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Structure and Function of the Auditory and Vestibular Systems
(Fall 2010)

Auditory Cortex (1)

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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
The Notion of Tonotopic Organization in Auditory Cortex
What is unique about the auditory systems?

1. Long subcortical pathway
2. Time is an essential axis
3. Stronger anesthetics side effects
More spiking synapses in subcortical nuclei

Visual

Graded transmission

Retinal ganglion cell

1

Vision

Auditory

spiking

1

Receptor

Primary neuron

Cochlear nuc.

Sup. olive

Inf. colliculus

Thalamus

3

Cortex

Auditory
Auditory cortex

New World Monkey
(*Callithrix jacchus* – common marmoset)

Old World Monkey
(*Cercopithecus*)

Human

Organization of auditory cortex is largely preserved across primate species

Brodmann (1909)
Overall organization of auditory cortex

Cat
Imig and Reale (1980)

Primates
Morel and Kaas (1992)
Tonotopic organization of auditory cortex:
First demonstration in anesthetized cat (at Hopkins!)

Fig. 4. Expt. 2/1/41; right cortex; left cochlea; stimulation of nerve fibers at 6 mm. (basal turn) and 14 mm. (middle turn) from basal end. Note that there are two response areas for the 14 mm. point. See text p. 320 and p. 327. Labels identify sulci. $\frac{2}{3}X$. 
Fig. 5. Exp. 2/3/41; right cortex; left cochlea; nerve fibers stimulated at 1.5, 4, 6, 8, 14 and 19 mm. from the basal end of the spiral. See text p. 321. 2½ X.
CLASSIFICATION OF UNIT RESPONSES IN THE AUDITORY CORTEX OF THE UNANAESTHETIZED AND UNRESTRAINED CAT

BY E. F. EVANS AND I. C. WHITFIELD

From the Neurocommunications Research Unit, The Medical School, University of Birmingham

Is auditory cortex tonotopically organized?
Lack of an orderly organization in unanesthetized cat

“Standard cortex”

Suprasylvian sulcus

Goldstein et al. (1970), Neural Encoding Lab, BME, JHU
Is there a columnar organization in auditory cortex?
How reliable are anatomical landmarks?
Auditory cortex is tonotopically organized

Merzenich et al. (1975)
Systematic changes of CF across auditory cortex

Merzenich et al. (1975)
Tonotopical organization in marmoset auditory cortex

- High frequency
- Low frequency

Al

R

RT

1 mm

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

Bendor and Wang (2005)
Tonotopic organization across mammals

Morel and Kaas (1992)
“Why are Evans et al. and our single track penetrations so out of agreement with the orderly representation of the cochlea within AI reported by Merzenich et al.? First and foremost in our view is the different anesthetic state. There is no question that the sorts of anesthetics Merzenich et al. used render many cortical units unresponsive to sound. Further the effect is probably selective so that units with more indirect input pathways are more likely to be affected.” (p.190)

What have we learnt from the old debate?

- Anesthetized
- MGB input
- Multi-unit
- Near threshold
- Single hemisphere

Unanesthetized
Cortical response
Other layers
Single-unit
Supra-threshold stimulus
Averaging across hemispheres
“In this chapter and elsewhere, we have stressed the diversity of the neural coding properties of the units in the auditory cortex. This diversity makes the cortex a difficult region to study and makes it especially unattractive to those who like their science in neat packages. Let us hope that new studies, new techniques, and new findings will move us out of what will someday be called the early phases (or even the dark ages) of neuroscientific study of the cortex.”

Mysteries of Auditory Cortex

Why it’s so silent?
Because of anesthesia & non-optimal stimuli!

Onset responses to brief sounds (anesthetized rats)

Onset responses to continuous sounds (anesthetized marmosets)

DeWeese and Zador (2003)

deCharms and Merzenich (1996)
Auditory cortex is capable of sustained firing in awake animals

Primary Auditory Cortex
(Stimulus: Tone)

Non-Primary Auditory Cortex
(Stimulus: Noise)

Wang et. al. (Nature, 2005)
Auditory cortex neurons respond to preferred stimuli with sustained firing and adapt quickly to non-preferred stimuli.

Wang et. al (Nature, 2005)
Sustained firing evoked by temporally modulated stimuli

Wang et. al (Nature, 2005)
How responsive is auditory cortex during sleep? (unlike under anesthesia!)

Issa and Wang (2008)
Auditory cortex is as responsive to sounds during sleep as during awake state

A

SWS (A1)

Fraction of units

\[ \text{Gain (SWS-Awake)} \]

B

Best driven (A1)

\[ \text{SWS (spikes/s)} \]

\[ \text{Awake (spikes/s)} \]
Firing pattern and stimulus selectivity in auditory cortex of awake monkeys

Auditory cortex neurons respond to preferred stimuli with sustained firing and adapt quickly to non-preferred stimuli
From a stimulus’ point of view:

Responses to one particular sound by all neurons

“When a sound is heard, a particular population of auditory cortex neurons fire continuously throughout the duration of the sound. Responses of other, less optimally driven neurons fade away quickly after the onset of the sound.” (Wang et al. *Nature* 2005)
From a neuron’s point of view:

Responses of one neuron to entire acoustical parameter space

Acoustic parameter space

Preferred stimulus (sustained firing)

Non-preferred stimuli (onset firing)

Outside RF (no response)

Wang (Hearing Research, 2007)
Responses of one neuron to entire acoustical parameter space

Acoustic parameter space

From a neuron’s point of view:
Increased stimulus selectivity along ascending auditory pathway

Wang (Hearing Research, 2007)
Summary of observations from auditory cortex in awake condition

1) Neurons in auditory cortex are high selective to acoustic stimuli.
   - Each neuron is only responsive to a small region of acoustic
   - As a result, each stimulus only excites a small number of neurons (“spatial sparseness”)

2) Neurons in auditory cortex are also highly responsive (fire plenty of spikes), but only to stimuli they like.
   - “spatial sparseness” does not result in sparse firing (i.e., transient responses)

3) “Selectivity” and “responsiveness” are closely coupled.
   - Stimulus selectivity is a more useful measure than “sparseness” if you want to understand what a neuron actually does.
Suggested readings:

**Tonotopic organization:**


**Firing pattern and stimulus selectivity:**
