# Neural Constraints in Auditory Cortex

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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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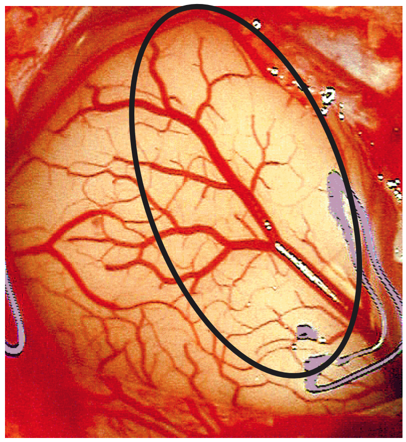
- **Constraints on Neural Connectivity**

# Basics

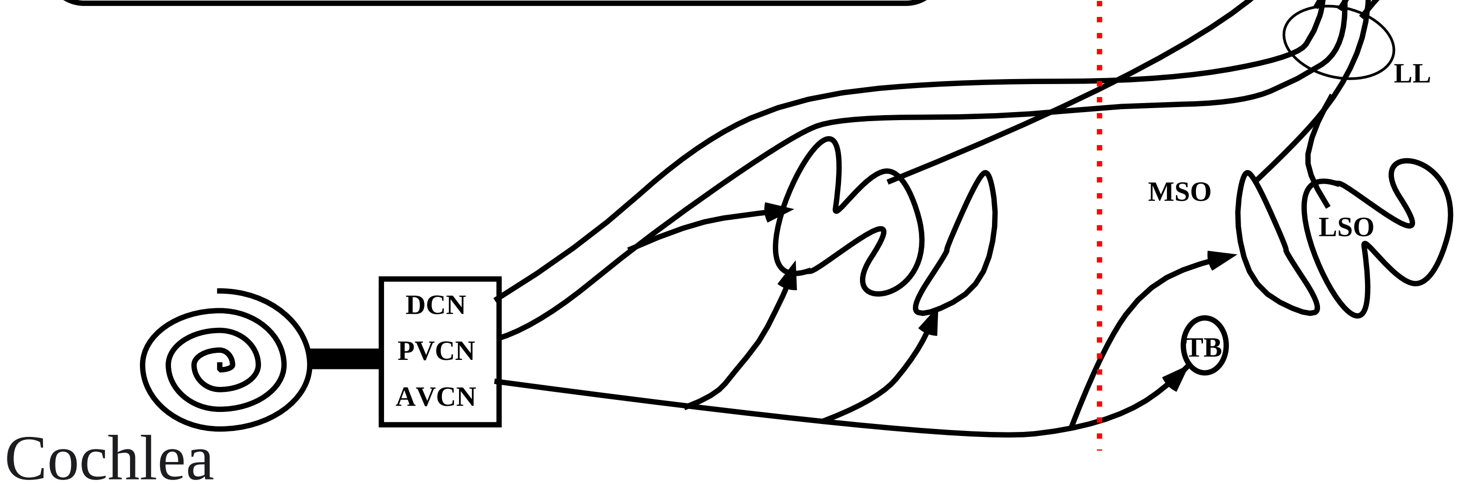
- **Most important auditory cues are acoustically non-trivial**
  - e.g. speech, speaker ID, emotional content, pitch, timbre, sound location, and many, many others
- **Enormous parallel and serial neural processing in multiple stages** from auditory nerve to cortex
- **Neural code is essentially unknown** 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*

# Motivation

- **The Quest**

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

  ≈ { which sounds/features evoke responses?
  how are they encoded into spike trains? }

- **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

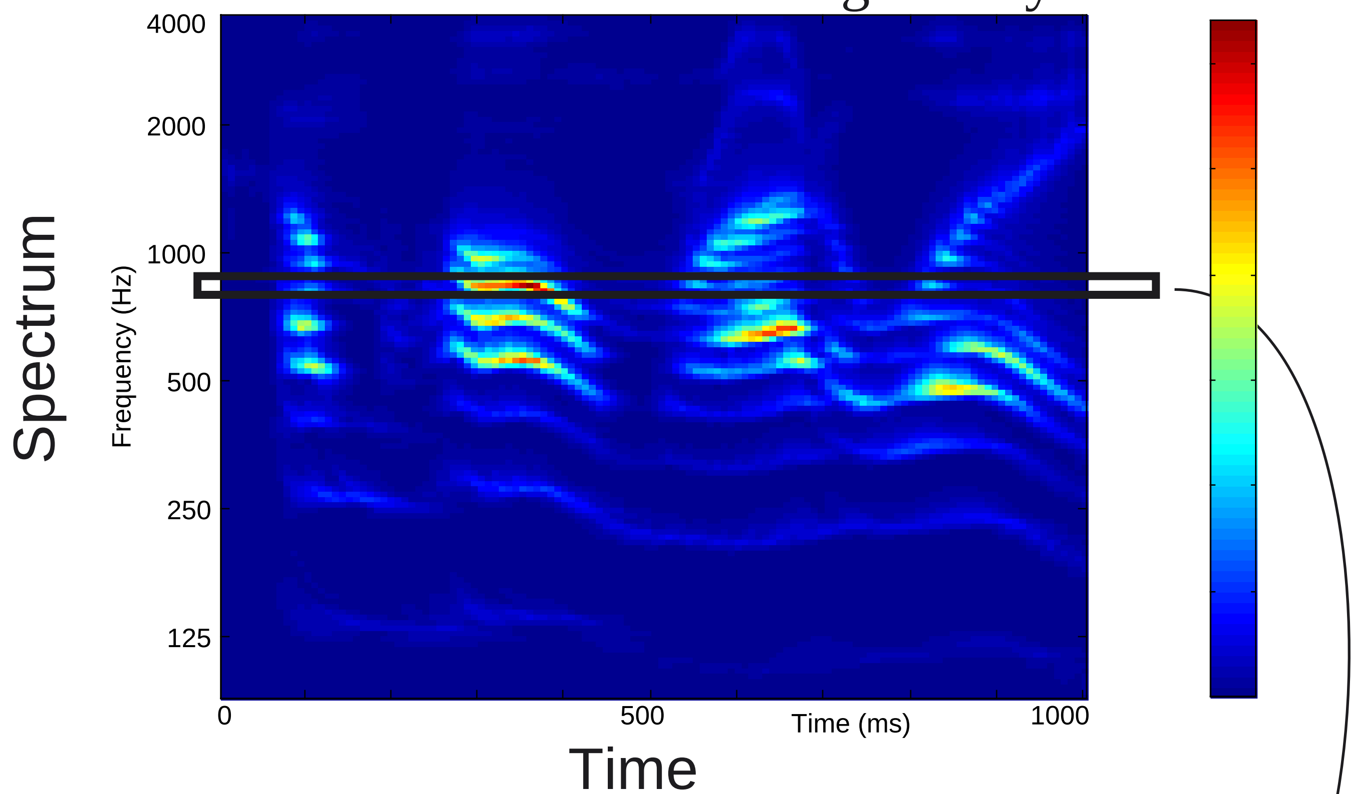
# Sound Features

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

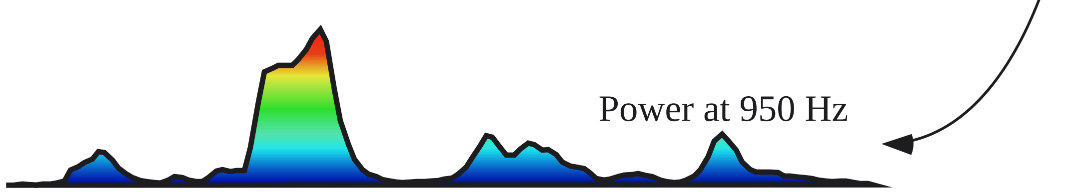
- Spectral content of sound as a function of time.

  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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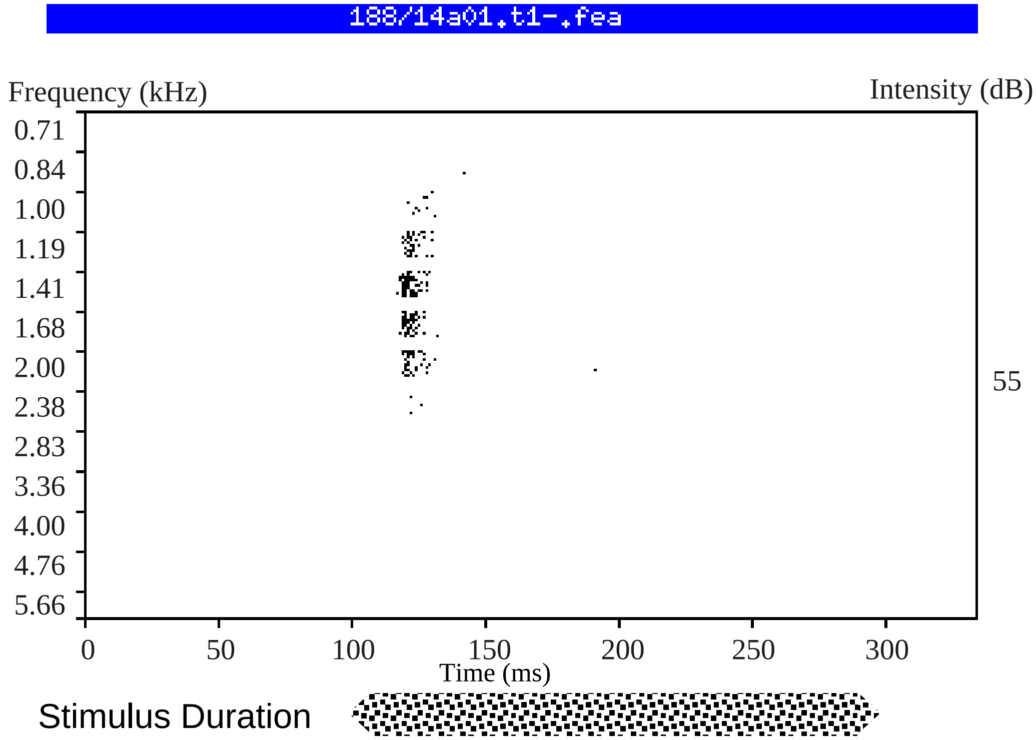
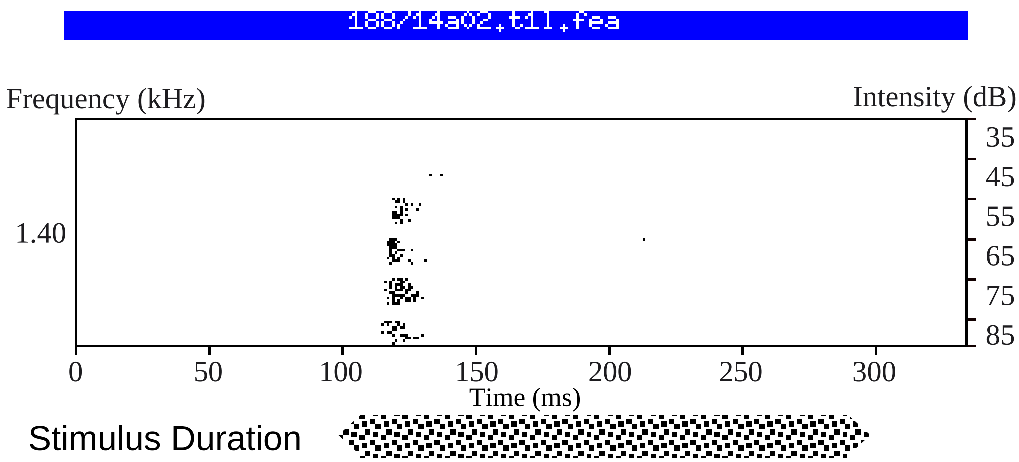
# Response to Pure Tones



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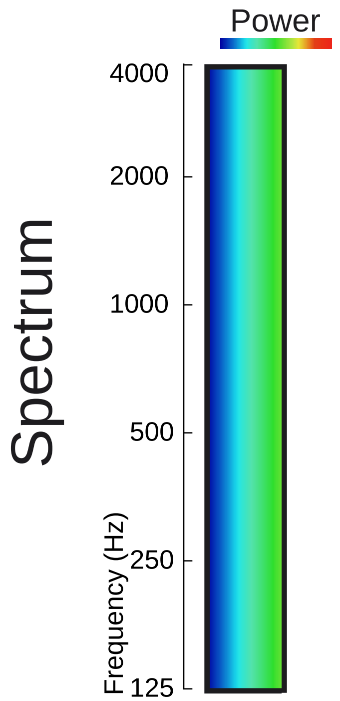
# Stimulus Construction

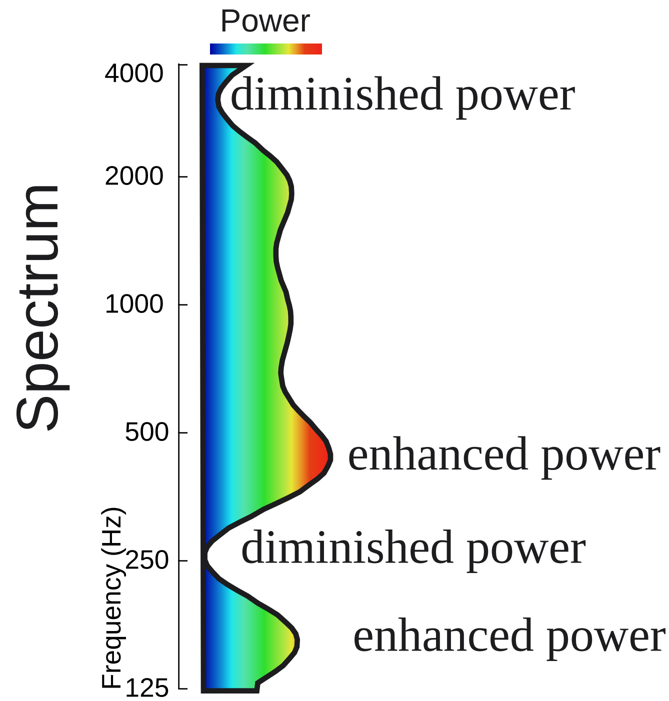
- Pink Noise = flat power density in octaves (log *f*)
  not white

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

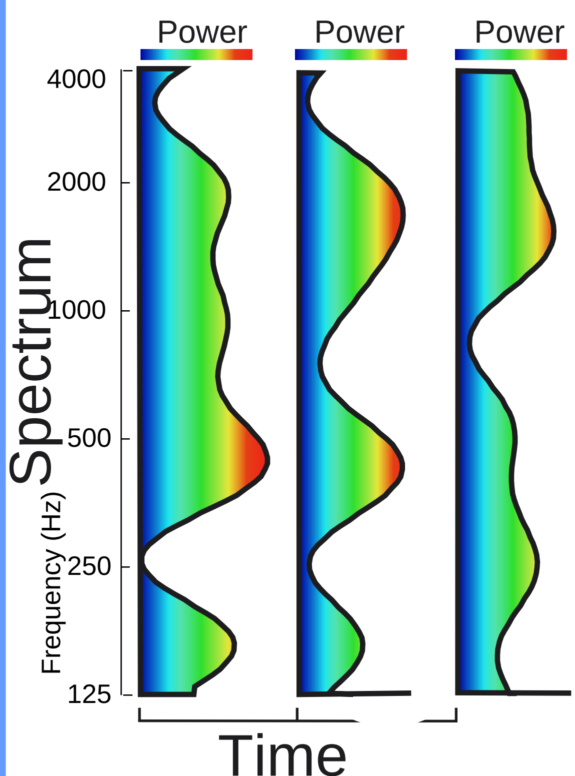



flat
power
over
entire
spectrum

- ***Spectrally modulated noise***




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

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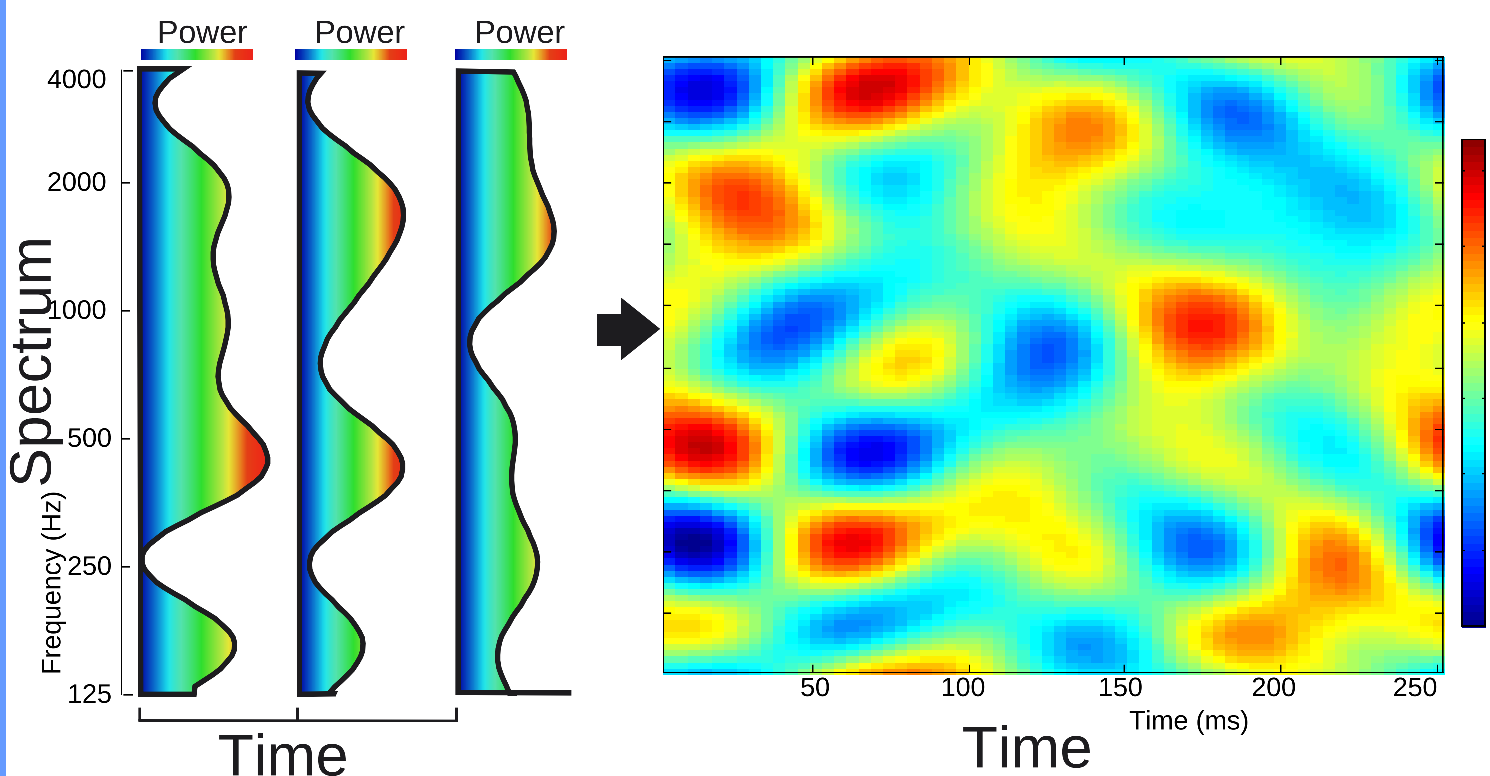
# Stimulus Construction

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



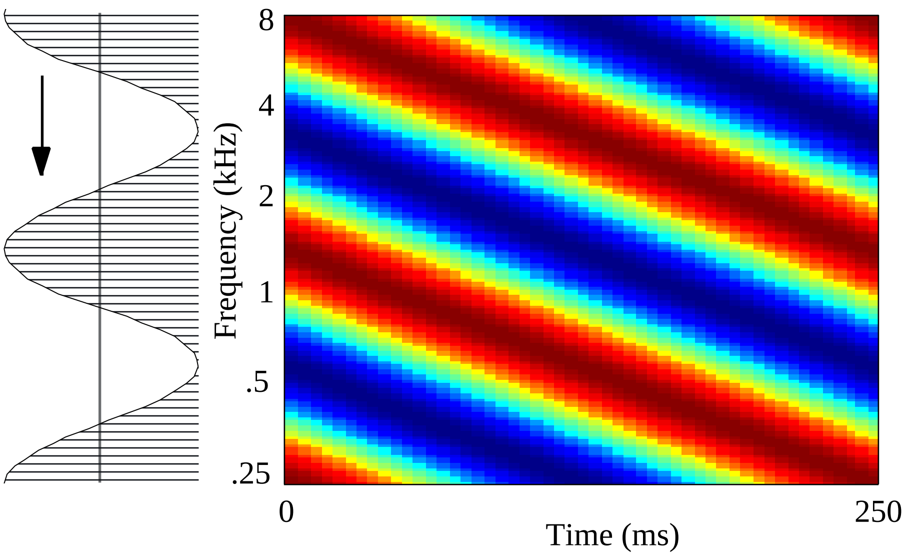
# Single Moving Ripple

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
$\Omega$ = ripple density,
e.g. 0.4 cycles/octave
= 2 cycles/5 octaves

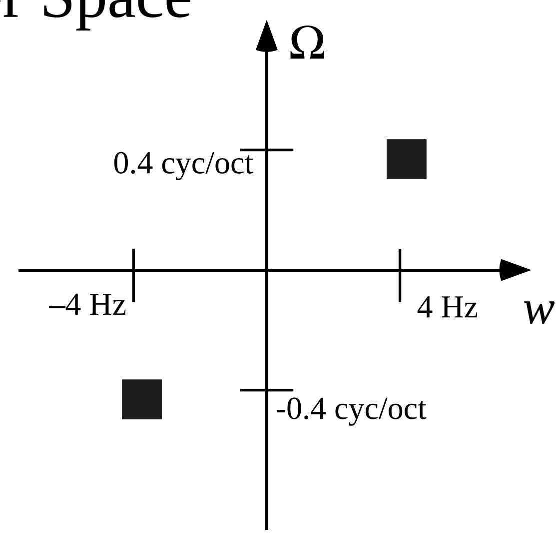
in Spectro-Temporal Space (*Spectrogram*)




c.f. visual contrast gratings

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

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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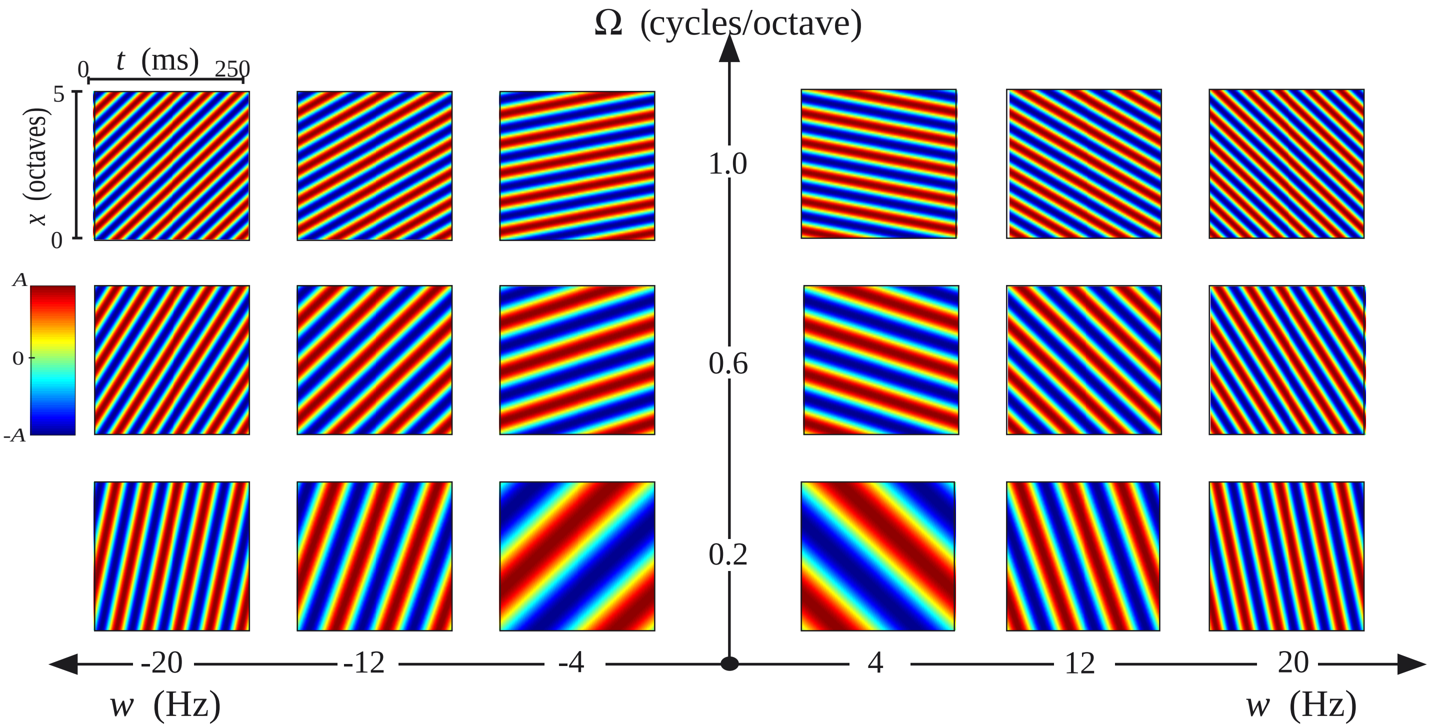
# Multiple Individual Ripples

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

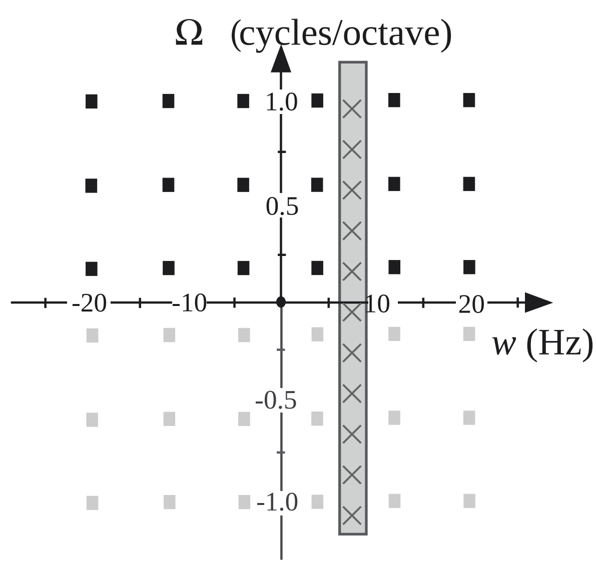
$x = \log_2(f / f_0)$

$w$ = ripple velocity (Hz)

$\Omega$ = 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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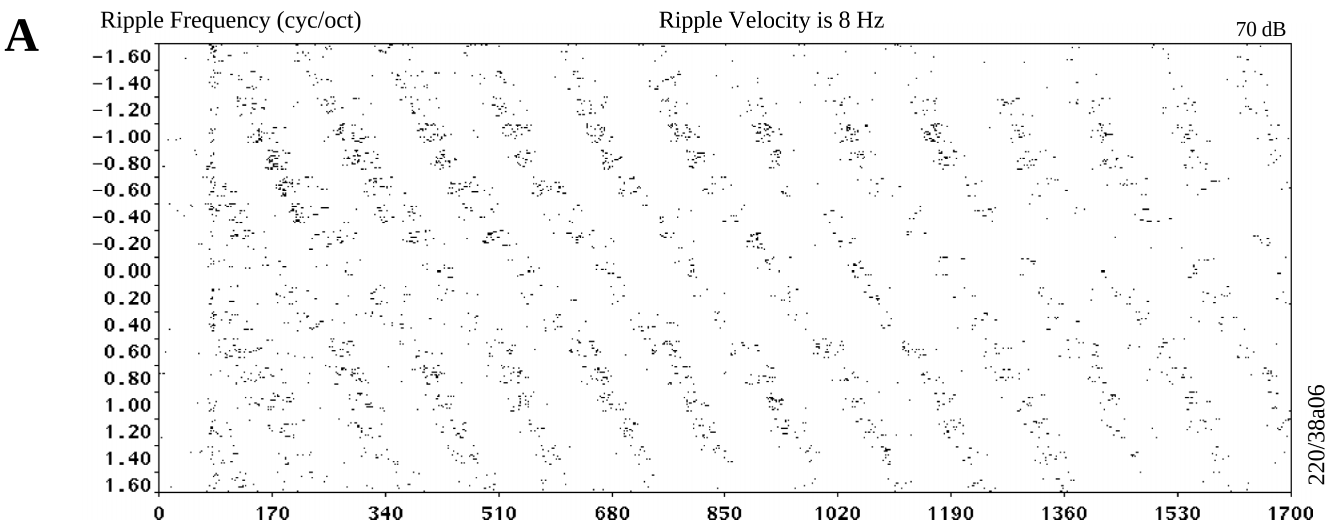
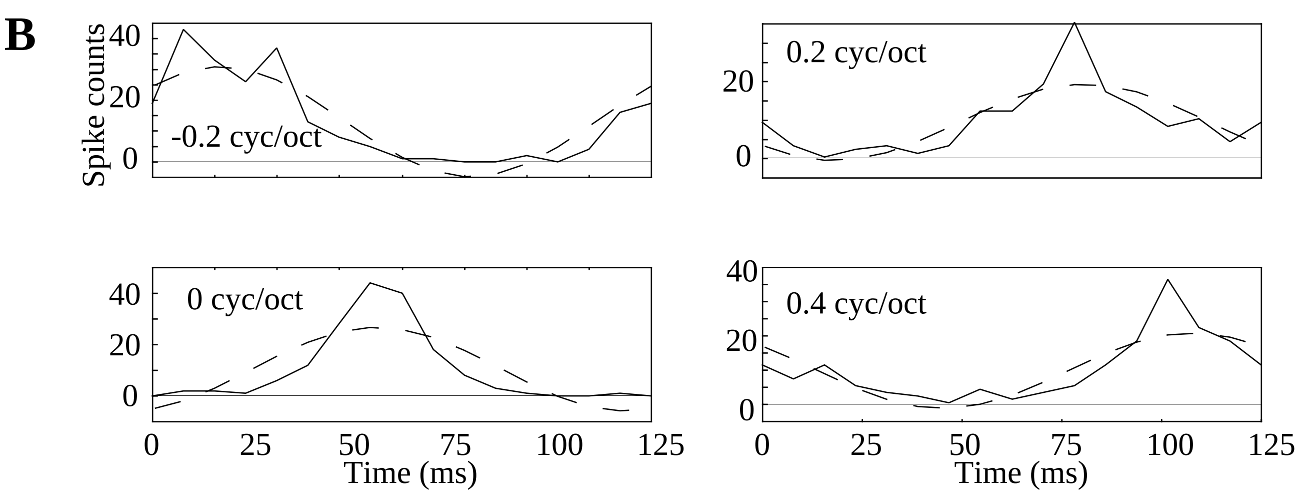
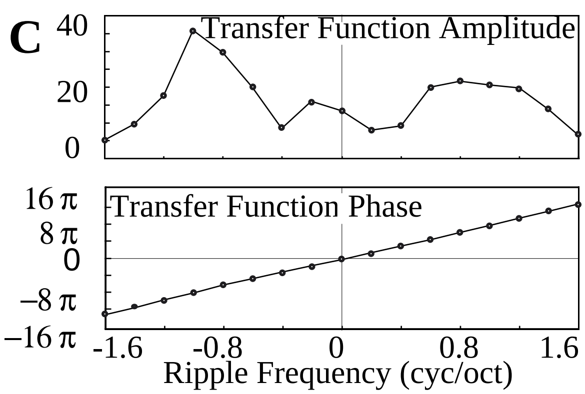
# Spike Train Measurements

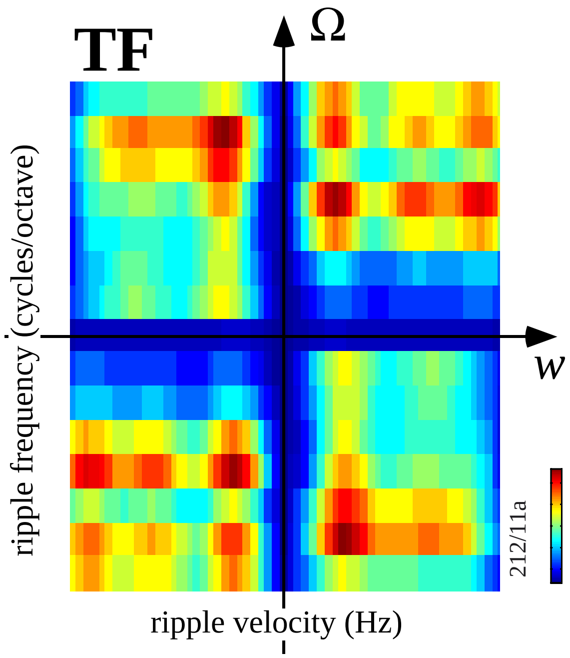



Spike events in (**A**) are turned into period histograms in (**B**). The amplitudes and phases give the transfer function in (**C**).

# Spectro-Temporal Response Field (STRF)



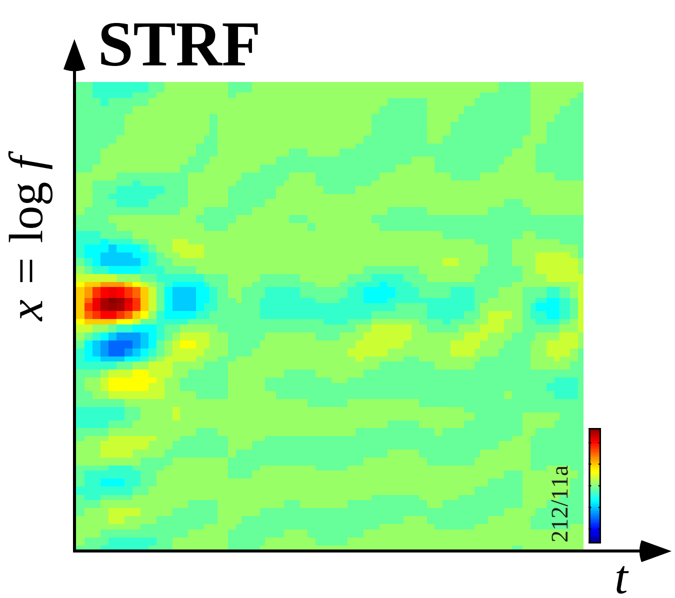

## 2 Dimensional Transfer Function

- 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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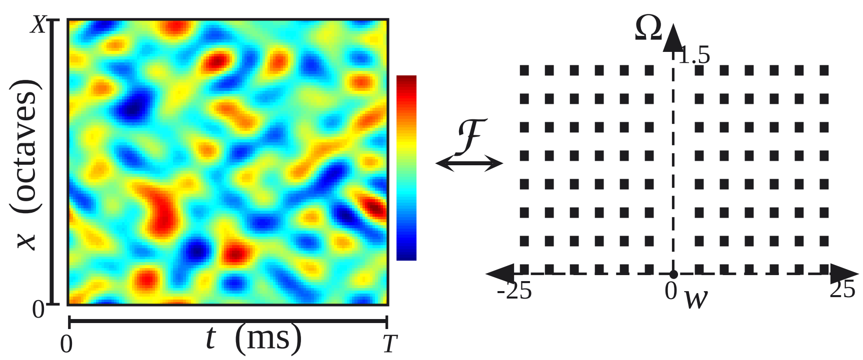
# Spectro-Temporal Noise

To speed up the characterization of a cell's response, we use combinations of ripples of *all* velocities $w$ and densities $\Omega$, 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

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 $S_j$

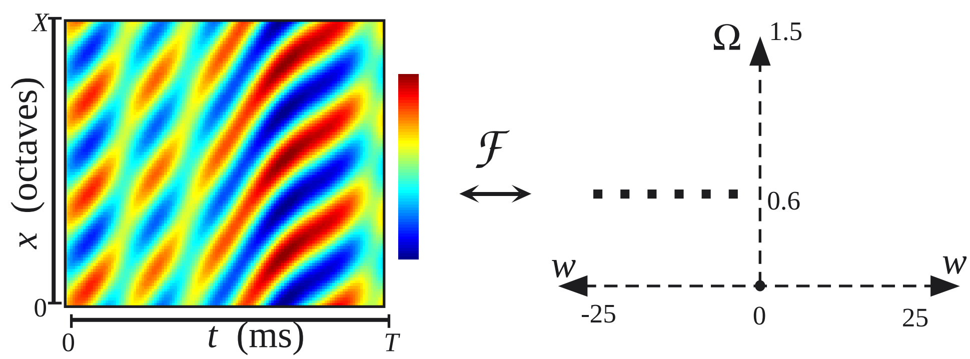
$$\text{STRF}_{\text{est}}(\tau, x) = \frac{1}{m}\sum_{j=1}^{m} C_j(-\tau, x)$$

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

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

= Spike-Triggered Average

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

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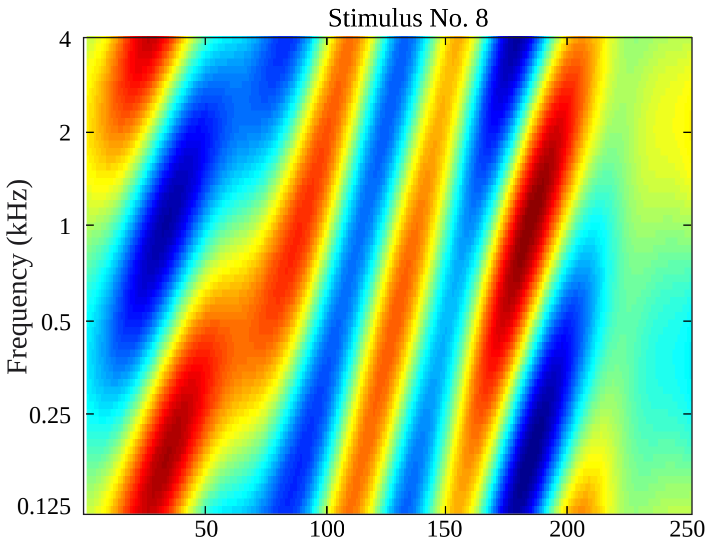
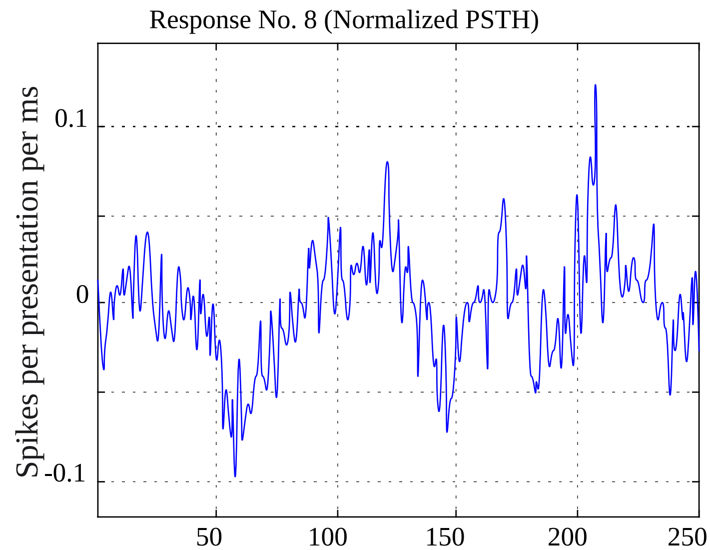
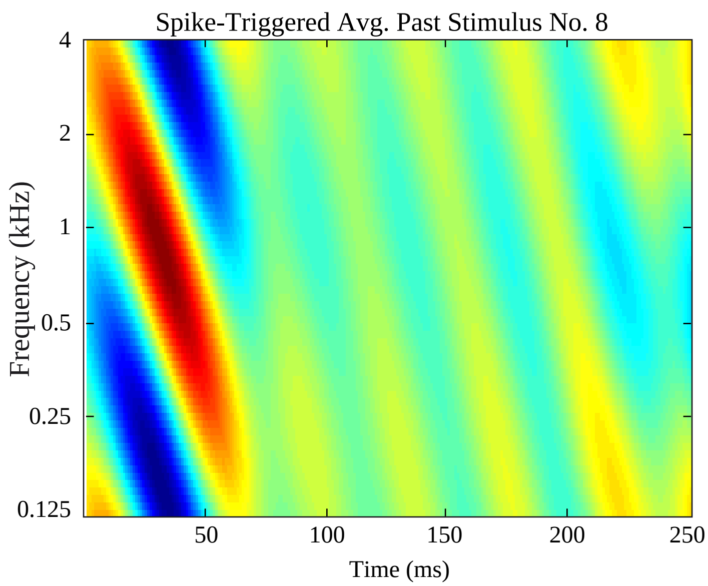
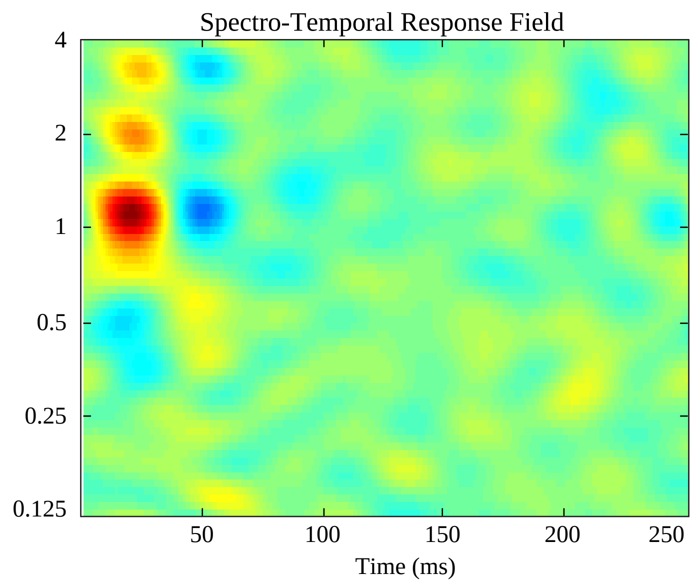
# Spike Averaged Data

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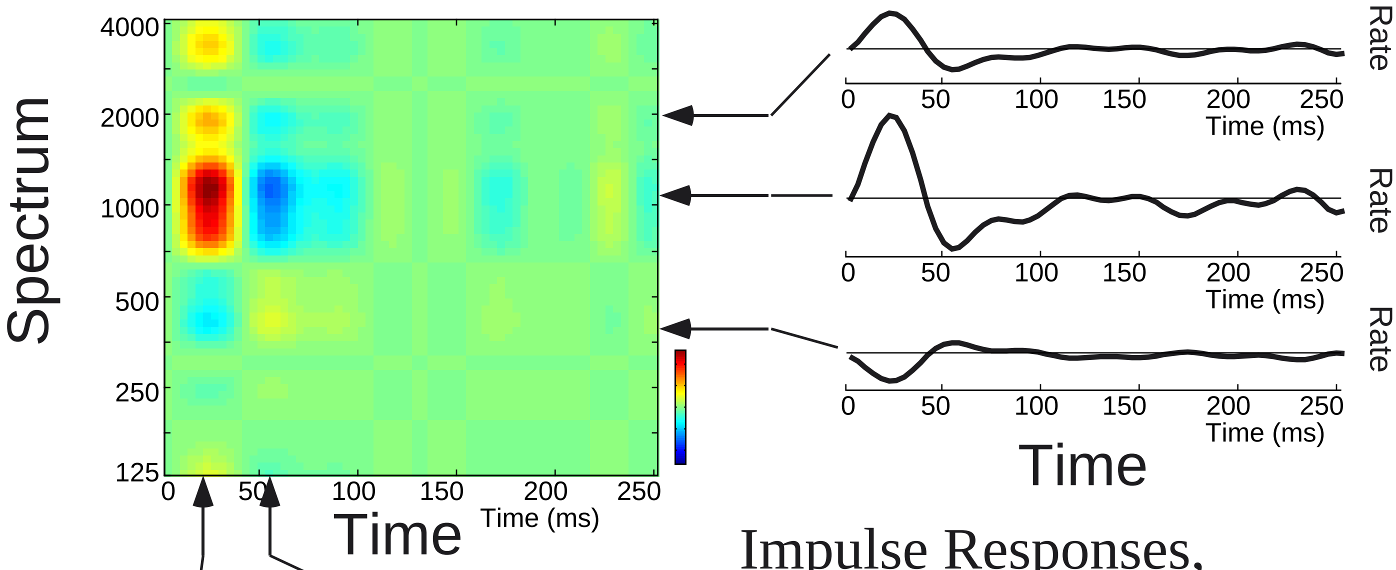
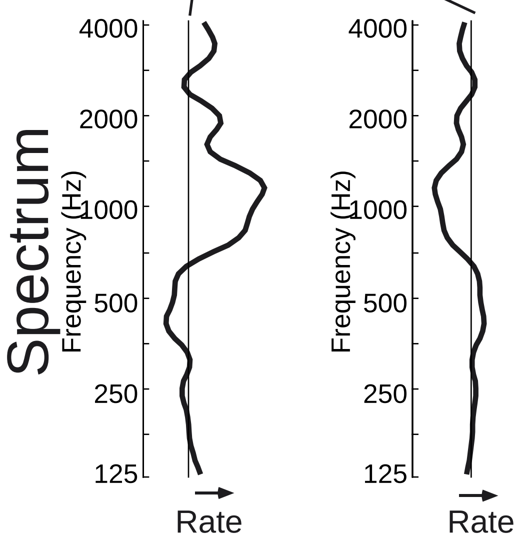
# Interpreting STRFs

## Cross-section interpretations

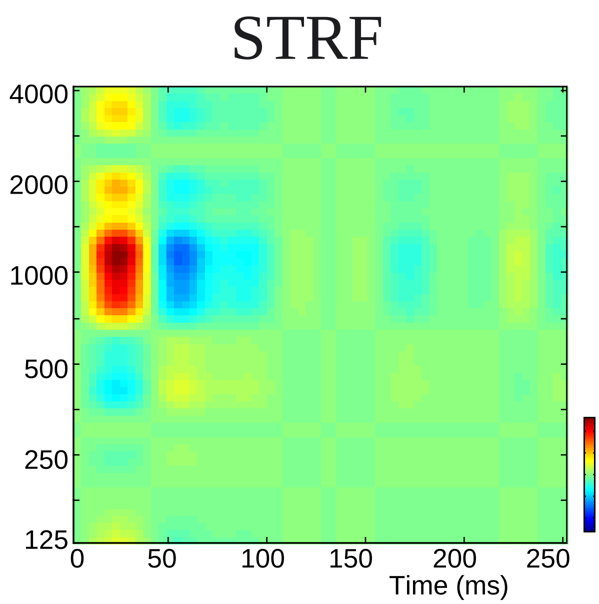


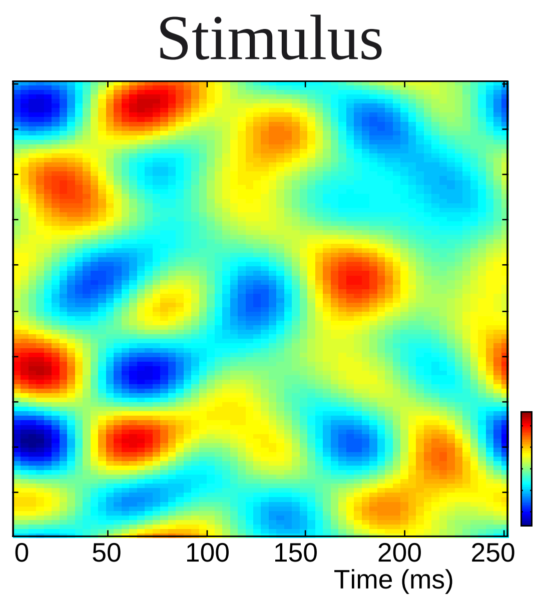

Impulse Responses,
*parametrized by spectral band*




Spectral Response Fields,
*evolving in time*

# Interpreting STRFs



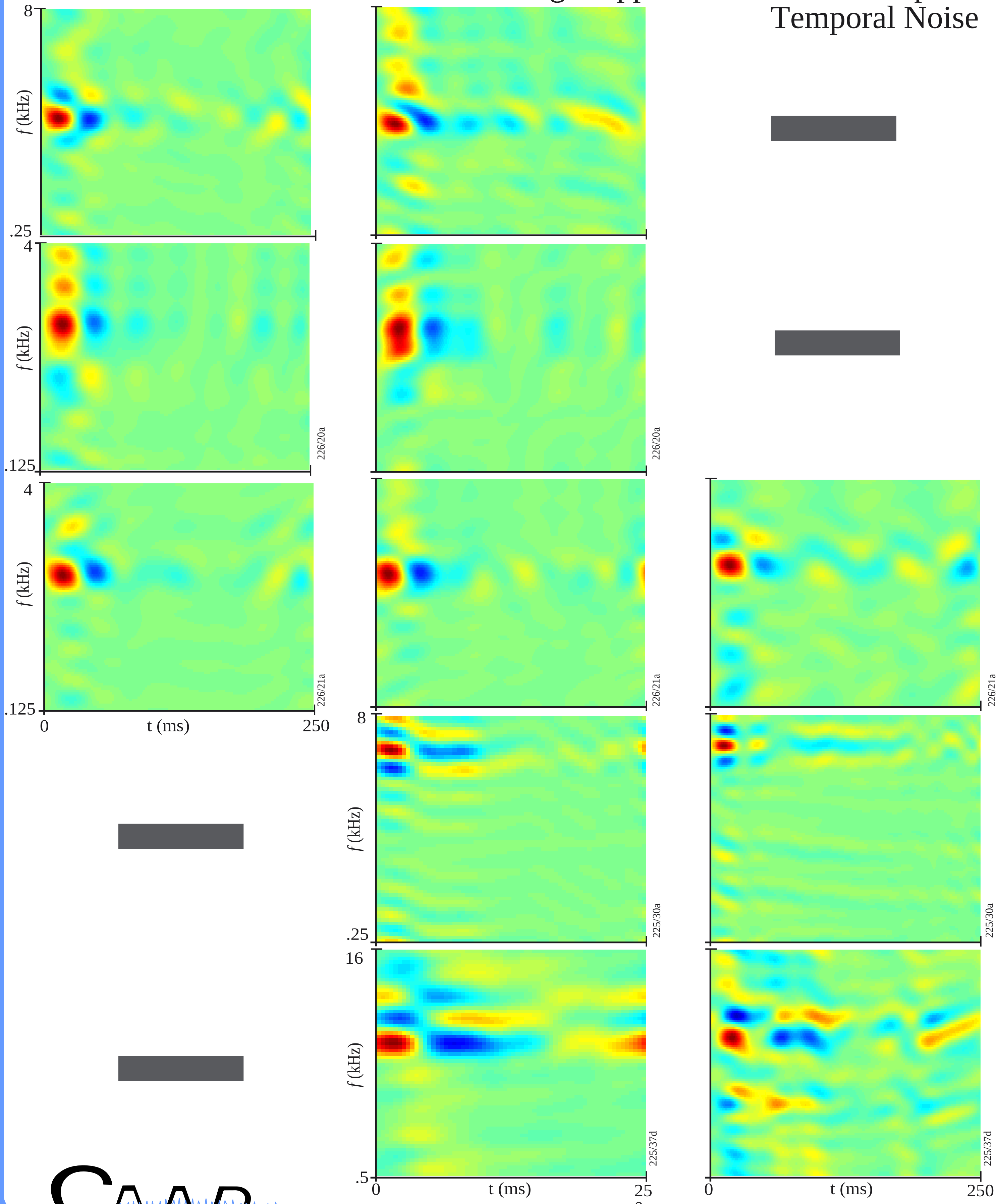

## Stimulus Effect on Rate

| 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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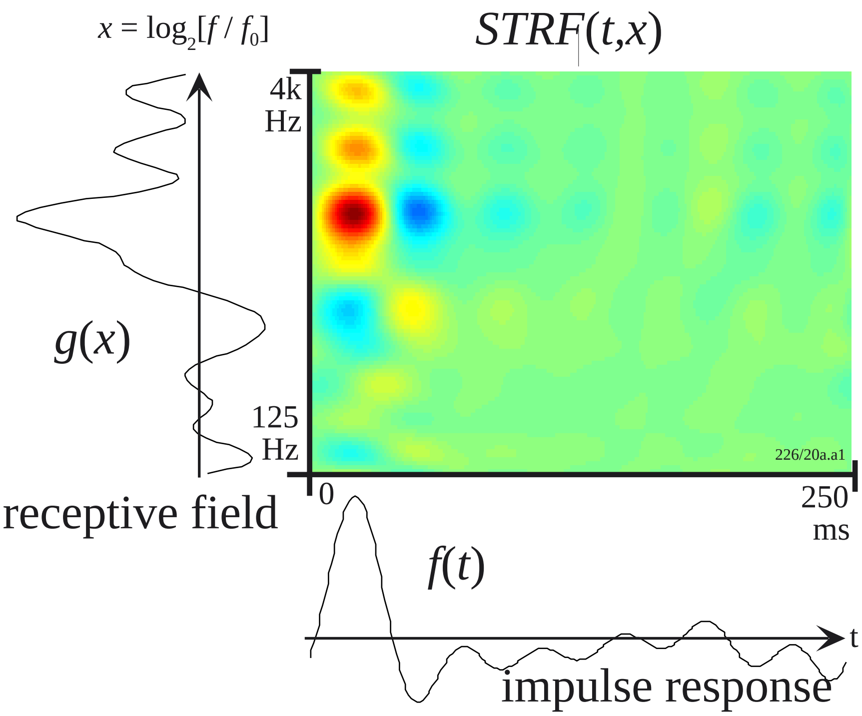
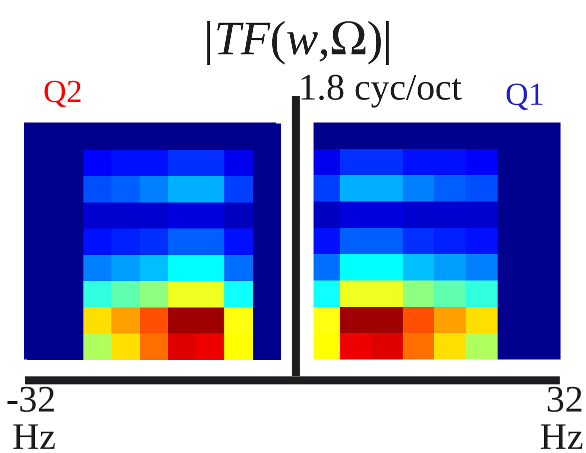
# Full Separability




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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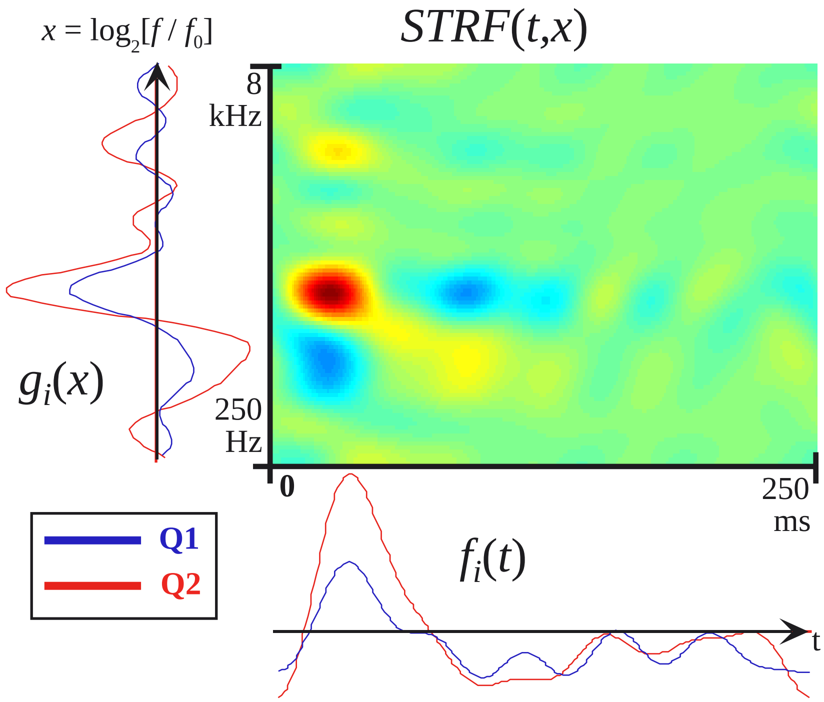
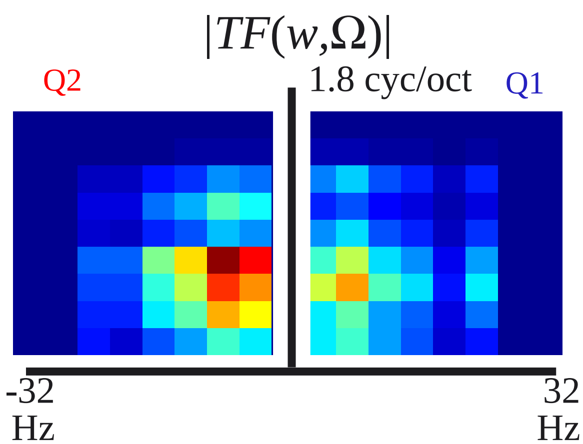
# Quadrant Separability




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.

$|\mathcal{F}\{\ \}|$ ↕




| | |
|---|---|
| $f_i(t)$ | $g_i(x)$ |
| ↕ | ↕ |
| $F_i(w)$ | $G_i(\Omega)$ |

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

for $\Omega > 0$: $T(w,\Omega) = T^*(-w,-\Omega)$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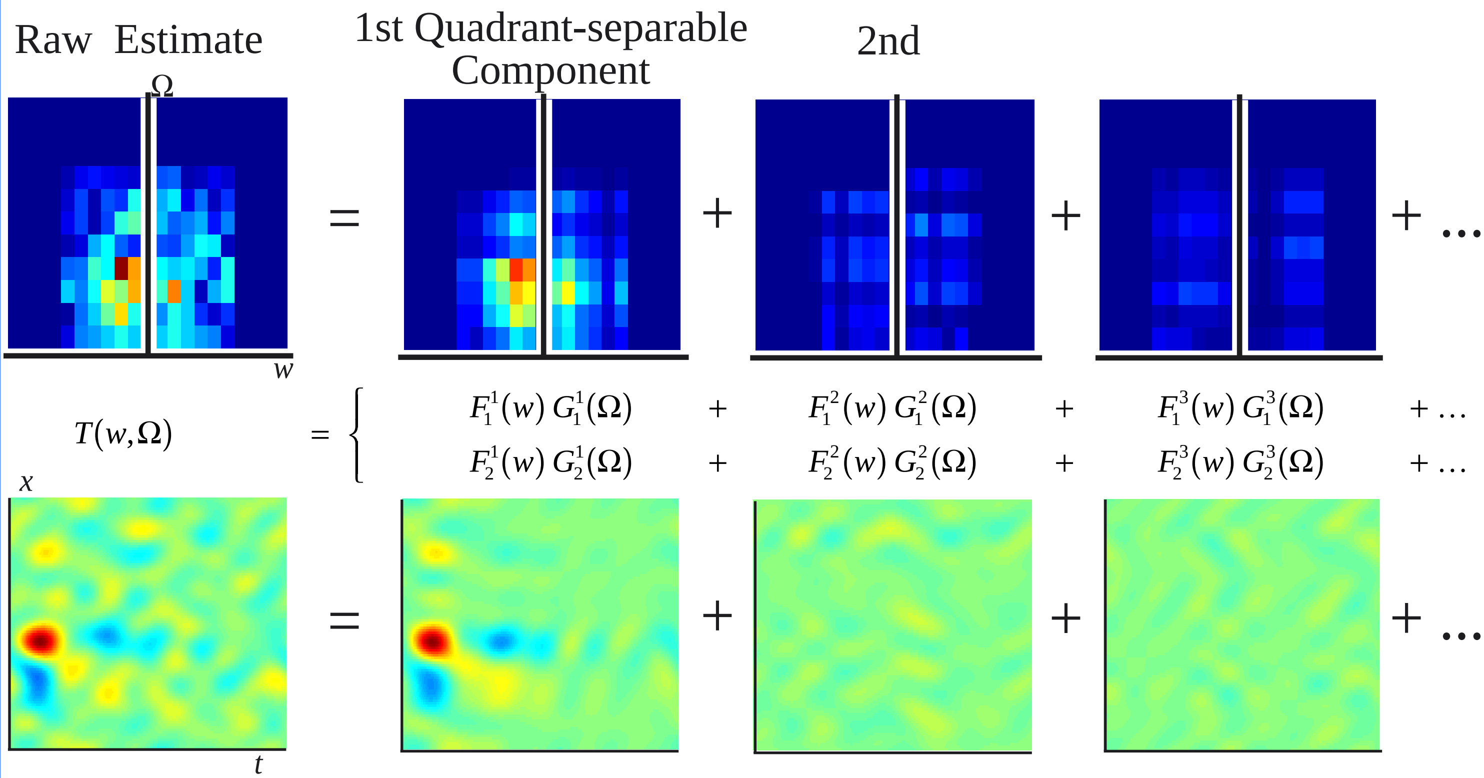
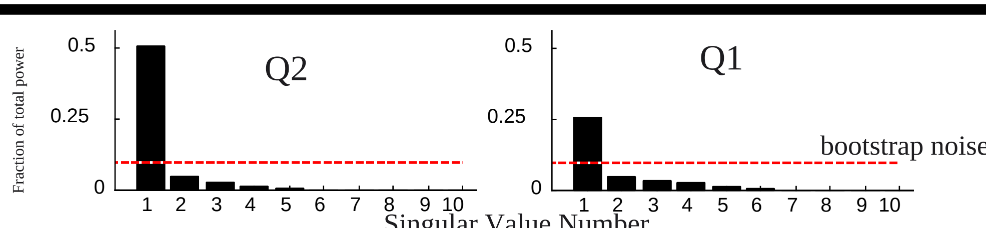
# Measuring Separability with SVD

- 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).




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





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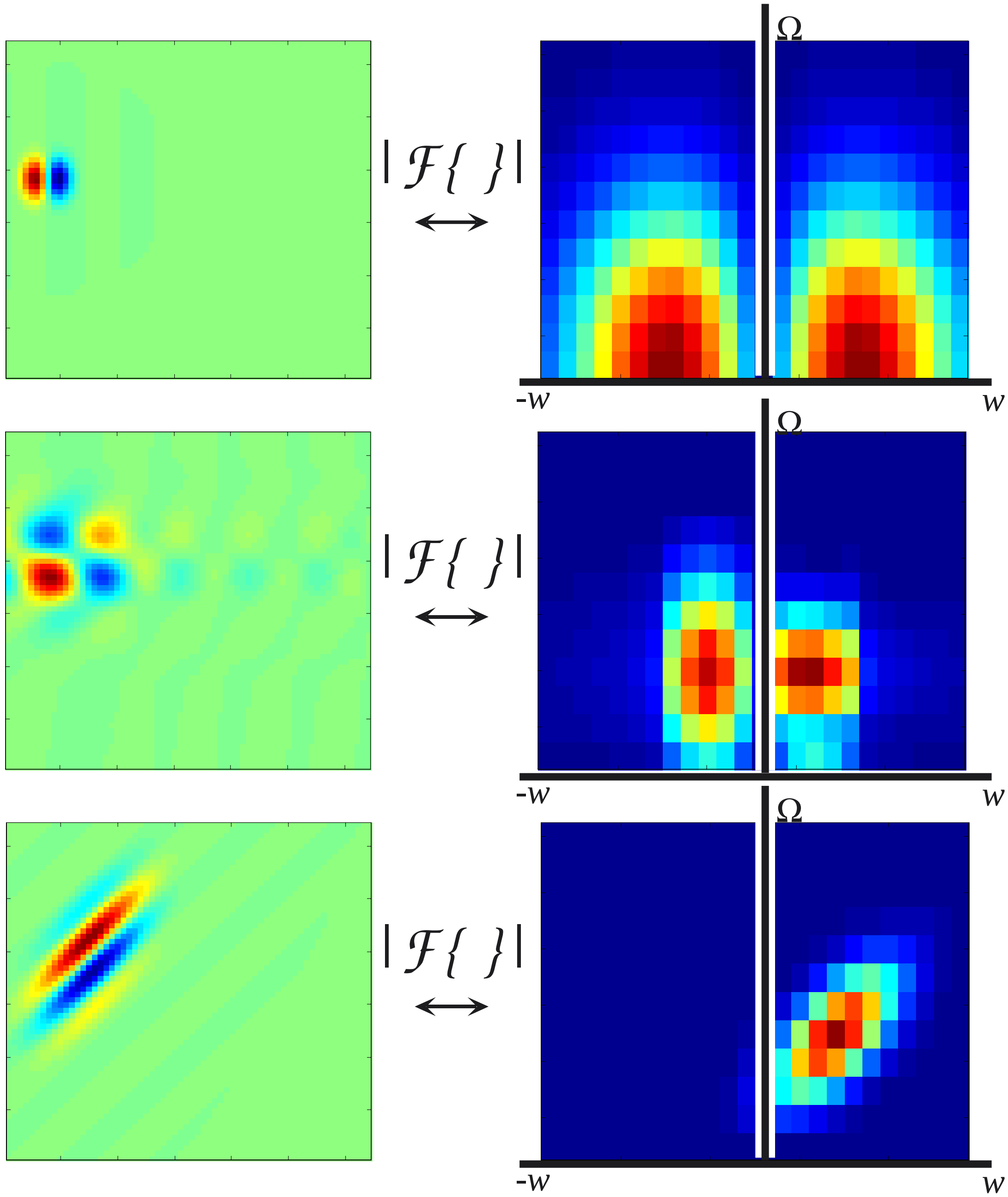
# Separability Examples

Fully Separable

Quadrant Separable

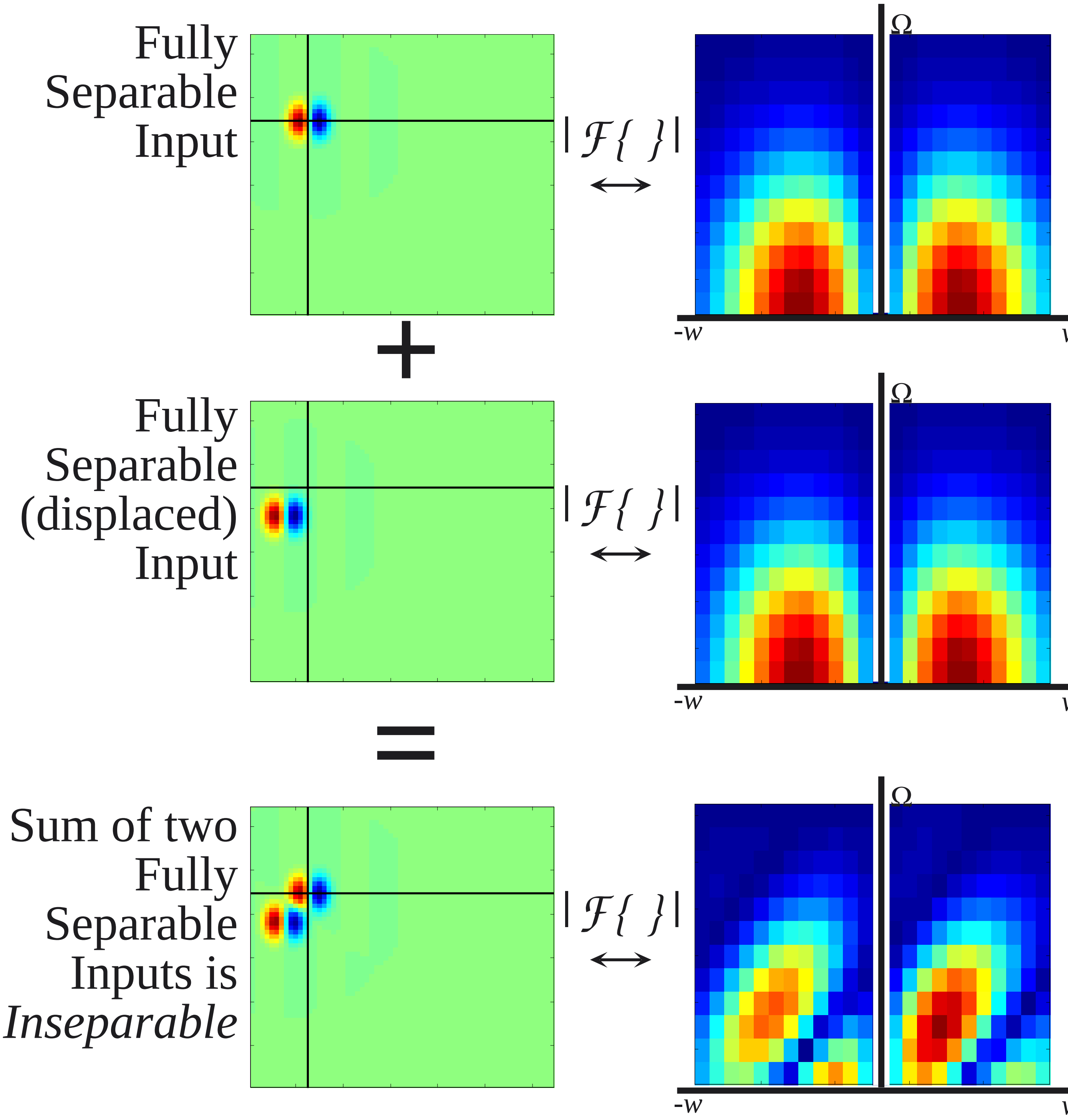
Velocity Selective is *Inseparable*




Quadrant separability is incompatible with velocity selectivity.

*Simulation*

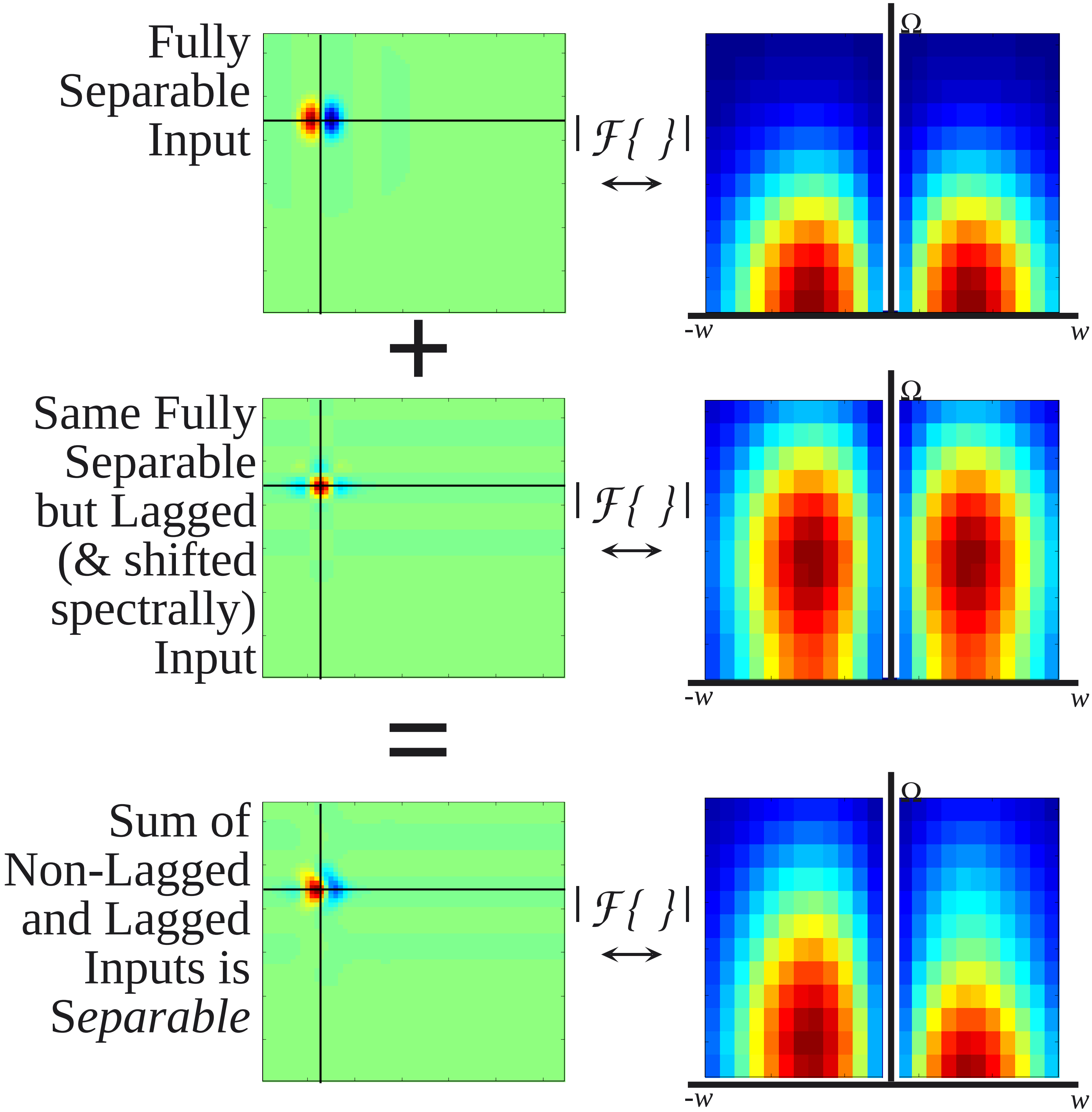
# Separability Counterexample




Naive sum of two fully separable input STRFs is inseparable.

*Simulation*

# Separability Example




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

*Simulation*

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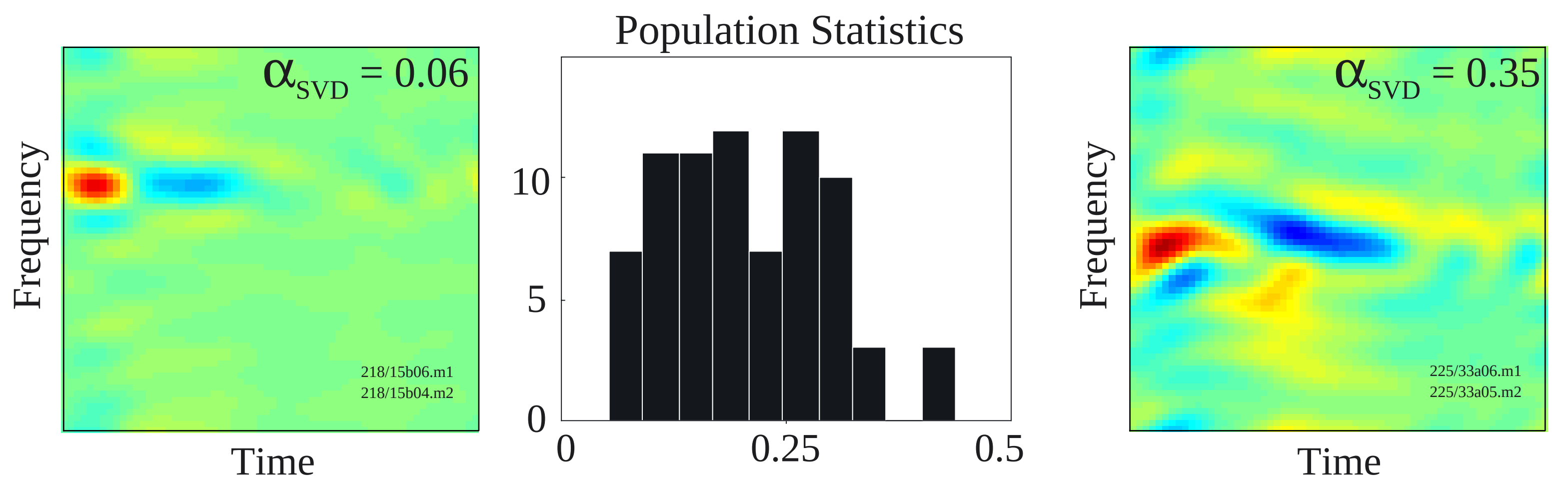
# Measure of Separability

- SVD supplies a natural measure of separability, $\alpha_{SVD}$

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

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

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# Symmetry by Power

- $\alpha_d$: Power asymmetry breaks full separability, producing quadrant separability

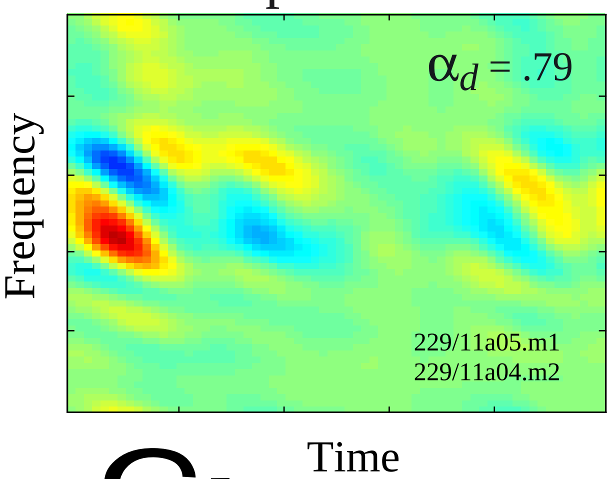
$$\alpha_d = (P_1 - P_2)/(P_1 + P_2)$$

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

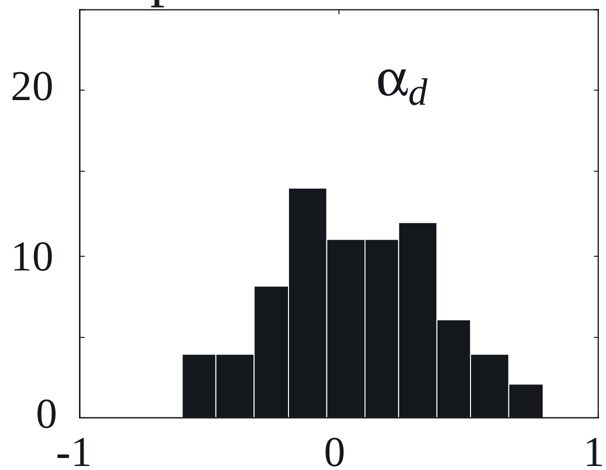
$$P_2 = (\text{Power in quadrant 2}) = (\lambda_2)^2$$

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

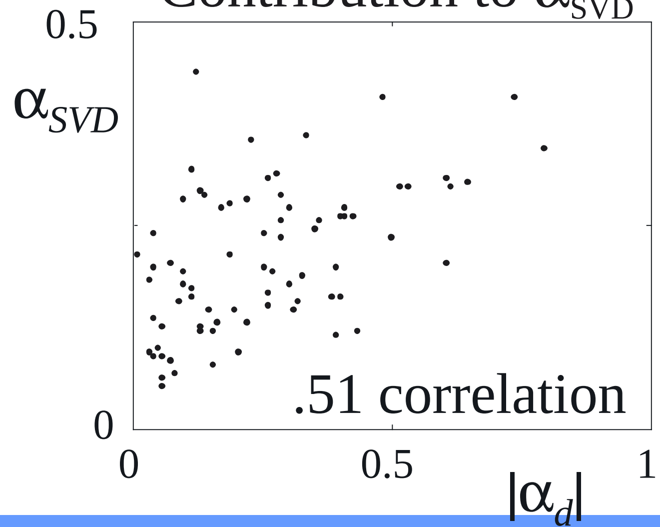
Example STRF




Population Statistics




Contribution to $\alpha_{SVD}$



# Spectral Symmetry

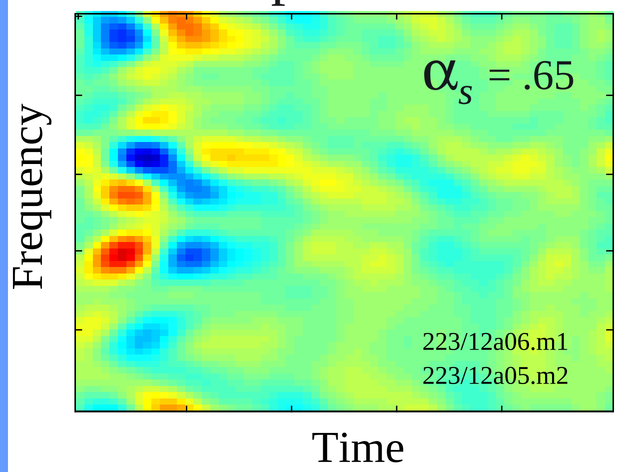
- $\alpha_s$: Asymmetry between spectral cross-sections $G_i(\Omega)$:

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

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

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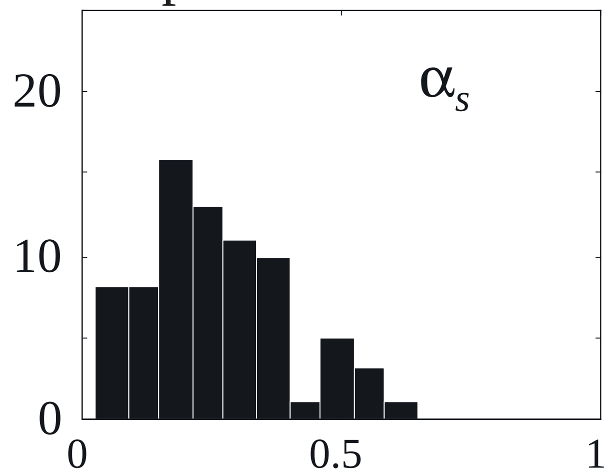
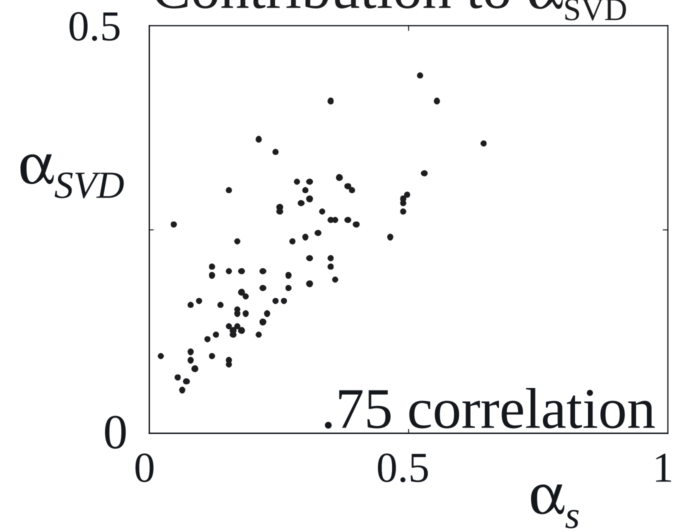



Contribution to $\alpha_{SVD}$





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# Temporal Symmetry

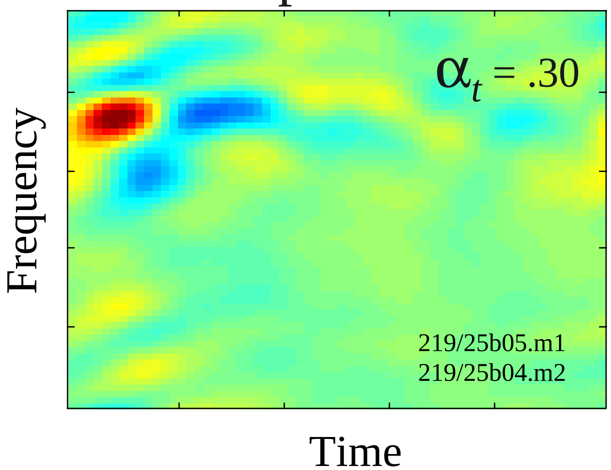
- $\alpha_t$: Asymmetry between temporal cross-sections $F_i(w)$:

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

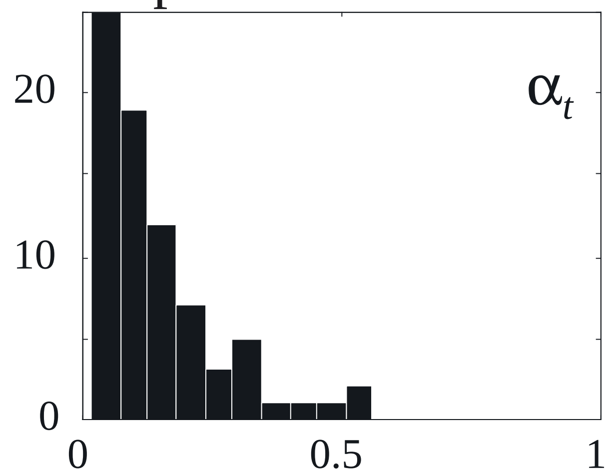
where the quantity inside the big absolute value bars is the (complex) correlation between $F_1(w)$ and $F_2^*(-w)$

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

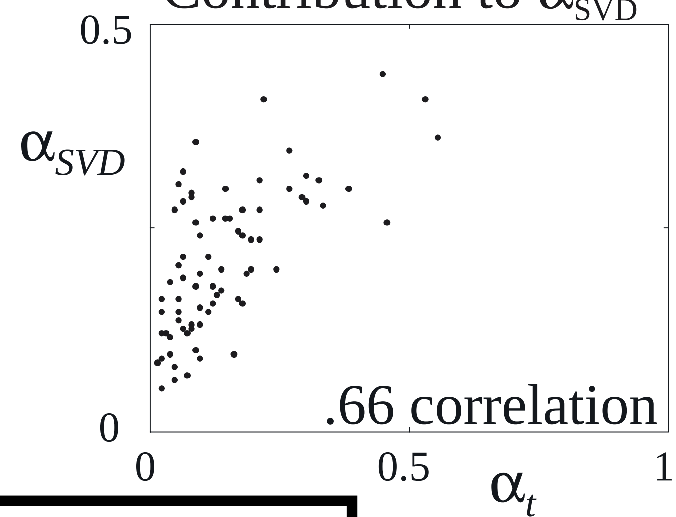
Example STRF




Population Statistics




Contribution to $\alpha_{SVD}$




**Distribution is strongly skewed toward temporal symmetry.**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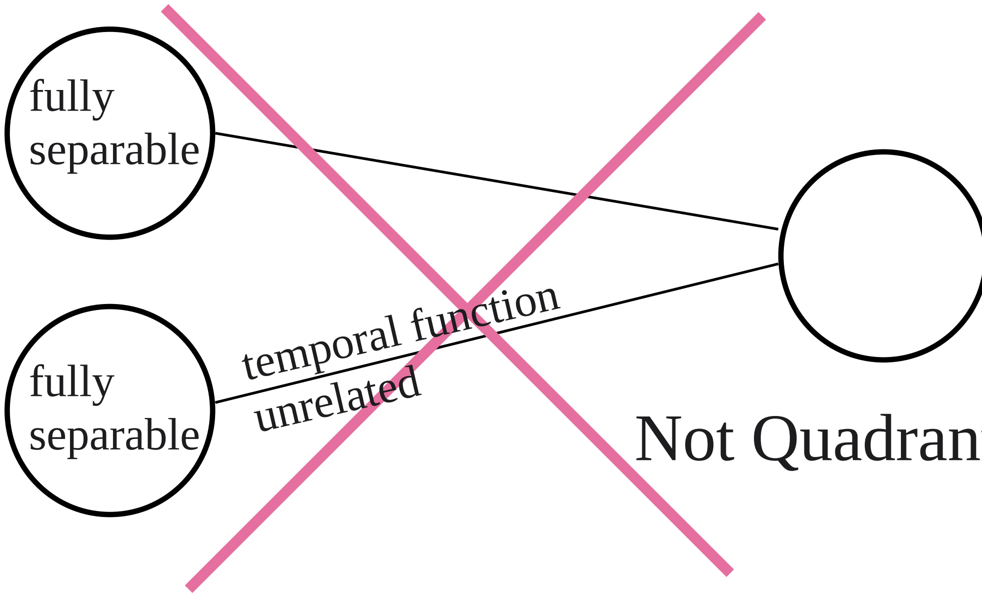
# Neural Connectivity Constraints

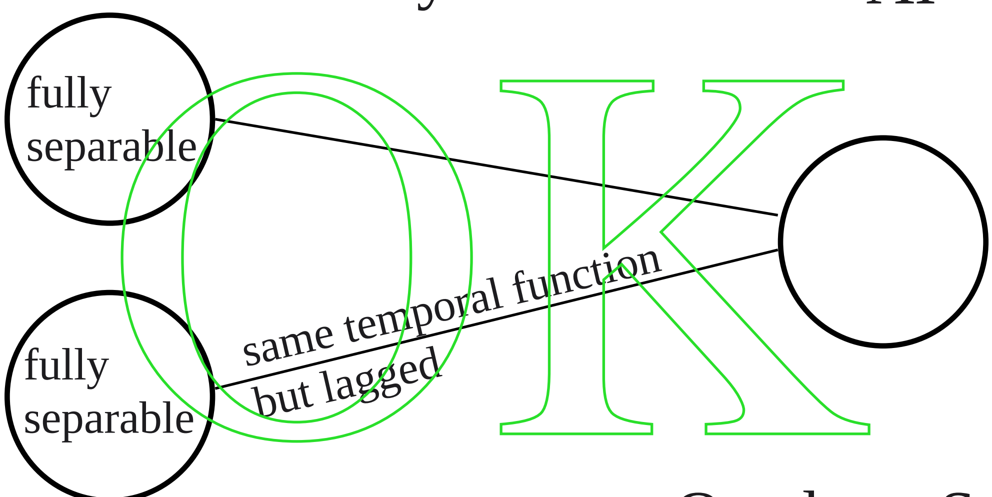
Input to AI =
Medial Geniculate Body

AI




Input to AI =
Medial Geniculate Body

AI




Quadrant Separable

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# 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*

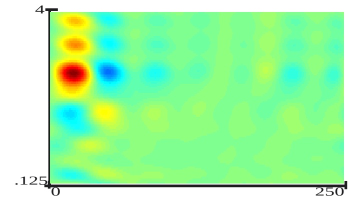
- **Spectro-Temporal Response Field (STRF)**
  - **Descriptor** of response to broadband dynamic stimuli
  - **Predictor** of spike train for stimuli of dynamic, spectral modulations of noise
    - STRFs agree despite measurement method
    - Linear processing conveys most of the information
  - **Visual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

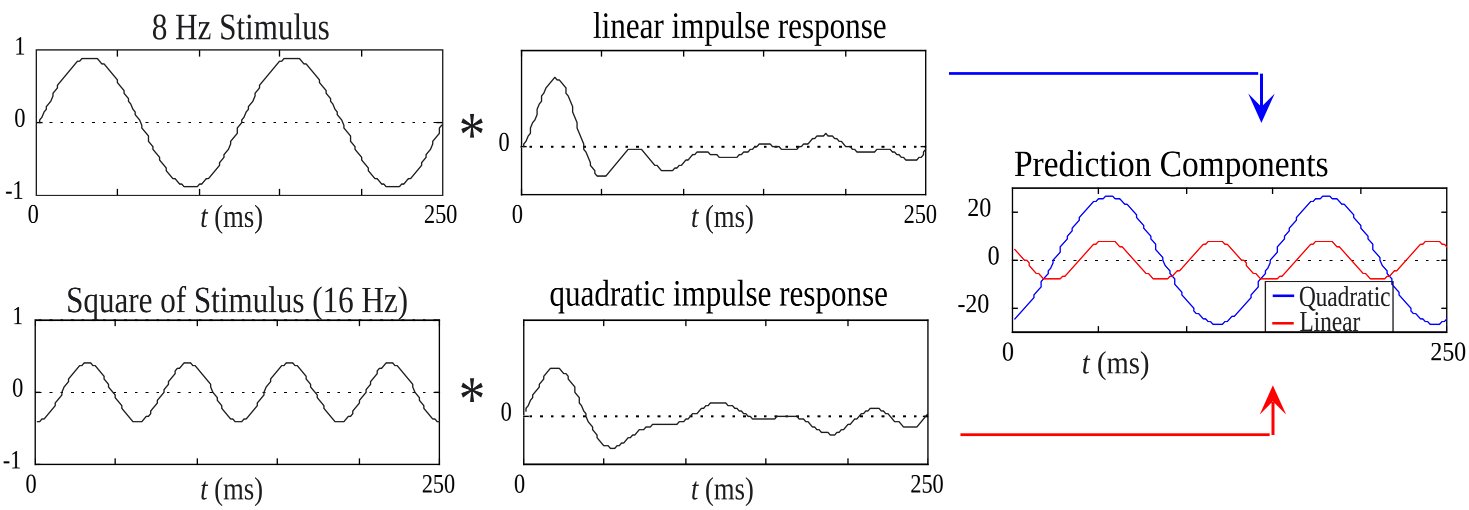
- **Constraints of Quadrant Separability**
  - Limits possible network dynamics

- 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)
- Predicting Responses to Novel Stimuli
- **Non-Linearities**

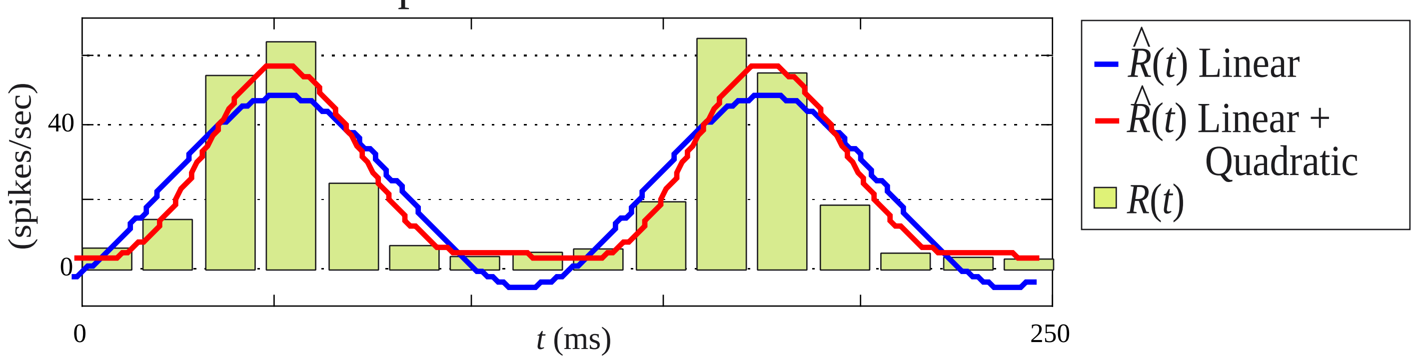
# Non-Linearity—Predictions

- 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.

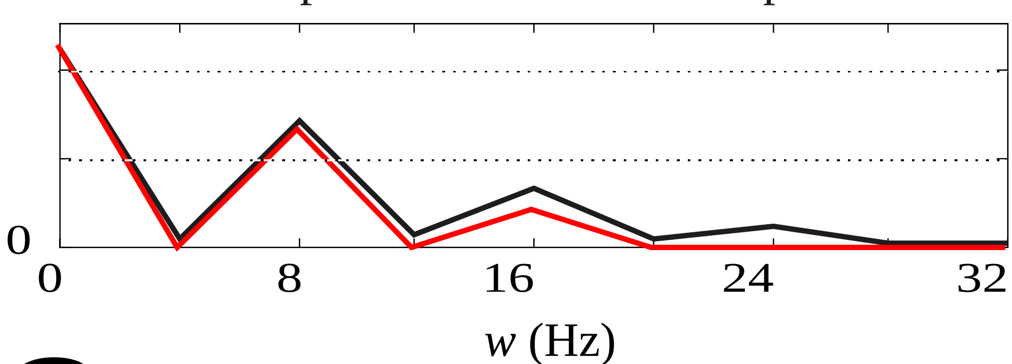



Response and Predictions




Response and Prediction Spectra

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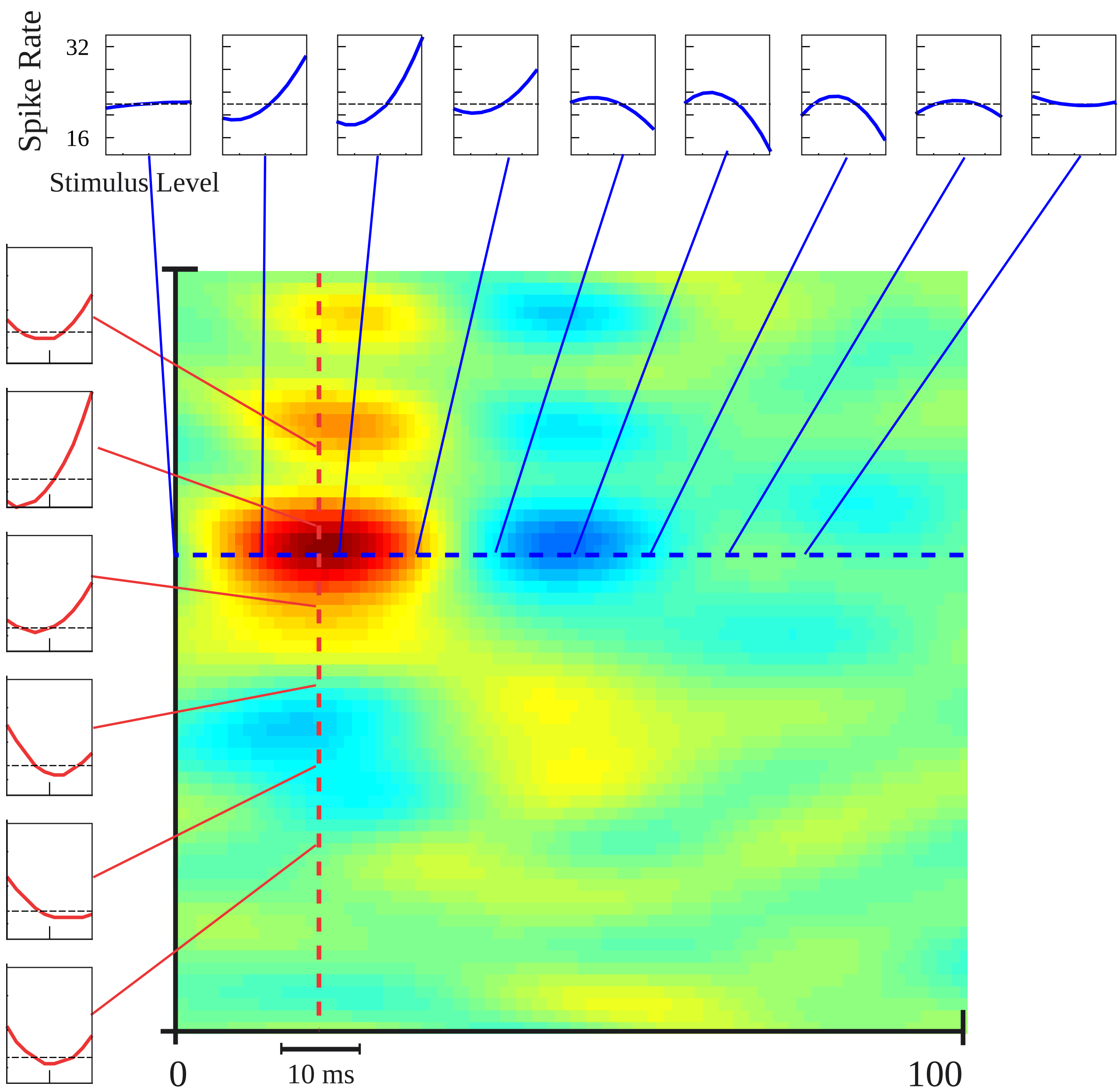
# Spectro-Temporal Rate-Level Functions

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

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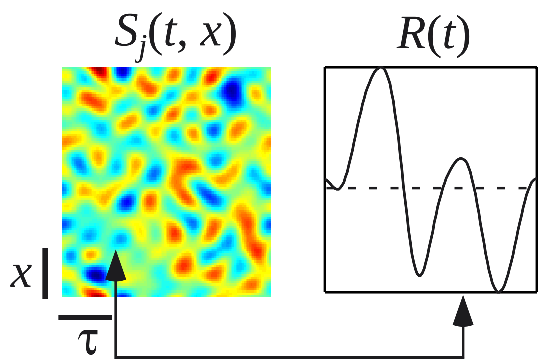
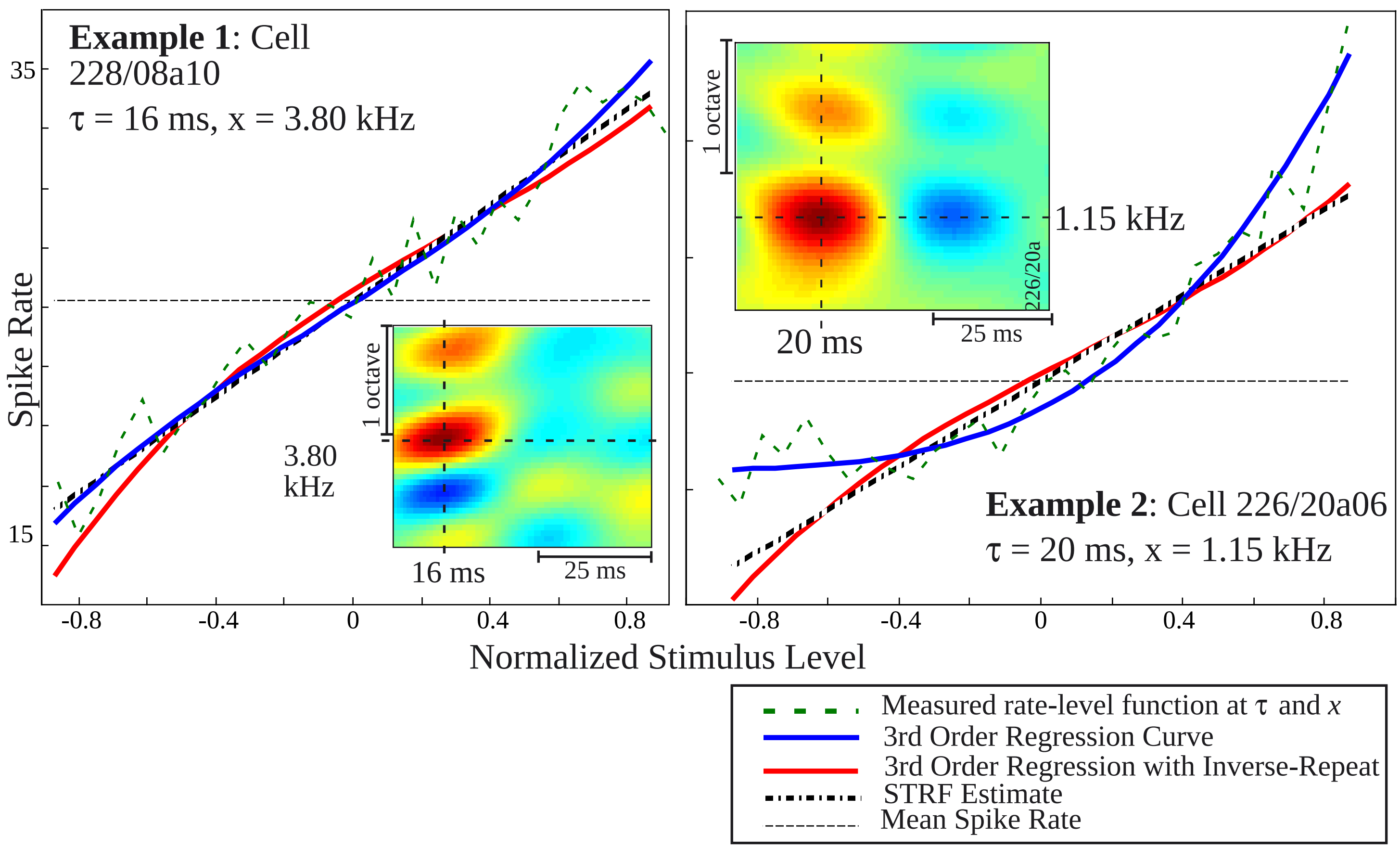
# Non-Linearity—Theory

- The value of the STRF at each point ($\tau$, $x$) 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 ($\tau$, $x$) 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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