# Response-Field Dynamics in the Auditory Pathway

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# Abstract

We investigated the response properties and functional organization of Primary Auditory Cortex (AI), to determine how the shape of the acoustic spectrum is represented in single-unit responses. The experiments employ broadband stimuli with sinusoidally modulated spectral envelopes (ripples), and systems theoretic methods to derive unit response fields and to characterize their spectro-temporal properties. These methods assume linearity of auditory responses with respect to the stimulus spectral envelope. We also address the degree of separability of response fields with respect to upward and downward moving sounds. We verified that unit responses to complex sounds with both upward and downward components can be predicted from their responses to simple ripples.

# Introduction

**Natural sounds** are characterized by loudness (intensity), pitch (tonal height) and timbre (the rest, e.g. dynamic envelope of spectrum).
**Question**: How is timbre encoded in primary auditory cortex (AI)?

**Our Approach**:
Beyond the sensory epithelium (cochlea or retina), principles used by neural systems are universal. To lowest order, we view the basilar membrane as a 1-D retina, and use the method of gratings to study single units in AI.

**Important Concepts**:
• *Response Field* (RF): the range of frequencies that influence a neuron. In general, RF is a function of time.
• *Ripples*: broadband sounds with sinusoidally modulated spectral envelope; i.e. auditory gratings.
• Data analysis based on *linear systems* to characterize response field. By varying ripple frequency and velocity, we measure the transfer function. The inverse Fourier transform gives the *spectro-temporal* RF (STRF).

**We find:**
• Cells can be characterized by a STRF. The STRF can be separable or non-separable.
• Cells behave like a linear system: when cells are presented with a sound made of up the sum of several profiles, the response of the cell (assuming a rate code) is the sum of the responses to the individual profiles.

**We show** predictions of single-unit responses in AI to complex spectra, verifying:
• *Linearity* of AI responses to all types of dynamic ripples: responses to both upward and downward moving ripples can be superimposed linearly to predict responses to arbitrary combinations of these ripples.
• *Separability* of spectral and temporal measurements of the responses: spectral properties can be measured independently of the temporal properties (such as the impulse response).

**We conclude:**
The combined spectro-temporal decomposition in AI can be described by an affine wavelet transformation of the input, in concert with a similar temporal decomposition. The auditory profile is the result of a multistage process which occurs early in the pathway. This pattern is projected centrally where a multiscale representation is generated in AI by STRFs with a range of widths, asymmetries, BFs, time lags and directional sensitivities.

# Captions

The next few figures illustrate spectro-temporal functions and their Fourier transforms.

Since the cochlea performs (to first order) a Fourier transform along the logarithmic frequency axis, we also measure spectral distance in log(frequency). Since the Fourier transform is time-windowed, we also require a time axis. For this reason we will focus attention on two-dimensional functions of log(frequency) and time.

Consider the (Fourier) space dual to this two-dimensional spectro-temporal space. For linear systems, the spectro-temporal domain and its Fourier domain are equivalent. Analysis is often conceptually simpler in the Fourier domain. Note that real functions in the spectro-temporal domain give rise to complex conjugate symmetric functions in the Fourier domain.

The next panel **Spectro-Temporal Fourier Transform** illustrates the envelope of a speech fragment, in both its spectro-temporal and Fourier representations. Notice that in the Fourier representation, the function is highly concentrated.

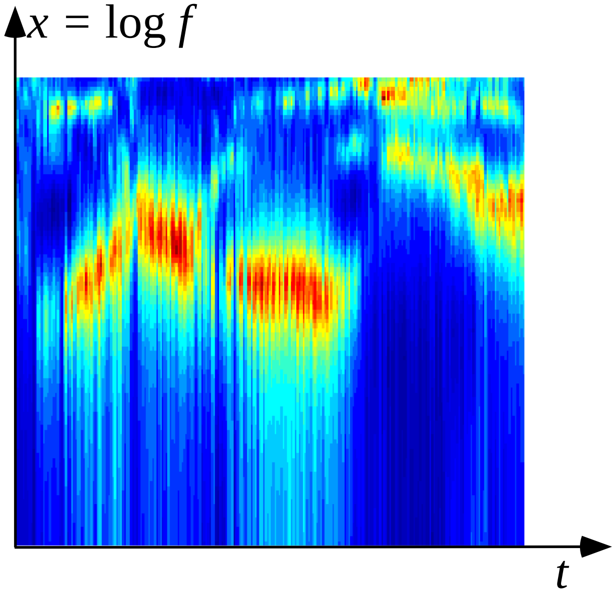
The subsequent panel **Spectro-Temporal Fourier Transform Response** illustrates the spectro-temporal response field of a neuron, and its Fourier dual, the transfer function.

The panel **Spectro-Temporal Fourier Transform Stimulus** shows an example of the usefulness of the Fourier domain. The envelope of a speech fragment is Fourier transformed. The Fourier transform is then approximated by its 100 largest components and then inverted, giving an excellent approximation to the original envelope.

The panel **Ripples** demonstrates that points in the Fourier space correspond to broadband sounds with a sinusoidally modulated spectral and temporal envelope.

# Spectro-Temporal Fourier Transform

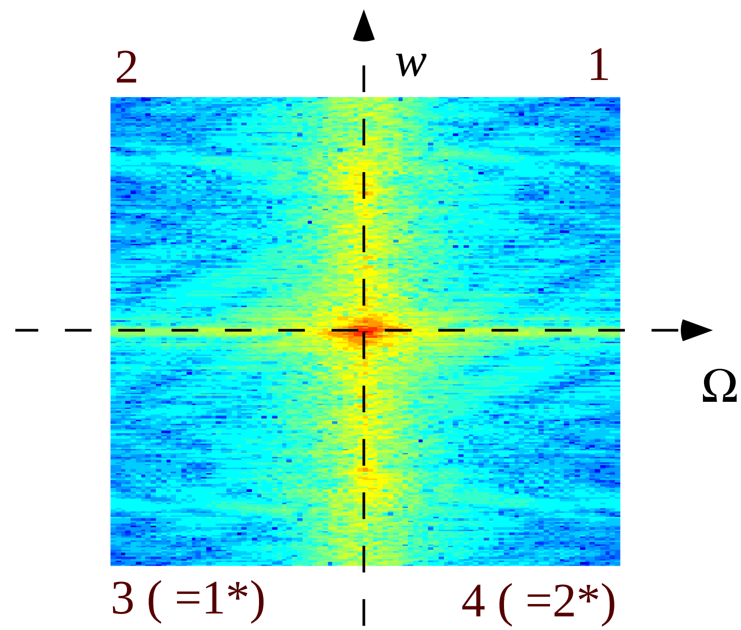
## Spectrogram (log frequency)




*Fourier Tranform*

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

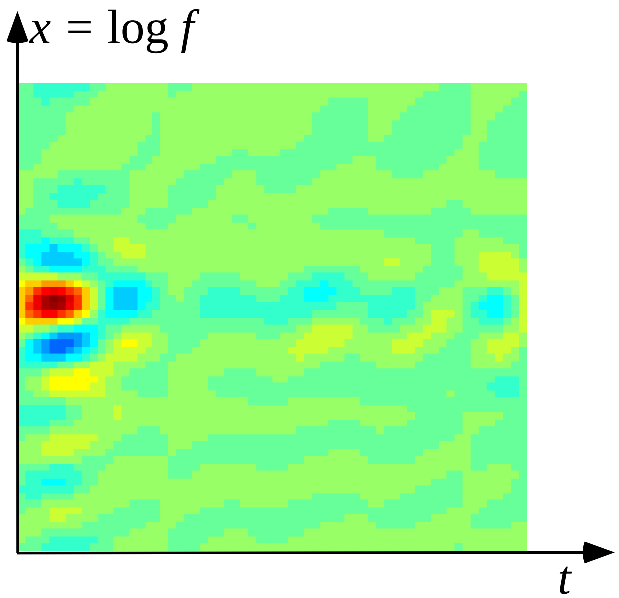
*Inverse Tranform*




$w$ = “ripple velocity”
$\Omega$ = “ripple frequency”

# Spectro-Temporal Fourier Transform Response

## Spectrogram (log frequency)

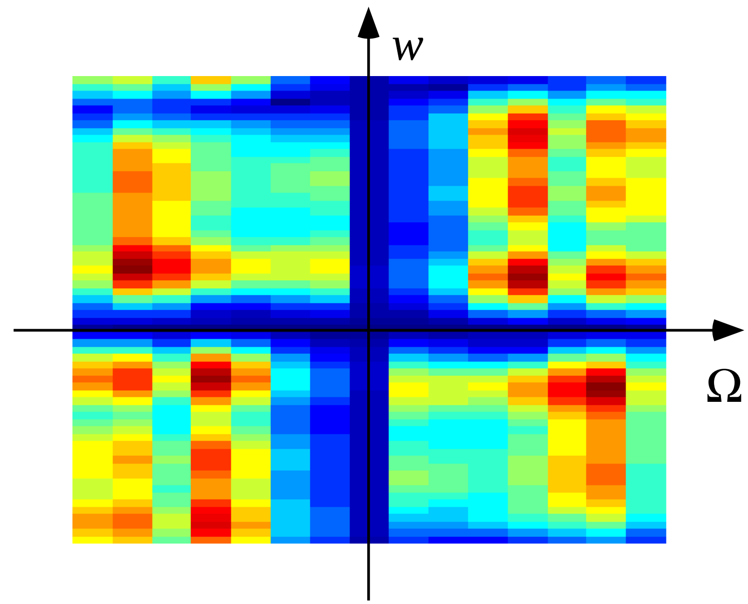



Spectro-Temporal
Response Function (STRF)
of a cortical neuron

*Fourier Tranform*

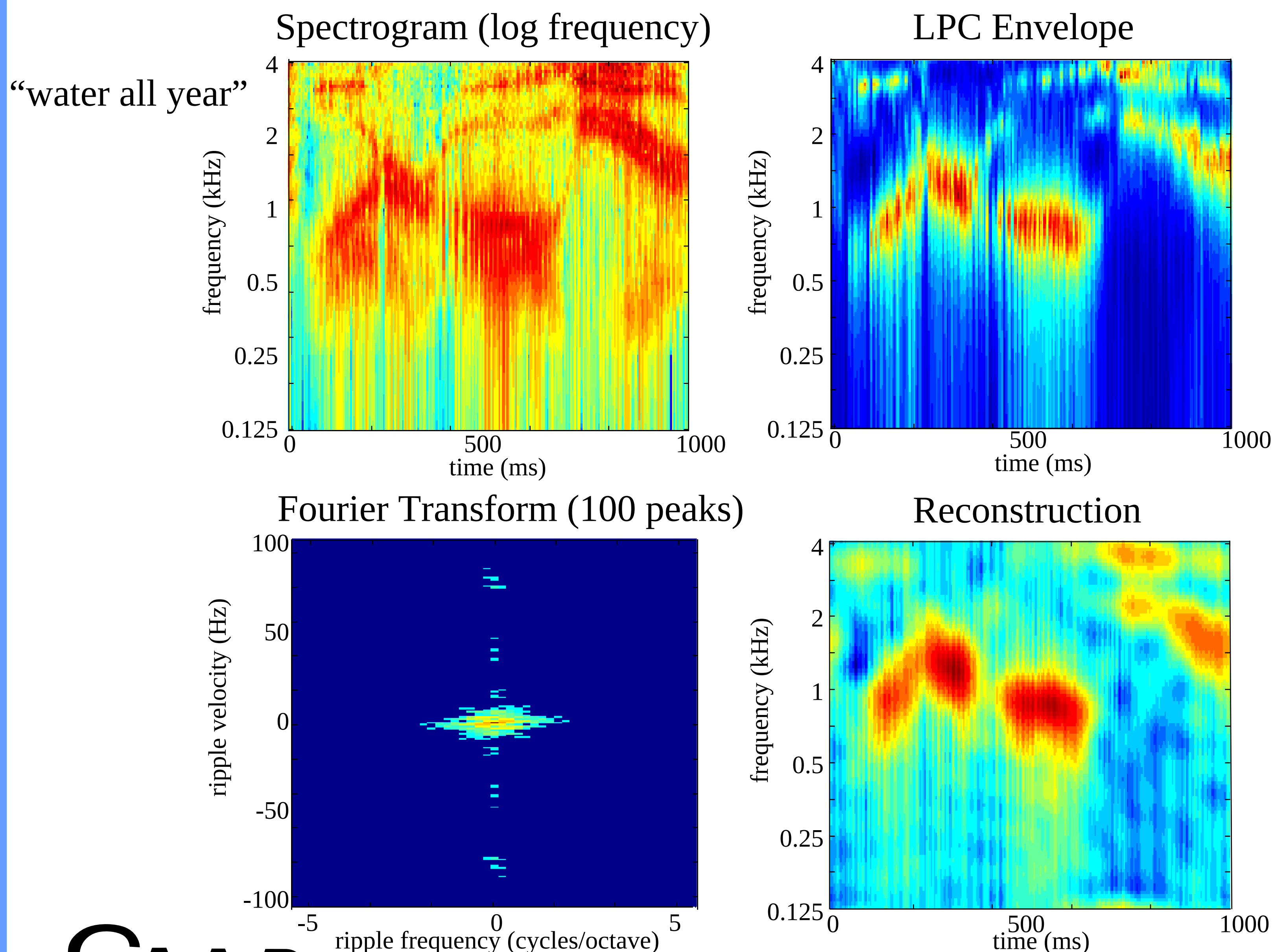
$\int [\cdot] \exp(\pm 2\pi j \Omega x \pm 2\pi j w t)$

*Inverse Tranform*




2 Dimensional
Transfer Function
of a cortical neuron

# Spectro-Temporal Fourier Transform Simulus

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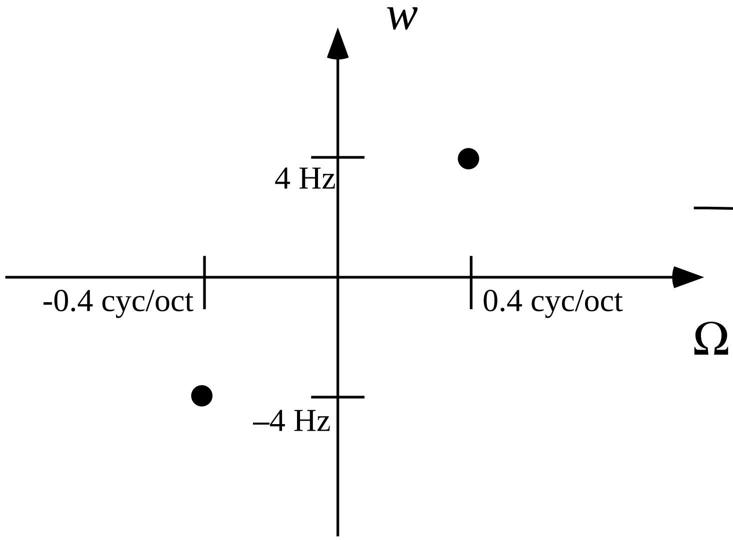
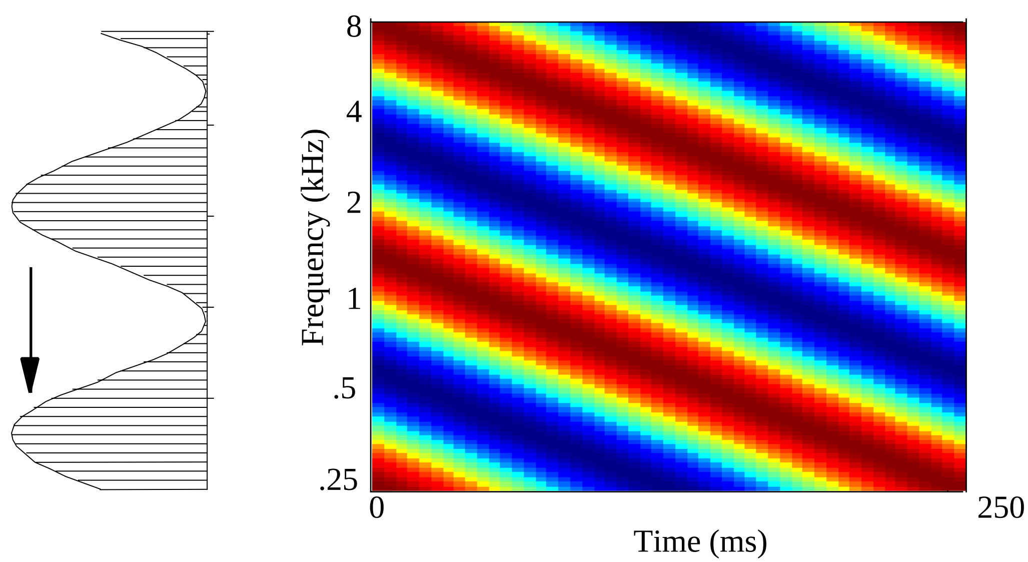
# Ripples

## Ripple in Fourier Space




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

## Ripple in Spectro-Temporal Space (Spectrogram)





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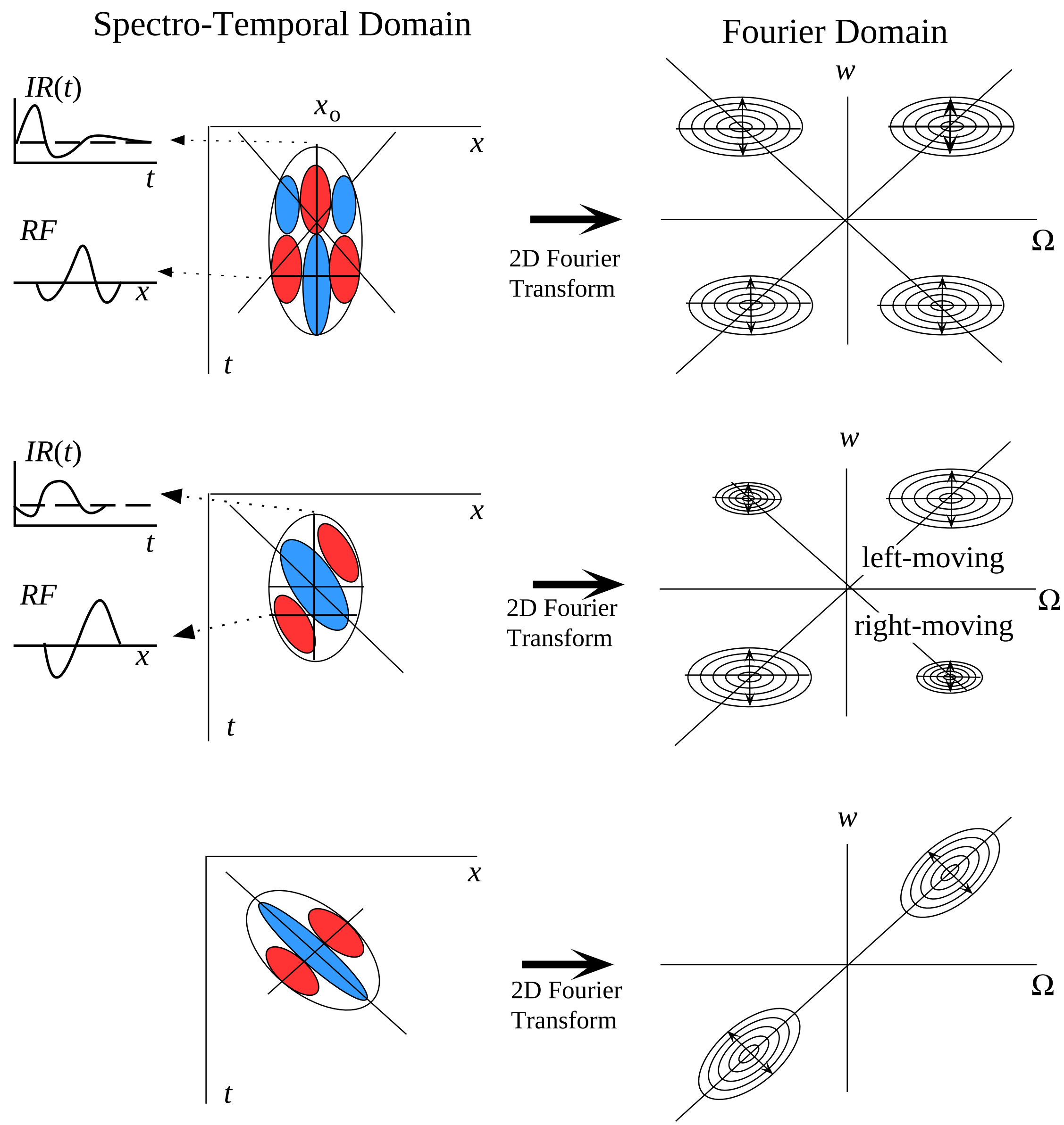
# Quadrant Separability




Fully Separable

Quadrant Separable

Inseparable

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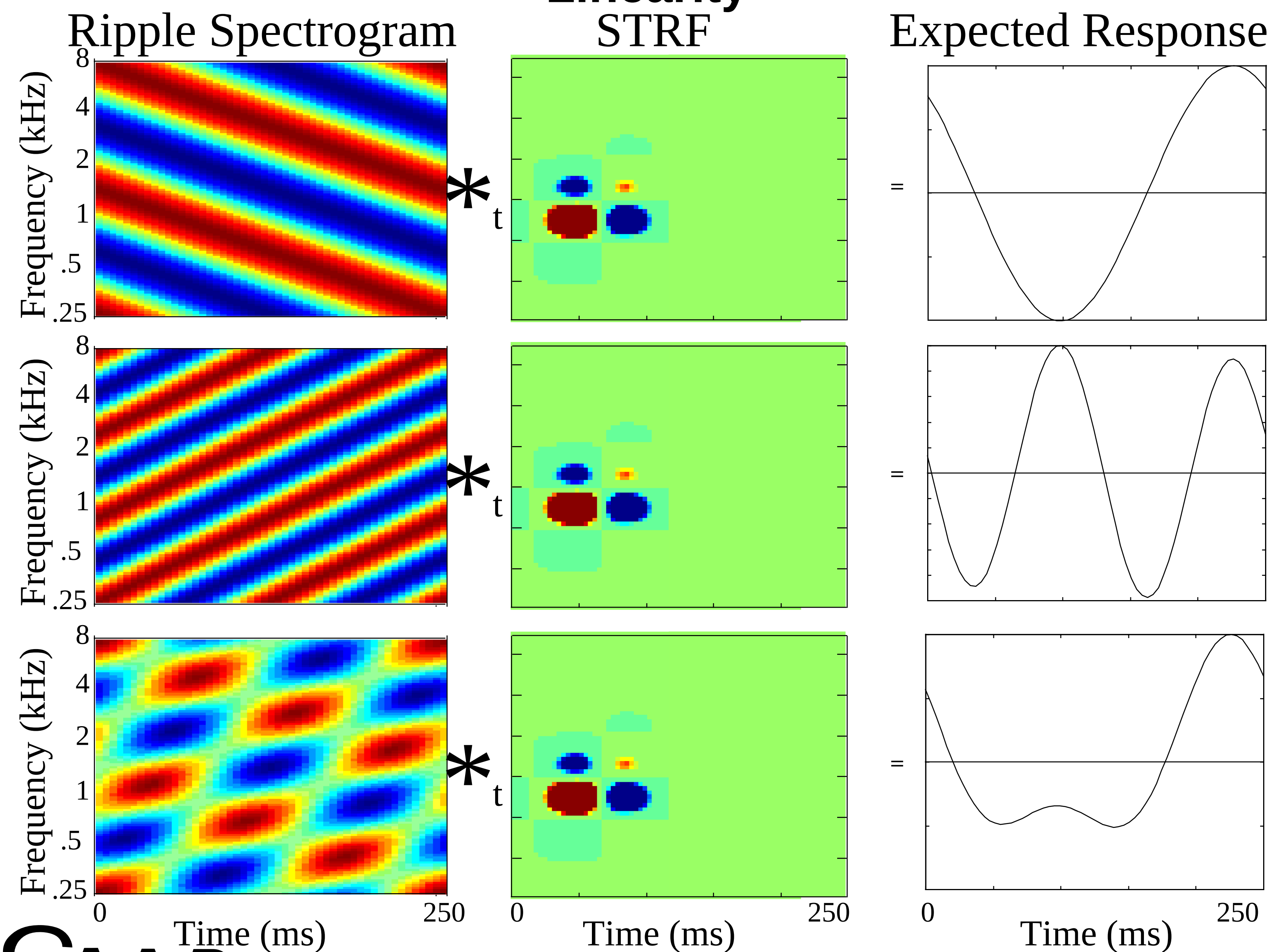
# Linearity

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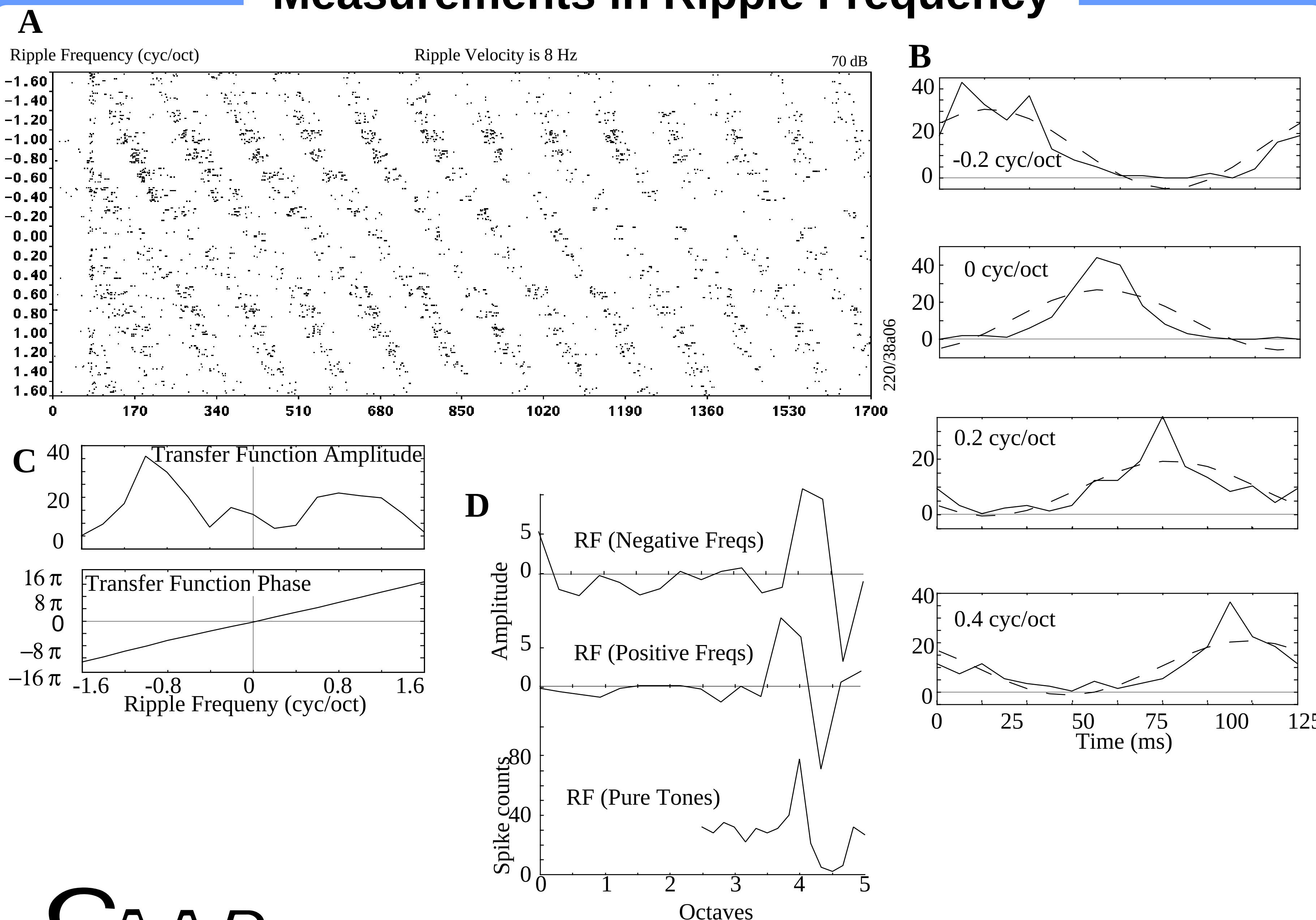
# Measurements in Ripple Frequency

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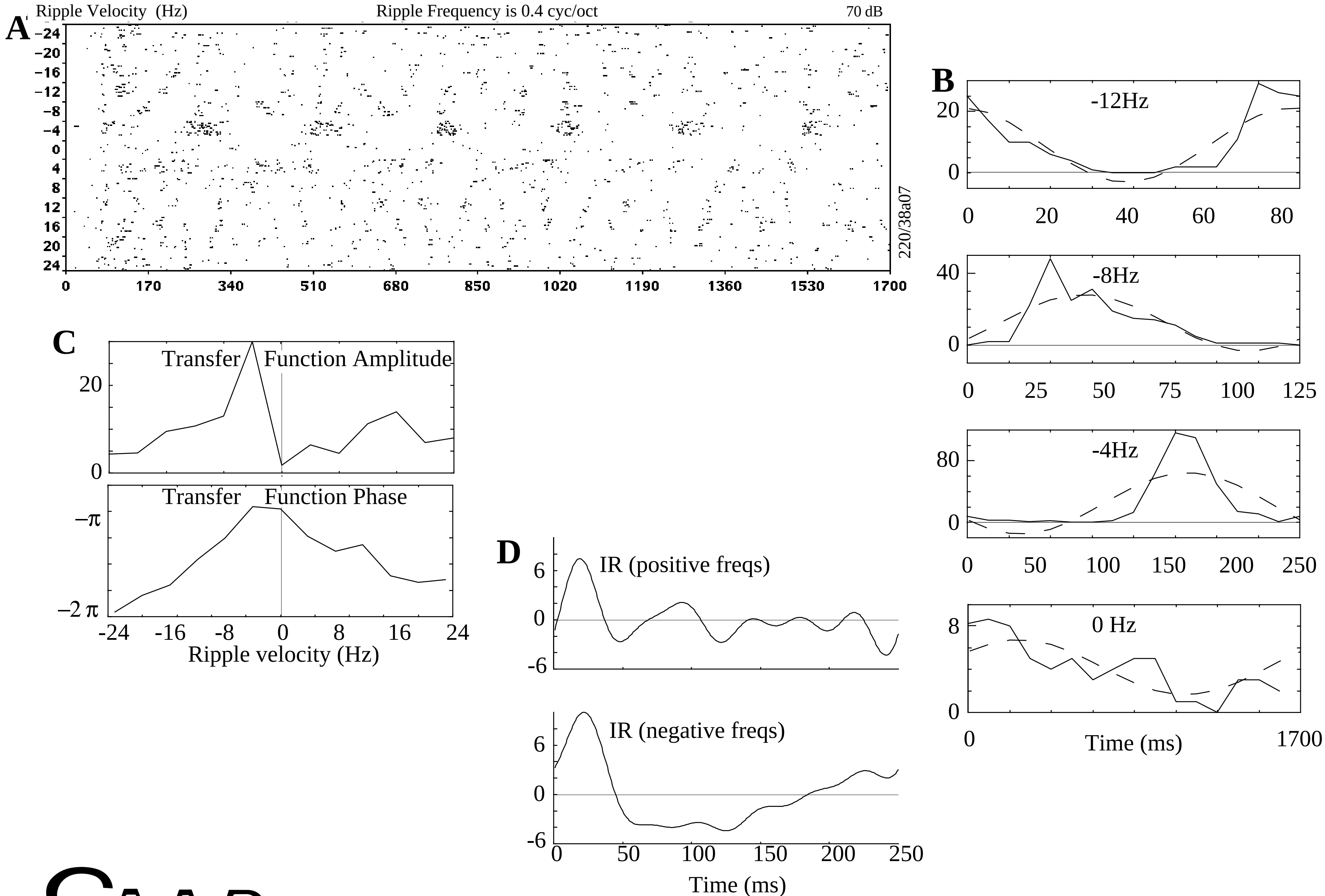
# Measurements in Ripple Velocity

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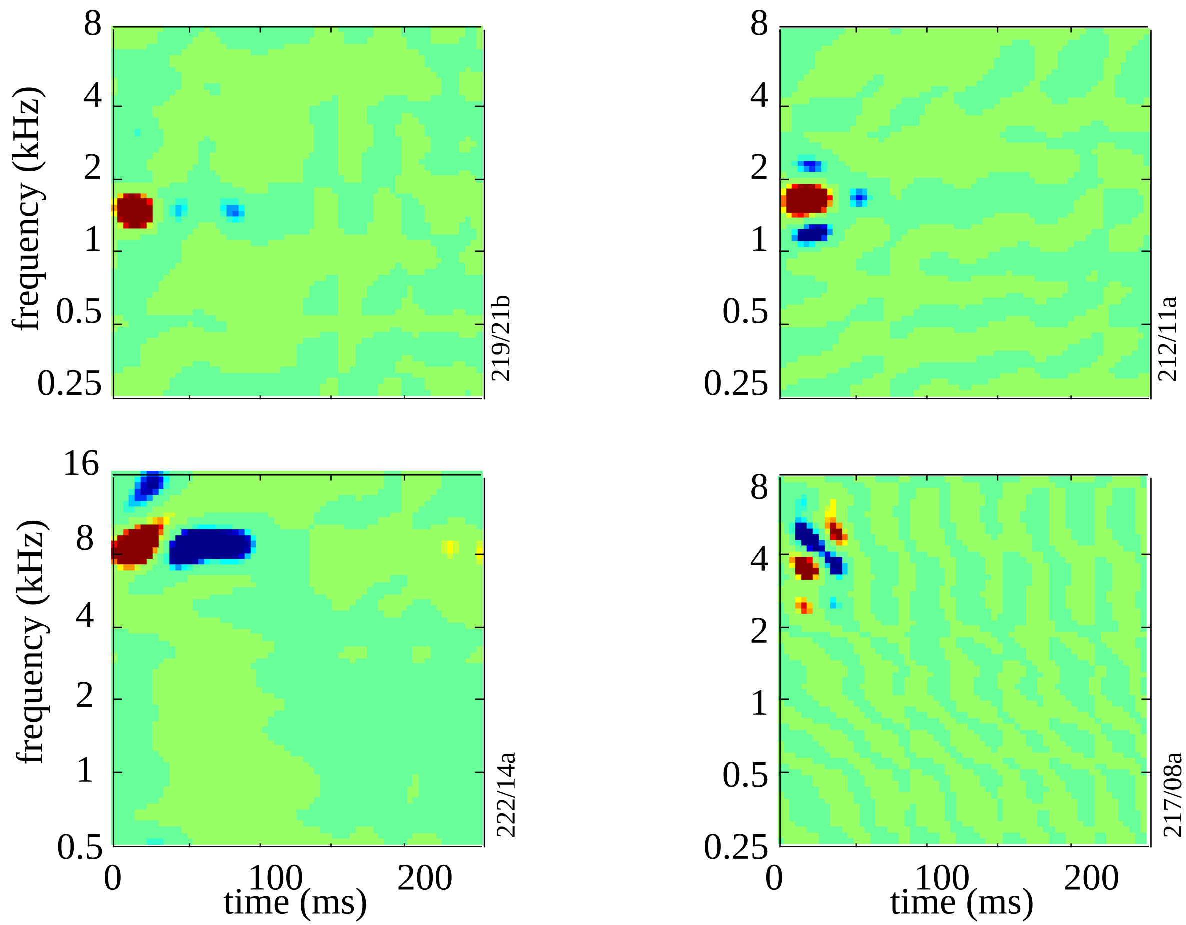
# Spectro-Temporal Response Fields

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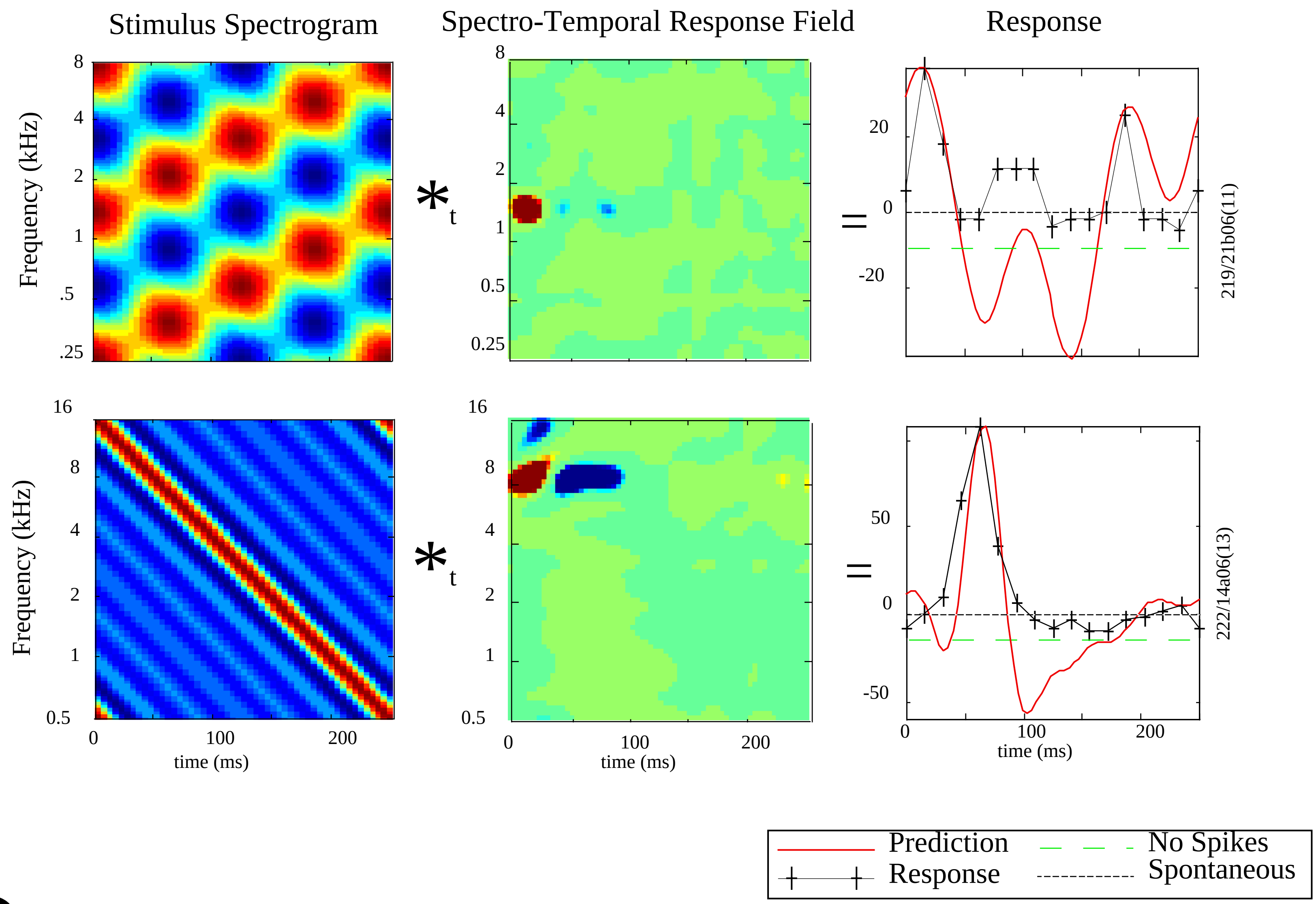
# Predictions

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# Ripple Decomposition

## Response field modeling

The response of the spatial filter is

$$H_n(\Omega) = (\Omega / \Omega_n)^2 e^{-(\Omega/\Omega_n)^2} \max(\Omega, 0)$$

$$h_n(x) = h_{n,r}(x) + j\hat{h}_{n,r}(x)$$

where $h_{n,r}(x) = \frac{k_n}{2}(1-(k_n x)^2)e^{-(k_n x)^2/2}$
and $k_n = 2\pi\Omega_n$

The response of temporal filter is

$$G_m(w) = (w / w_m)^2 e^{-(w/w_m)^2} \max(\mathrm{sgn}(w_m)w, 0)$$

$$g_m(t) = g_{m,r}(t) + j\,\mathrm{sgn}(w_m)\hat{g}_{m,r}(t)$$

where $g_{m,r}(t) = \frac{\omega_m}{2}(1-(\omega_m t)^2)e^{-(\omega_m t)^2/2}$
and $\omega_n = 2\pi w_n$

## Direction selectivity

The multiscale-multirate response for an auditory spectrogram is

$$p_{mn}(t,x) = p(t,x) *_t g_m(t) *_x h_n(x)$$

The composite spatiotemporal impulse response shows the nature of directional selectivity.

## Representation

The phase of the complex response is indicated by colors:
green = 0°, red = 90°, purple = ±180° and blue = -90°.
The magnitude is linearly represented by the saturation of the color.

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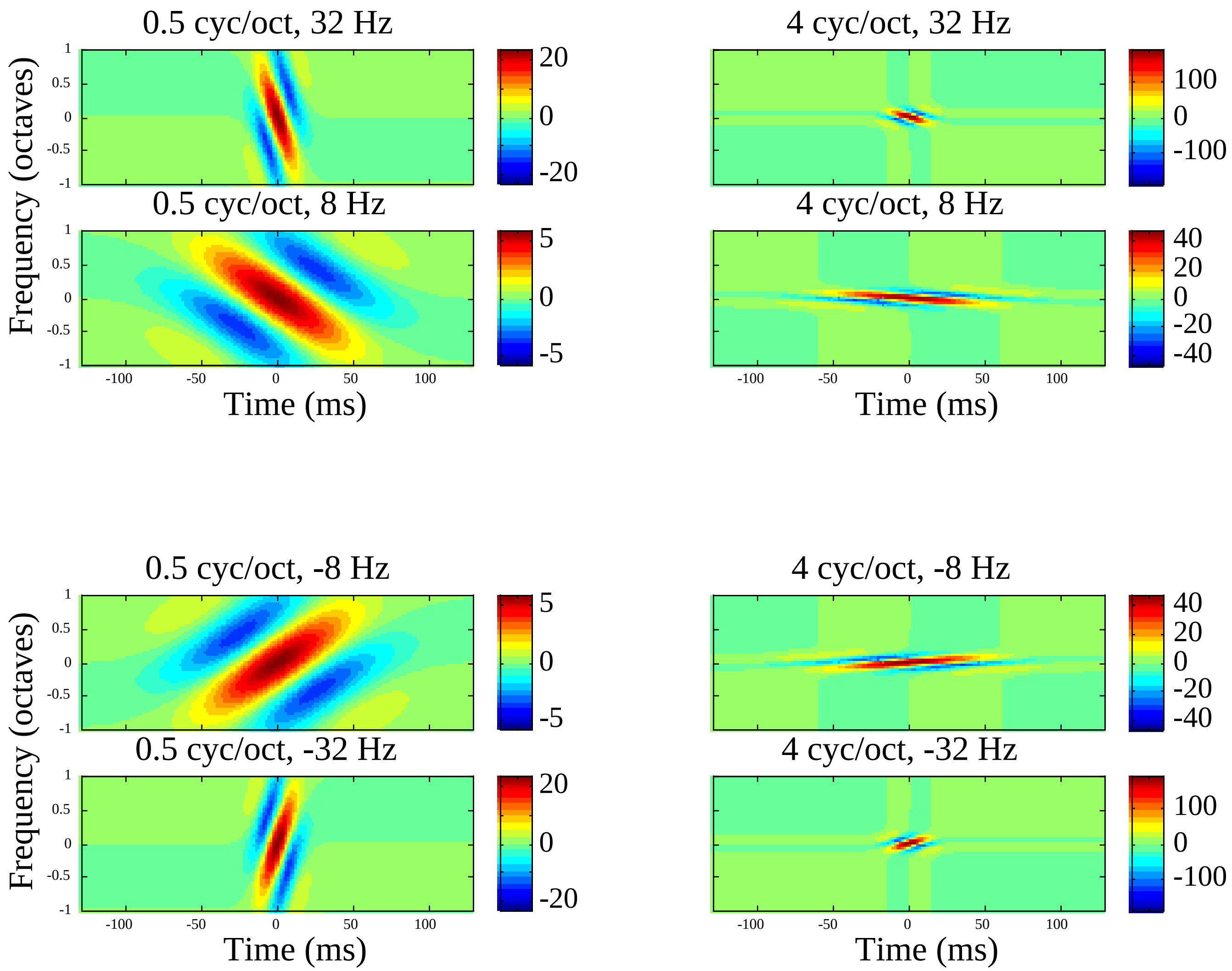
# Ripple Filters





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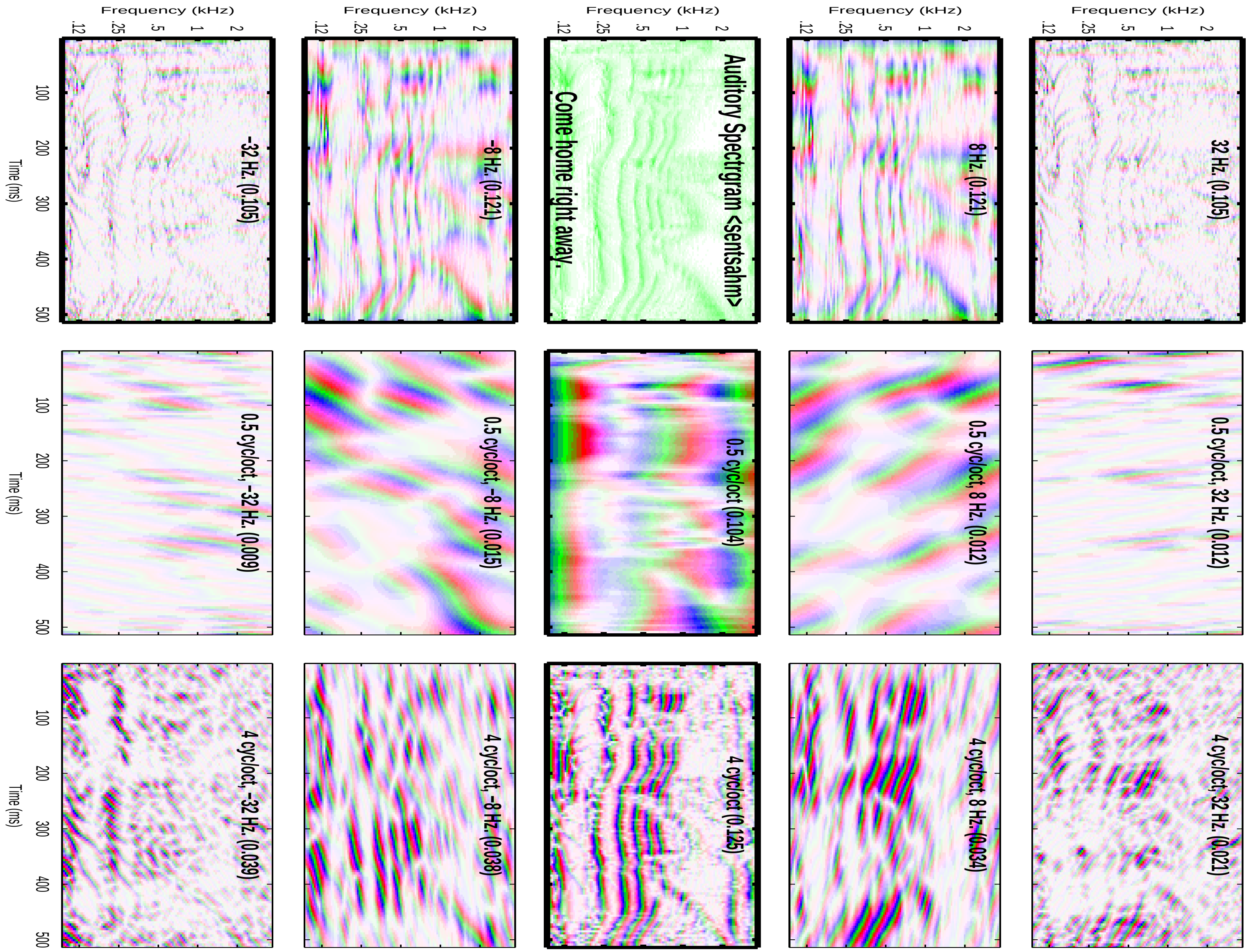
# Ripple Decomposition Example

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- Shamma SA, Versnel H and Kowalski NA, J. Auditory Neuroscience (1) (1995) 233-254, and 255-270, and 271-285.
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- Wang K and Shamma SA, IEEE Trans. on Speech and Audio 2(3) (1994) 421-435, and 3(2) (1995) 382-395
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