Modulation Encoding in Auditory Cortex

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Introduction

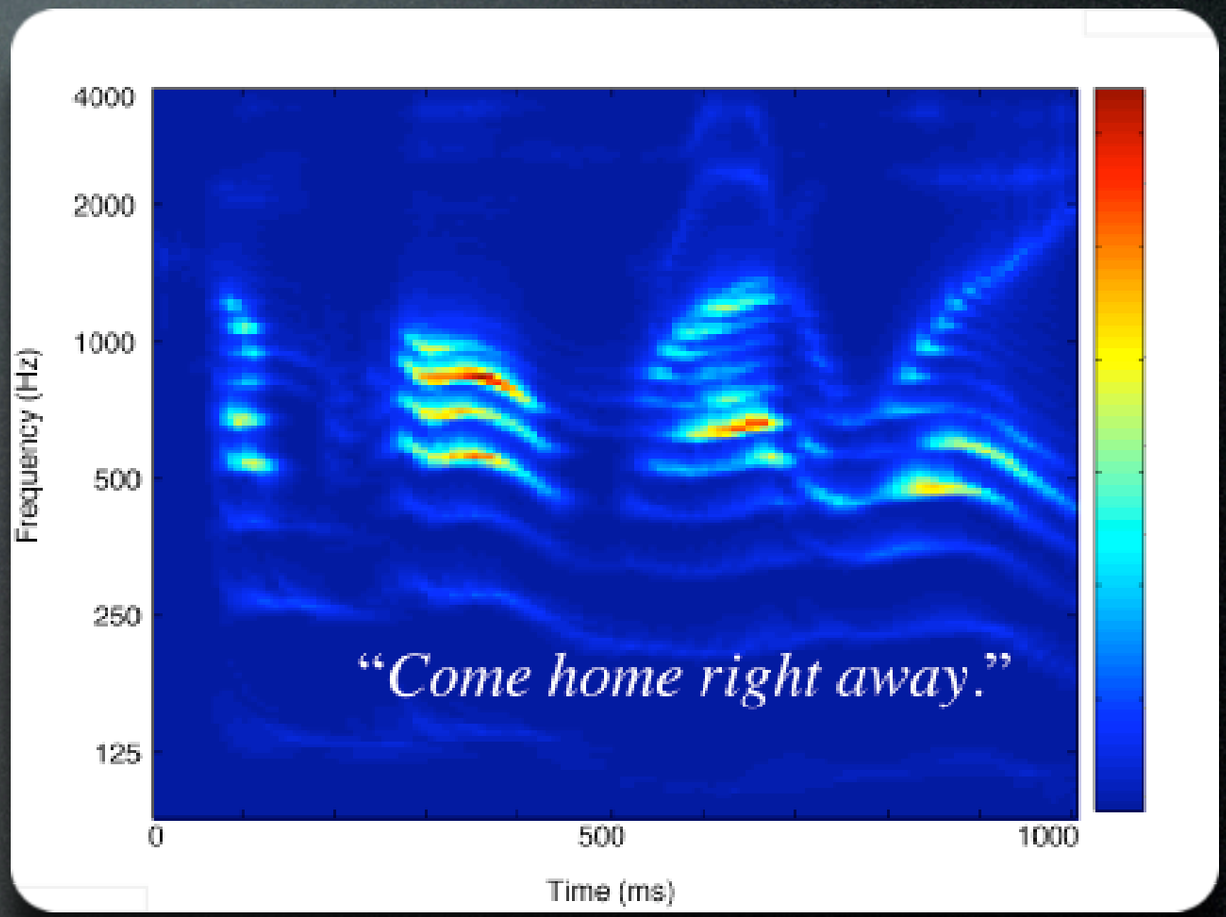
- Modulations—what are they?
- Modulation Encoding—What is it?
- Simple Examples: Modulation Transfer Functions (MTF)
- Complex Examples: Encoding of compound modulations, multi-AM, AM & FM
- Effects of Attention & Hemisphere

Experimental Technique

- Magnetoencephalography (MEG)
- Awake, behaving, healthy human subjects
- ~150 channels (whole head) sampled at 1 kHz

Auditory Modulations

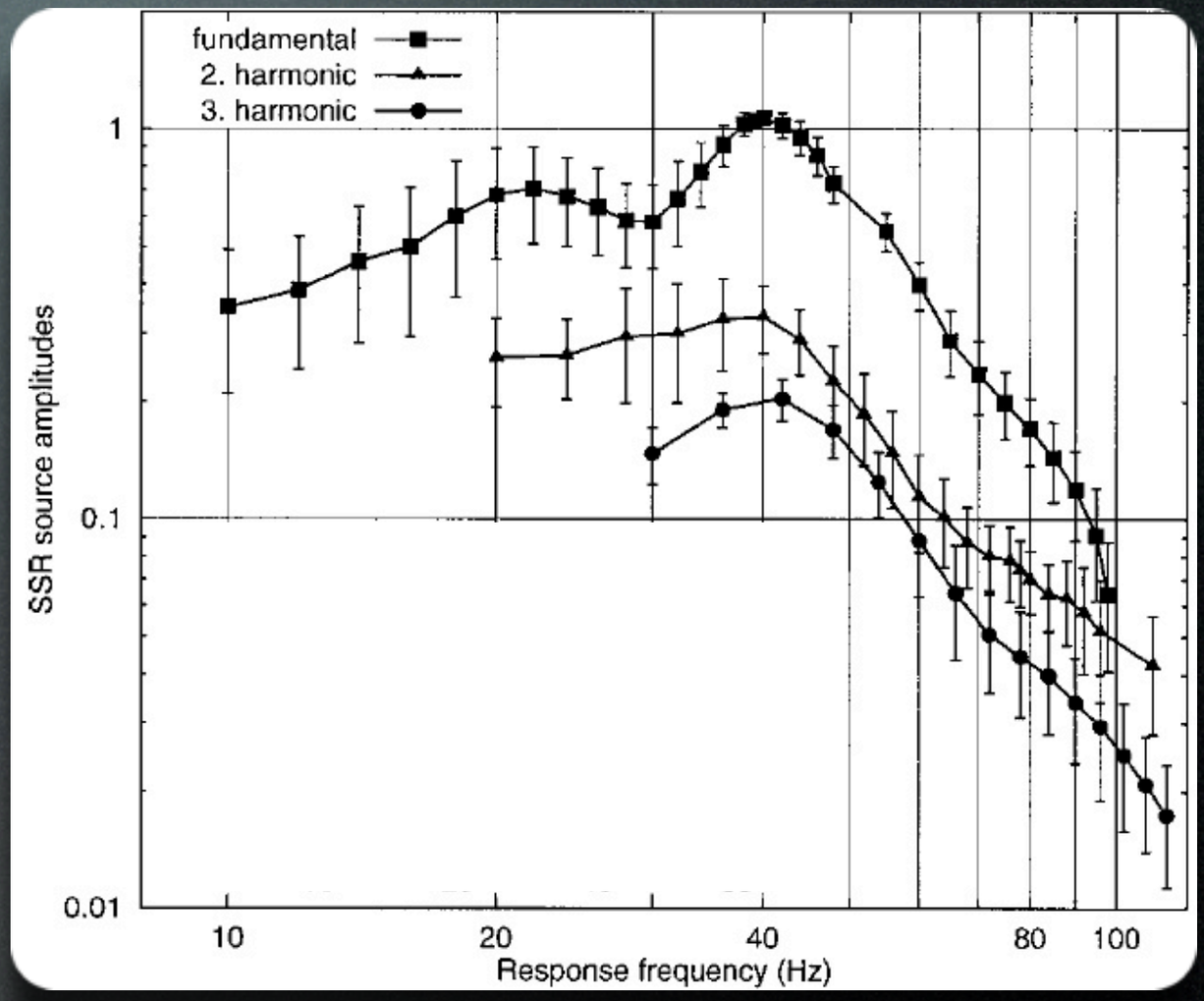
- Amplitude Modulation (AM)
- Frequency Modulation (FM)
- Other (e.g. binaural)



Modulation Transfer Functions (MTF)

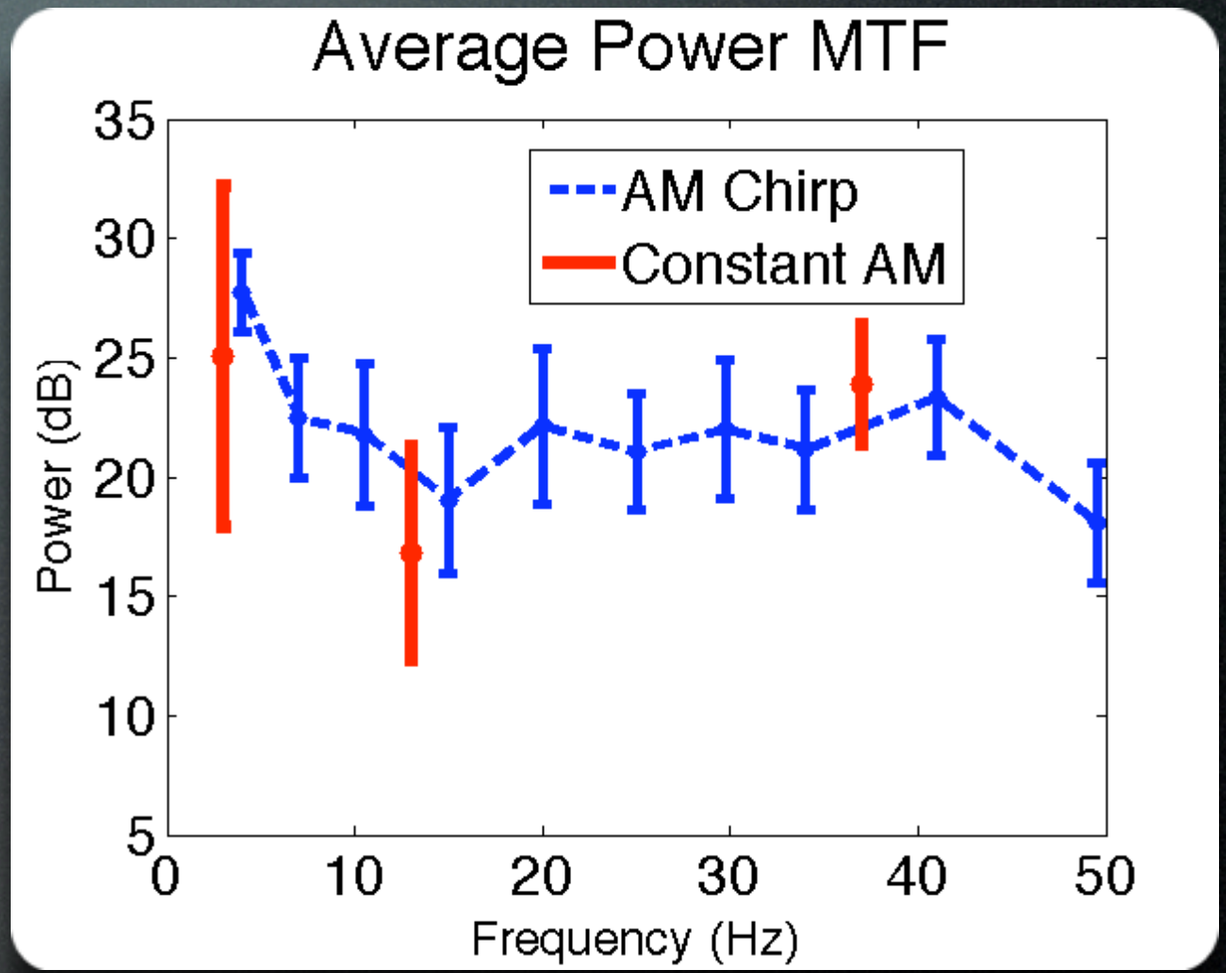
- Neural response for each stimulus modulation
- Response measured in both amplitude and phase

Steady State Response (SSR) MTF



Ross et al. 2000

Modulation Frequency Sweep MTF: Amplitude



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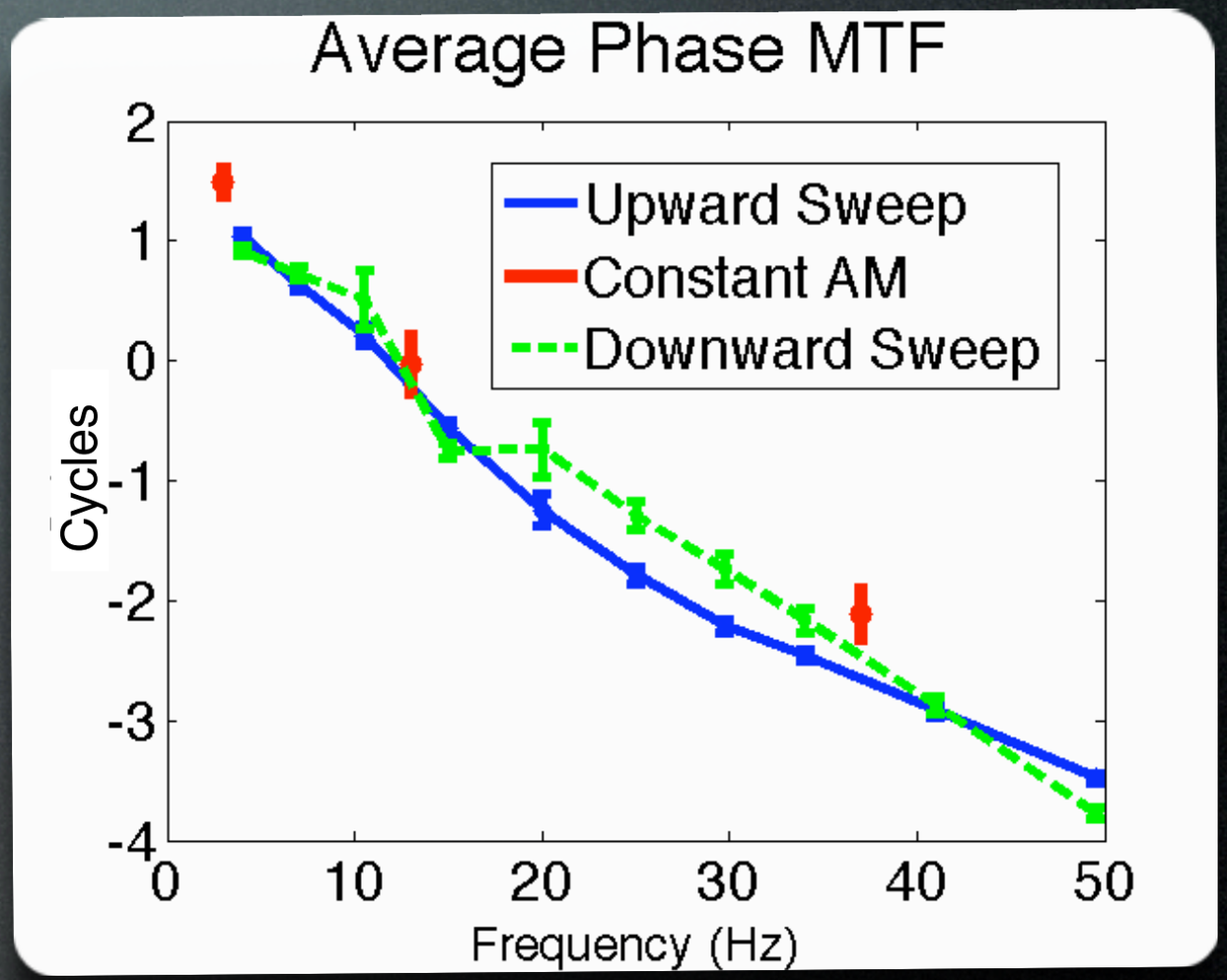
Modulation Frequency Sweep MTF: Phase



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MTF Strengths & Weaknesses

Strengths

- Linear Measure
- Very Powerful for Linear Systems
- Often Decent Characterization of modulation tuning
- Latency from Phase

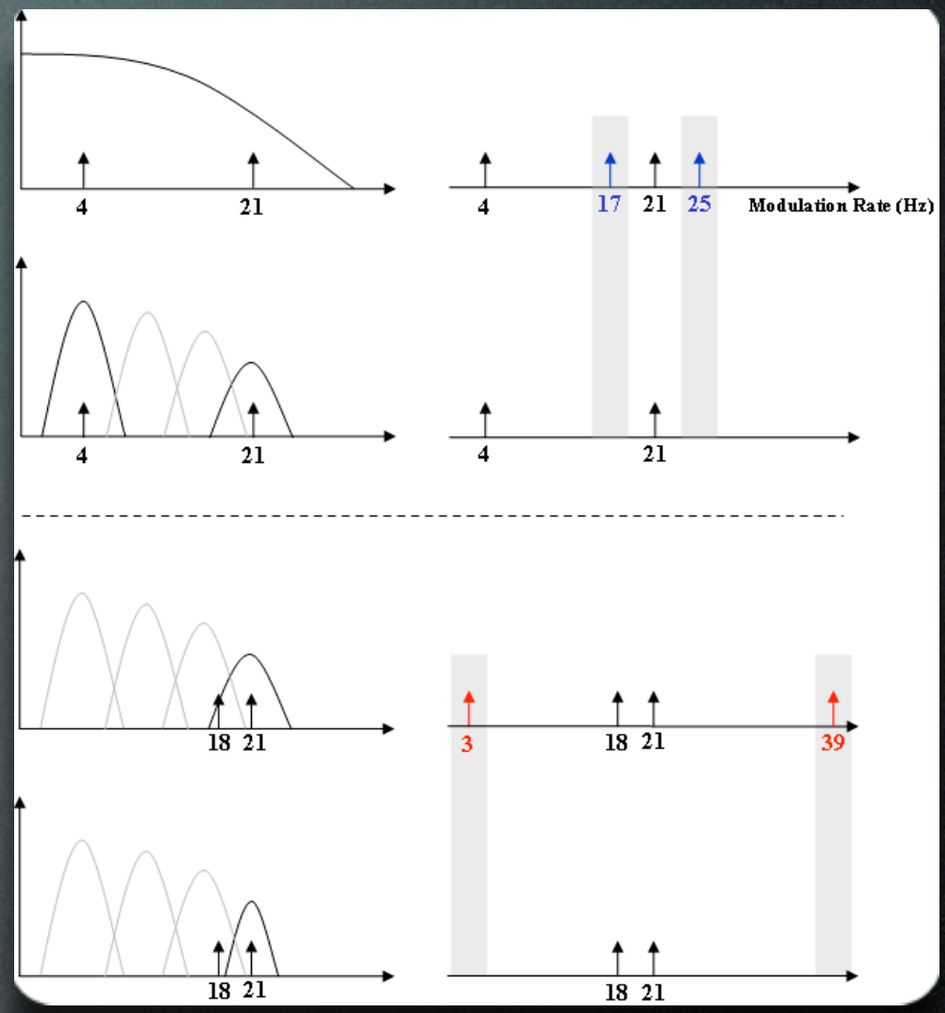
Weaknesses

- Linear Measure
- Misses known non-linear coding strategies:
  - fine structure response properties
  - history dependence

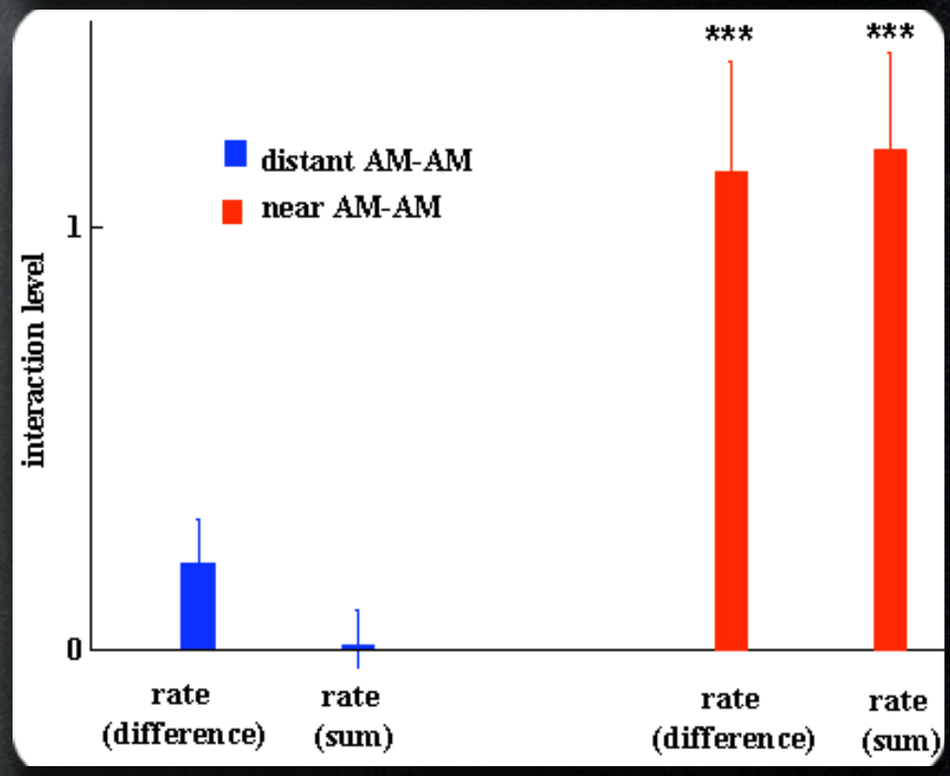
Beyond the MTF: Modulation Interaction

- Multiple simultaneous modulation rates may interact with each other
- When they interact can elucidate how modulations are processed
- Analogy with cochlear filterbank?
- Modulation Filterbank?

Modulation Filterbank Evidence



Cortical encoding of multiple modulations may be analogous to cochlear encoding of multiple frequencies



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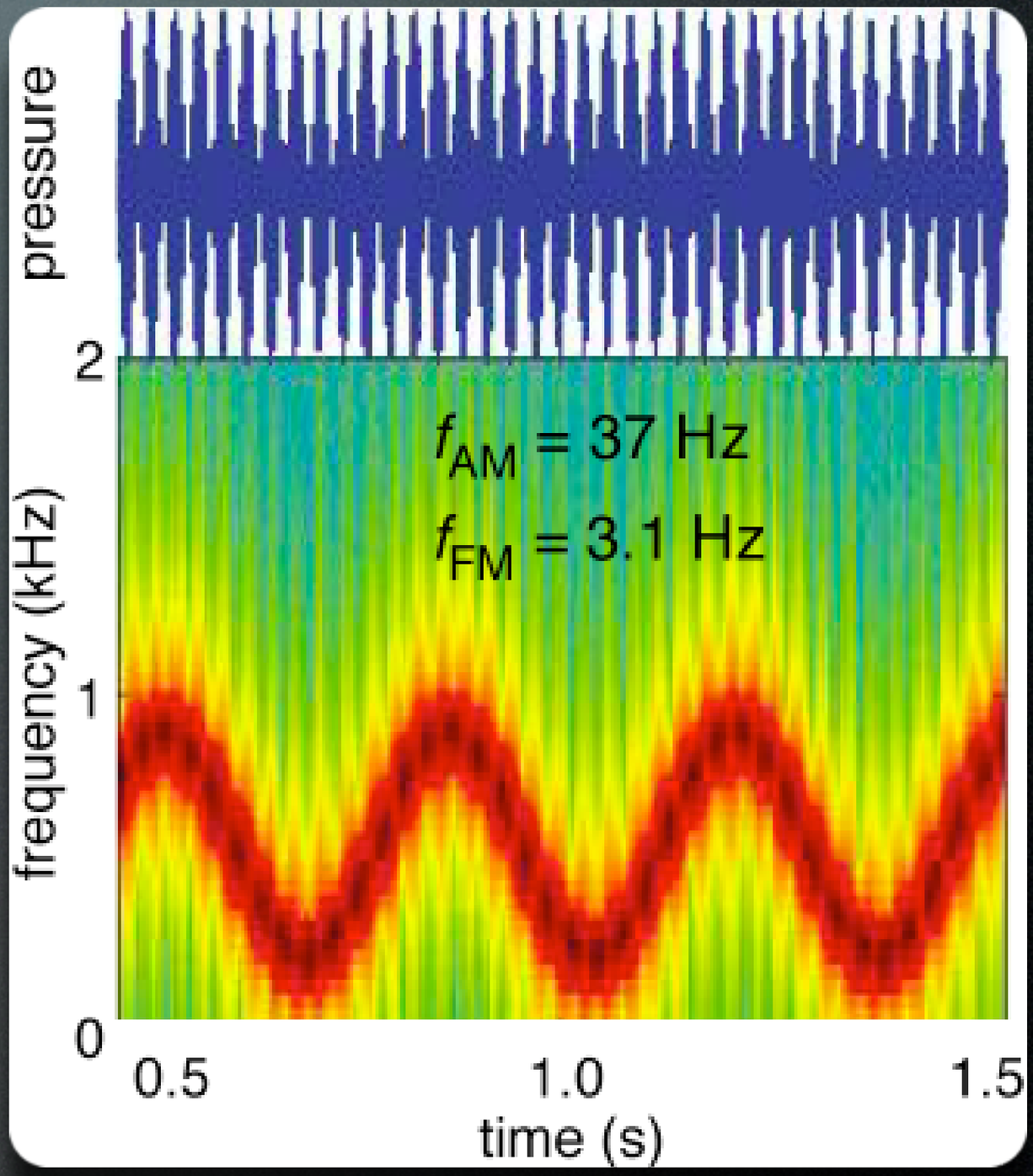
Frequency Modulations

- FM represents different information in the stimulus than AM (e.g. formant transition)
- FM should therefore be processed differently than AM
- Single-unit studies often show FM MTFs similar to AM MTFs

Combined AM-FM Stimuli



Luo et al., J. Neurophysiol (2006, 2007)

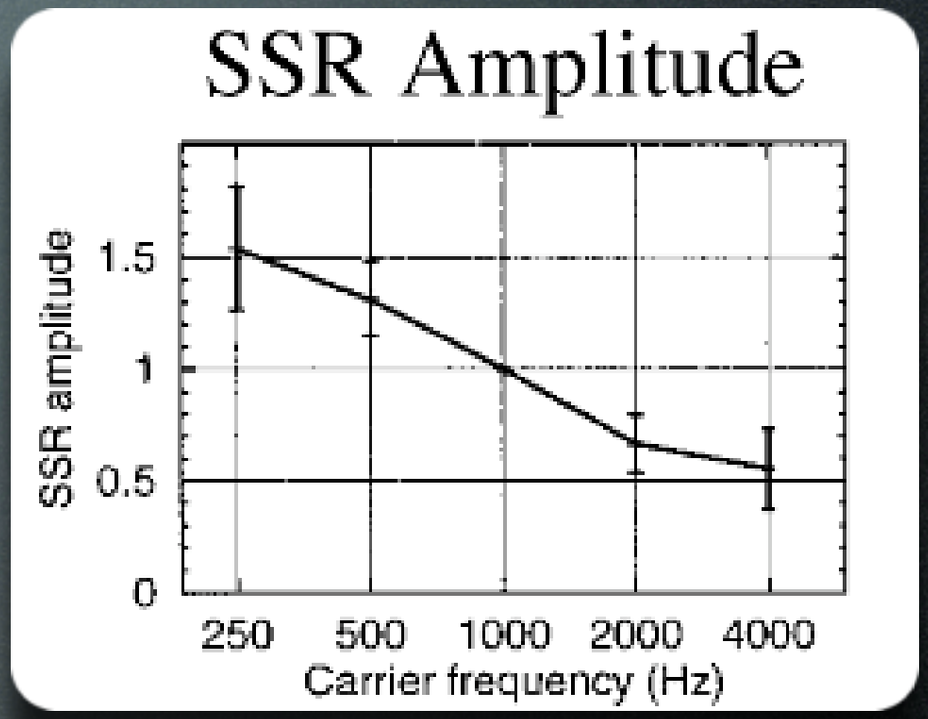
Combined AM & FM

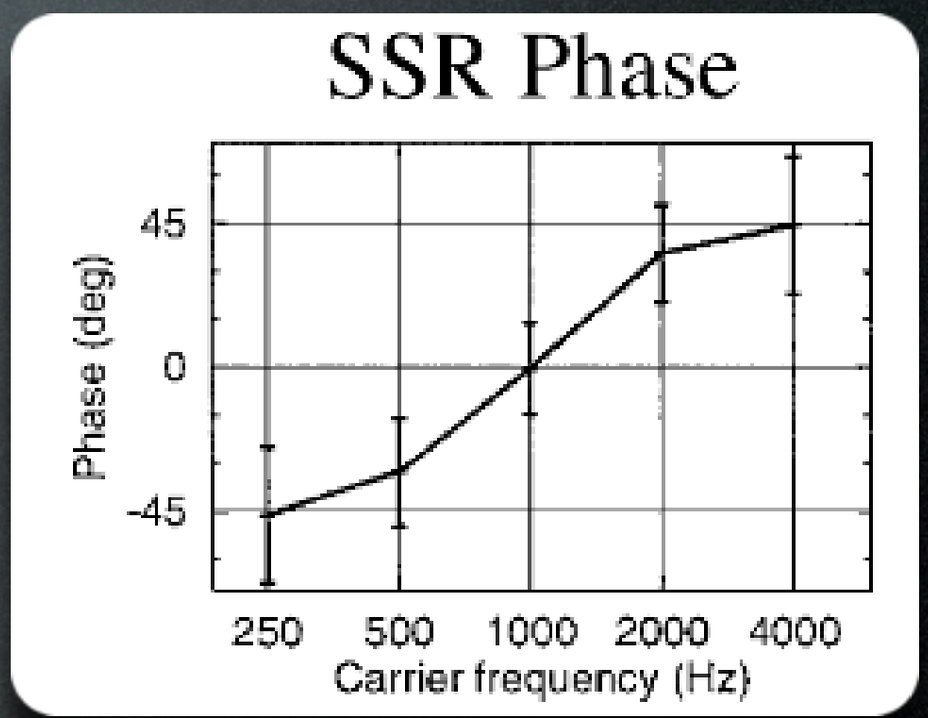
- Expect direct SSR for both f_{AM} & f_{FM}
- Additional encoding of slower modulations: faster SSR may itself be modulated at rate of slower SSR

➡ e.g. neural "carrier" at faster f_{AM} may be modulated at slower rate f_{FM}

- Phase modulation? Amplitude modulation? both?

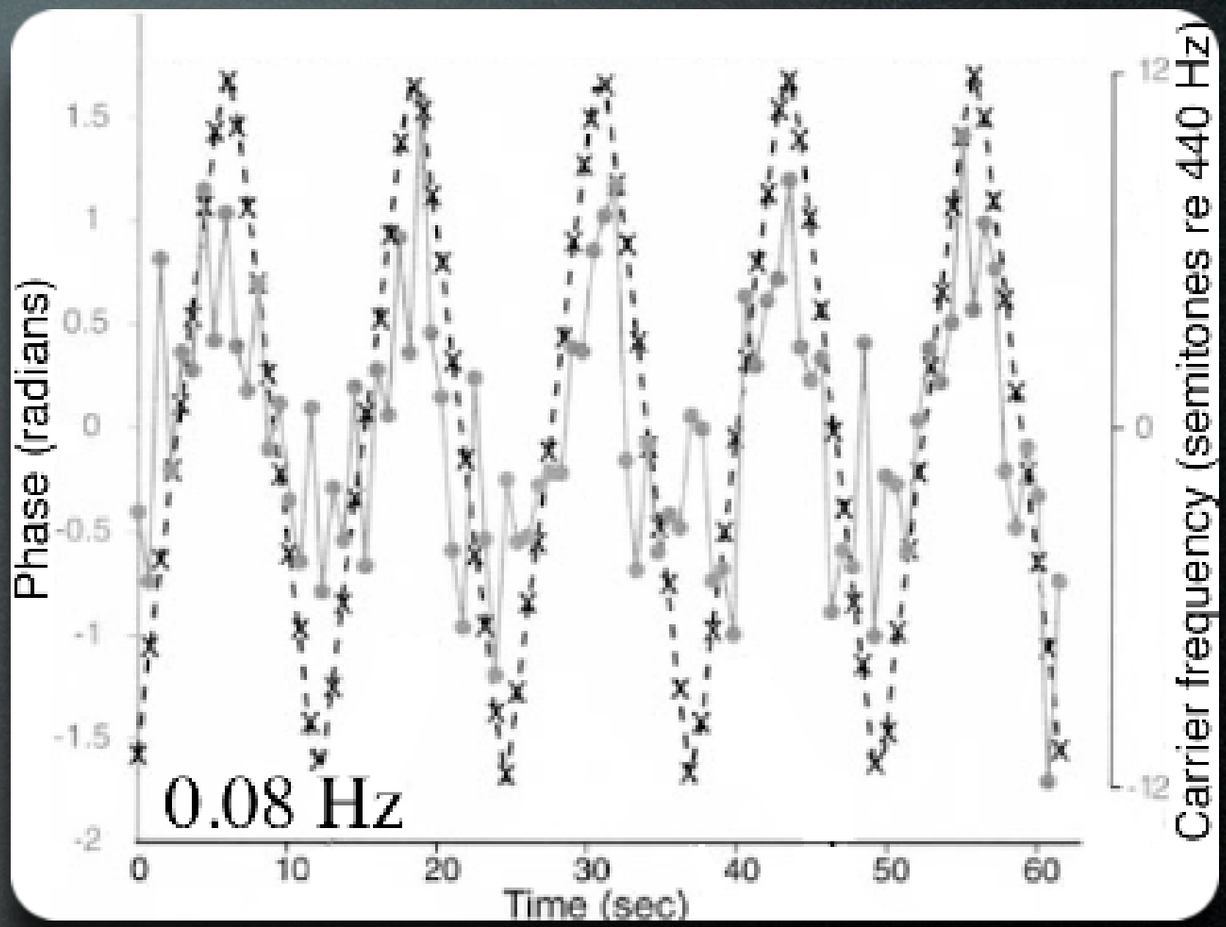
Why expect neural modulation?





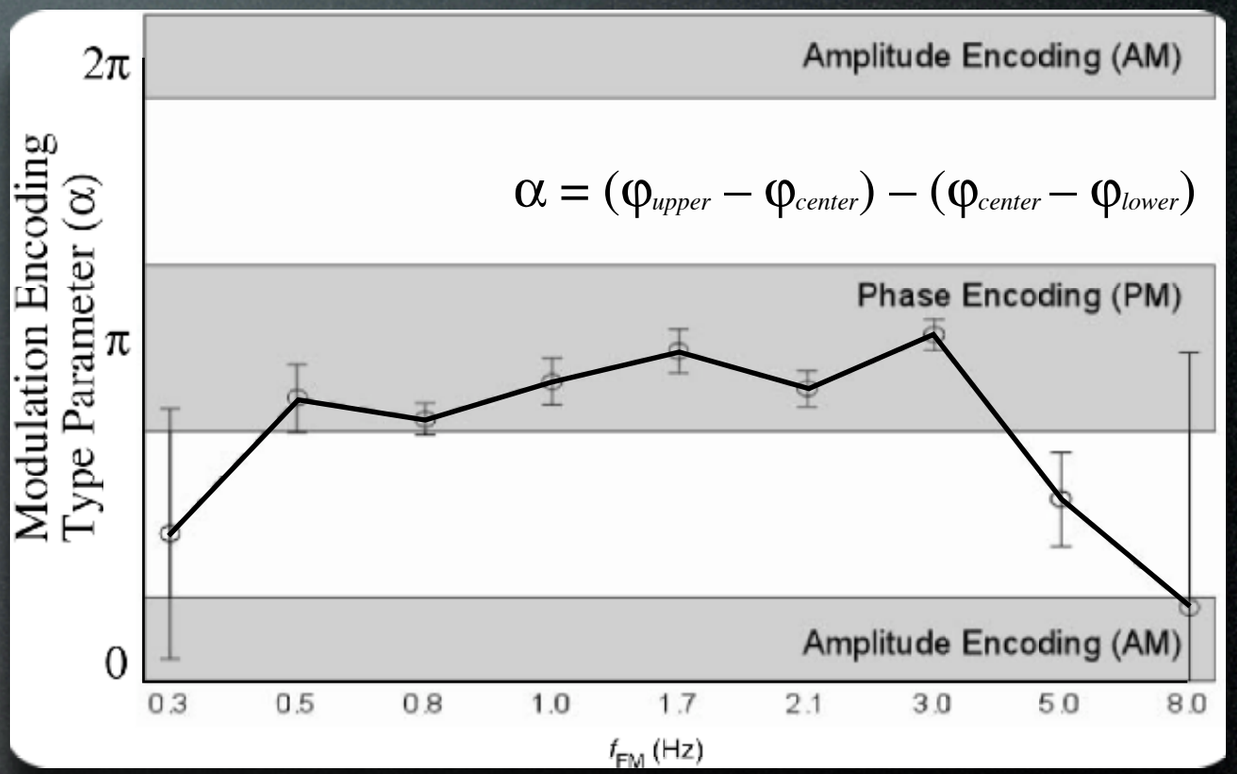
Ross et al. (2000)

Slowest FM rates → phase modulation only



Patel & Balaban (2004)

Phase Modulation only below f_{FM}~5 Hz



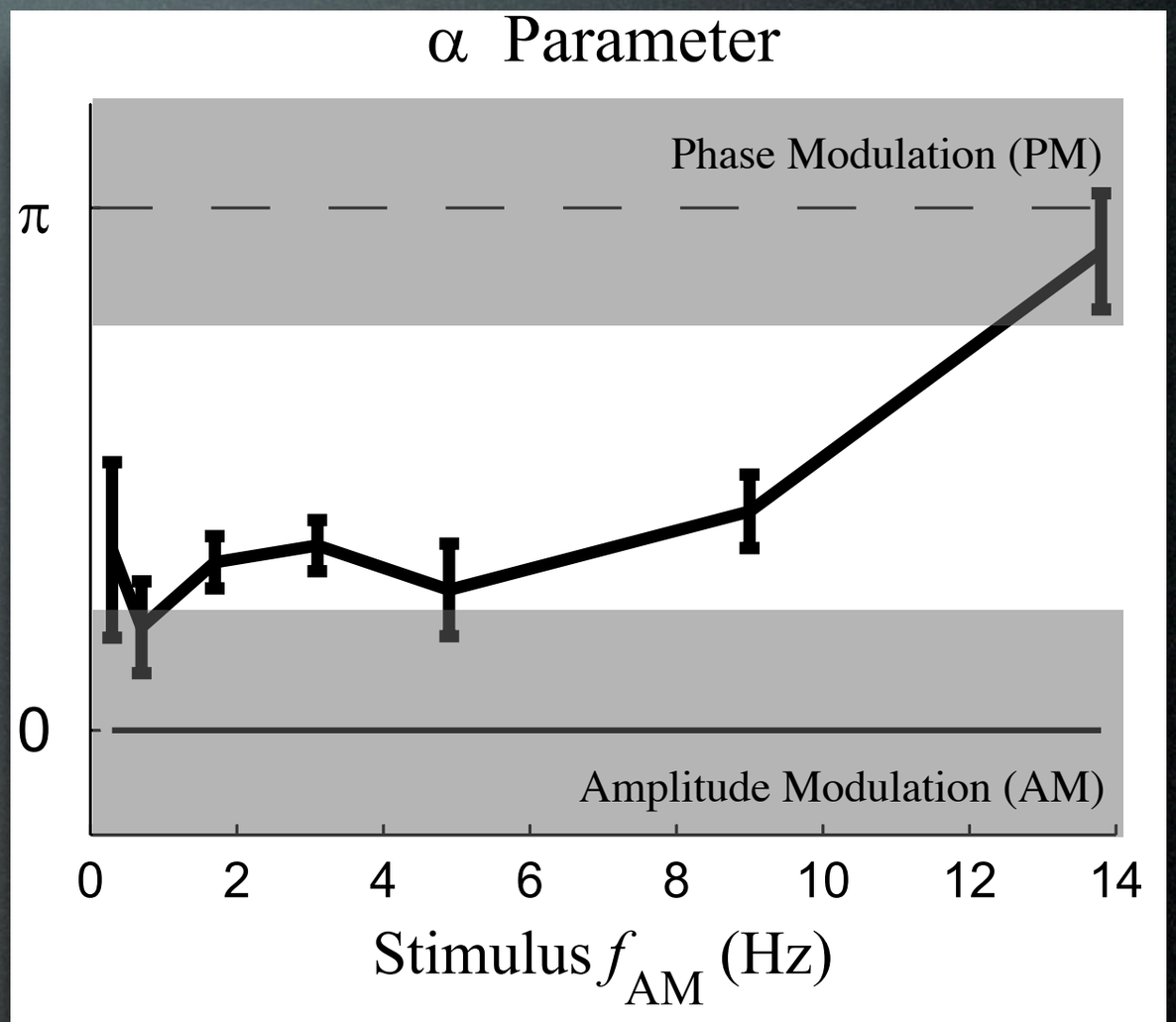
Luo et al., J. Neurophysiol (2006, 2007)

Additional analysis shows...

- Transition in modulation type at f_{FM} ~ 5 Hz
- Above 5 Hz, modulation type changes to Single Sideband modulation
- f_{FM} ~ 5 Hz also corresponds to transition in FM psychophysics

FM modulations can be encoded twice: directly, and as a secondary modulation whose coding changes at 5 Hz

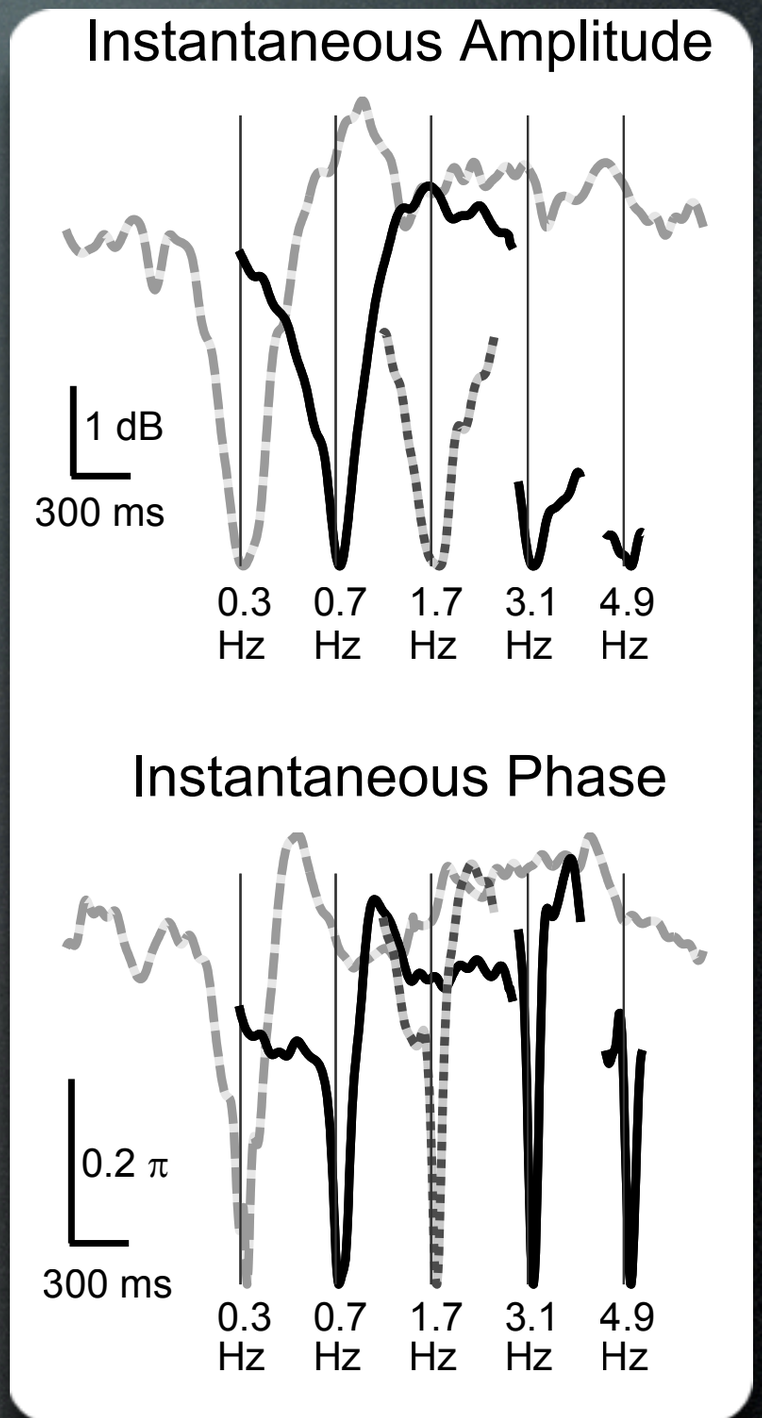
The reverse (slow AM + fast FM) is different



Ding & Simon, J Neurophysiol (in press)

Secondary modulation temporally sharp

Ding & Simon, J Neurophysiol (in press)



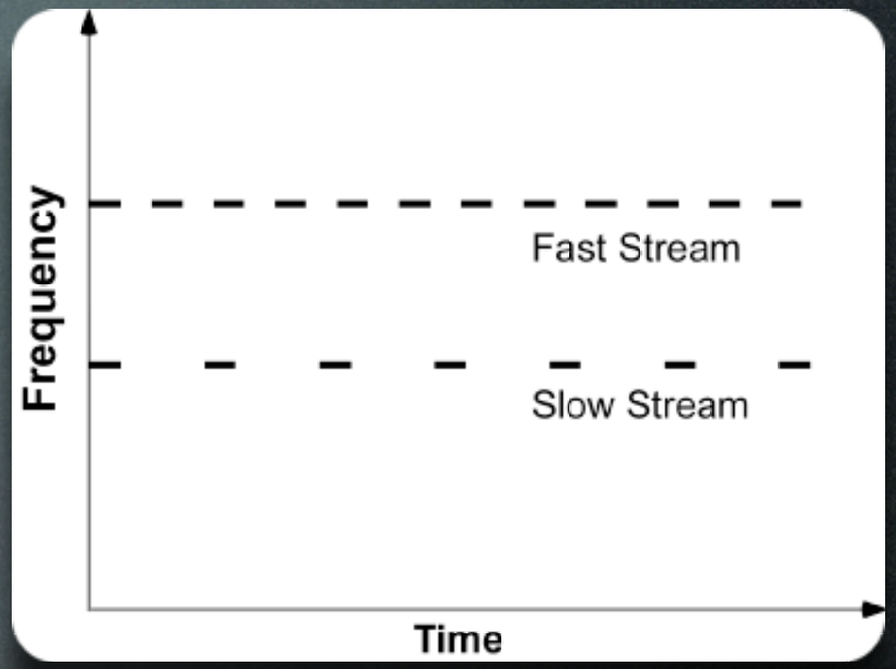
Redundant Coding of Concurrent Modulations

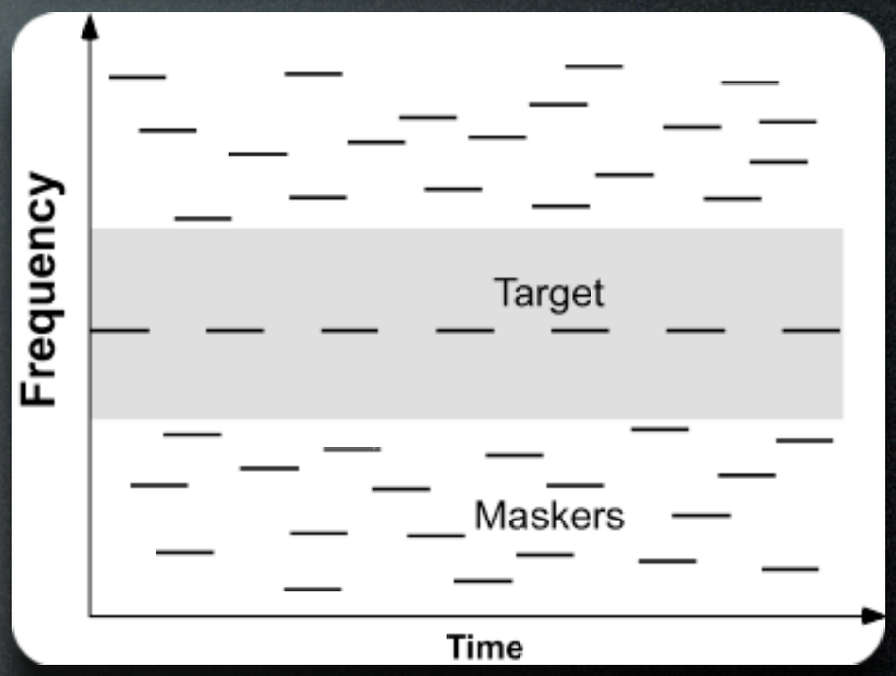
- In the presence of a fast AM, a slower FM can be encoded twice: directly, and as a secondary modulation whose coding changes at 5 Hz
- In the presence of a fast FM, a slower AM can be encoded twice: directly, and as a secondary modulation with sharpened temporal tuning

Attentional Effects

- In complex auditory scenes, modulatory patterns aid segregation of auditory objects
- Attention to different sound components affects neural processing of the (modulated) objects

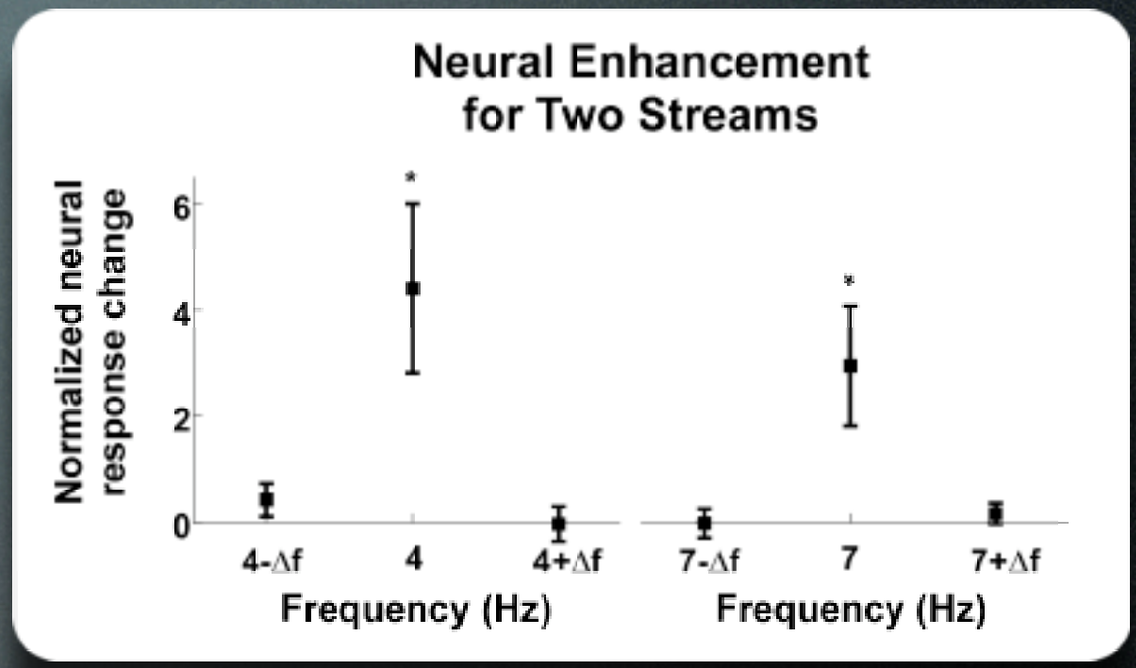
Streaming with simple modulations

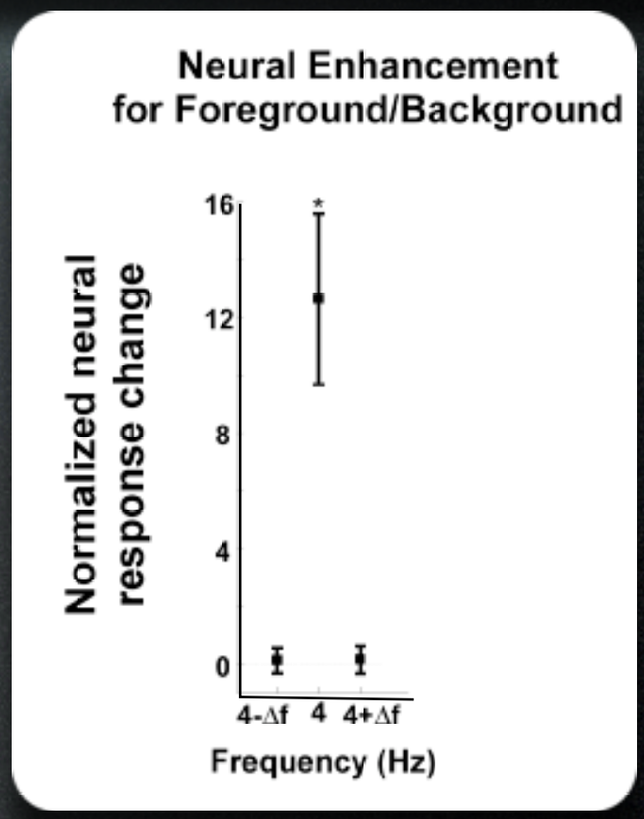




Elhilali et al., PLoS Biology (2009)
(& more in preparation)

Attentional Enhancement





Elhilali et al., PLoS Biology (2009)
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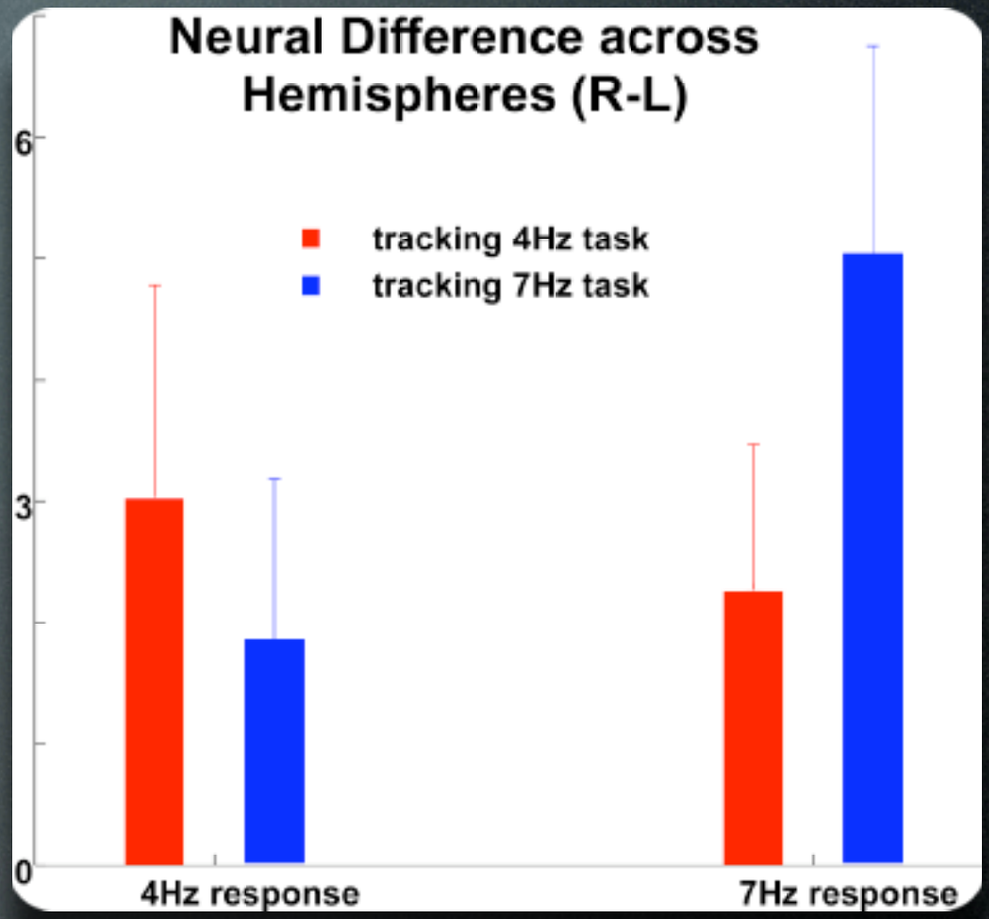
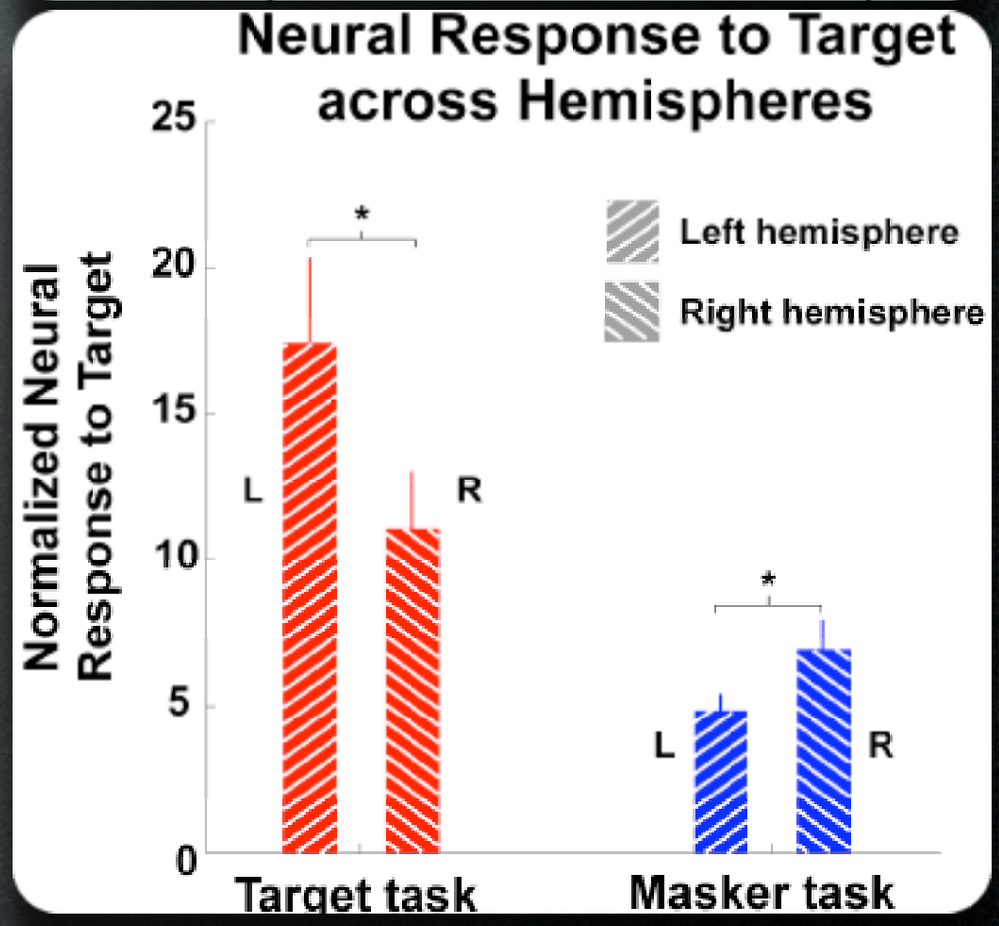
Hemispheric Asymmetries





Elhilali et al., PLoS Biology (2009)
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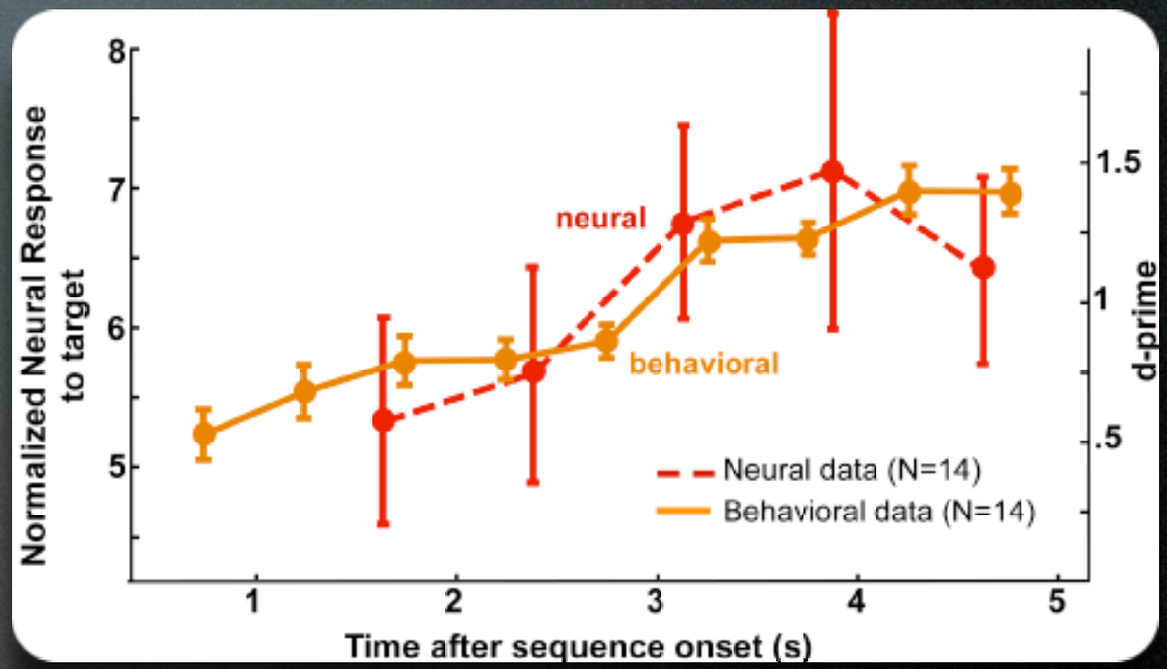
Neural enhancement tracks behavior along stream



Elhilali et al., PLoS Biology (2009)
(& more in preparation)

Attention Modulates Modulation Encoding

- Attending to one stream over another enhances modulation representation
- Attentional modulation is hemispherically asymmetric (and task dependently so)
- Attentional modulation tracks behavior, over the course of the stream

Conclusions

- Encoding of modulations, even just as neural modulations, can be done using many different (non-linear) strategies
- Using stimuli with multiple modulations allows non-linear modulation encoding to shine through
- Modulation encoding depends on attentional state