Auditory Cortex (4)

Prof. Xiaoqin Wang

Laboratory of Auditory Neurophysiology
Department of Biomedical Engineering
Johns Hopkins University

web1.johnshopkins.edu/xwang
Outline

Lecture 1: Anatomy of auditory thalamus and cortex
   a) Subdivisions of medial geniculate body (MGB)
   b) Multiple fields of auditory cortex
   c) Thalamo-cortial and cortico-cortical connections

Lecture 2: Tonotopic organization and stimulus selectivity
   a) Tonotopic organization of auditory cortex
   b) Firing patterns and tuning to preferred stimulus

Lecture 3: Temporal processing
   a) Temporal-to-rate transformation in A1
   b) Temporal-to-rate transformation outside A1

Lecture 4: Spectral, intensity and spatial processing
   a) Spectral processing
   b) Intensity processing
   c) Pitch and harmonicity processing

Lecture 5: Complex sound processing
   a) Spatial processing
   b) Vocalization processing
Tonotopic organization in cat A1 (anesthetized)

Suprasylvian sulcus

AES

PES

Merzenich et al. (1975)
Spectral processing:

• Frequency axis is expanded from one-dimension to two-dimension (tonotopic & iso-frequency)

• Iso-frequency axis allows additional processing of spectrally overlapping information from the periphery
Bandwidth of Excitatory RF

Analysis based on RF derived by pure tones: Frequency response area (FRA)

Schreiner and Mendelson (1990)
Neurons in the center of A1 are more sharply tuned

Schreiner and Mendelson (1990)

\[ Q_{10} = \frac{CF}{BW_{10}} \]
Distribution of BW along iso-frequency axis
Single units vs. multi-units

Schreiner and Sutter (1992)
Distribution of BW along iso-frequency axis

Dorsal-Central-Ventral A1

Schreiner and Sutter (1992)
Inhibition probed by two tone paradigm

Shamma et al. (1993)
Organization along iso-frequency axis:
Asymmetry of inhibitory sideband

Shamma et al. (1993)

Asymmetry measure:

\[
M = \frac{R_{>BF} - R_{<BF}}{R_{>BF} + R_{<BF}}
\]

Shamma et al. (1993)
Frequency response area (FRA) in awake marmoset auditory cortex (A1)

Sadagopan and Wang (J. Neurosci. 2008)

"I"/"V"-shaped

~60% neurons in awake condition

"O"-shaped
Non-monotonic “O”-shaped FRA resulted from inhibition

Sadagopan and Wang (J. Neurosci. 2008)
Sound level representation in auditory cortex
Rate-level Functions of Auditory Nerve Fiber (ANF)

Monotonic and saturated

- Low spontaneous ANF (SR<20 spk/s, high threshold, less saturation)
- High spontaneous ANF (SR>20 spk/s, low threshold, rate saturation at high sound levels)

Sachs and Young (1979)
Rate-level Functions of Auditory Cortex Neurons
(awake mustached bat)

Suga (1977)
Rate-level Functions of Auditory Cortex Neurons
(Awake and behaving macaque monkeys)

“Monotonic” Neurons

“Non-monotonic” Neurons

Pfingst and O'Connor (1981)
Non-monotonic Rate-level Functions

Examples of narrowly tuned non-monotonic rate-level functions

Normalized Discharge Rate

Sound Level (dB SPL)
Non-monotonic rate-level function and “O”-shaped FRA (awake marmoset)

SI = BW (loudest level) / BW (best level)
MI = R (loudest level) / R(best level)

Sdagopan and Wang (2008)
Representations by “O”-shaped and “V”-shaped neurons

Sadagopan and Wang (J. Neurosci. 2008)
Spectral-temporal integration and non-linear processing in auditory cortex
"Combination sensitive" neurons in auditory cortex of echo-locating bats

Suga (1997)
Specialized auditory cortical area for processing sonar signals in echo-locating bats

Suga (1994)
Marmoset Vocalizations (recorded in captivity)

High F0 harmonics

Low F0 harmonics

(Wang Lab, JHU)
Auditory cortex neurons are selective for complex sounds

Responses to 20 types of marmoset vocalizations

Sadagopan and Wang (J. Neurosci 2009)
Some cortical neurons are really hard to drive…

Sadagopan and Wang (J. Neurosci 2009)
Two-two responses suggest local non-linear integration

Sadagopan and Wang (J. Neurosci 2009)
Non-linear interaction explains “highly selective” response
Non-linear neurons are more often found in upper layers

Sadagopan and Wang (J. Neurosci 2009)
Probing spectral sensitivity using random spectrum stimuli (RSS)


Linear estimate:

$$\bar{R}_{\text{lin}} = \bar{R}_0 + \Lambda \tilde{w}$$

$$\tilde{w}_{\text{ls}} = (\Lambda^T \Lambda)^{-1} \Lambda^T (\hat{R} - \hat{R}_0) = \Lambda^T \hat{R}/n\sigma_{\Lambda}^2$$
Cortical responses to random spectrum stimuli (RSS)

Cortical neurons’ spectral tuning is not widened at high sound levels when listening to broadband signals

High-Contrast Preference Neuron


Unit M42m25a

Driven Rate (sp/s)

Weight (sp/s/dB)

Frequency (kHz)

Level re Mean (dB)

Driven Rate (sp/s)

Attenuation (dB)

Driven Rate (sp/s)

Contrast (dB SD)

High contrast (20 dB SD)
Low-Contrast Preference Neuron


Low contrast (5 dB SD)
Harmonic processing in auditory cortex
Auditory cortex RF derived by two-tone stimuli

Schreiner et al. (2000)
Neurons with multi-peak RF in dorsal A1 of cat

Sutter and Schreiner (1991)
Neurons with multi-peak RF in A1 of marmoset

Two-tone Facilitation and Inhibition in single-peak Neurons

One-tone Responses

![Graph showing discharge rate vs frequency for one-tone responses with CF = 4.53 kHz (11 spikes/sec) and CF = 12.25 kHz (38 spikes/sec).]

Two-tone Responses

![Graph showing percent change in discharge rate vs S2 frequency for two-tone responses with CF = 7.1 kHz (28 spikes/sec) and CF = 3 CF (38 spikes/sec).]


Facilitation

Inhibition
Harmonic structures in marmoset auditory cortex responses

Multi-peak Neurons
(facilitation)

Single-peak Neurons
(facilitation, inhibition)

What is Pitch?

A sound’s periodicity or harmonic structure determines its pitch (unresolved or resolved pitch)

Pure tone (pitch: 100 Hz)

“Missing fundamental” harmonic complex (pitch: 100 Hz)
Non-linear processing by pitch-selective neurons

Pure tone response

Individual harmonics response

“Missing fundamental” response

Bendor and Wang (Nature, 2005)
Responses of pitch-neurons are not due to cochlear distortion products

Pressnitzer and Patterson (2001)

Cochlear distortion product

Pitch-selective neuron

Pressnitzer and Patterson (2001)

Noise Masker

Bendor and Wang (*Nature*, 2005)
Pitch-selective responses are not due to cochlear distortion products

Bendor and Wang (J Neurophysiol, 2010)
Properties of pitch neurons:
sensitive to temporal irregularity

Regular click trains:
repetition rate = pitch

Irregular click trains:
pitch strength decreases with irregularity

Population average for irregular click trains (n=10)

(Bendor and Wang 2005)
Properties of pitch neurons: sensitive to pitch salience

Population average for IRN

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<th>Iterations</th>
<th>Normalized discharge rate</th>
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<tr>
<td>1</td>
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n=15
* p<0.05
** p<0.01
Lower order harmonics evoke stronger responses than higher order harmonics

Population average for harmonic order of harmonic complex tone

Population average for lowest frequency harmonic of complex tone

Lower harmonic must be less than ~5 kHz to evoke a response in most neurons

(Bendor and Wang 2005)
A “Pitch Region” in Auditory Cortex

High frequency

Low frequency

RT

Left Hemisphere M2P
- Recording site (519 total units)
- Pitch neuron site (19 pitch units)

Bendor and Wang (2005)
Similar locations of “Pitch region” in auditory cortex of humans and Monkey

Bendor and Wang (2006)
Topographic Organization of Auditory Cortex in Primates

New World Primates (owl monkey)

(Morel and Kaas 1992)

Pitch-selective region
Functional Organization of Auditory Cortex in Mustached Bats

Nobuo Suga (1994)
Harmonic structures in auditory cortex connectivity

Diagram showing connectivity between the auditory cortex and thalamus, illustrating CF, CF/2, and 2CF frequencies.
Information Processing in Auditory System

Transformations

Sound → Isomorphic representations (auditory periphery, brainstem) → Non-isomorphic representations (midbrain, primary auditory cortex) → Perceptual representations (Non-primary auditory cortex)
Suggested readings:

**Spectral Processing:**


**Intensity Processing:**


**Pitch and harmonicity processing:**
