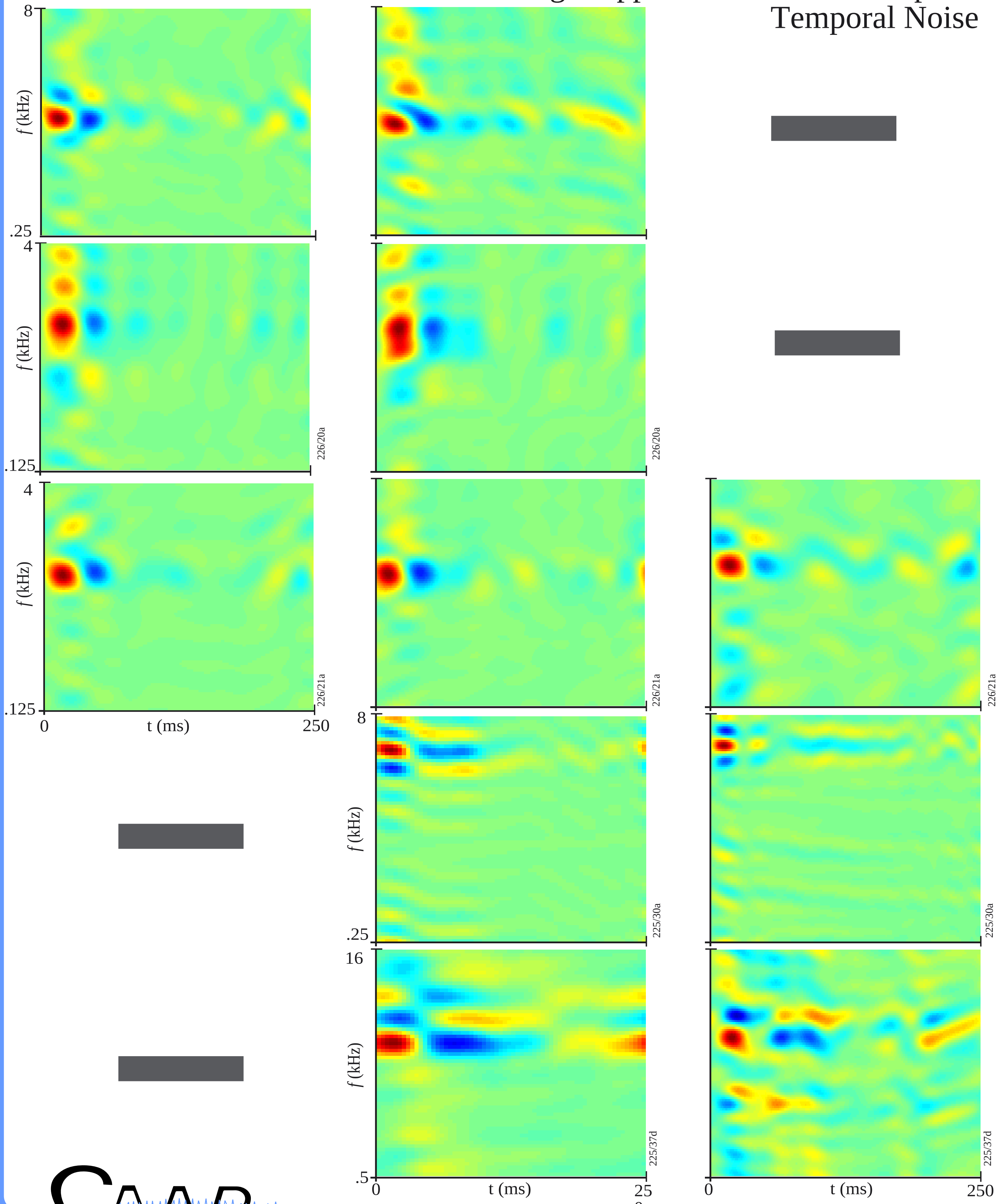
Animation Demo

STRFs Compared

STRF from TORCs

STRF from single ripples

STRF from Spectro-Temporal Noise



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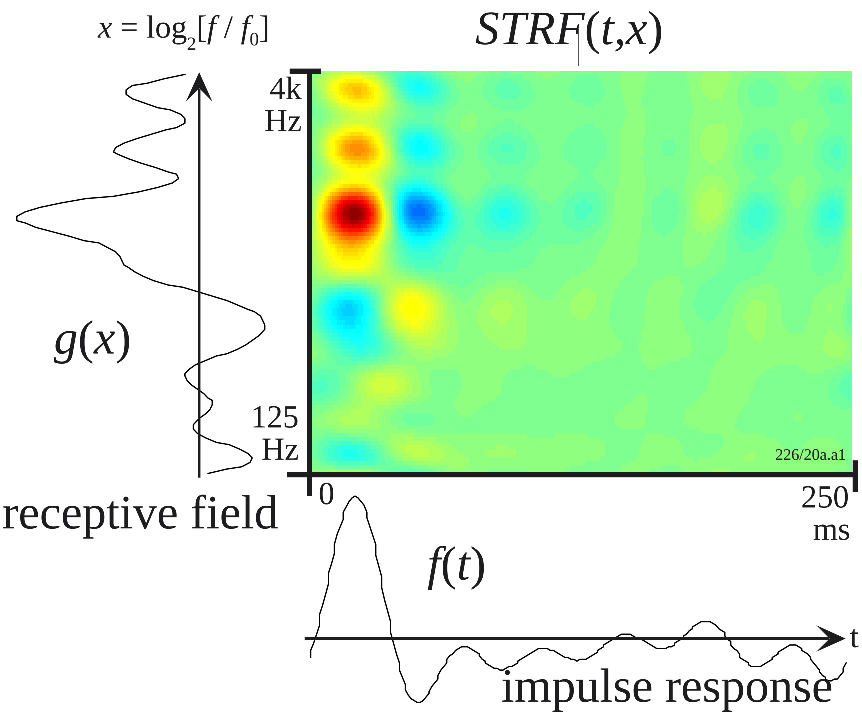
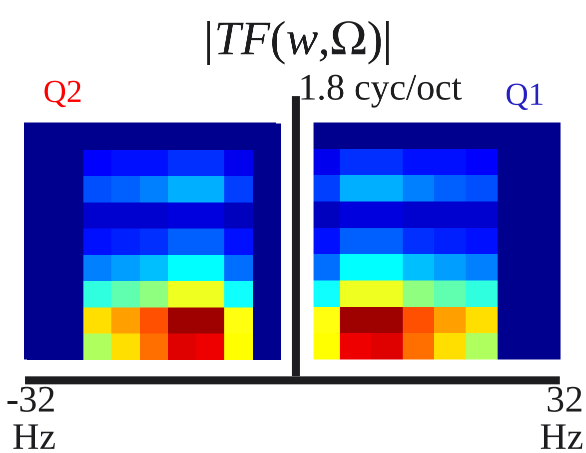
Full Separability



The STRF is a simple product of a single spectral response function with a single temporal response function.

$$STRF(t,x) = f(t)\, g(x)$$

$$|\mathcal{F}\{\ \}| \updownarrow$$

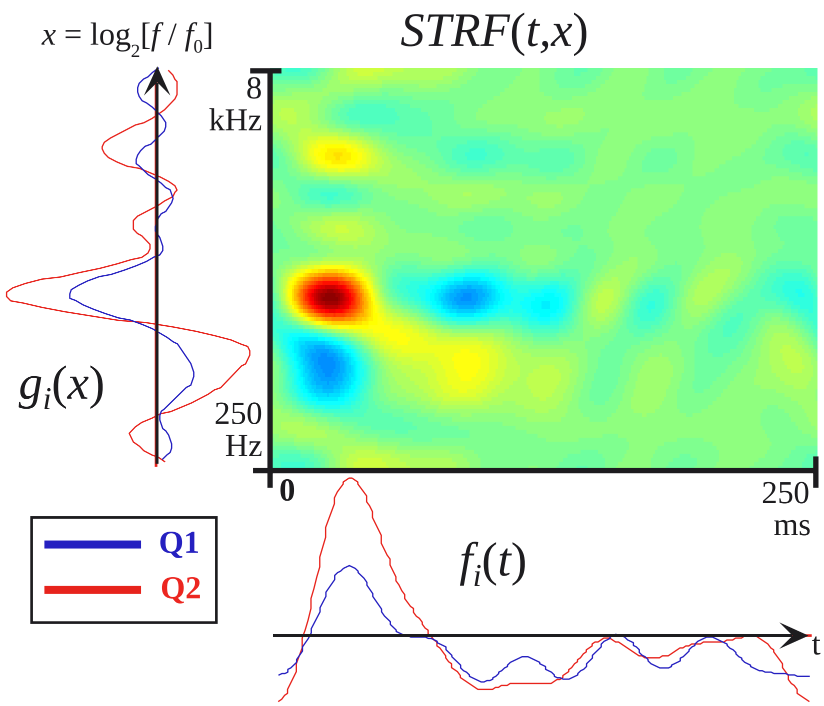


$f(t)$	$g(x)$
$\updownarrow$	$\updownarrow$
$F(w)$	$G(\Omega)$

$$TF(w,\Omega) = F(w)\, G(\Omega)$$

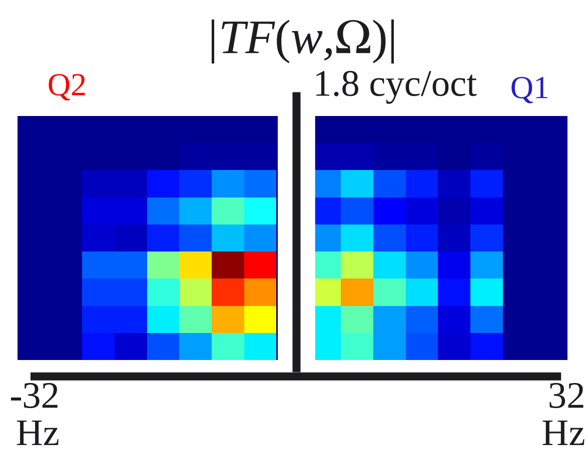
Therefore the TF is also a simple product

Quadrant Separability



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.

$|\mathcal{F}\{\ \}| \updownarrow$



$f_i(t)$	$g_i(x)$
$\updownarrow$	$\updownarrow$
$F_i(w)$	$G_i(\Omega)$

$$T(w,\Omega) = \begin{cases} F_1(w)\,G_1(\Omega) & w > 0,\ \Omega > 0 \\ F_2(w)\,G_2(\Omega) & w < 0,\ \Omega > 0 \end{cases}$$

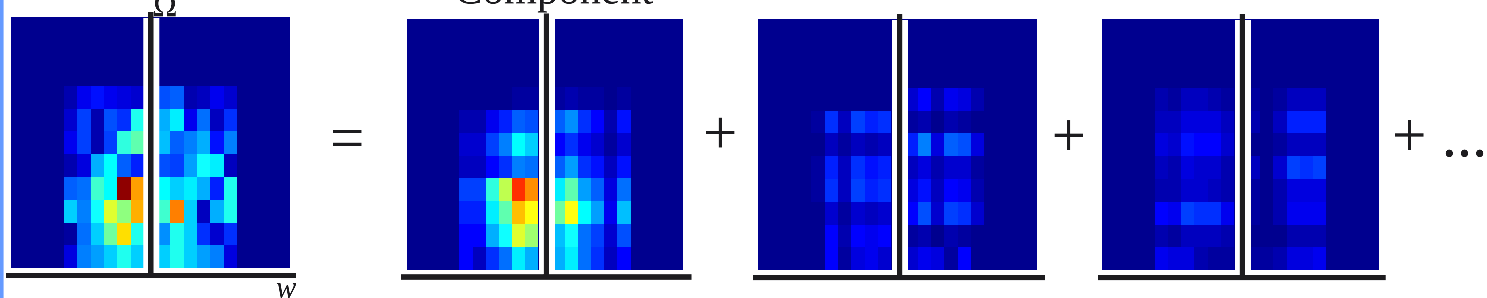
for $\Omega > 0$: $T(w,\Omega) = T^*(-w,-\Omega)$

Measuring Separability with SVD

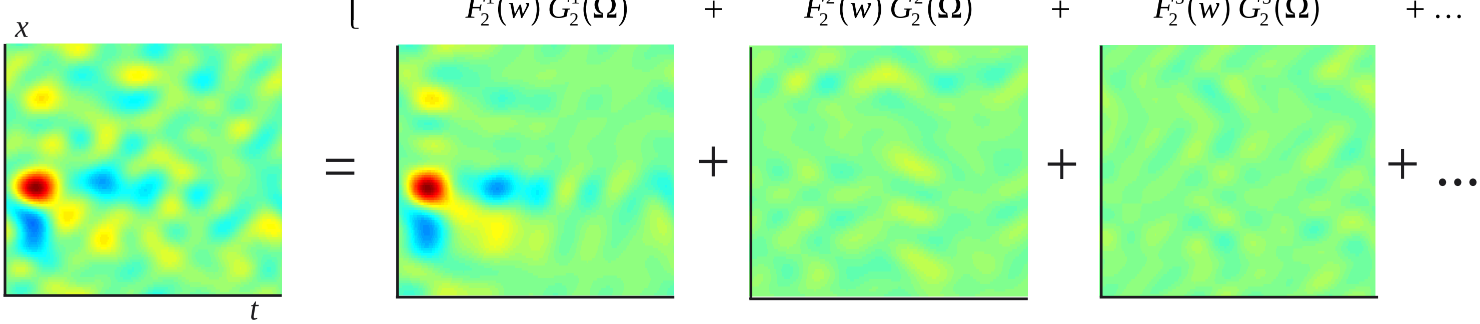
- Singular Value Decomposition (SVD) can be used to estimate the separability of a Transfer Function (possibly corrupted by noise). It decomposes the Transfer Function into a sum of Quadrant Separable Transfer Functions, ordered by their power.

- Large jumps in the singular values separate signal from noise (& straddle bootstrap estimate of noise).

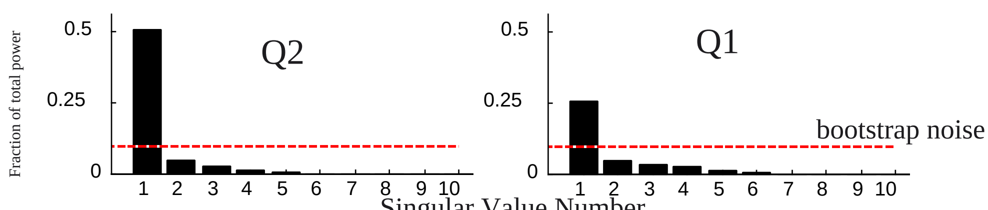
Raw Estimate | 1st Quadrant-separable Component | 2nd



$$T(w,\Omega) = \begin{cases} F_1^1(w)\,G_1^1(\Omega) + F_1^2(w)\,G_1^2(\Omega) + F_1^3(w)\,G_1^3(\Omega) + \dots \\ F_2^1(w)\,G_2^1(\Omega) + F_2^2(w)\,G_2^2(\Omega) + F_2^3(w)\,G_2^3(\Omega) + \dots \end{cases}$$



All units measured in AI are quadrant separable (or fully separable).



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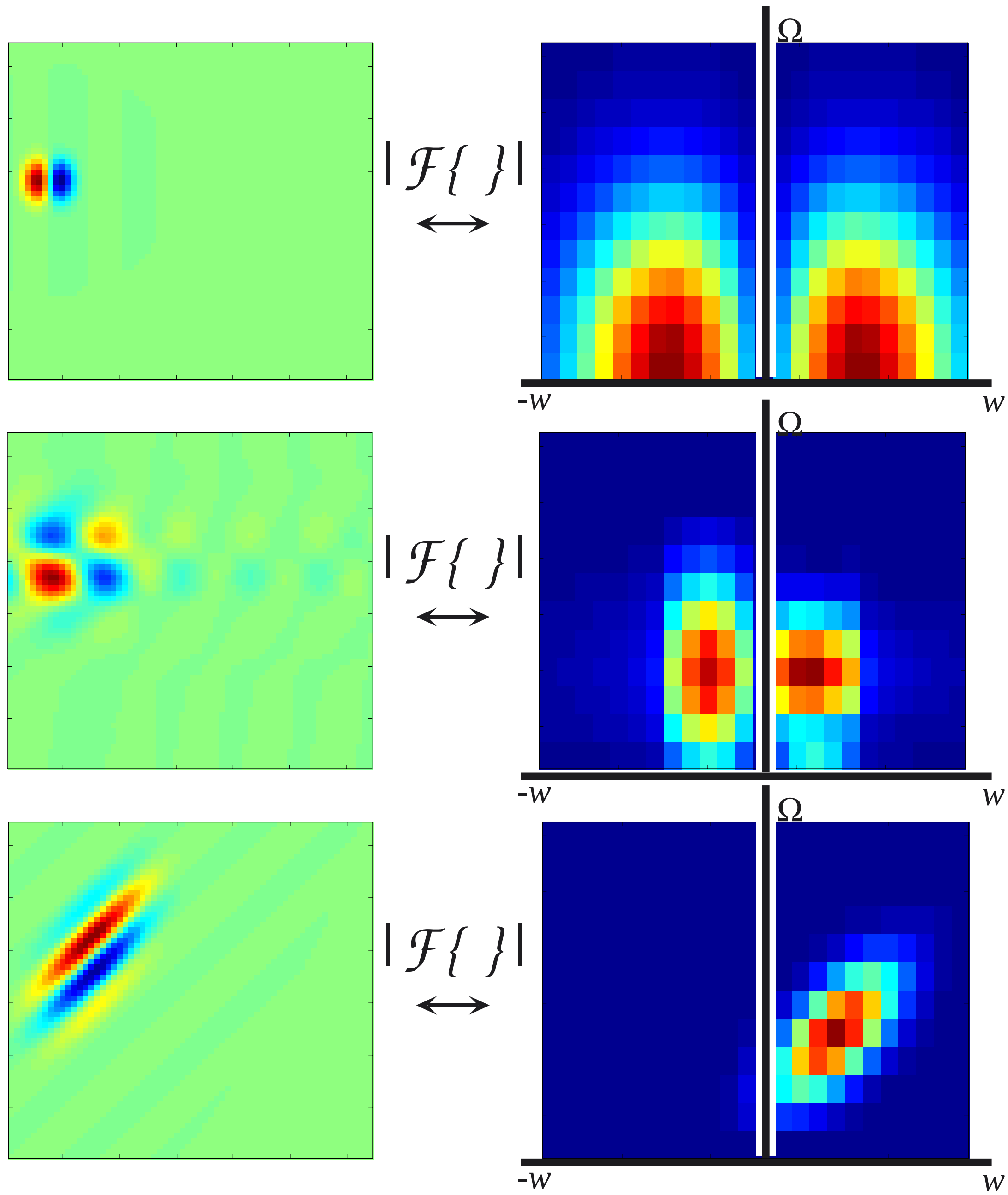
Separability Examples

Fully Separable

Quadrant Separable

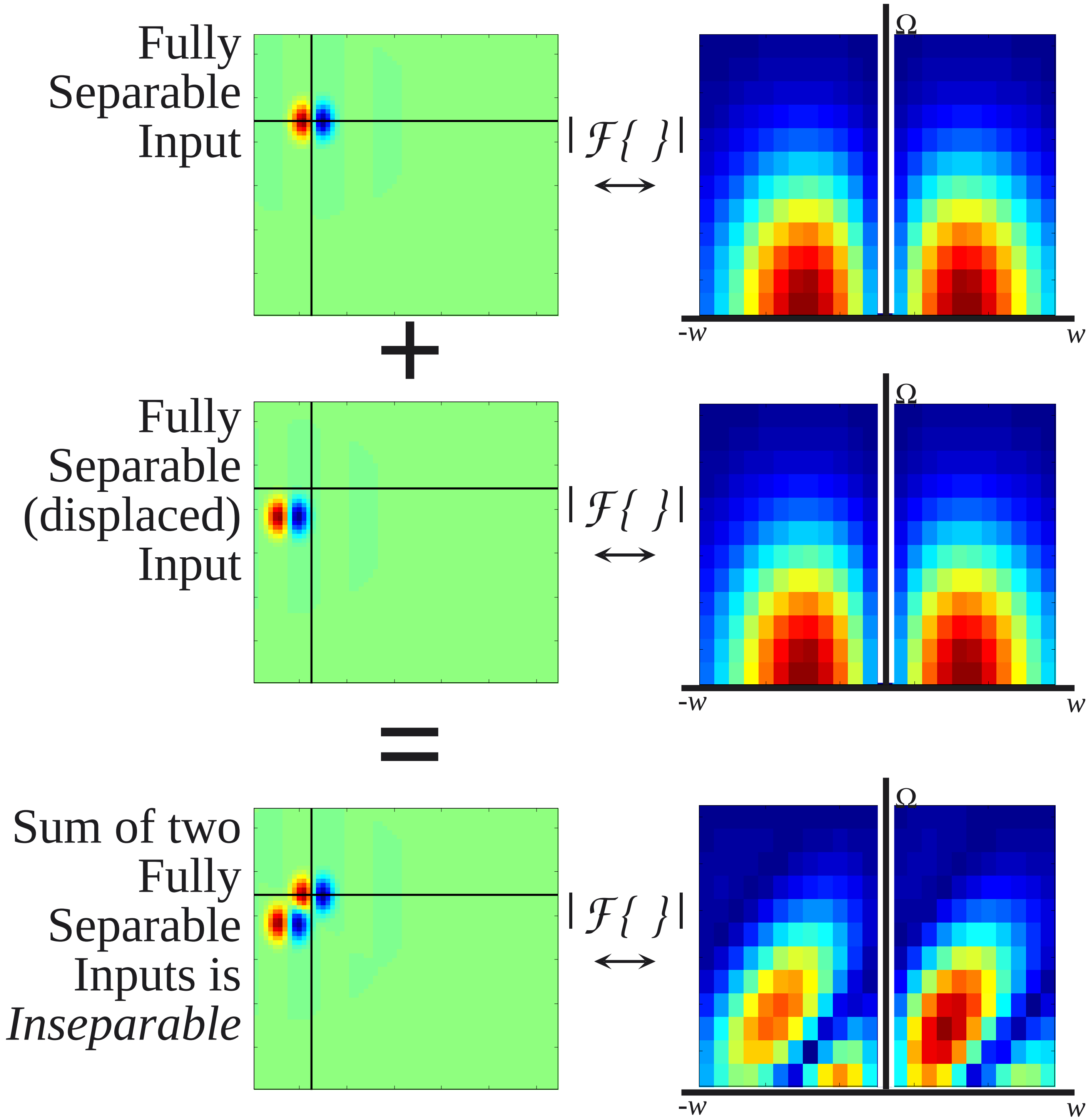
Velocity Selective is *Inseparable*



Quadrant separability is incompatible with velocity selectivity.

Simulation

Separability Counterexample



Naive sum of two fully separable input STRFs is inseparable.

Simulation

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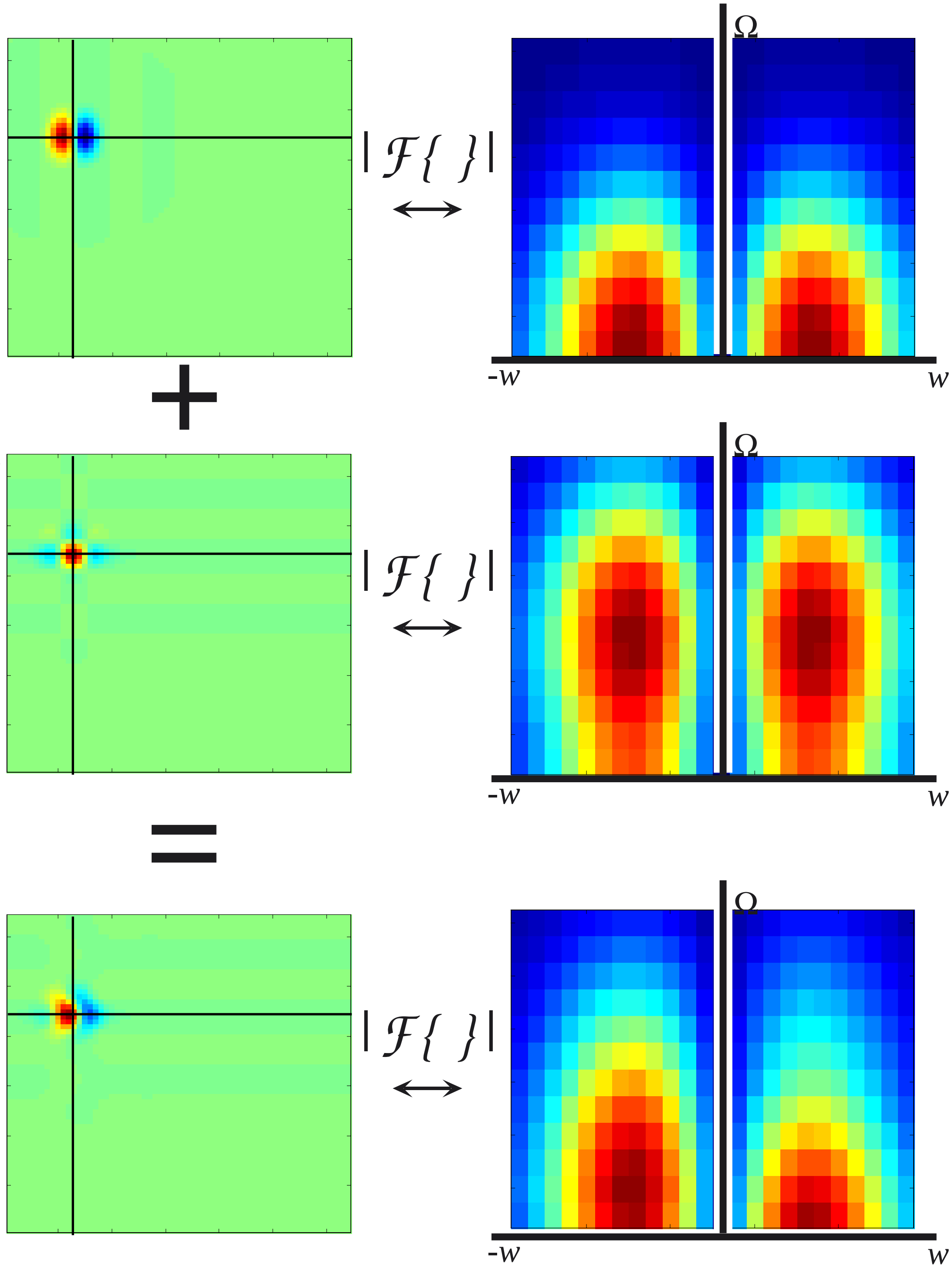
Separability Example

Fully Separable Input

Same Fully Separable but Lagged (& shifted spectrally) Input

Sum of Non-Lagged and Lagged Inputs is *Separable*



Sum of two fully separable input STRFs is separable if the temporal processing is in quadrature.

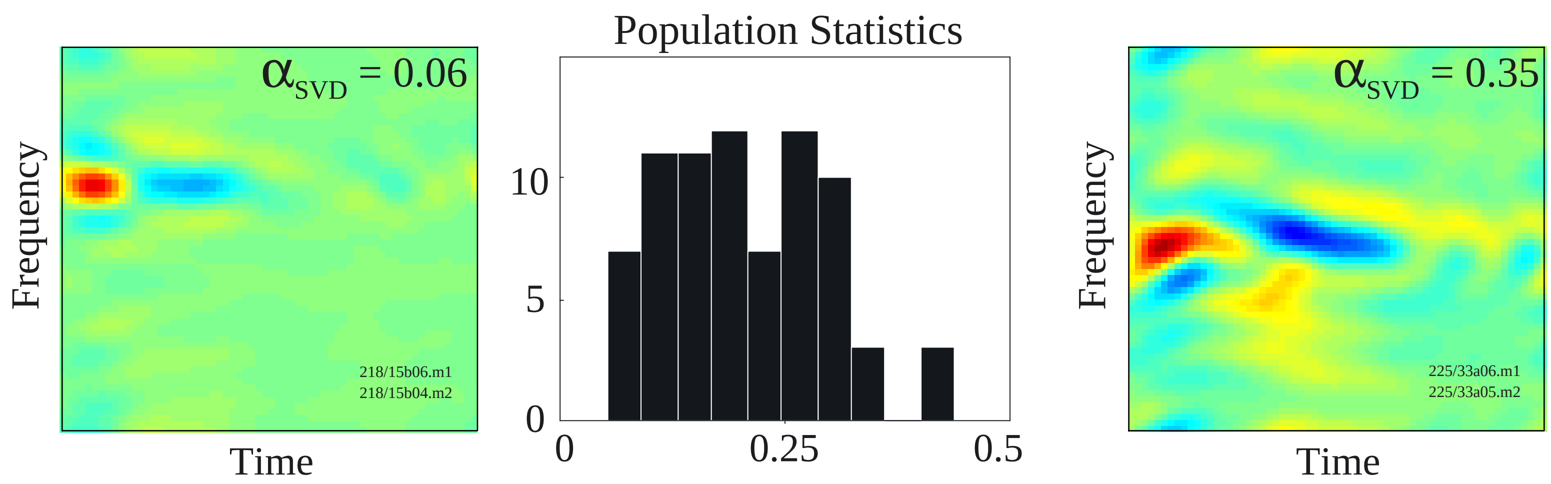
Simulation

Measure of Separability

- SVD supplies a natural measure of separability, α_{SVD}

$$\boxed{\alpha_{\mathrm{SVD}} = \left(1 - \frac{\lambda_1^2}{\sum_i \lambda_i^2}\right)}$$

- $\alpha_{SVD} \approx 0$ is fully separable
- $\alpha_{SVD} > 0.3$ is strongly inseparable



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Symmetry by Power

- α_d: Power asymmetry breaks full separability, producing quadrant separability

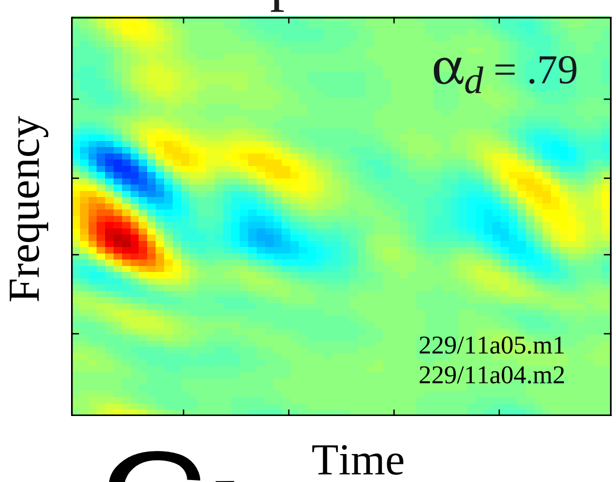
$$\alpha_d = (P_1 - P_2)/(P_1 + P_2)$$

$$P_1 = (\text{Power in quadrant 1}) = (\lambda_1)^2$$

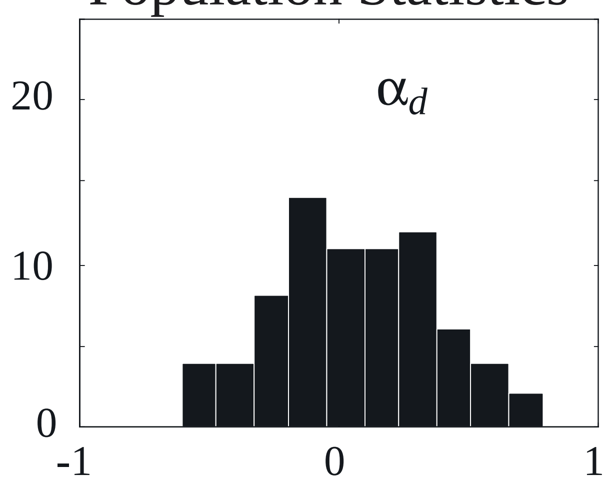
$$P_2 = (\text{Power in quadrant 2}) = (\lambda_2)^2$$

- $\alpha_d \approx 0$ is symmetric in power
- $|\alpha_d| > 0.3$ is quite asymmetric in power—strongly inseparable

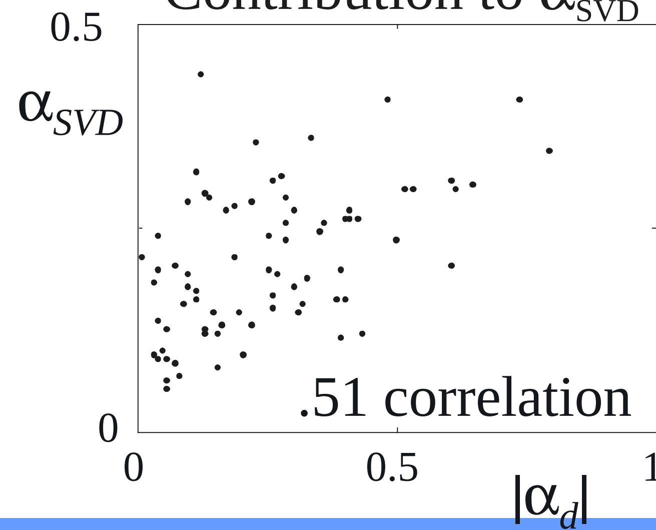
Example STRF



Population Statistics



Contribution to α_{SVD}



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Spectral Symmetry

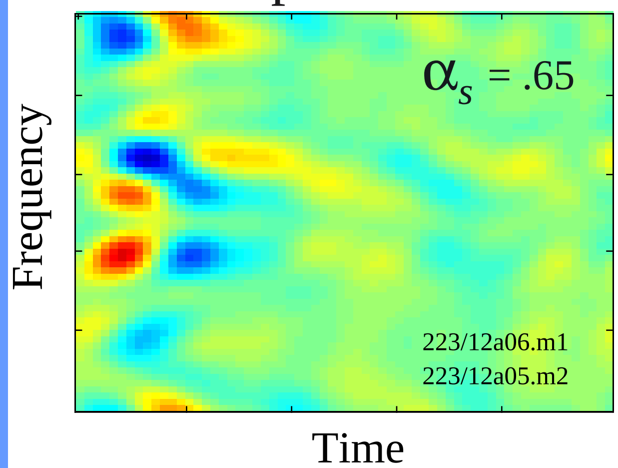
- α_s: Asymmetry between spectral cross-sections $G_i(\Omega)$:

$$\boxed{\alpha_s = 1 - \left| \frac{\sum_{\Omega>0} G_1(\Omega)\, G_2^*(\Omega)}{\sqrt{\sum_{\Omega>0} |G_1(\Omega)|^2\, |G_2(\Omega)|^2}} \right|}$$

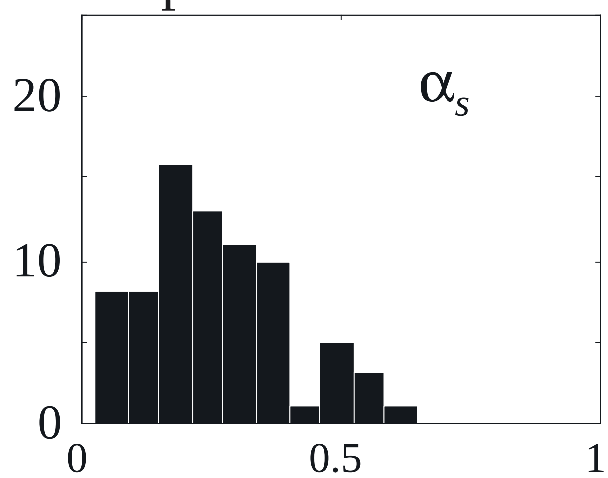
where the quantity inside the big absolute value bars is the (complex) correlation between $G_1(\Omega)$ and $G_2(\Omega)$

- $\alpha_s \approx 0$ is spectrally symmetric
- $\alpha_s > 0.3$ is spectrally asymmetric—strongly inseparable

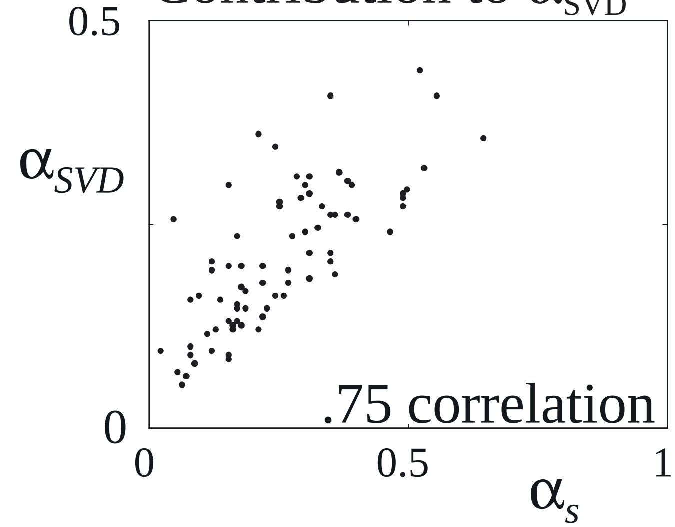
Example STRF



Population Statistics



Contribution to α_{SVD}



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Temporal Symmetry

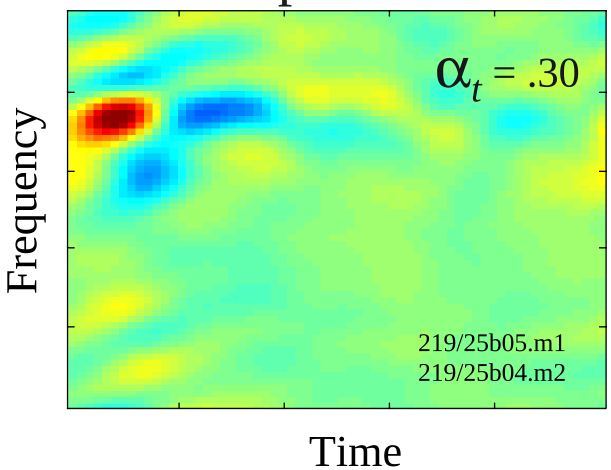
- α_t: Asymmetry between temporal cross-sections $F_i(w)$:

$$\alpha_t = 1 - \left| \frac{\sum_{w>0} F_1(w)\, F_2(-w)}{\sqrt{\sum_{w>0} |F_1(w)|^2\, |F_2(-w)|^2}} \right|$$

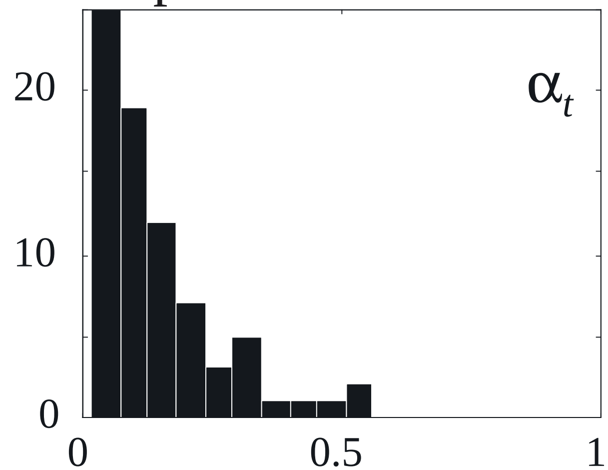
where the quantity inside the big absolute value bars is the (complex) correlation between $F_1(w)$ and $F_2^*(-w)$

- $\alpha_t \approx 0$ is temporally symmetric
- $\alpha_t > 0.3$ is temporally asymmetric—strongly inseparable

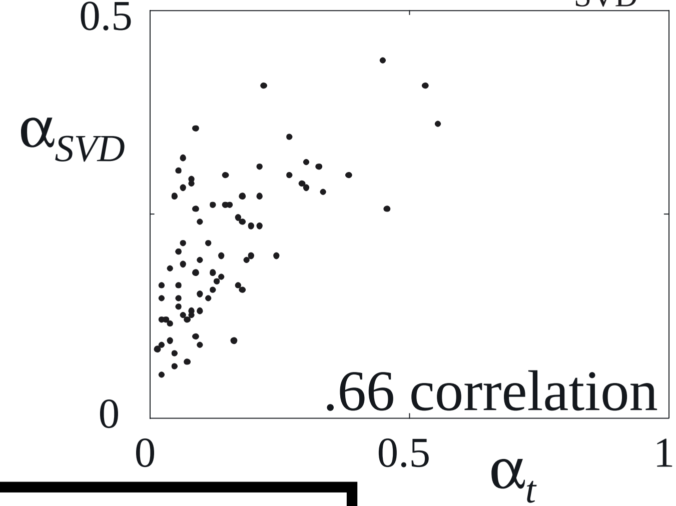
Example STRF



Population Statistics



Contribution to α_{SVD}



Distribution is strongly skewed toward temporal symmetry.

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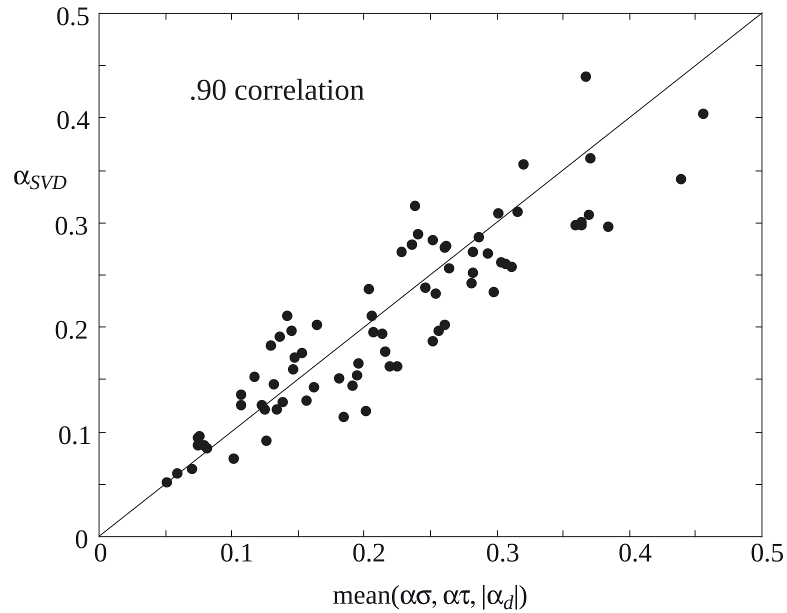
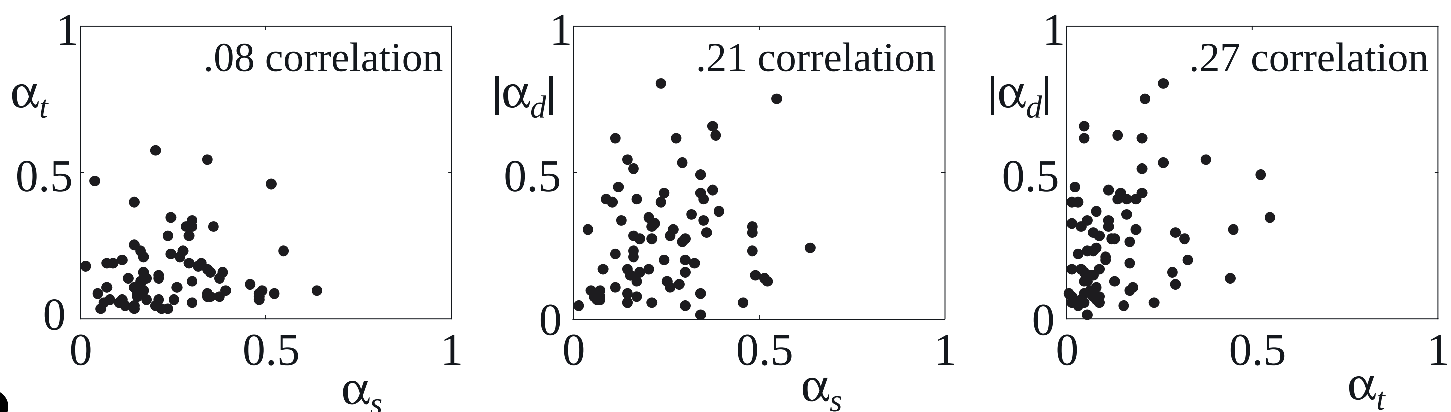
Symmetry Correlations

- Mean of 3 separate symmetry measures correlates well with full separability index.



- Individual indices only partially correlated with each other.



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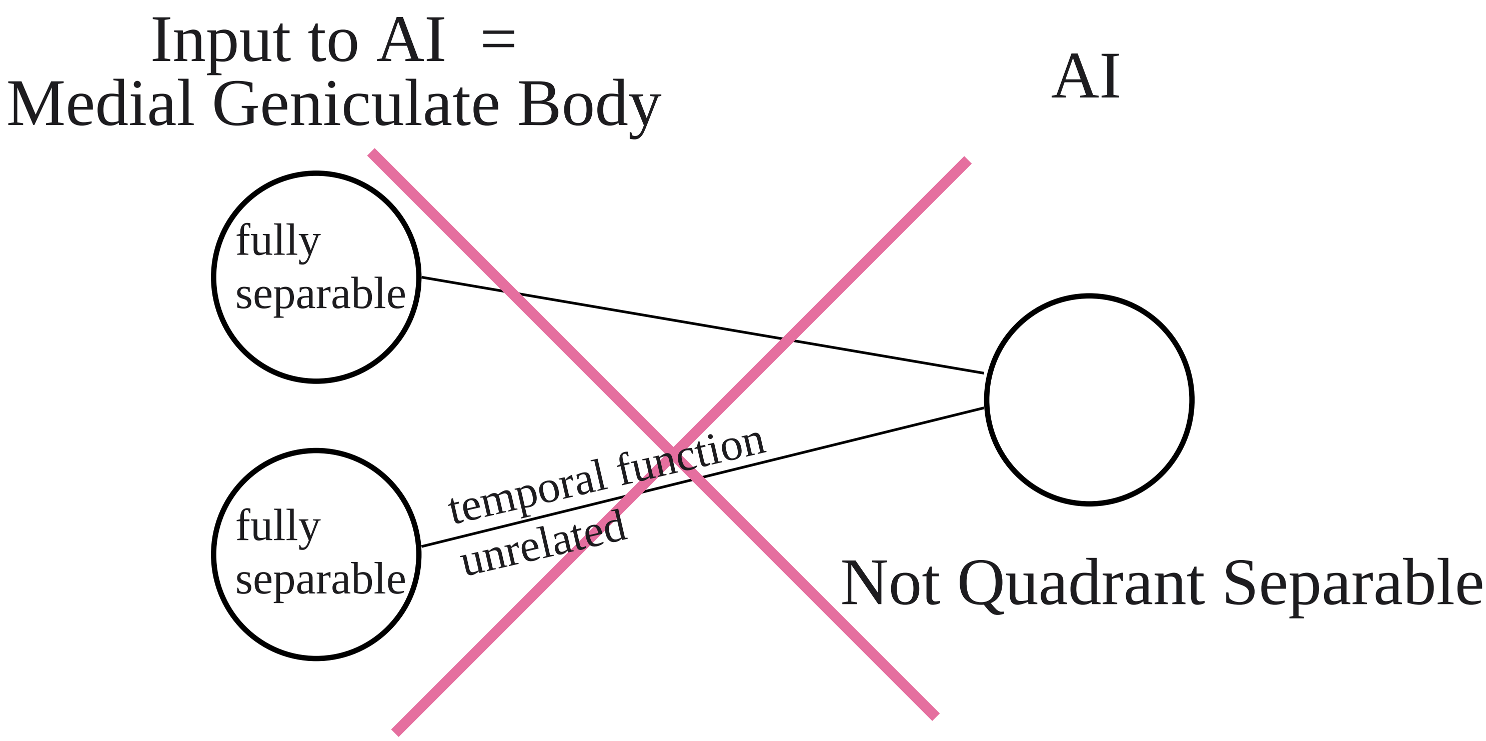
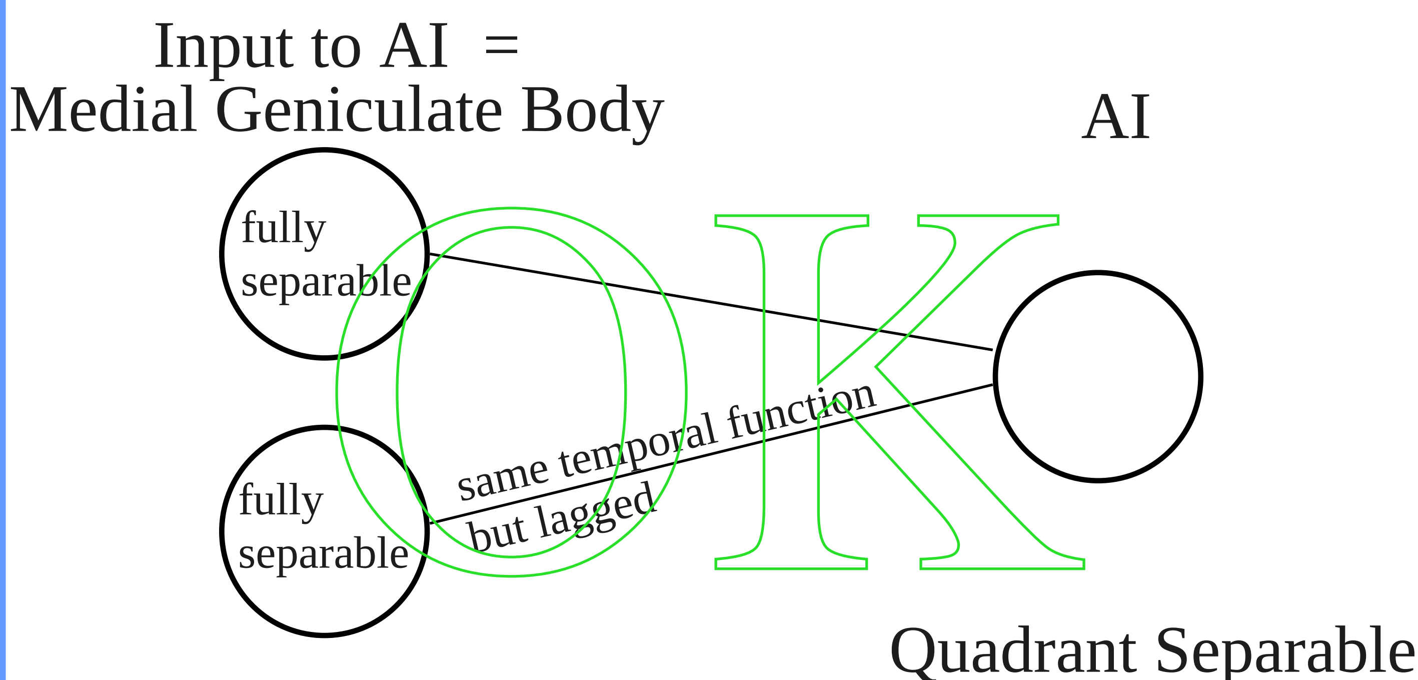
Neural Connectivity Constraints





Summary

- **The function of AI**

  To encode spectro-temporal features of sounds

  spectrally: to ~1 cycles/octave

  temporally: ~2 to ~20 Hz (in ferret)

  plus encoding other sound features not addressed here

- **Spectro-Temporal Response Field (STRF)**
  - **Descriptor** of response to broadband dynamic stimuli
  - **Predictor** of spike train for stimuli of dynamic, spectral modulations of noise
    - STRFs agree despite measurement method
    - Linear processing conveys most of the information
  - **Visual Tool** conveys spectro-temporal regions of excitation and inhibition

- **Constraints of Quadrant Separability**
  - Limits possible network dynamics

Selected References

Moving Ripple / STRF / Ripple Transfer Function

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- ❑ Simon JZ, Depireux DA and Shamma SA, *Psychophysical and Physiological Advances in Hearing*, Ed.: A. R. Palmer, A. Rees, A. Q. Summerfield, and R. Meddis, Whurr London, 1997.
- ❑ Depireux DA, Simon JZ and Shamma SA, *Comments in Theor. Biol.* 5 (1998) 89-118.
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- ❑ deCharms RC, Blake DT, and Merzenich MM *Science* 280 (1998) 1439–1443.
- ❑ Eggermont JJ, *Hearing Research* 66 (1993) 177-201.

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- ❑ Watson AB and Ahumada AJ, *J. Opt. Soc. Am.* A2(2) (1985) 322–341.
- ❑ Saul AB and Humphrey AL, *J. Neurophysiol.* 64 (1990) 206-224.

Singular Value Decomposition

- ❑ Hansen PC, *Rank-Deficient and Discrete Ill-Posed Problems*, SIAM 1998.
- ❑ Press WH, Flannery BP, Teukolsky SA, and Vetterling, WT, *Numerical Recipes*, Cambridge University Press 1986.

- Introduction to Auditory Spectro-Temporal Processing
- Stimuli—Dynamic & Broadband: Ripples, Ripple Combinations
- Examples & Properties of Spectro-Temporal Response Fields
- Constraints on Neural Connectivity
- **MagnetoEncephaloGraphy (MEG)**

MEG

- **MagnetoEncephaloGraphy**

- **Supercooled SQuIDs**
  - measure evoked magnetic fields ~ 200 fT
    created by ~ 10^4 neurons carrying current in parallel

- **Features**
  - **Non-invasive** can be used in human subjects
  - **Magnetic fields *not* attenuated by tissue**: c.f. EEG
  - **Excellent temporal resolution**: ~ 1 ms
  - **Coarse spatial resolution**: ~150 sensors ↔ ~ 1 cm^2
  - **Complementary to EEG**

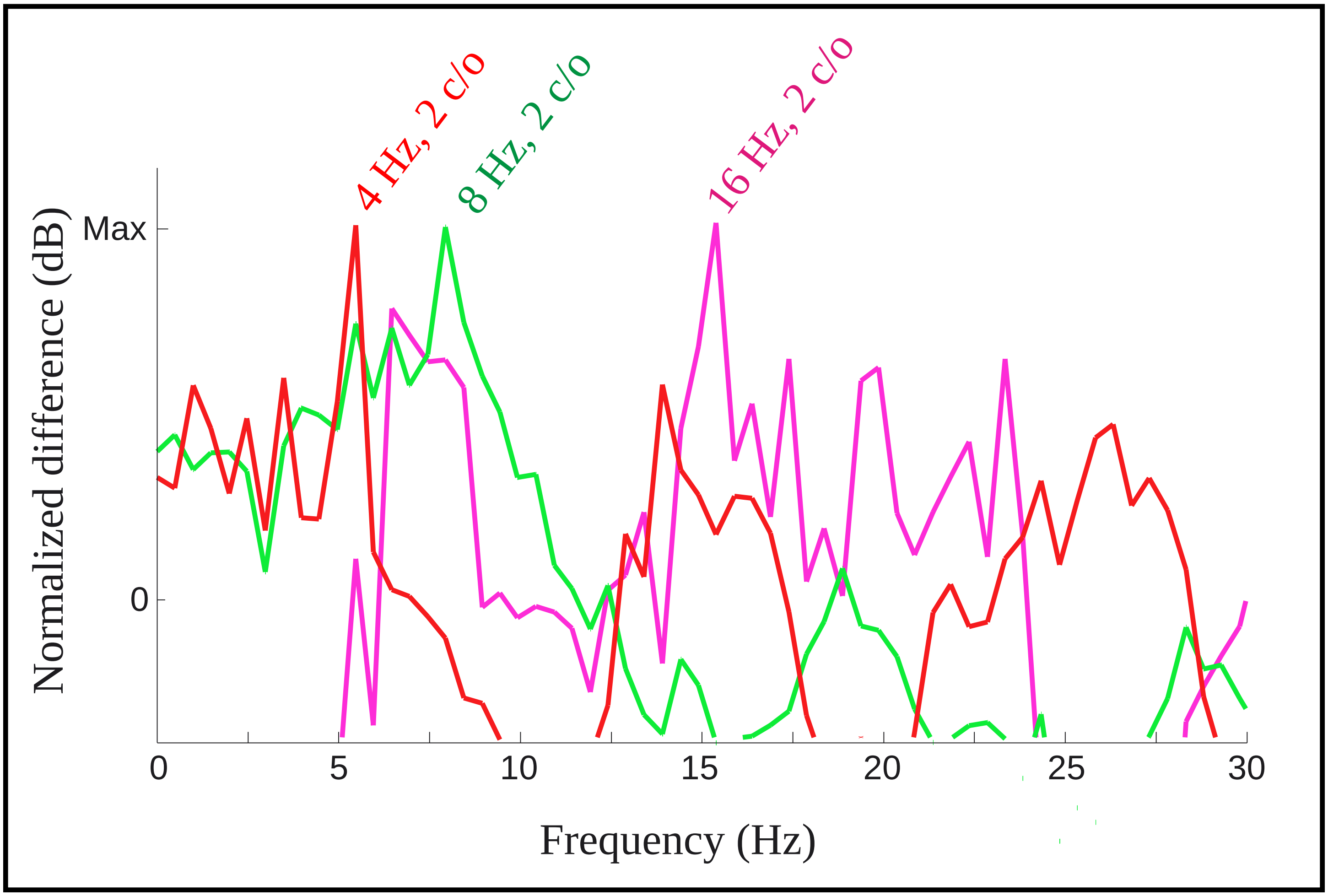
- **Preliminary Study**
  - 5 subjects, ~4 Gig data/subject, analysis in progress
  - single ripple stimuli

- **Goals**
  - Demonstrate magnetic
    correlate of single neurons
  - Characterize spatial response

Preliminary Data

- **Peaks in Power Spectral Density** (of magnetic field) correspond to stimulus ripple velocity
- **Left-Right Processing Asymmetry**

Power Spectral Density, R – L



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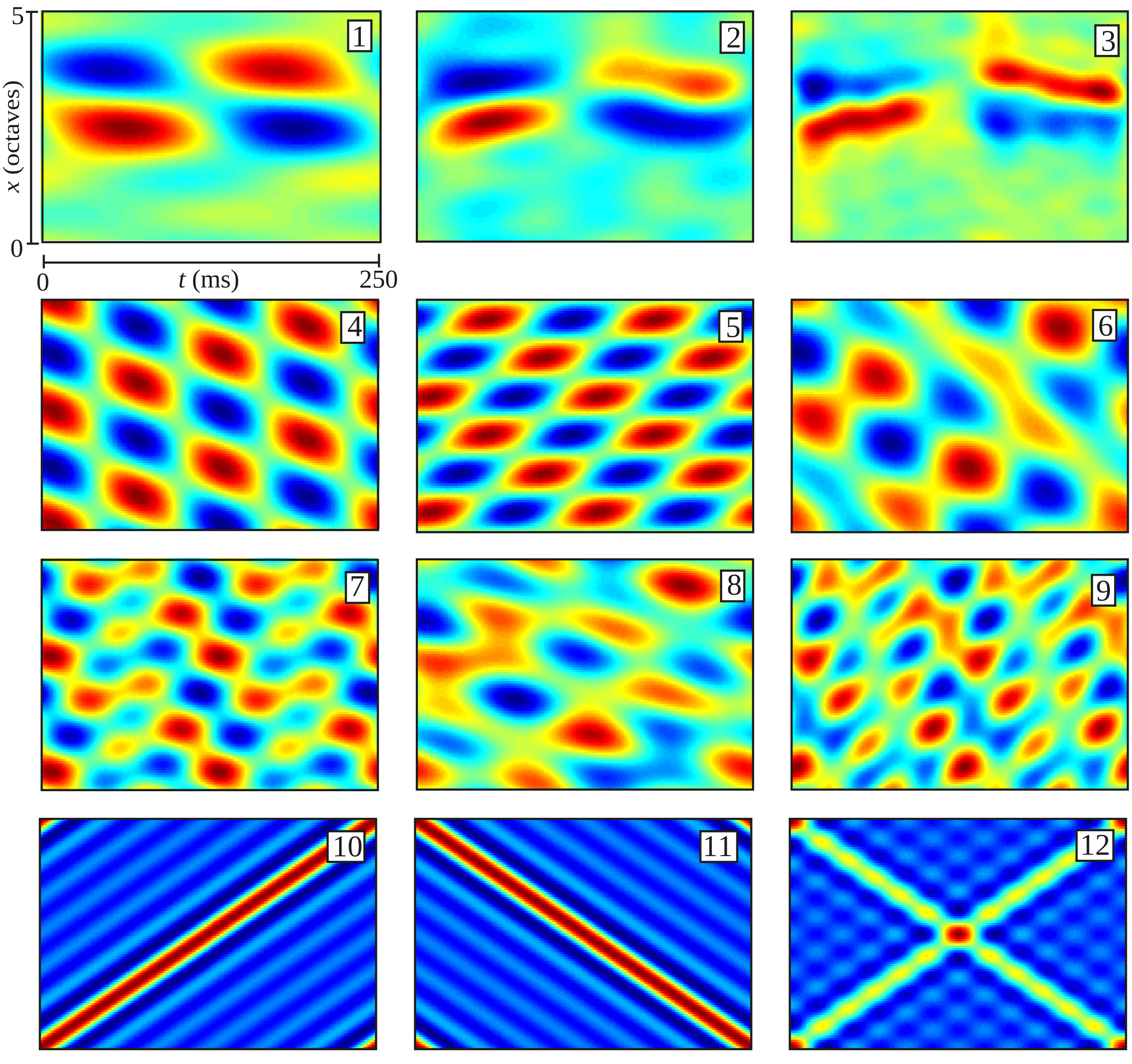
- **Predicting Responses to Novel Stimuli**

Predicting Responses

- **Predictions of Responses to Novel Stimuli**

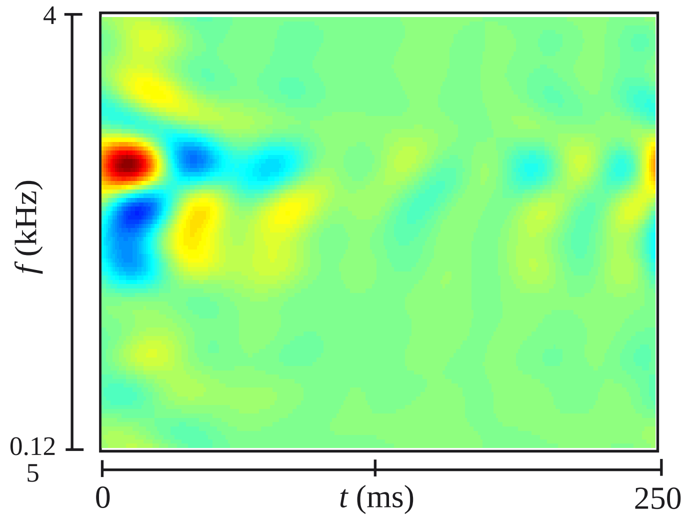
  Good test of linearity

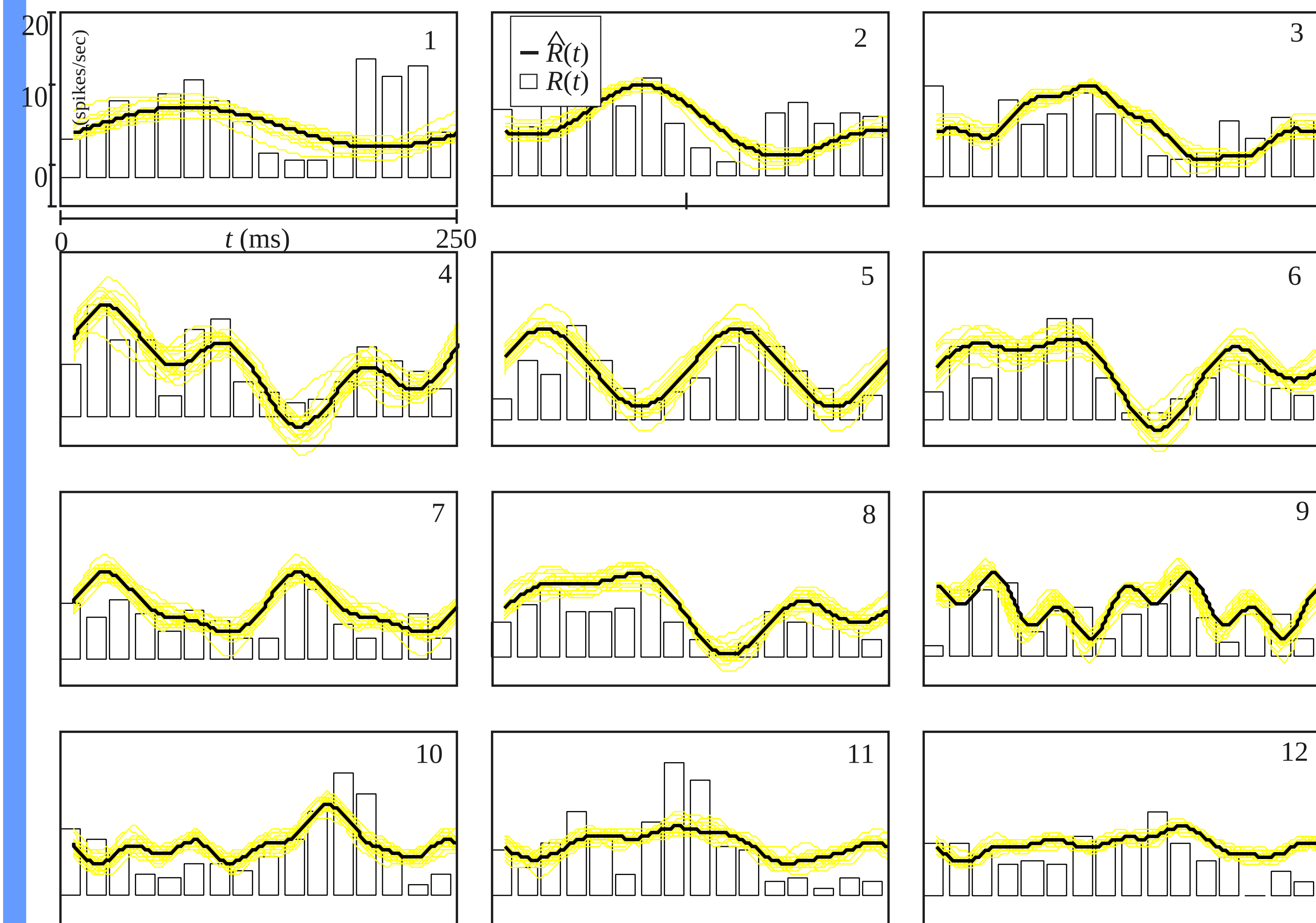
Stimuli Used for Predictions



Predictions and Responses

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





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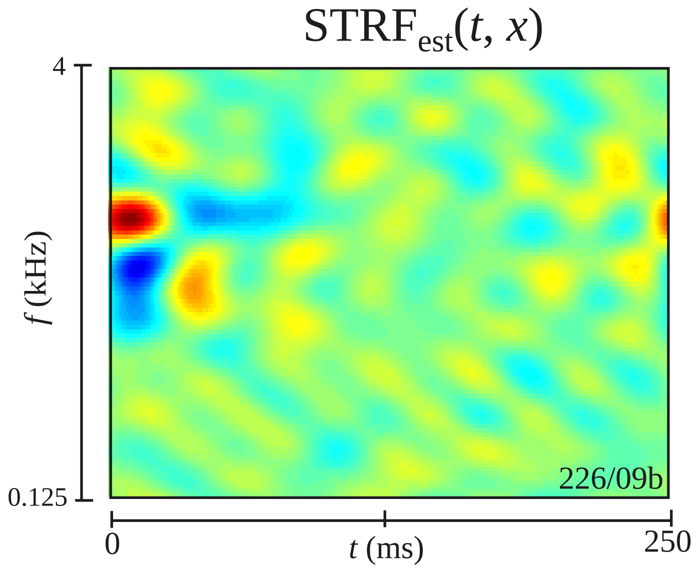
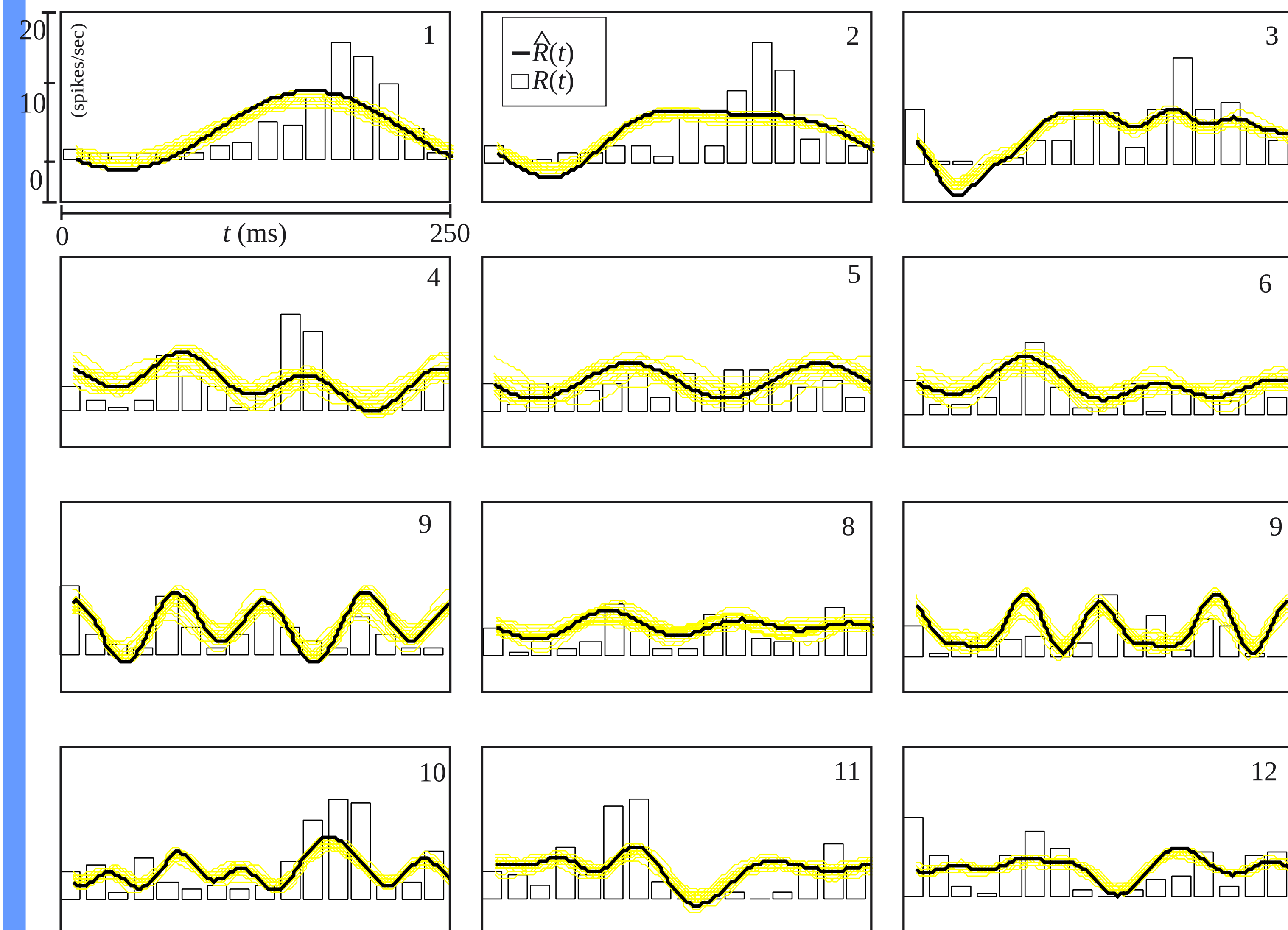
Predictions and Responses II





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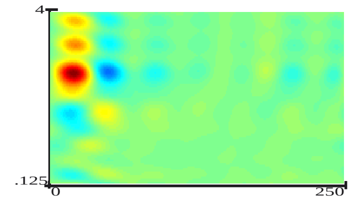
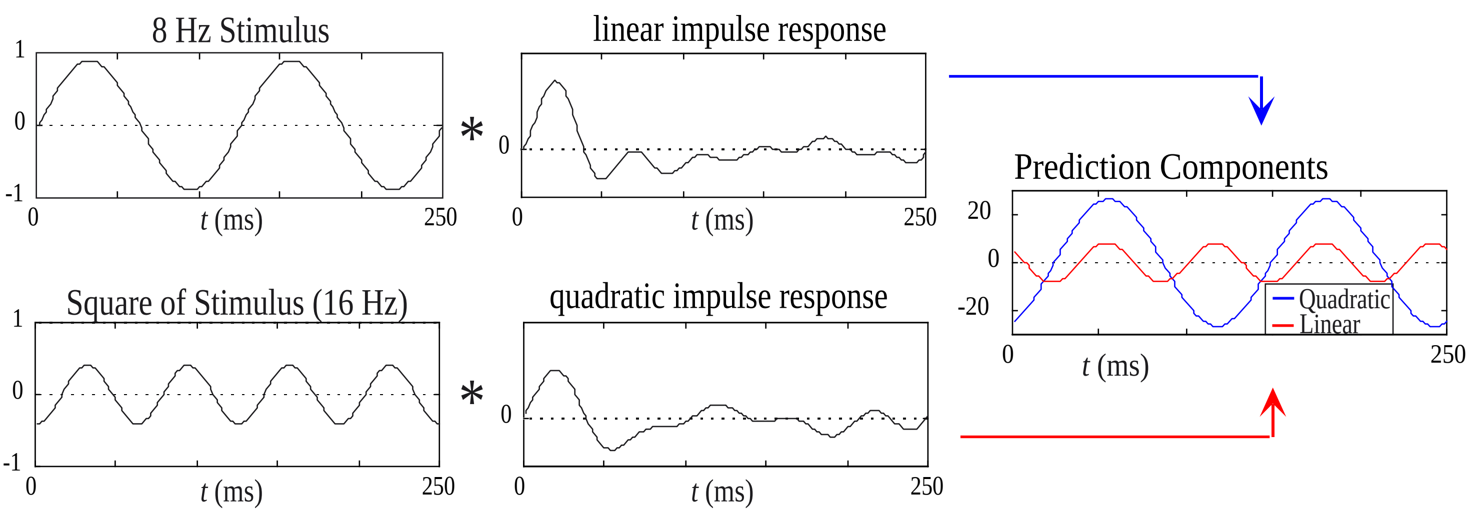
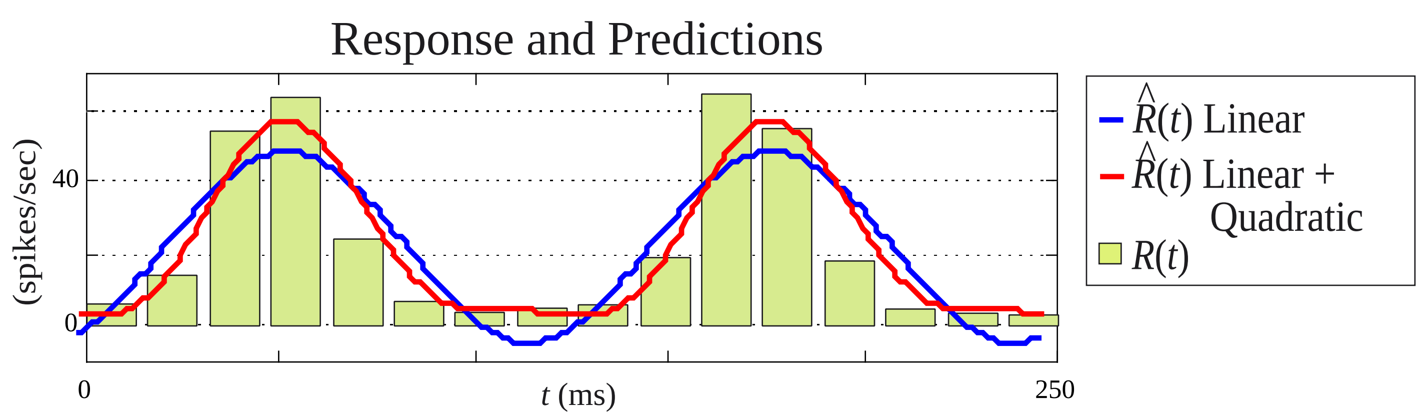
- **Non-Linearities**

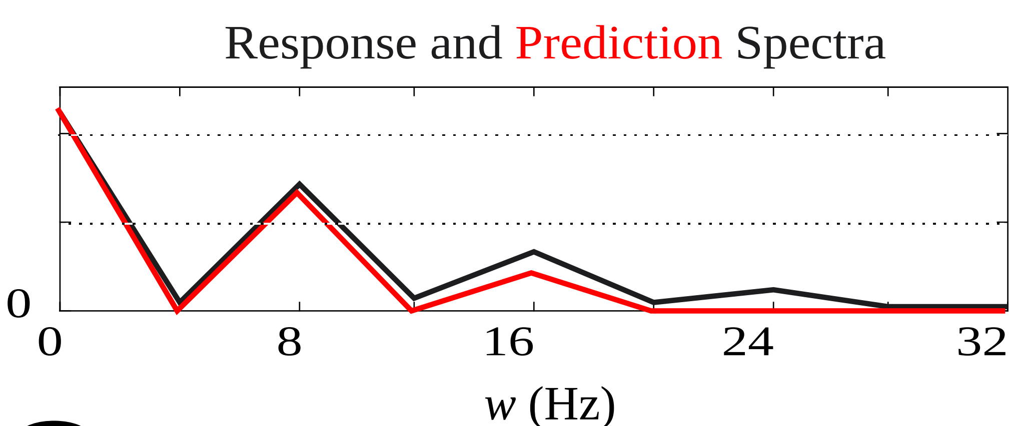
Non-Linearity—Predictions

- 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.









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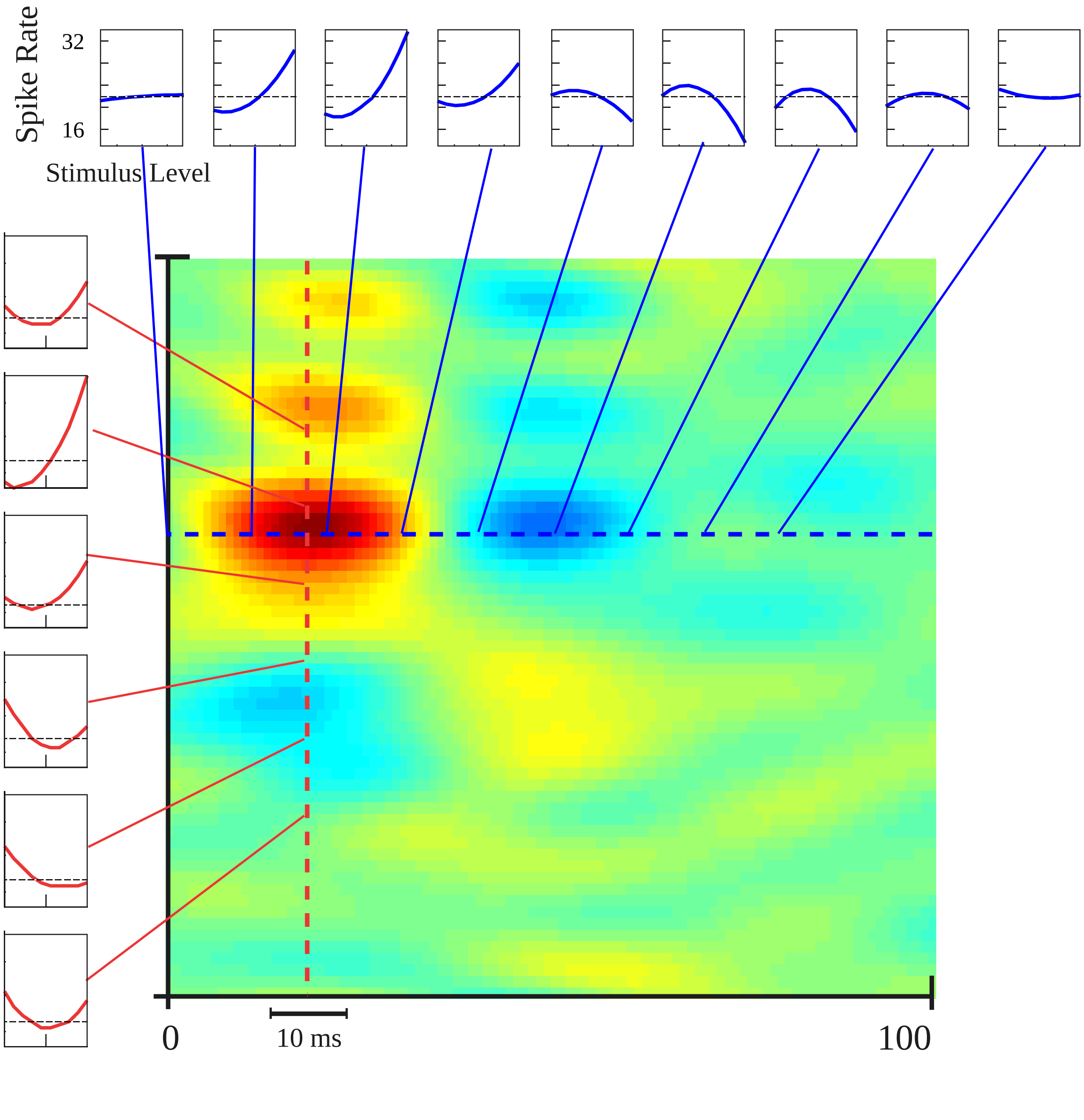
Spectro-Temporal Rate-Level Functions

Rate-level functions change with τ and *x*.



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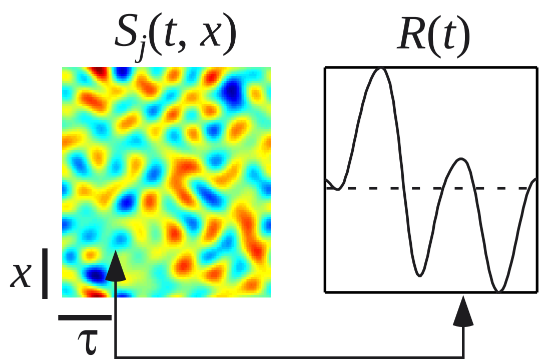
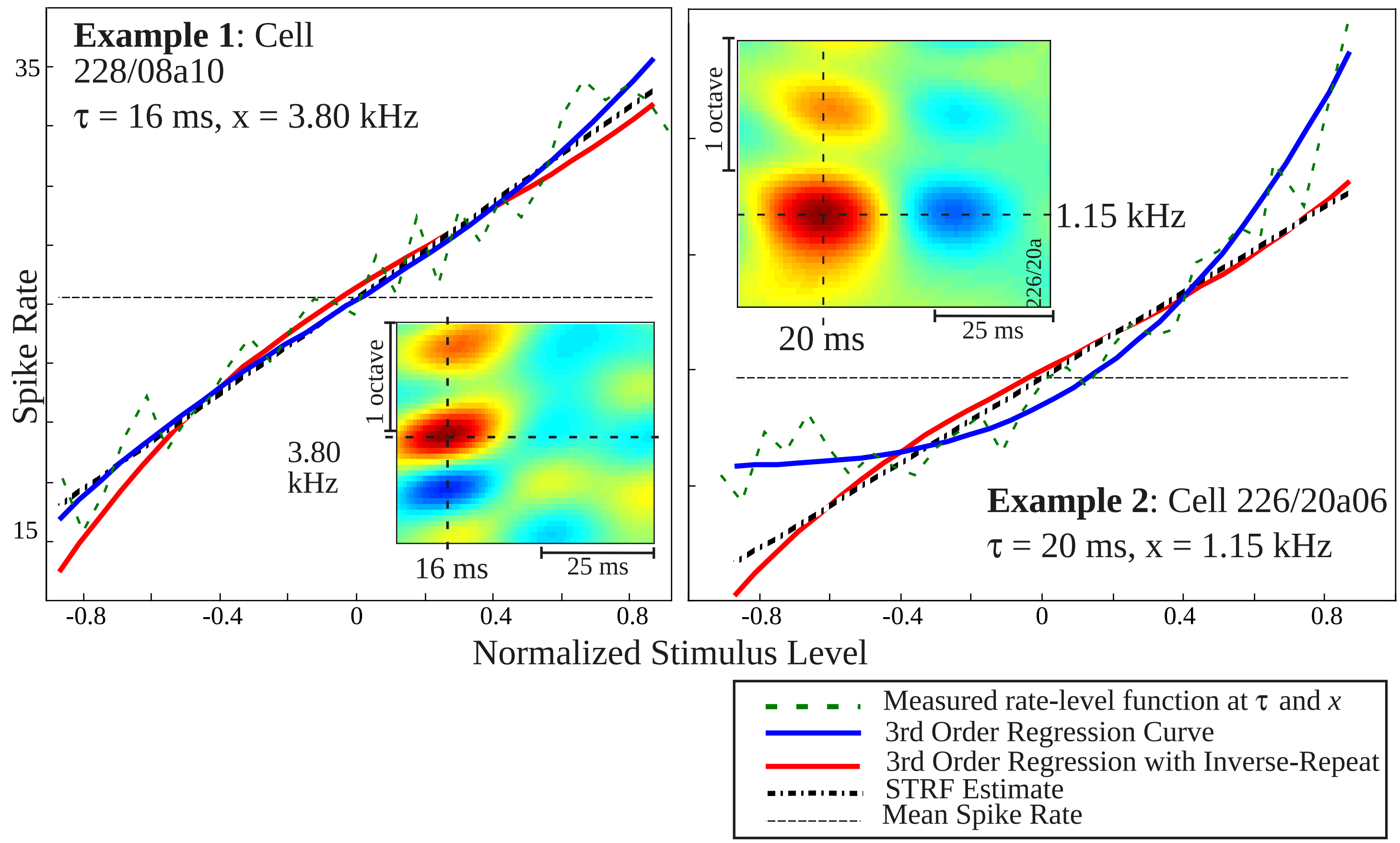
Non-Linearity—Theory

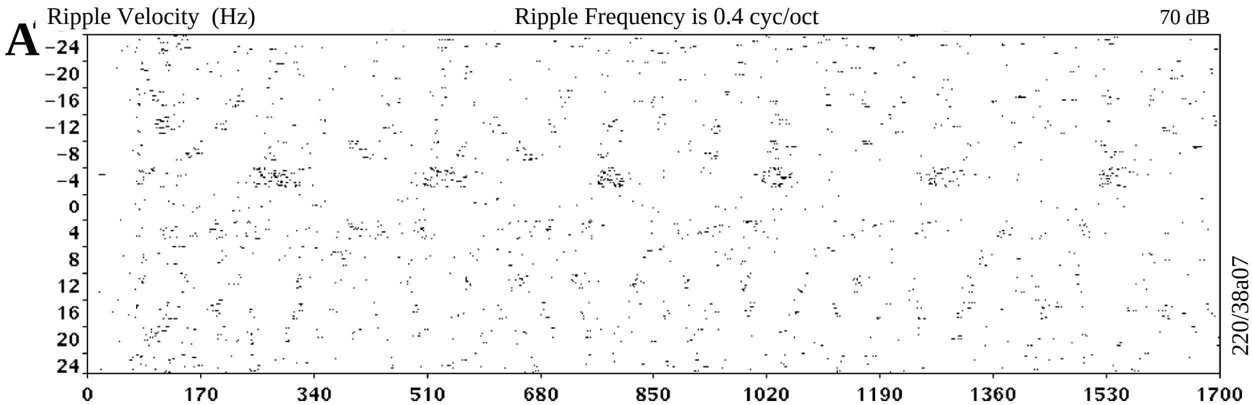
- The value of the STRF at each point (τ, x) is the slope of a linear rate-level function: $R_{\tau,x}(t) = [\mathrm{STRF}(\tau, x)] \cdot S(t-\tau, x)$.
- Polynomial rate-level curves measured at every (τ, x) improve the description. These are potentially non-linear functions.

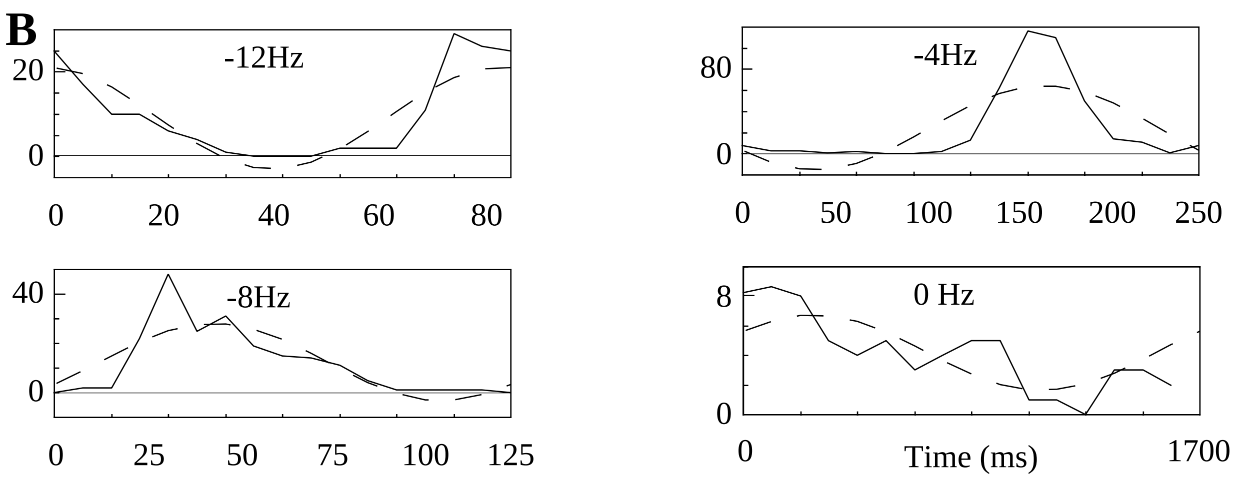


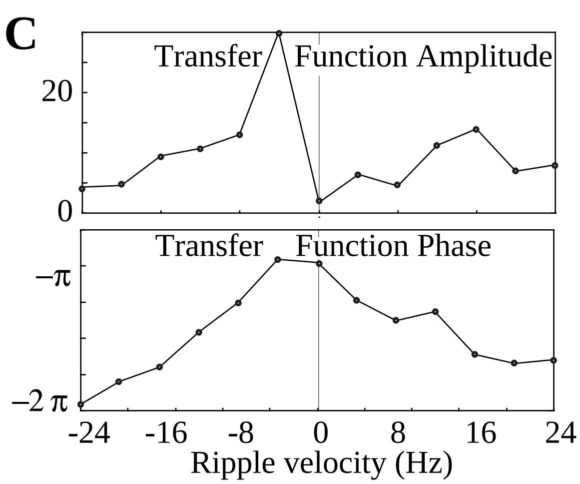


- **Using cubic polynomials, we have shown that either the non-linearities are absent, or they are dominantly second order.**
- **Subtraction of the response to the inverted envelope gives a nearly linear polynomial fit. This would be expected, for example, from a purely even order (e.g., rectifying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

Spike Train Measurements 2

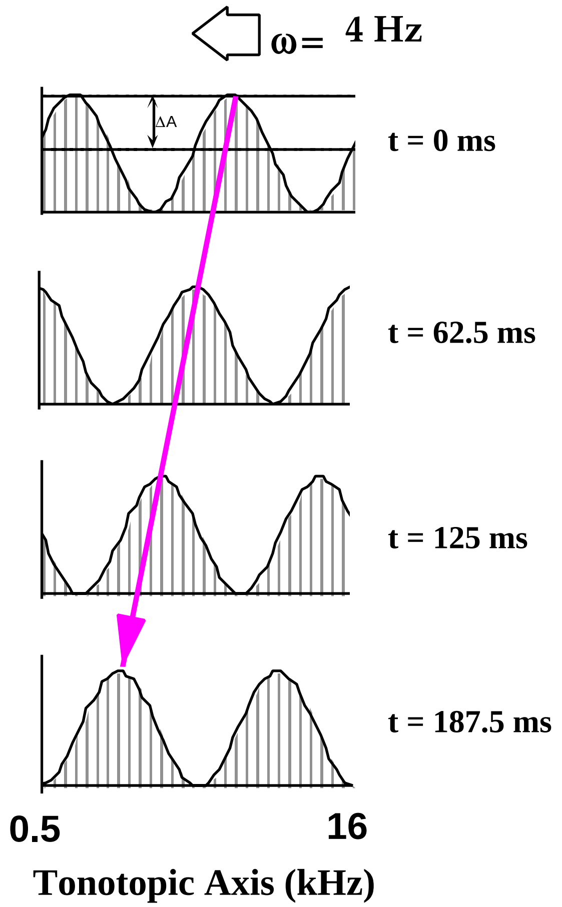


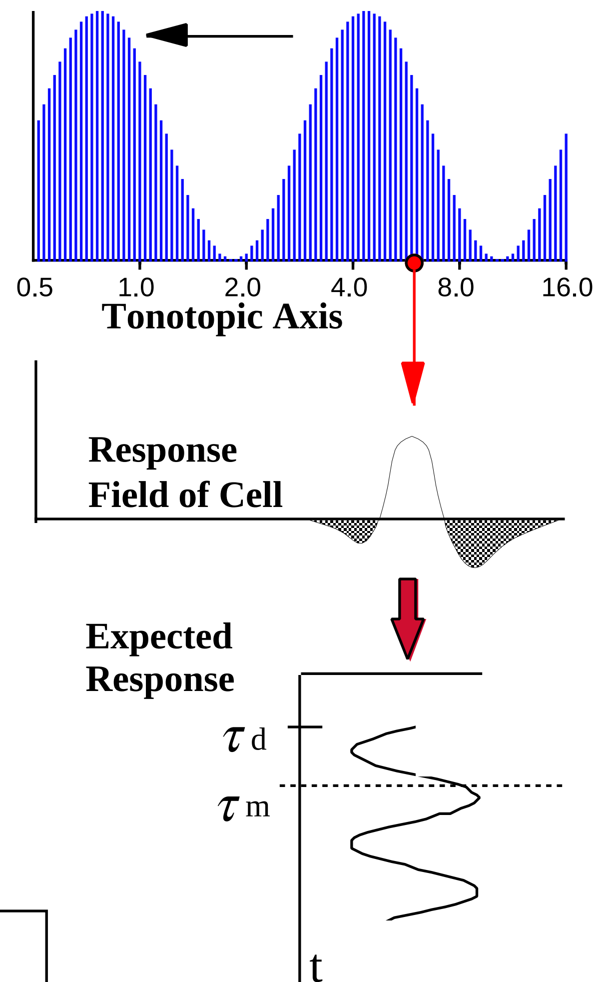




Spike events in (**A**) are turned into period histograms in (**B**). The amplitudes and phases give the transfer function in (**C**).

Simple Spectral Response Model





- Ω = ripple frequency in cycle/octaves
- ω = temporal frequency in Hz

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