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Structure and Function of the Auditory and Vestibular Systems
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Auditory Cortex (2)

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Outline

Lecture 1: Tonotopic organization and stimulus selectivity
   a) Anatomical structure of the mammalian auditory cortex
   b) Tonotopic organization of auditory cortex
   c) Firing patterns and tuning to preferred stimulus

Lecture 2: Temporal processing
   a) Coding of time-varying signals
   b) Temporal-to-rate transformation in A1
   c) Temporal-to-rate transformation outside A1

Lecture 3: Spectral and intensity processing
   a) Spectral processing
   b) Intensity processing
   c) Other topics
Temporal processing:

• How does auditory cortex represent time-varying signals?
Spectral and Temporal Characteristics of Speech

Spectrum

Formant

- RELATIVE LEVEL (dB)
- FREQUENCY (KHZ)

Temporal

Fine structure (“carrier”)

Coarse structure (“envelop”)
Reduction of spike timing precision in CN:
Fine temporal structure

Synchronization Index

Best Frequency (kHz)

AN

CN (primary-like cell)

CN (chopper cell)

(Blackburn and Sachs, 1989)
Reduction of spike timing precision in CN:
Envelope

Rohde and Greenberg (1994)
Further reduction of spike timing precision in IC: “Low-pass” to “band-pass”
Thalamus (MGB) spiking faster than auditory cortex (AC)

Increasing modulation frequency

10 Hz

140 Hz

Creutzfeldt et al. (1980)
Modulation Frequency Selectivity Independent of Spectral Contents

Liang et al. (2002)
Stimulus-locked responses are progressively “slowed down” along ascending auditory pathway.

(AN: Johnson, 1980, CN: Blackburn and Sachs, 1990)
Distributions of tBMF in different auditory cortical areas of the cat

\[ \text{tBMF: } R_{f_0} + R_{2f_0} \]
Awake versus Anesthetized Condition

Goldstein, Kiang and Brown (1959)
Click trains produce largely synchronized discharges in anesthetized condition

Anesthetized Cat A1

~ 80%

~ 20%

2-11

Lu and Wang (2000)
Click trains produce both synchronized and non-synchronized discharges in awake condition

Stimulus

Click Trains

10 Hz (100 ms)

100 Hz (10 ms)

333 Hz (3 ms)

Synchronized Responses

Unit M1K-366, CF 3.83 kHz, 50 dB

Non-Synchronized Responses

Unit M49L-048, 70 dB

Lu et al. (2001)
Cortical Representations in Different Time Scales:
A two-stage mechanism

Implicit rate-coding  Explicit temporal-coding

![Graph showing normalized percent of units against response boundary (ICI ms).](image)

- **Awake marmoset**
- **Anesthetized cat**

(Lu and Wang *J. Neurophysiology*, 2000)
Summary: A1 representations to sequential events

In awake condition:

- Synchronized population can explicitly represent slowly occurring sound sequences by their temporal discharge patterns.
- Non-synchronized population can implicitly represent rapidly occurring sound sequences by their firing rate.

In anesthetized condition:

- Discharge synchronization rates are lower than those observed in awake condition.
- Non-synchronized responses are largely absent.
Why are auditory responses “slowed down” in cortex?

For the purpose of multi-sensory integration.

Other sensory systems (visual, tactile) are much slower at the periphery, but discharge synchrony rates are similar across sensory cortex. This “slow-down” allows auditory information to be integrated with information from other sensory modalities at the same “clock rate”.

For the purpose of auditory object processing

which requires temporal integration over longer time windows.
What about spike timing in auditory cortex?

Auditory cortex marks sparse acoustic events (or onsets) with precise spike timing and transform rapidly occurring acoustic events into firing rate-based representations.
Synchronized and non-synchronized responses are also observed for dynamically changing stimuli.

Dual Temporal and Rate Representations in Auditory Cortex

Spike timing is more precise at the first event than at successive events, more precise with sparse events than with densely packed events.

$$CV \text{ [spike latency]} = \frac{\text{std}}{\text{mean}}$$
Entropy computed from ISI distribution shows little temporal structure in non-synchronized responses

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Lu and Wang (J. Neurophysiol. 2004)
The question is not whether spike timing is important, but under what stimulus conditions and for which population of cortical neurons.

**Synchronized Responses**

Unit M58L-051, CF 14.9 kHz, 80 dB

**Non-Synchronized Responses**

Unit M49L-074, 23.39 kHz, 40 dB
What about thalamus in awake condition?
Sustained firing also observed in auditory thalamus (MGB)

Bartlett and Wang (J. Neurophysiol., 2007)
Greater extent of sustained firing in auditory cortex than in MGB

Bartlett and Wang (J. Neurophysiol., 2007)
Progressive increase of non-synchronized firing from brainstem to cortex

Bartlett and Wang (J. Neurophysiol., 2007)
How does auditory cortex process sound sequences?

• Cortical processing of sound streams operates on a “segment-by-segment” basis rather than on a “moment-by-moment” basis as found in the auditory periphery.

• Auditory cortex neurons mark sparse acoustic events (or onsets) with precise spike timing and transform rapidly occurring acoustic events into firing rate-based representations.
What else can firing rate-based representations encode?

(There are always surprises …)
Stimulus synchronization in the range of acoustic flutter

n = 274

Percent of samples

$\text{Flutter perception}$

Mean vector strength

Synchronized ($n = 83$)

Unsynchronized ($n = 107$)

$\text{Flutter perception}$

Bendor and Wang (Nature Neuroscience 2007)
Firing rate-based representations of acoustic flutter

Bendor and Wang (Nature Neuroscience 2007)
Non-synchronizing firing also encodes low repetition rates

“Non-synchronizing responses” (Lu et al. 2001)
Transformation of firing rate-based representations from A1 to rostral fields

Bendor and Wang (Nature Neuroscience 2007)
Spectral/temporal integration pathways in primate auditory cortex

Bendor and Wang (J. Neurophysiology, 2008)
A common coding strategy between the tactile and auditory system

Synchronizing neuron in S1

Positive and Negative monotonic neurons in S2

Romo and Salinas (2003)

Salinas et al. (2000)
What is the implication of these experiments?

“Non-synchronized responses” are the results of temporal-to-rate transformations and represent processed (instead of preserved) information.

The auditory cortex transforms stimulus features into internal representations that are no longer faithful replicas of acoustic dimensions.
Challenges in understanding cortical processing of acoustical information:

1) Transformation from isomorphic (faithful) to non-isomorphic representation of acoustic signals

2) Transformation from acoustical to perceptual dimension
Suggested readings:
