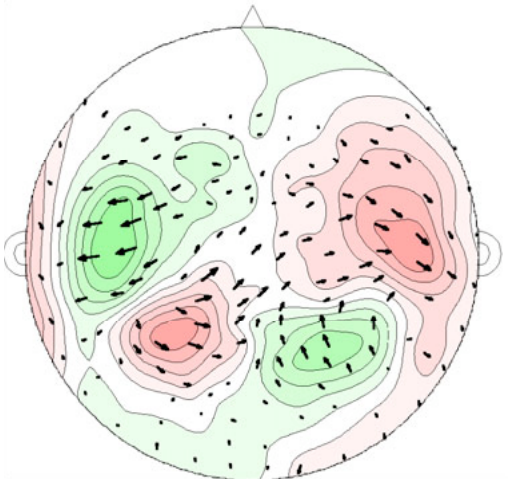
# Neural Coding of Multiple Stimulus Features in Auditory Cortex



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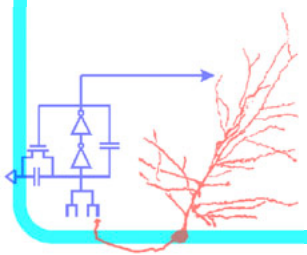
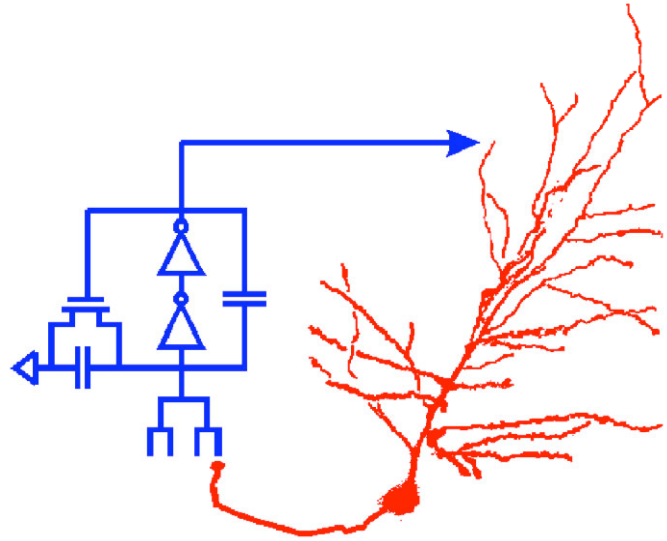


# Computational Sensorimotor Systems Laboratory



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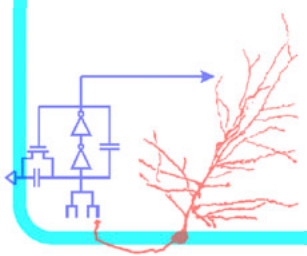
*Luo, H., Y. Wang, D. Poeppel & J. Z. Simon (2006), J. Neurophysiology*

# Outline

- Magnetoencephalography (MEG) as a tool of Non-Invasive Auditory Physiology
- MEG in the Frequency Domain
- Neural Encoding of Modulations



# Magnetoencephalography (MEG)

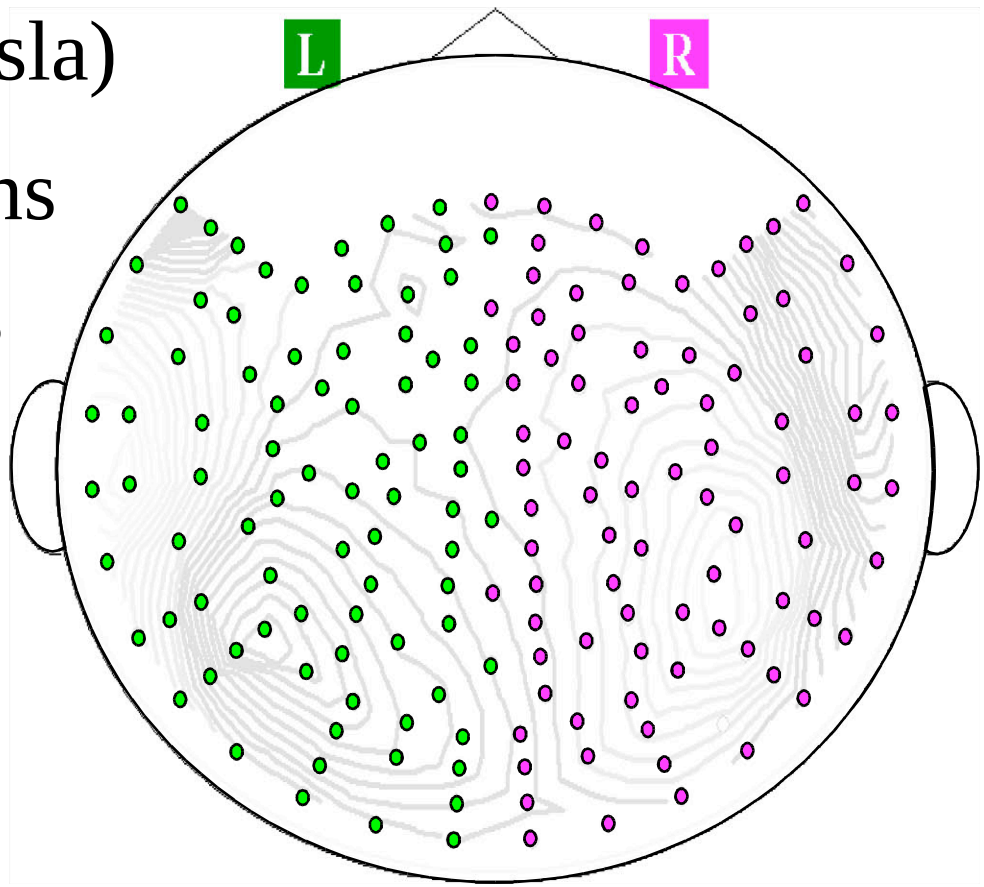
- Non-invasive, Passive, Silent Neural Recordings
- Simultaneous Whole-Head Recording (~200 sensors)
- Sensitivity

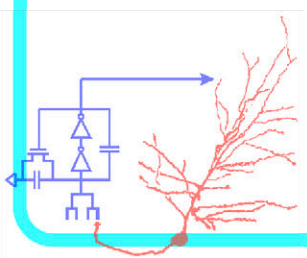
  high: ~100 fT ($10^{-13}$ Tesla)

  low: ~$10^4$ – ~$10^6$ neurons
- Temporal Resolution: ~1 ms
- Spatial Resolution

  coarse: ~1 cm

  ambiguous



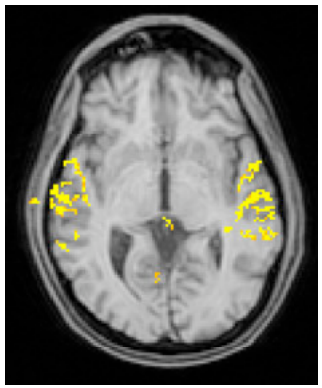



# Functional Imaging

**Non-invasive recording from human brain (Functional brain imaging)**

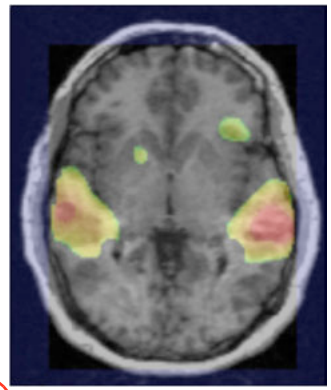
**Hemodynamic techniques**

**Functional magnetic resonance imaging**
**fMRI**



**Excellent *spatial resolution***
**( ~ 1-2 mm)**
**Poor temporal resolution**
**( ~ 1 s)**

**Positron emission tomography**
**PET**

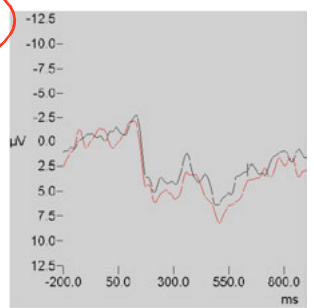


PET, EEG require across-subject averaging

fMRI and MEG can capture effects in single subjects

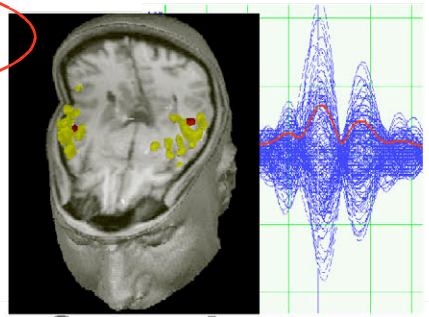
**Electromagnetic techniques**

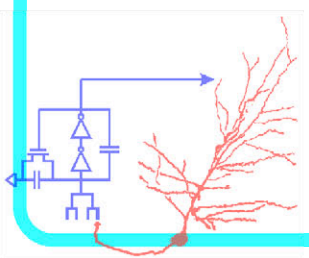
**Electroencephalography**
**EEG**



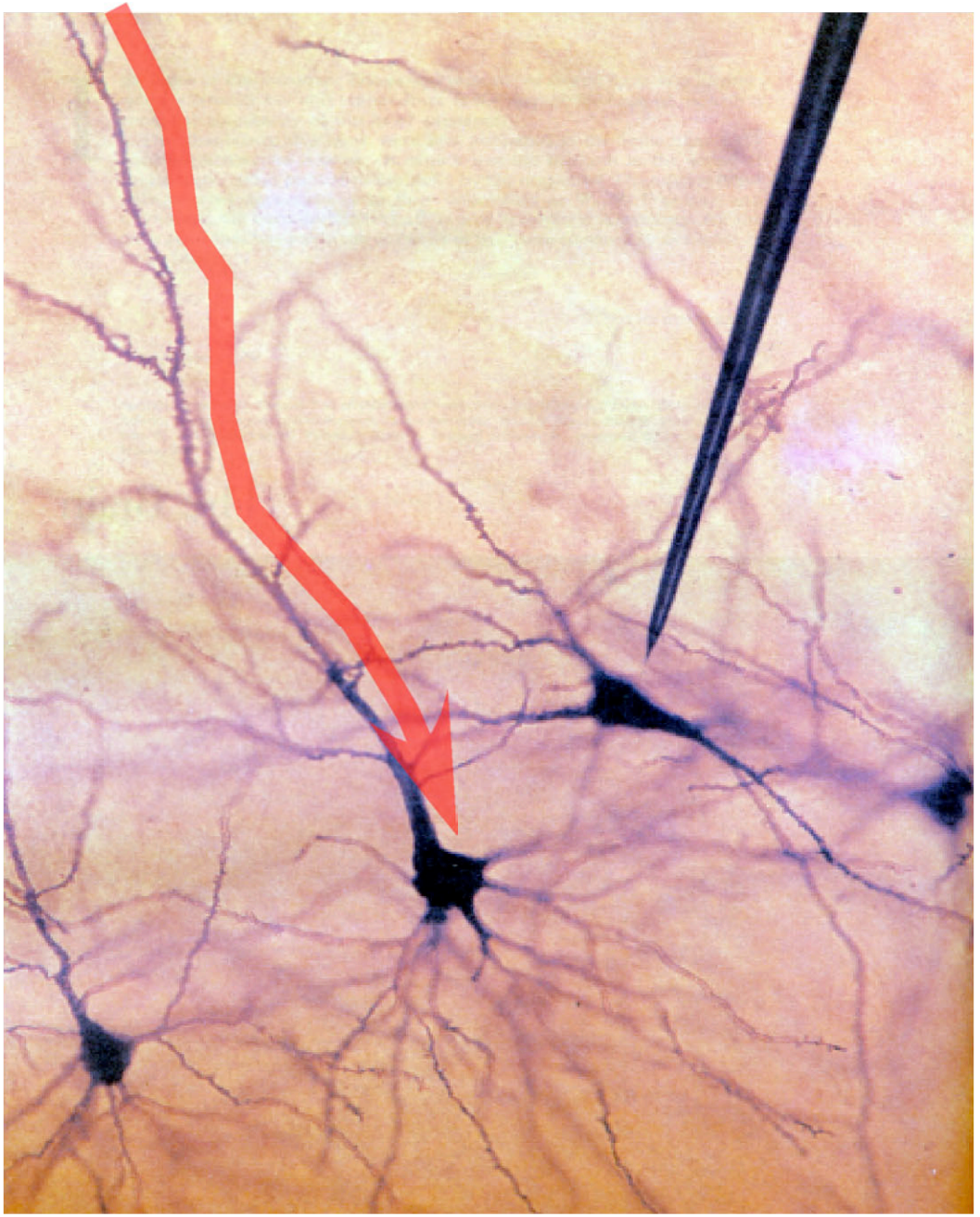

**Poor spatial resolution**
**( ~ 1 cm)**
**Excellent *temporal resolution***
**( ~ 1 ms)**

**Magnetoencephalography**
**MEG**





# Primary Neural Current



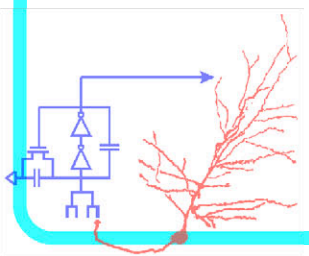
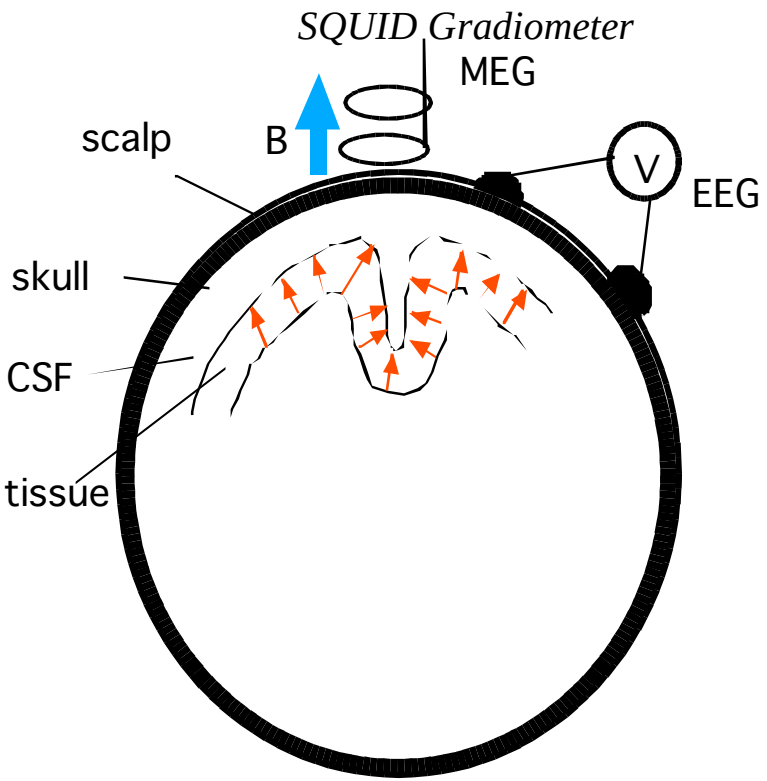
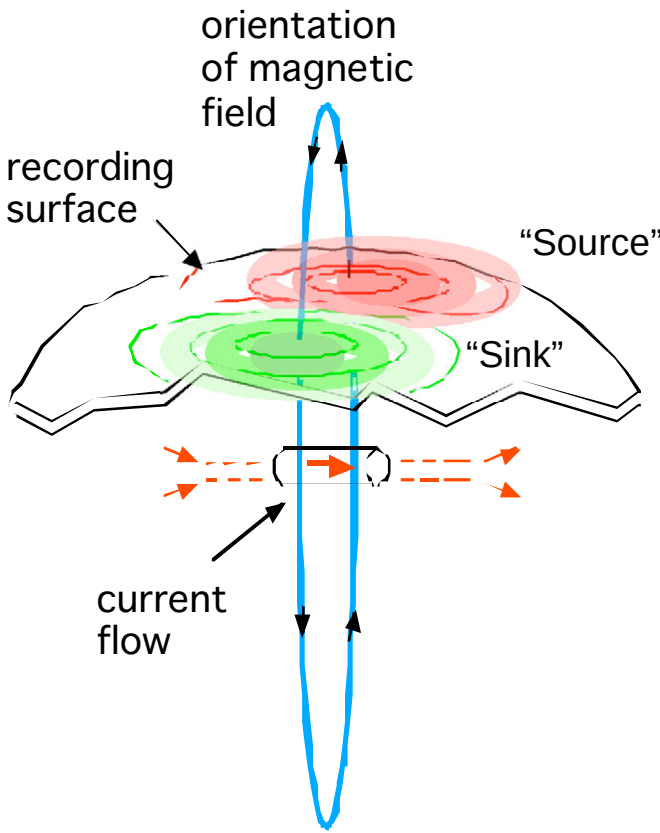


Photo by Fritz Goro

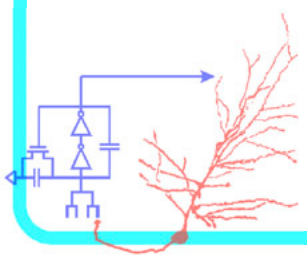
# MEG Measures Neural Currents



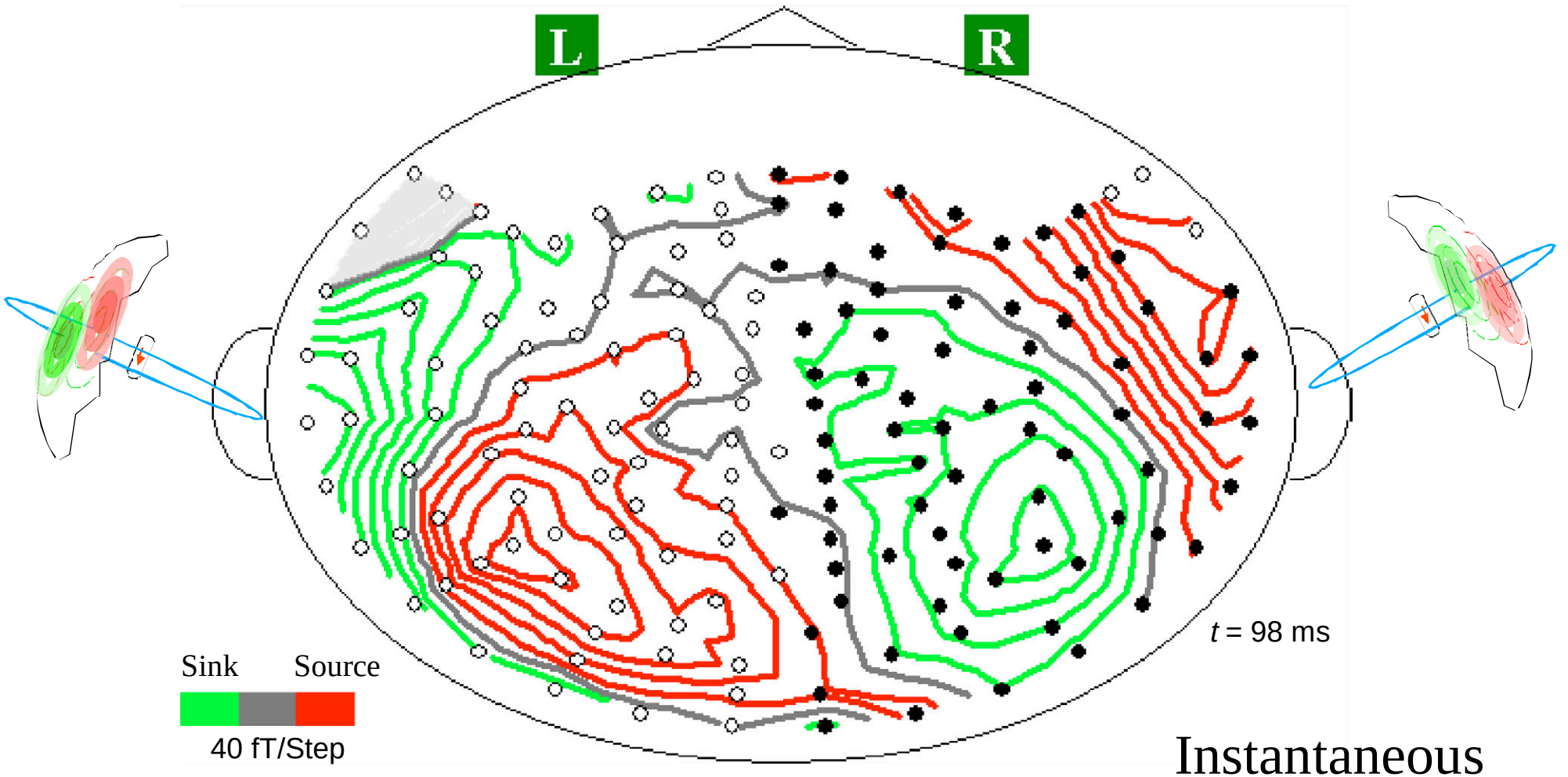

Magnetic Dipolar Field (Projection)

- Direct electrophysiological measurement
  - not hemodynamic
  - real-time
- No unique solution for distributed source

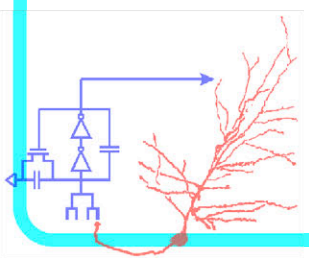


# MEG Response

## Flattened Isofield Contour Map

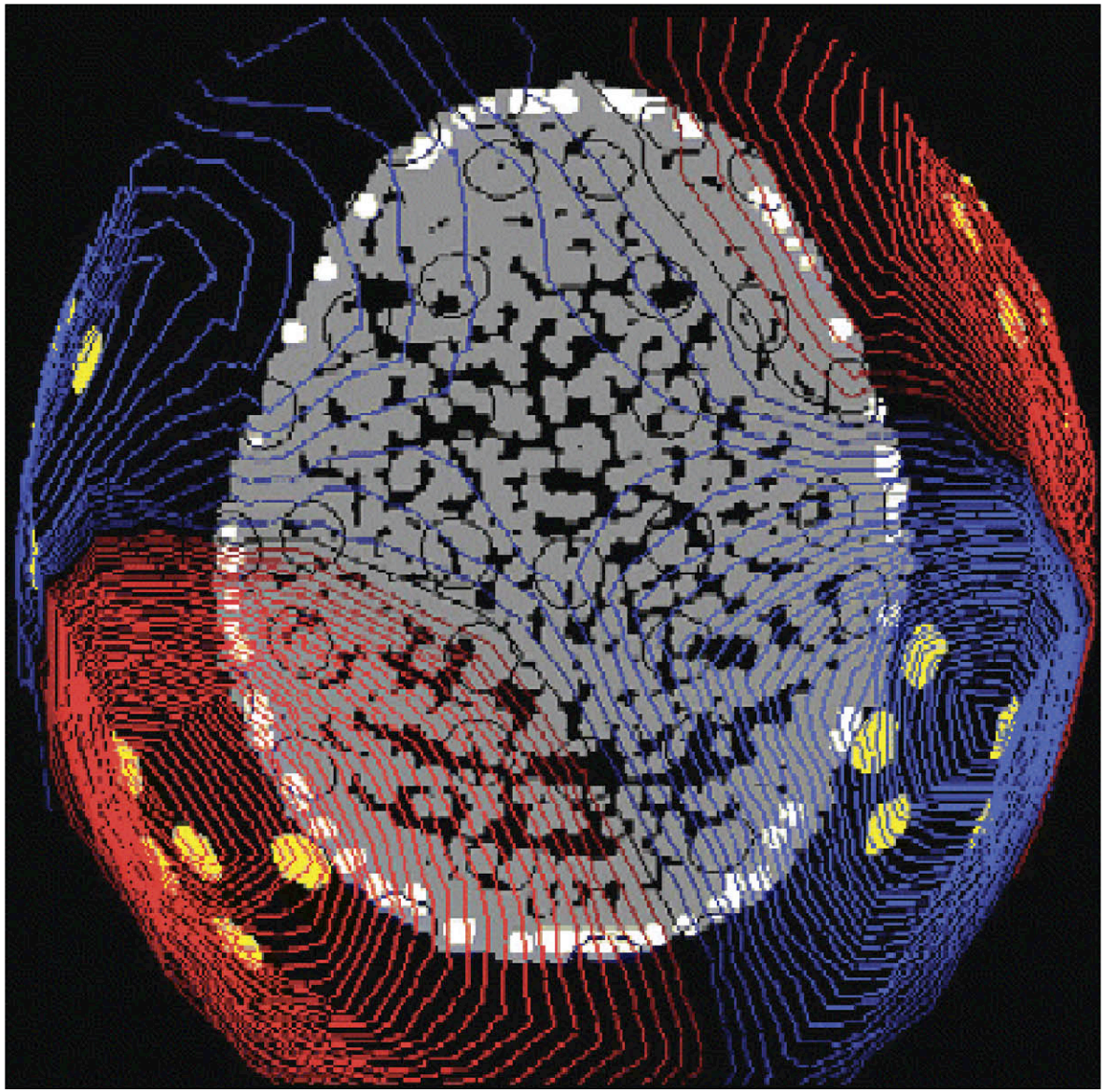



Instantaneous Magnetic Field

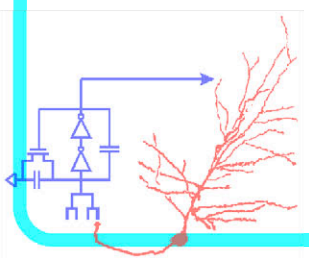


# MEG Response

## 3-D Isofield Contour Map

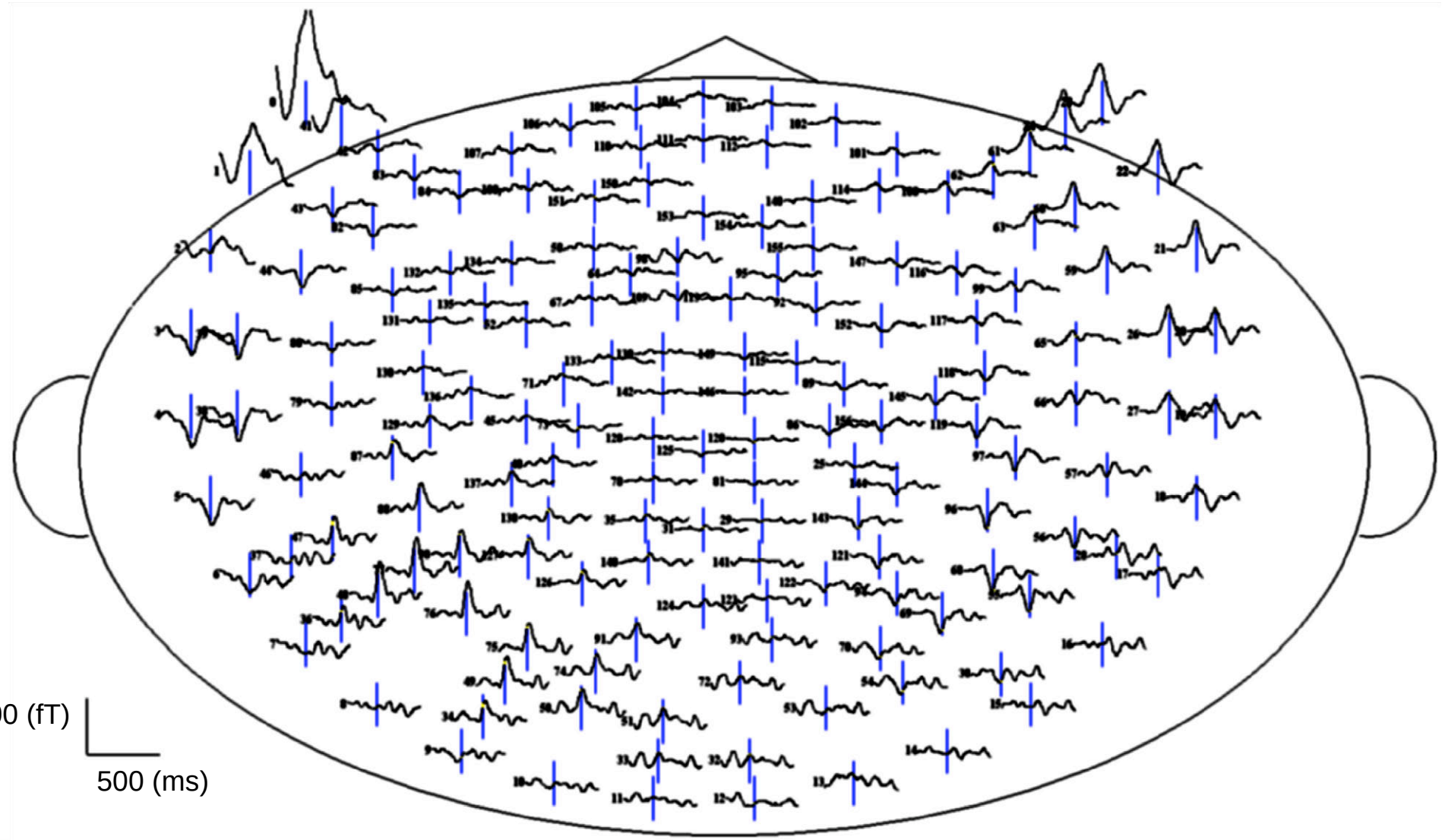


Chait, Poeppel and Simon,
Cerebral Cortex 2006



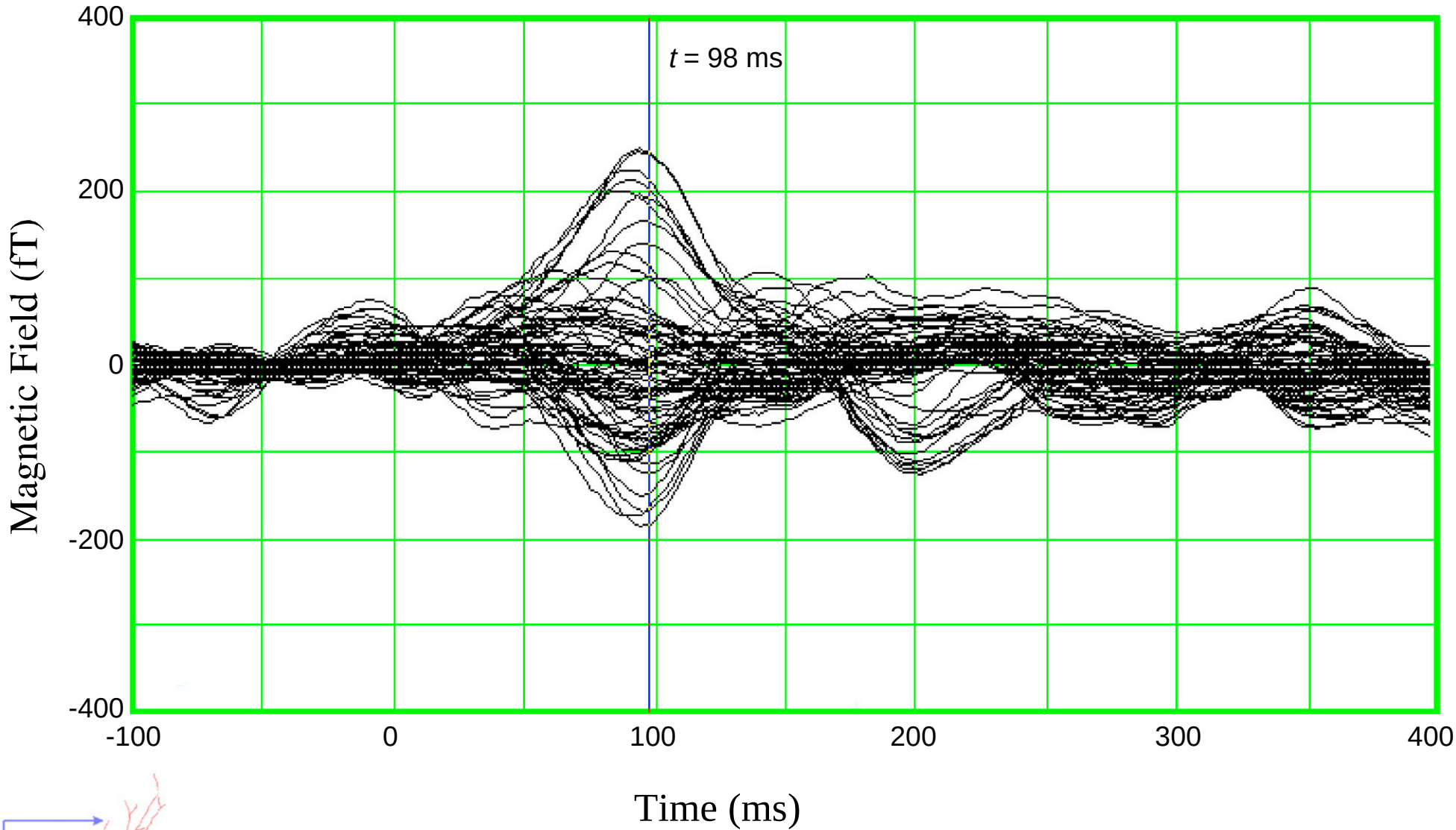
# MEG Response

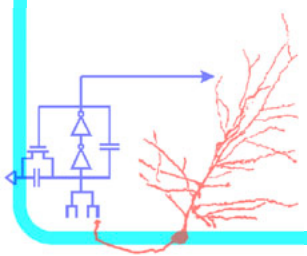
## Spatial Map of Time Series



# MEG Response

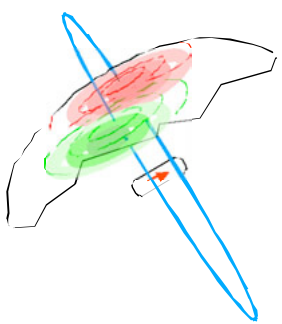
## Butterfly Plot



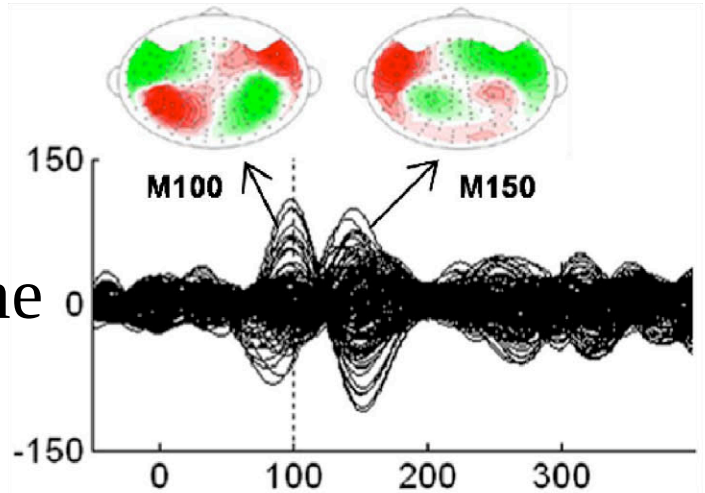



# Time Course of MEG Responses

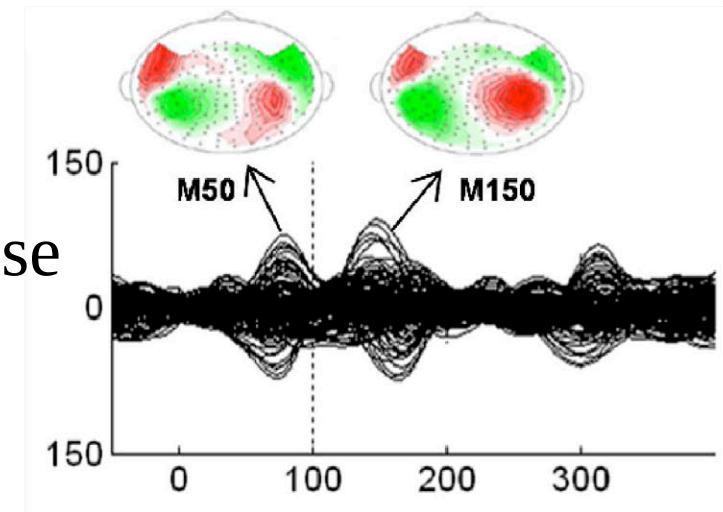
**Evoked Responses**
MEG Events Time-Locked
to Stimulus Event

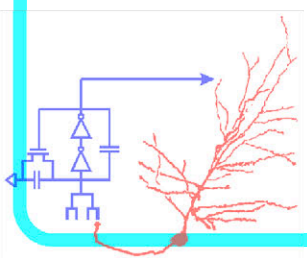


Pure Tone

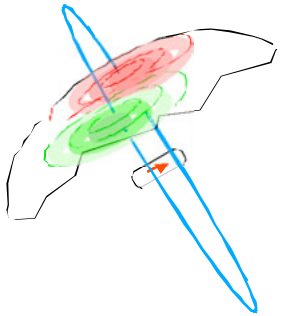



Broadband Noise

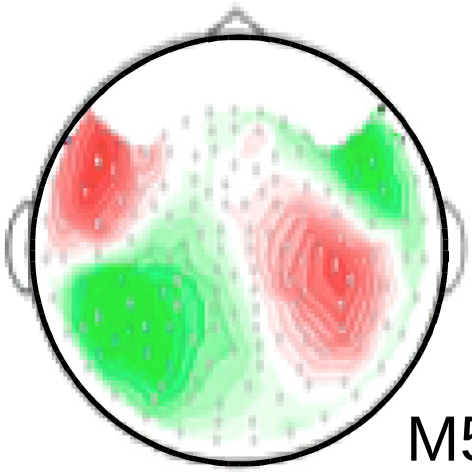


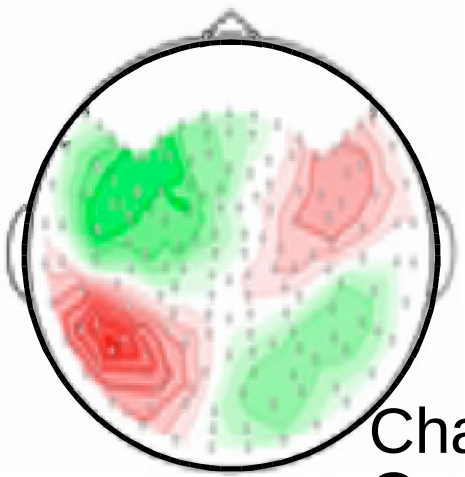
# Spatial Auditory MEG Responses



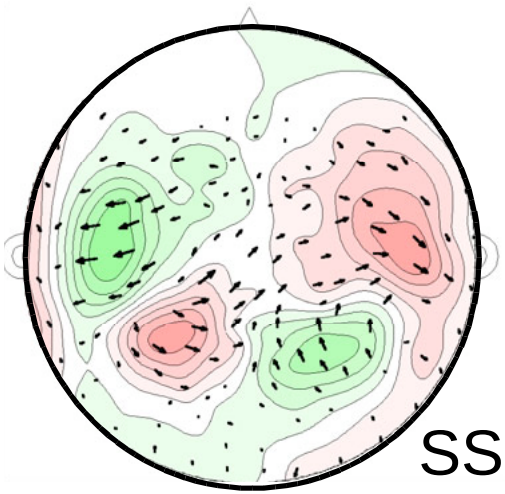
Auditory Responses
*Robust*
*Strongly Lateralized*



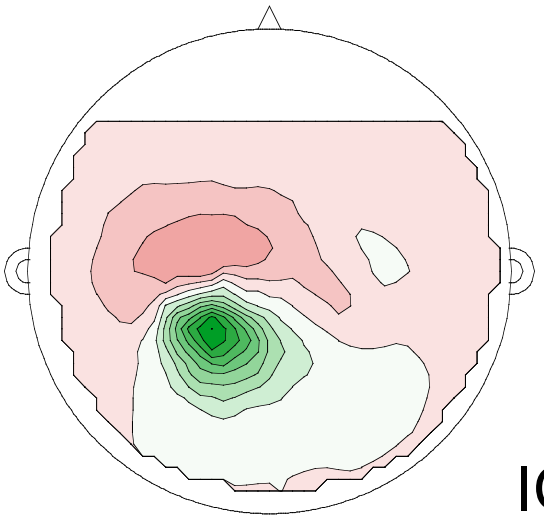
M50

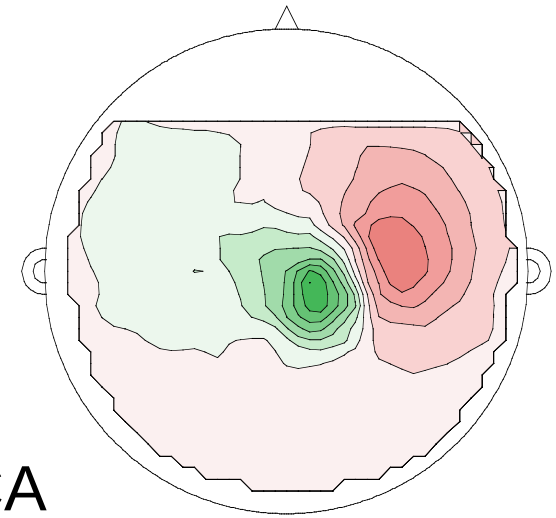


Change Onset

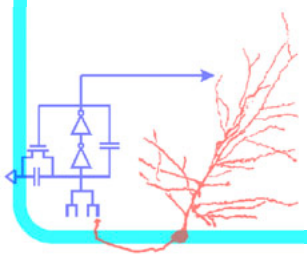


SSR



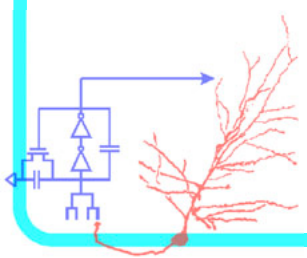


ICA



# MEG as Auditory Physiology Tool

- Advantages of humans over animals
  - Subjects can be rented (by the hour)
  - Subjects can be trained in minutes
  - Better grasp of subjects' perceptual space (?)
  - Access to Speech & Language processing (?)
- Advantage of Whole Head Recording
- Disadvantage of Neural Source Localization
  - Coarseness/Ambiguity in Source Location
  - Blindness to Many Kinds of Coding
- Neutral Aspects
  - Neural Source is Dendritic Current (not Spikes)
  - Humans not typical mammals (?)
  - New Technique/Immature Analysis Tools



# Outline

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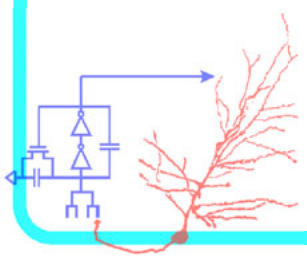
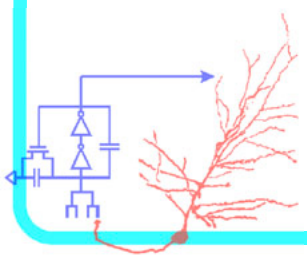
- MEG in the Frequency Domain
- Neural Encoding of Modulations



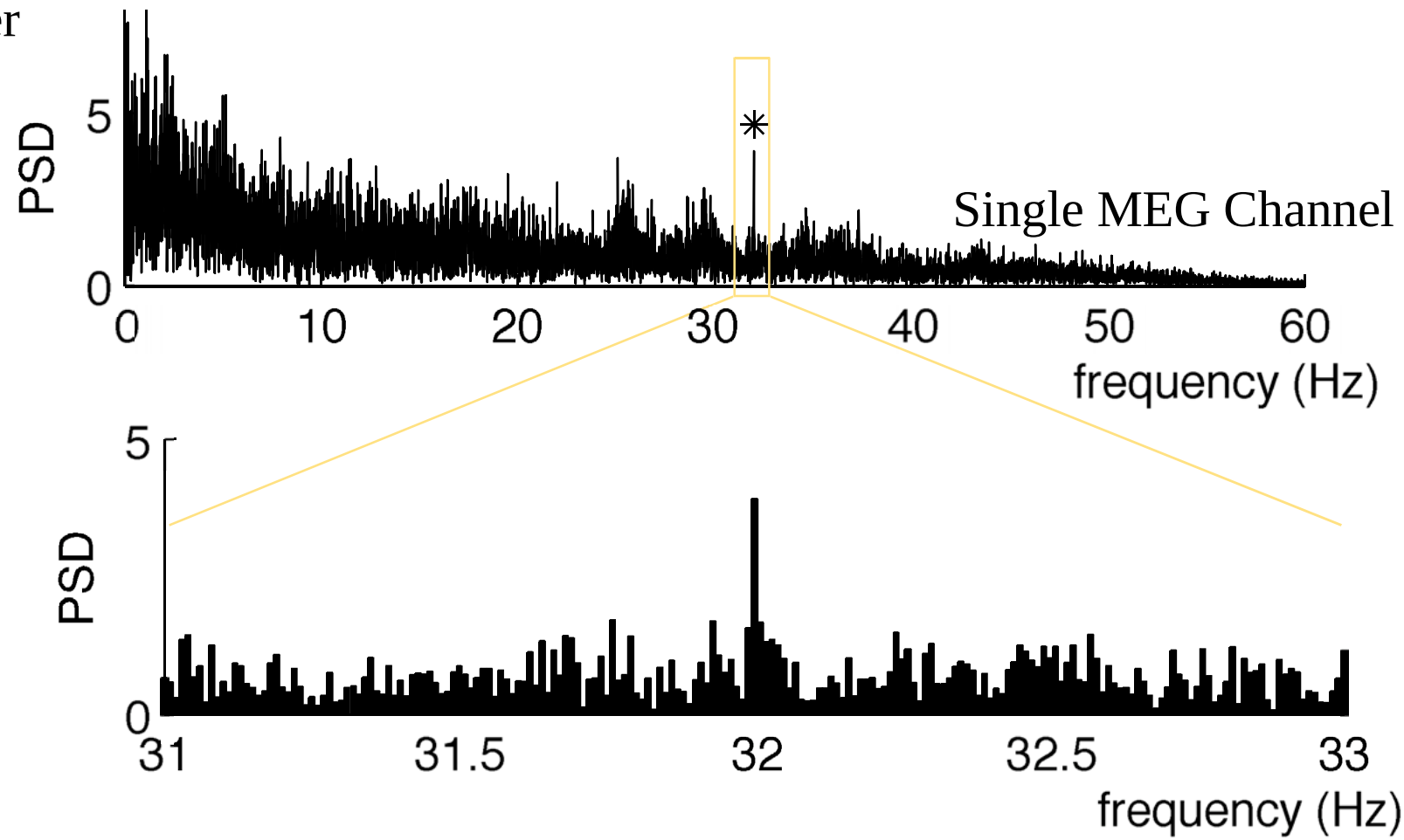
# An Alternative to Time: Frequency

- Use Stimuli localized in Frequency rather than time
- Examine Response at Same Frequency
- Steady State Response (SSR)
- Frequency Response/Transfer Function

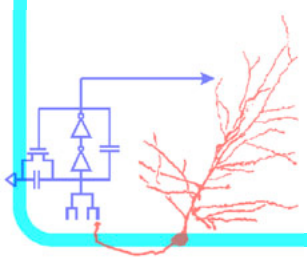


# Frequency Response

32 Hz Modulation
400 Hz tone carrier
100 trials @ 1 s
(concatenated)

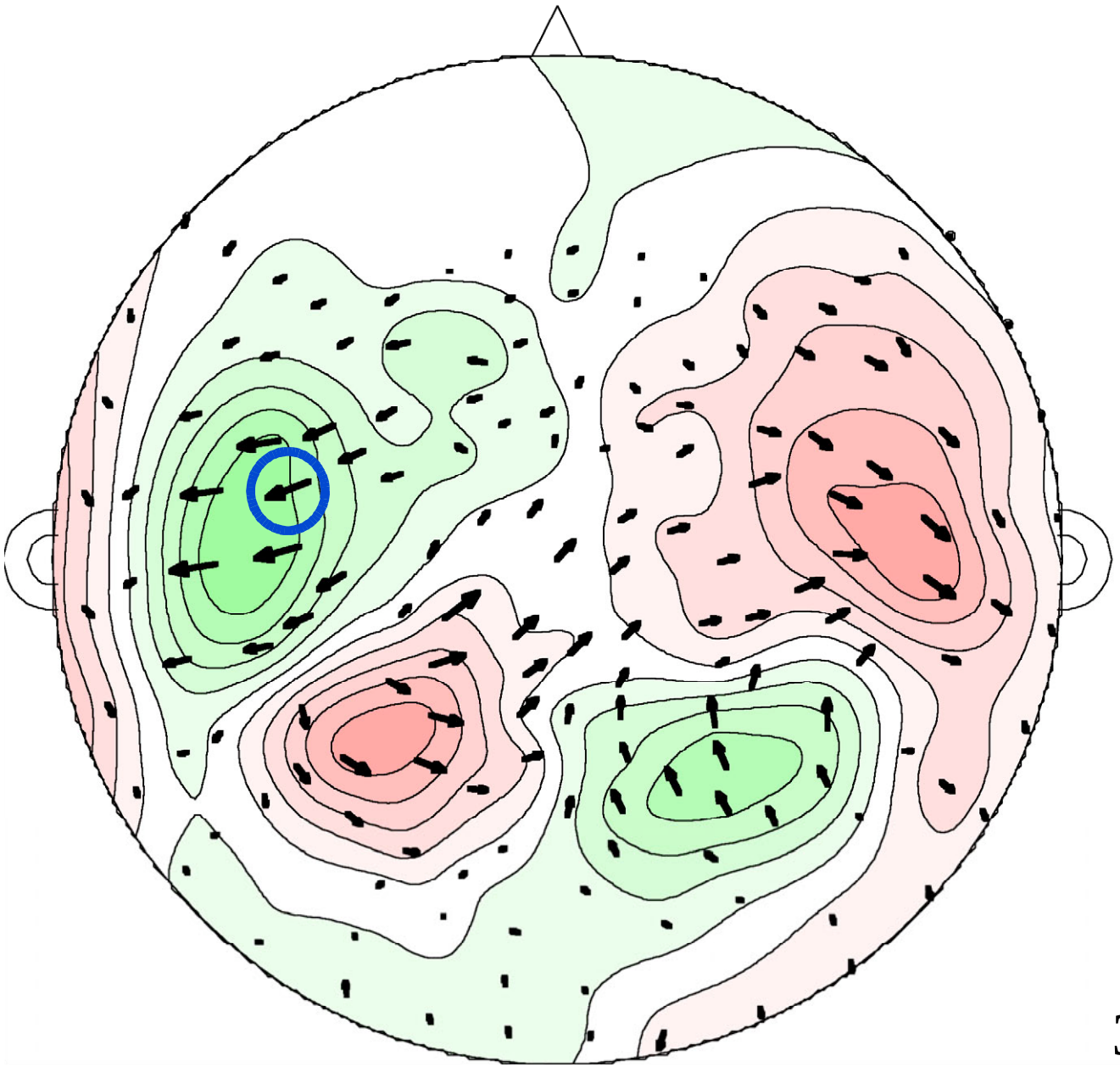



Precise Phase-Locking: 0.01 Hz
Little trial-to-trial jitter

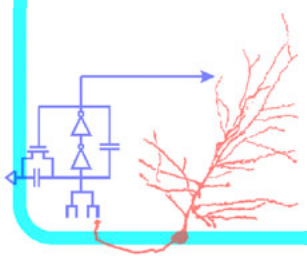


*Amplitude + Phase...*

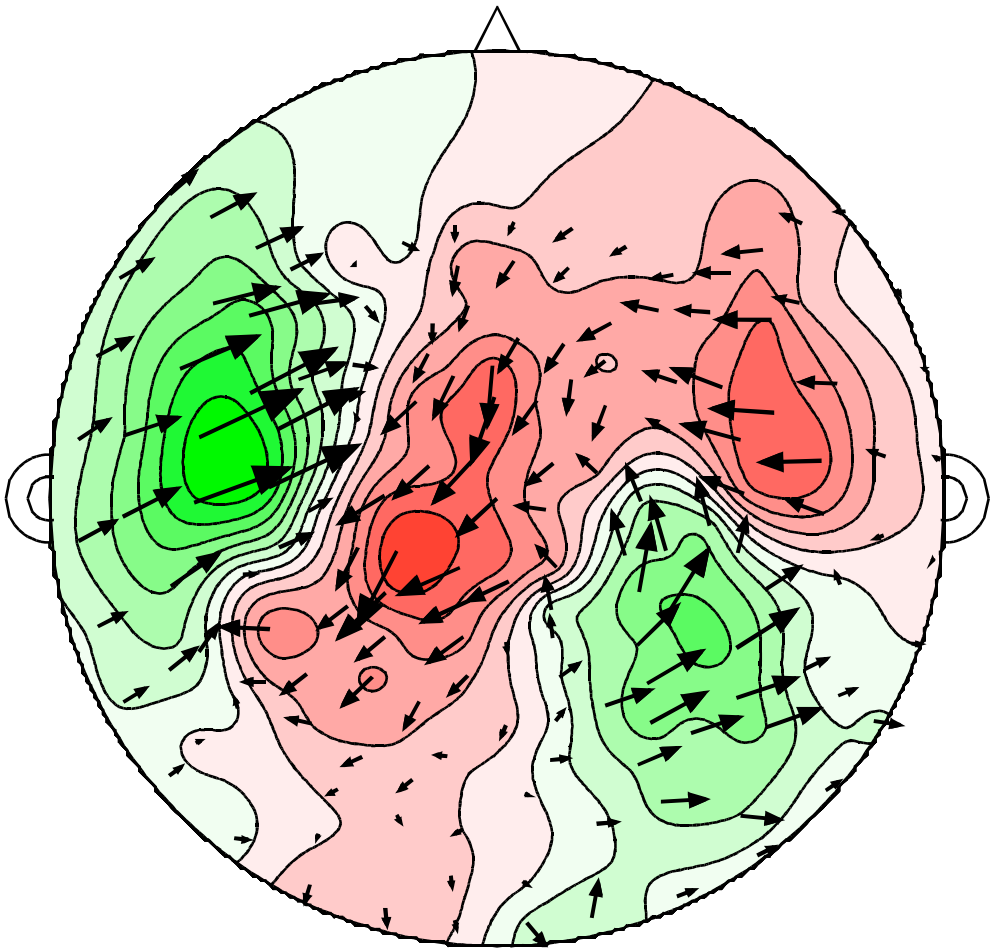
# Whole Head Steady State Response

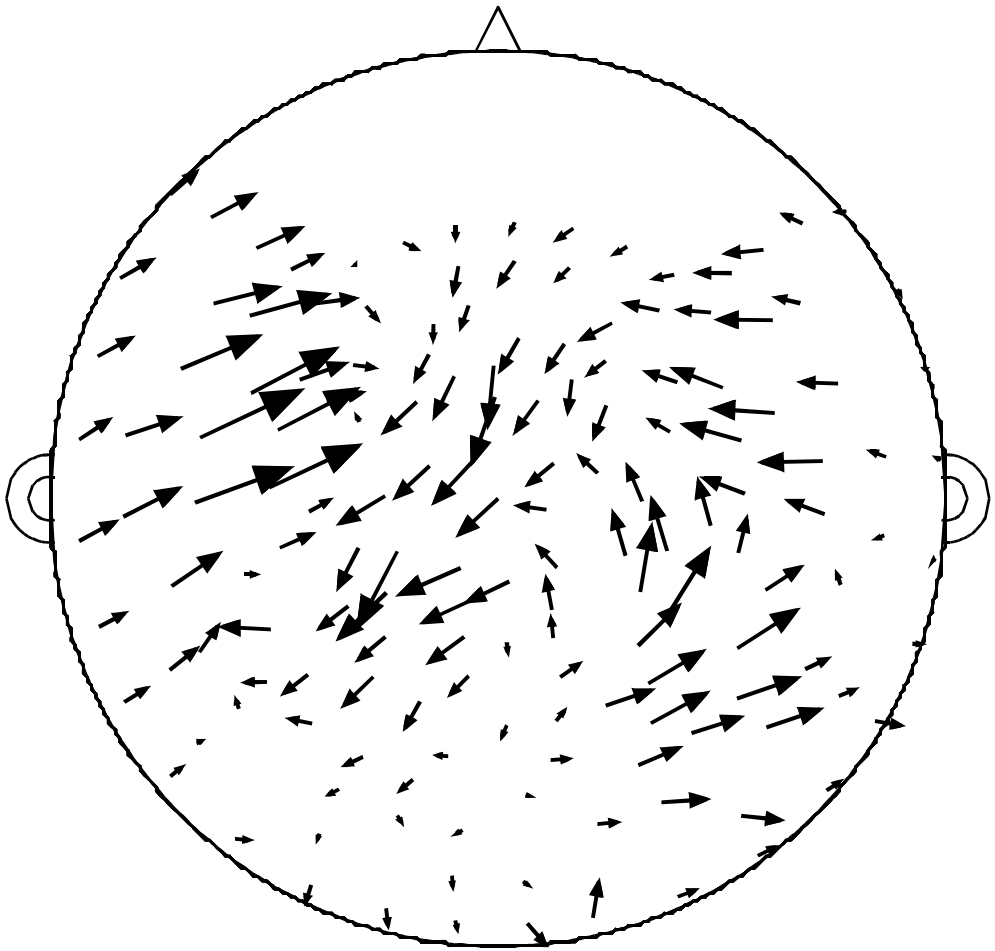


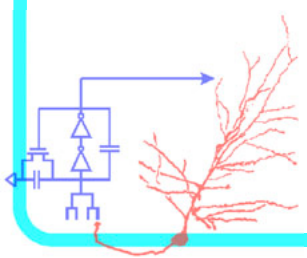
32 Hz



# Complex Magnetic Field



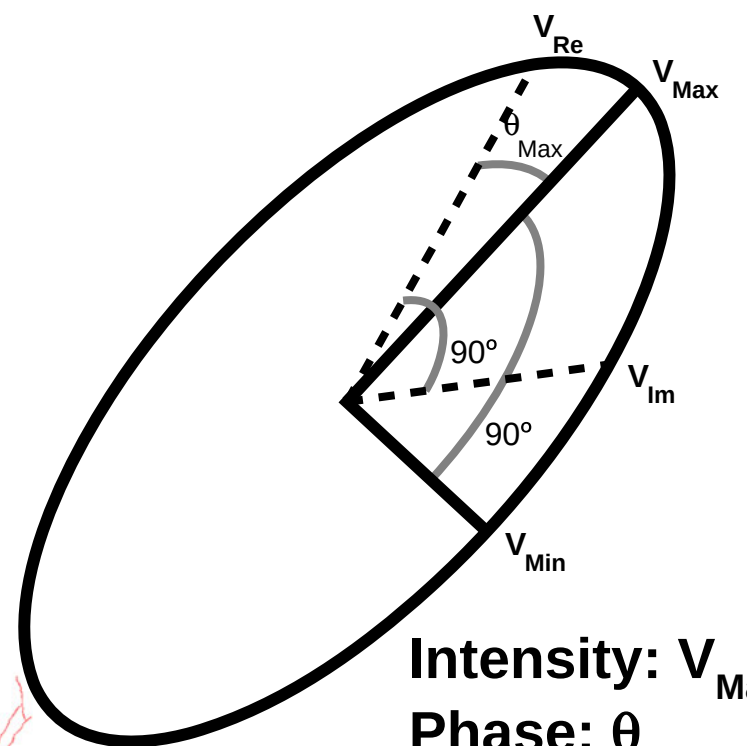


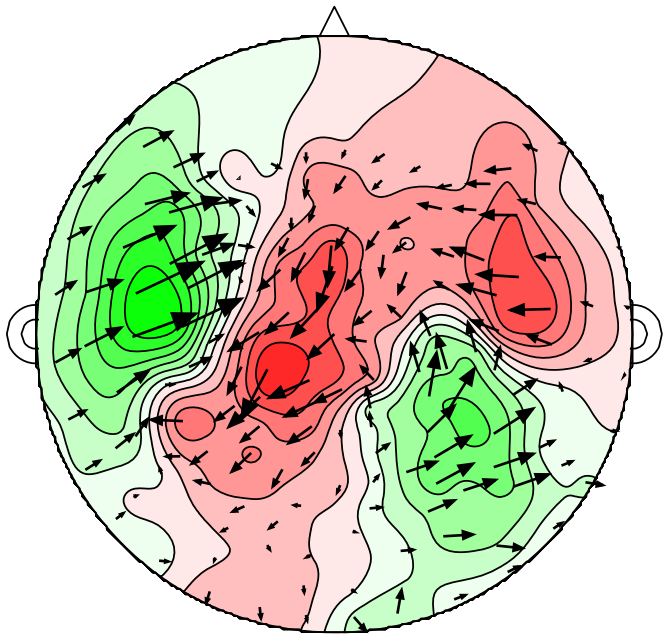


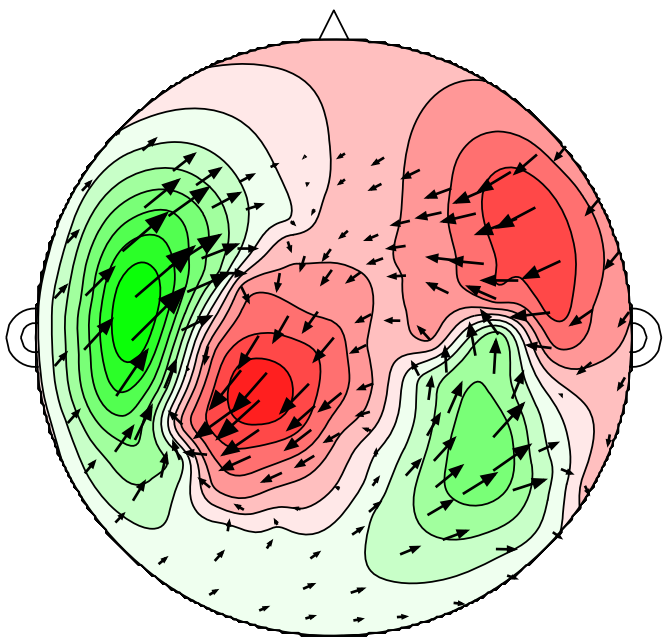
# Complex Neural Current Sources

$$\vec{V} = \vec{V}_{Re} + j\,\vec{V}_{Im}$$

$$\vec{V}(\theta) = \vec{V}_{Re}\cos(\theta) + \vec{V}_{Im}\sin(\theta)$$





**Intensity:** $V_{Max}$

**Phase:** $\theta_{Max}$

**Sharpness:** $\eta = V_{Min}/V_{Max}$

Simon and Wang,
J. Neurosci. Methods 2005

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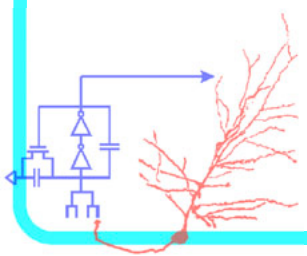
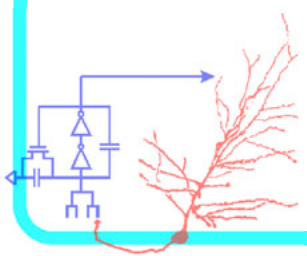


# Modulation Encoding

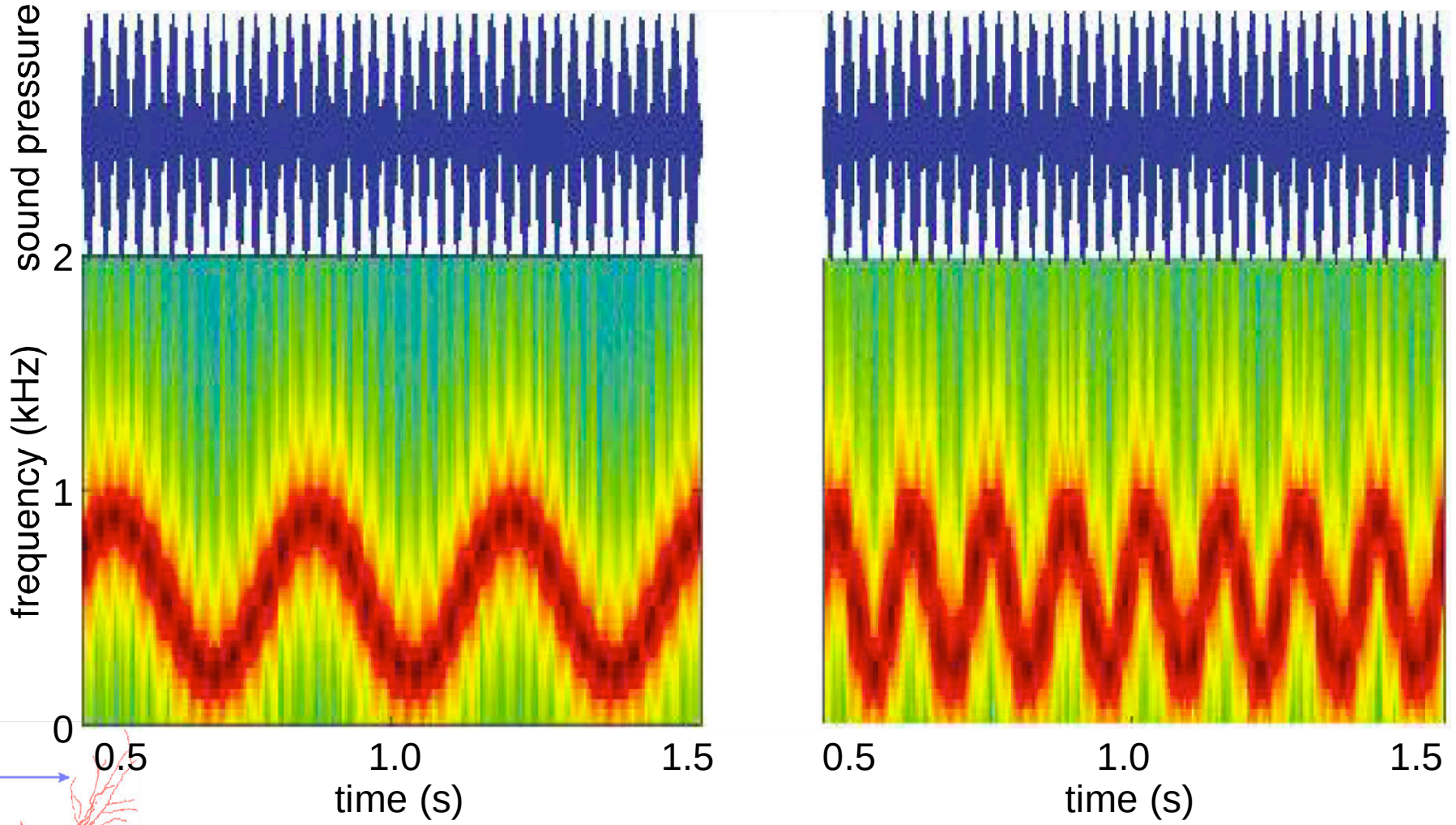
- Simple Modulations → Simple Cortical Encoding
  - *Simple Amplitude Modulation* coding often used for *slower* modulations
  - *Rate* coding (invisible to MEG) often used for *faster* modulations
- Applies to general modulations: AM, FM, other
- Simple Amplitude Modulation coding is easily detectable in Fourier/Spectral domain (SSR)
  = Spectral Peak at Modulation Frequency
- Coding for multiple modulations of different kinds?

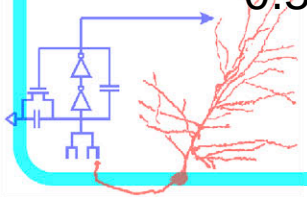


# Sample Dual Modulation Stimuli

$f_{FM}$ = 3.1 Hz
$f_{AM}$ = 37 Hz

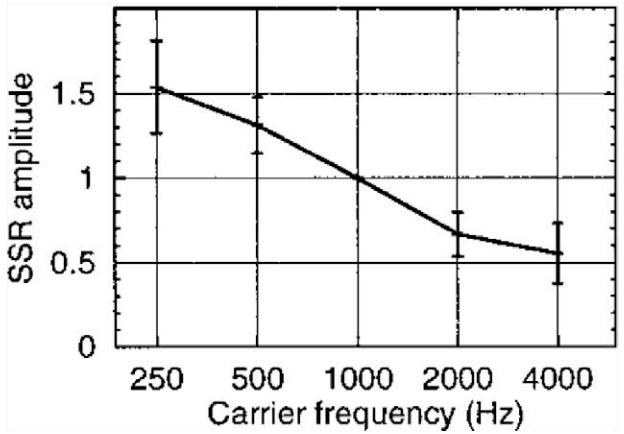
$f_{FM}$ = 8 Hz
$f_{AM}$ = 37 Hz



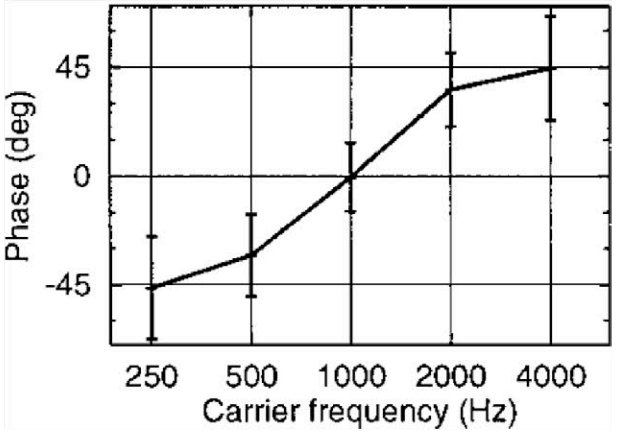



# SSR Carrier Dependence

SSR Amplitude




SSR Phase

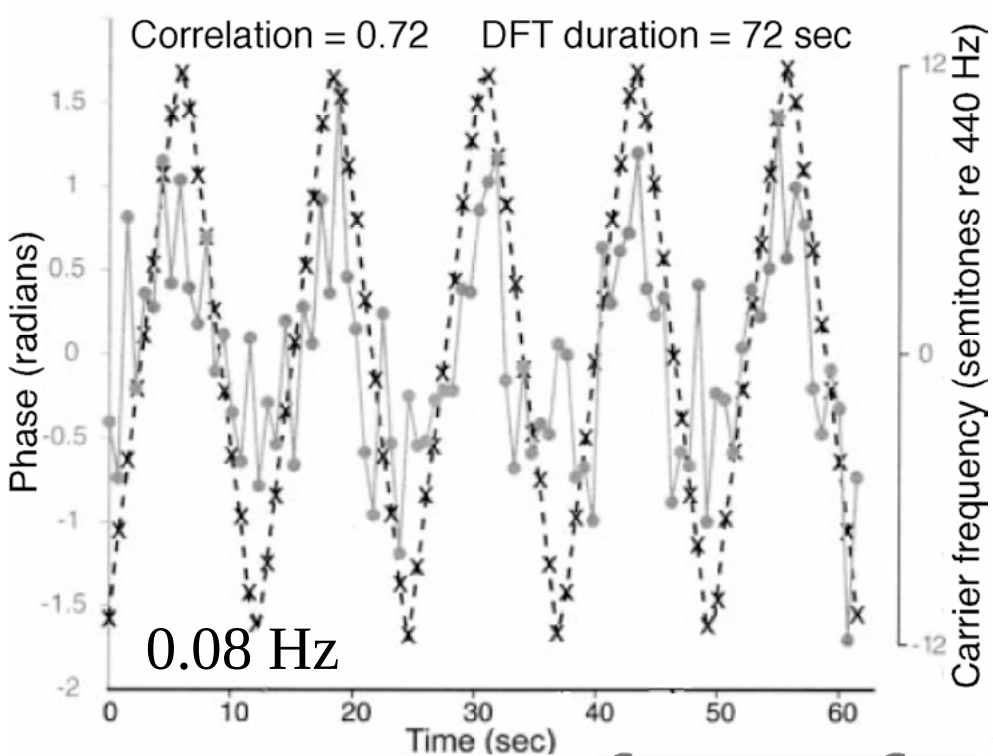



*Ross et al. (2000)*

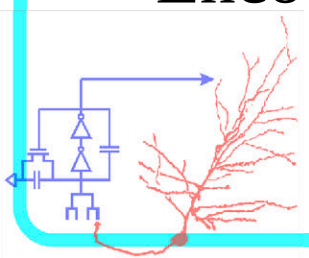
SSR Phase Follows Carrier

⬇

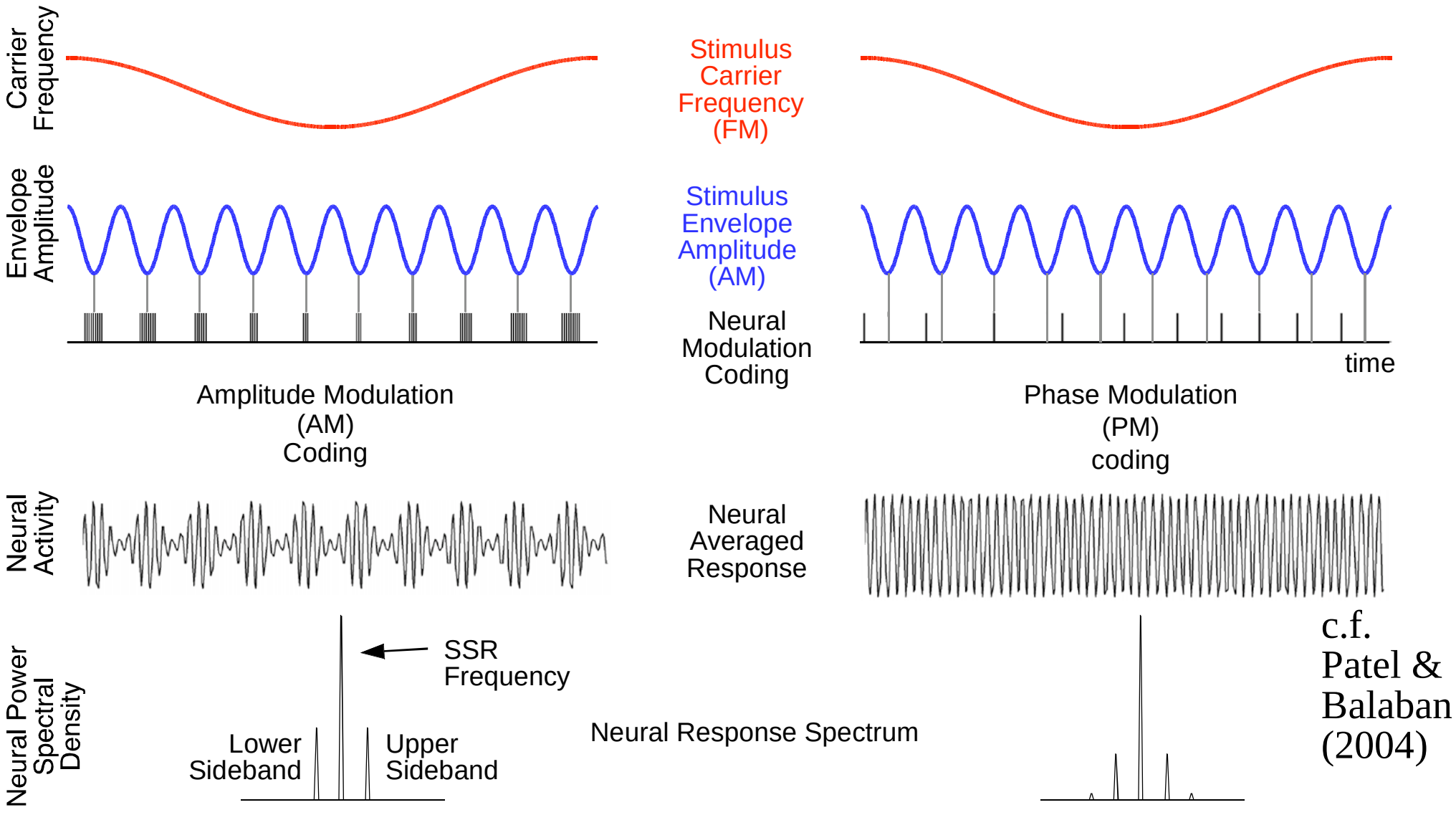
Phase Modulation Encoding




*Patel & Balaban (2004)*



# Neural Modulation Models




c.f. Patel & Balaban (2004)

$$\alpha = (\varphi_{upper} - \varphi_{SSR}) - (\varphi_{SSR} - \varphi_{lower})$$

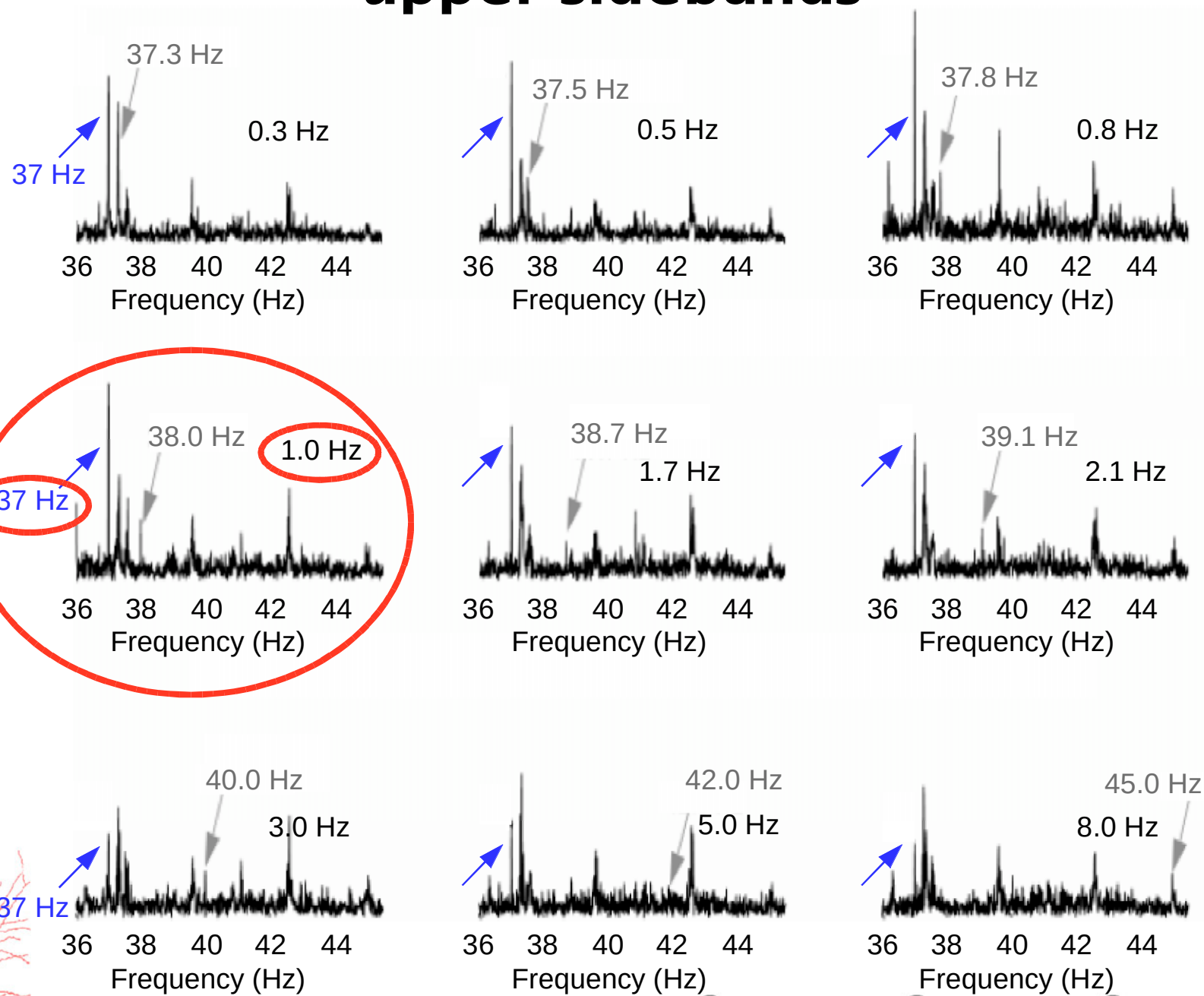
$\alpha_{AM} = 0$ or $2\pi$

Neural Response Phase Encoding Parameter

$\alpha_{PM} = \pi$

# Spectral Sideband Responses

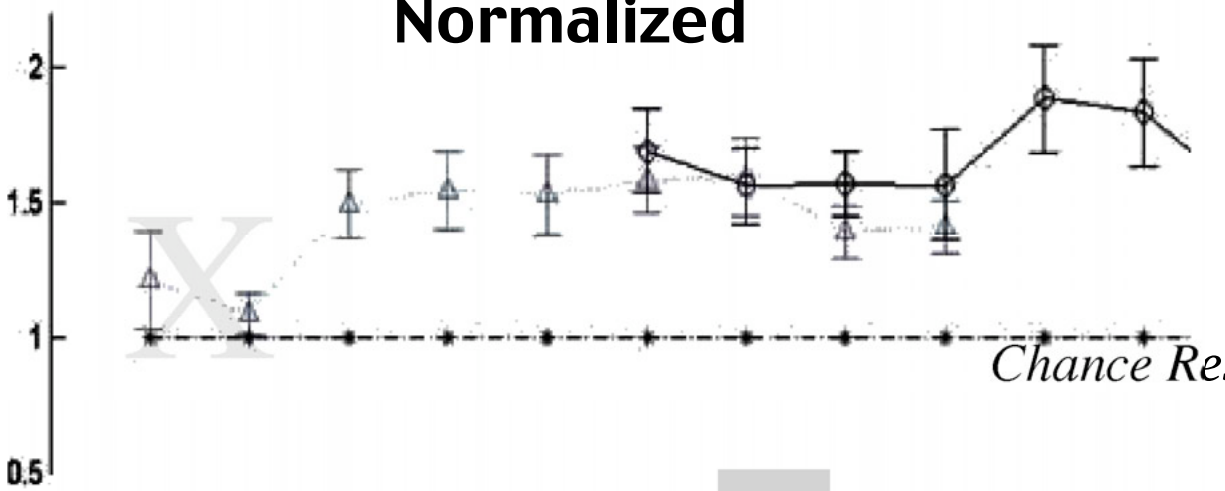
## upper sidebands



# Sideband Responses

Normalized

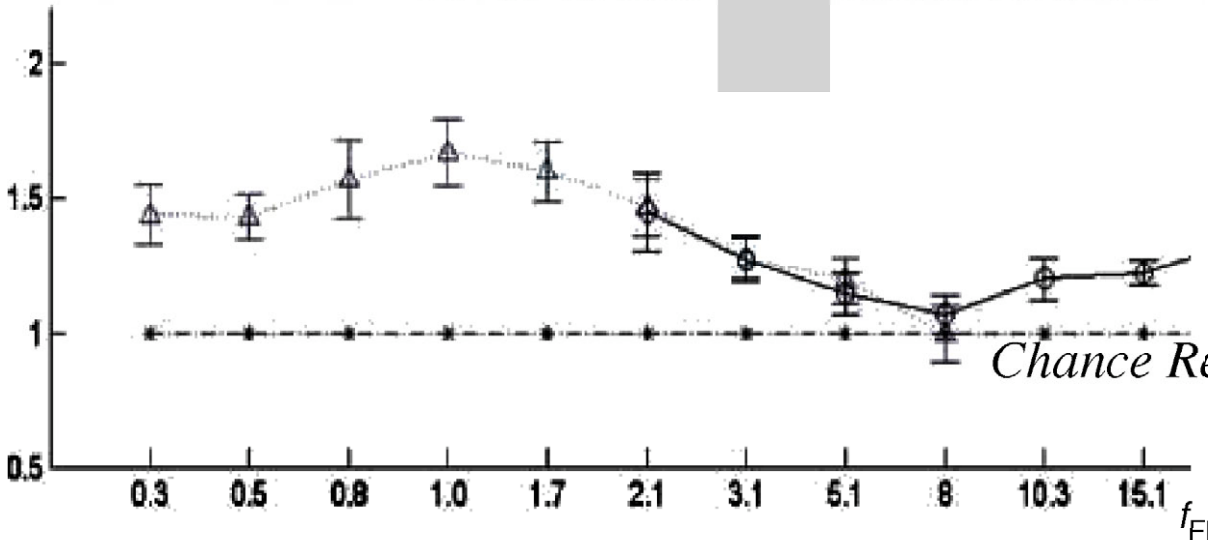
Upper Sideband Responses



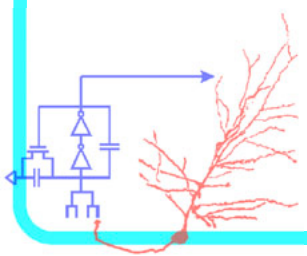

*Both Sidebands contribute*

*Only Upper Sideband contributes*

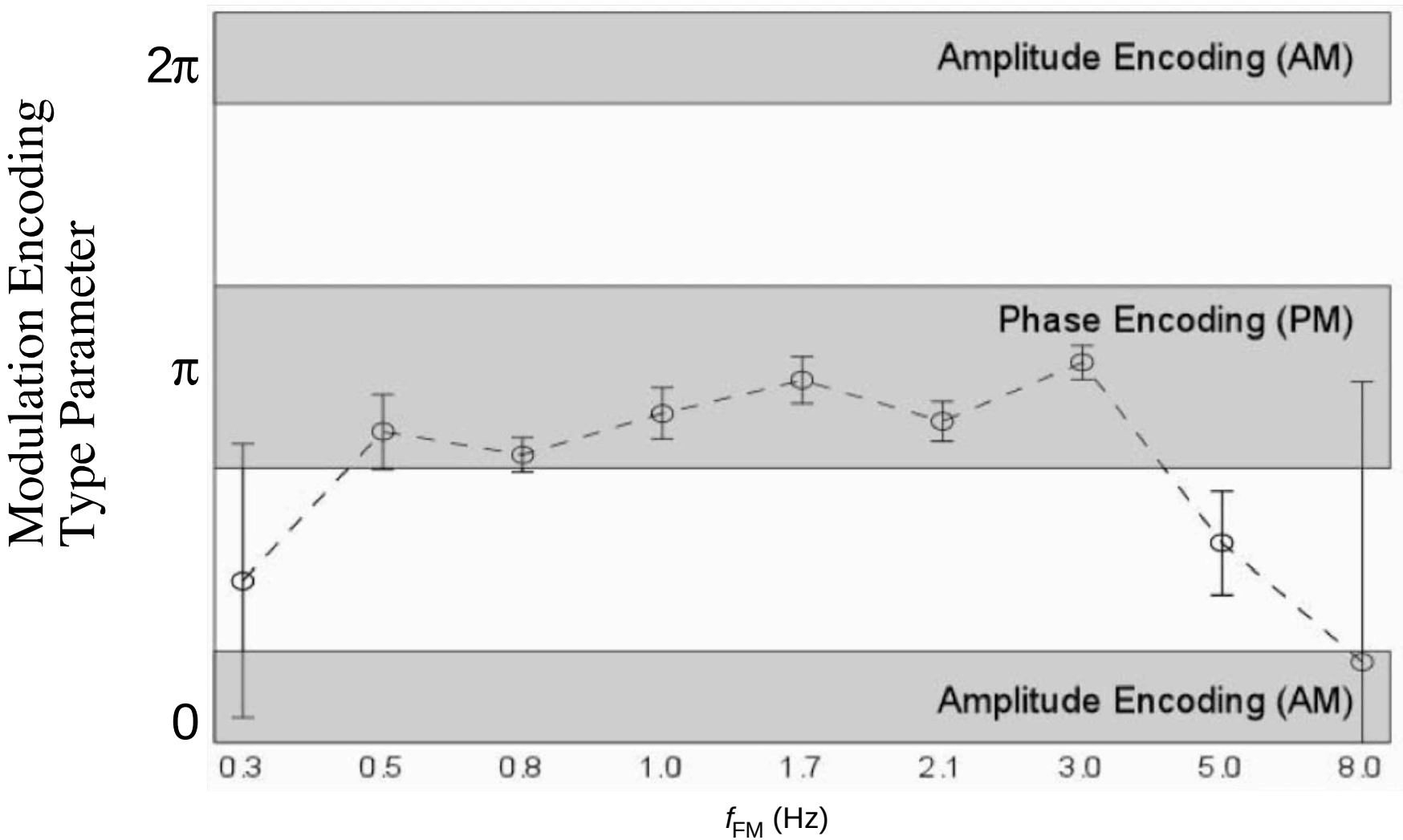
Lower Sideband Responses



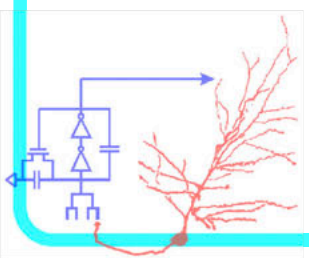

Modulation Encoding, with coding transition at $f_{FM} \sim 5$ Hz



# Modulation Encoding Type

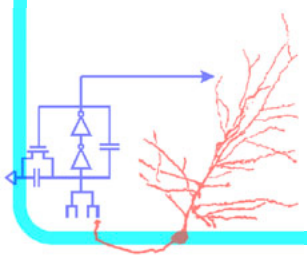



Phase Modulation Encoding below $f_{FM}$ ~ 5 Hz



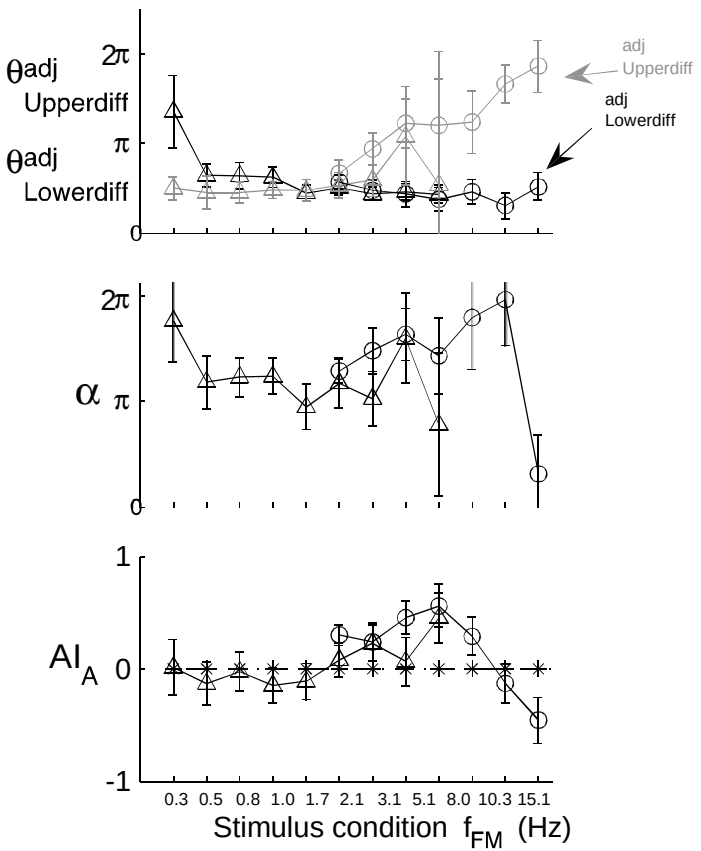
# Neural Population Model

$$S(t) = \underbrace{(1 + m\cos(2\pi f_{FM} t + \theta))}_{Amplitude\ Modulation} \times \underbrace{\cos(2\pi f_{AM} t + \frac{\pi}{8}\cos(2\pi f_{FM} t))}_{Phase\ Modulation} + GWN$$

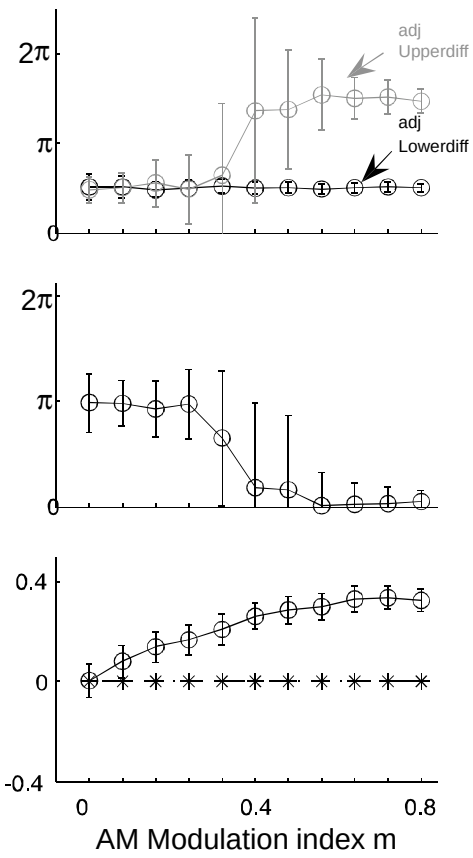


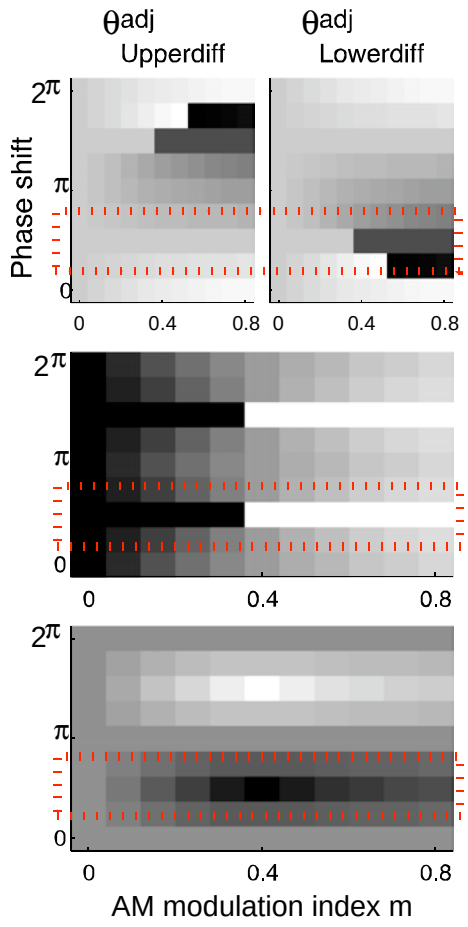
# Model Results

## Experimental Results




## Model Results



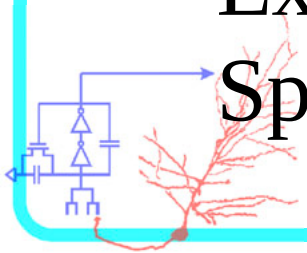




$$S(t) = \underbrace{(1 + m\cos(2\pi f_{FM} t + \theta))}_{Amplitude\ Modulation} \times \underbrace{\cos(2\pi f_{AM} t + \frac{\pi}{8}\cos(2\pi f_{FM} t))}_{Phase\ Modulation} + GWN$$

AM in quadrature with PM *Why?*

# Summary

- Combined AM/FM modulations are encoded in Auditory Cortex
  - Phase Modulation seen at lowest FM rates
  - Modulation Encoding changes at higher rates
- Single Sideband Modulation unexpected
  - Speculate: Single Modulation Encoding type?
  - Or: Two populations of AM and PM encoding neurons whose phase happens to cancel in lower sideband?
- Magnetoencephalography (MEG)
  - Directly generated by neural currents
  - Excellent time/frequency resolution
  - Spatial Localizability an open question



*Thank You*