Auditory Cortex (2)

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Outline

Lecture 1: Tonotopic organization and stimulus selectivity
   a) Tonotopic organization of auditory cortex
   b) Firing patterns and tuning to preferred stimulus

Lecture 2: Temporal processing
   a) Temporal-to-rate transformation in A1
   b) Temporal-to-rate transformation outside A1

Lecture 3: Spectral, intensity and spatial processing
   a) Spectral processing
   b) Intensity processing
   c) Spatial processing

Lecture 4: Complex sound processing
   a) Pitch and harmonicity processing
   b) Vocalization processing
What is unique about the auditory system?

1) Longer subcortical pathway
2) Spectrally overlapping, time-varying input signal
3) Sounds entering the ear from anywhere at anytime
4) Hearing-speaking: sensory-motor processing
Temporal processing:

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

Spectrum

Formant

Temporal

Fine temporal structure ("carrier")

Coarse temporal structure ("envelop")
Reduction of spike timing precision in CN:
Fine temporal structure ("carrier") – Phase-locking

(S Blackbourn and Sachs, 1989)
Reduction of spike timing precision in CN:
Coarse temporal structure ("envelop") – Modulation transfer function

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

Increasing modulation frequency (Stim: SAM)

Creutzfeldt et al. (1980)
Responses to SAM, SFM stimuli in awake marmoset A1

Liang et al. (2002)
Temporal modulation preference in A1 largely independent of spectral contents

BMF: Best modulation frequency
(rBMF: firing-rate based, tBMF: firing synchrony based)

Liang et al. (2002)
Modulation transfer functions in gerbil IC and A1

Ter-Mikaelian et. al. (J Neurosci, 2007)
Distributions of tBMF in different auditory cortical areas of the cat

$$tBMF: R_{f_0} + R_{2f_0}$$

Schreiner and Urbas (1988)

Imig and Reale (1980)
Stimulus-locked responses are progressively “slowed down” along ascending auditory pathway.

(AN: Johnson, 1980, CN: Blackburn and Sachs, 1990)
Slower stimulus-following responses in anesthetized condition

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

Anesthetized Cat A1

~ 80%

~ 20%

Lu and Wang (2000)
Click trains produce both synchronized and non-synchronized responses in awake condition.
Dual Temporal and Rate Representations in Auditory Cortex

Cortical Representations in Different Time Scales: 
A two-stage mechanism

Lu et al. (2001)
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.
How precise are spike timing 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 [spike latency] = std / mean

Lu and Wang (J. Neurophysiol., 2004)
Entropy computed from ISI distribution shows little temporal structure in non-synchronized responses

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

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Spike timing is more “sluggish” in awake than in anesthetized condition in auditory cortex, but not so in IC

Ter-Mikaelian et. al. (J Neurosci, 2007)
Spike timing is more precise IC than in A1

Ter-Mikaelian et. al. (J Neurosci, 2007)
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.
What about thalamus in awake condition?
Non-synchronized responses also observed in awake MGB

Bartlett and Wang (J. Neurophysiol., 2007)
Greater extent of non-synchronized responses in A1 than in MGB

Bartlett and Wang (J. Neurophysiol., 2007)
Progressive increase of non-synchronized responses from IC to A1

Bartlett and Wang (J. Neurophysiol., 2007)
Fewer synchronized responses in A1 than IC
Fewer synchronized responses in awake A1 than anesthetized A1
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 …)
Temporal-to-rate transformation at longer time scales

Non-synchronized (Negative monotonic)
Synchronized
Non-synchronized (Positive monotonic)

Thomas Lu (PhD Thesis, 2001)  
Lu et al. (Nat Neurosci. 2001)
Stimulus synchronization in the range of acoustic flutter

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

All neurons (synchronized, mixed and unsynchronized)

- Positive monotonic ($n = 75$)
- Negative monotonic ($n = 63$)

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

Unsynchronized neurons

Positive monotonic (n=47)
Negative monotonic (n=25)

Flutter
Pitch

“Non-synchronized responses” (Lu et al. 2001)

Bendor and Wang (Nat Neurosci. 2007)
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:

