Coding of auditory foregrounds and backgrounds in the auditory cortex

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Prelude
- Organization of the auditory system
- Auditory Scene Analysis

Case study 1: Responses to bird calls in noise
Case study 2: Responses to weak tones in naturalistic noise
Case study 3: Responses to rare stimuli in the context of common stimuli, or: on the splitting of the tuning curve
Methods

- Extracellular and intracellular recordings from auditory cortex of halothane-anesthetized cats
- 1-4 electrodes simultaneously
- Spike rates in cortex are low (typically, < 10/s)
- The analysis emphasizes changes in the temporal patterns of spikes caused by the stimulus

Prelude: Organization of the auditory system
Prelude: Simple feature detectors and complex sounds
Prelude: Complex feature detectors in the auditory system

Prelude: Organization of the auditory system

Visual system:
- Photoreceptors
- Retinal ganglion cells
- LGN
- V1
- IT
- Face cells

Auditory system:
- Hair cells
- Auditory nerve fibers
- Cochlear nucleus
- Superior Olive
- Inferior Olive
- MGN
- Auditory cortex

Localization and binaural detection
Species-specific calls?
Auditory scene analysis?
Cortical neurons are more complicated than neurons in the cochlear nucleus...

Optimizing Sound Features for Cortical Neurons
R. Christopher deCharms, David T. Blake, Michael M. Merzenich*

Spectro-temporal filtering by neurons in auditory cortex...

From Schnupp et al.,
Nature 2001, in press
...sometimes work and sometimes not...

...(but mostly do, at least for virtual space stimuli)
But may still be governed by simple energy summation rules?

Auditory scene analysis: Source separation
Foregrounds and backgrounds in auditory cortex

**Bottom line:**
Neurons in AI respond to weak and rare acoustic components, even in the presence of much stronger components, in “natural” settings.

Thus, neurons in AI perform auditory source separation: they distinguish between weak and strong sounds, narrowband and wideband sounds, common and rare tones.

These results cannot be explained by energy summation models (but I do believe that the response is related to the PHYSICS of the sound!)

Case study 1: Responses to bird calls in noise
Separating a natural sound into its components

Responses of cortical neurons to Natural and Main should be similar… But are they?
Some responses to Natural are similar to responses to Noise, not to Main

Responses to Main are often weaker than responses to Natural
Low correlations between responses to similar stimuli

What about lower stations?

Go to MGB data
Transformations of Stimulus Representation Along the Ascending Auditory System

In the IC:
Mike Anderson and Eric Young
Transformations of Stimulus Representation Along the Ascending Auditory System

![Graphs showing different types of auditory responses and their representations along the ascending auditory system.](image)
Transformations of Stimulus Representation Along the Ascending Auditory System

Main ≡ BF

Main ≡ 4 kHz

And in the auditory thalamus…
Quantifying the relationships between stimulus and response

When the response does not depend on the stimulus, this matrix should have identical rows. The amount of departure from this condition is measured by the mutual information, \( I(\text{response};\text{stimulus}) \).

Quantifying relations between neurons

- The way neurons interact to code the presence of stimuli is revealed when comparing the information about the stimulus provided by joint and by independent neuronal activity. Formally,
  \[
  R_S = I(\text{Cell}_i, \ldots, \text{Cell}_N ; S) - \sum I(\text{Cell}_i ; S)
  \]
- This measure can be shown to have two contributions, one arising, roughly speaking, from neuronal interactions (‘two neurons should respond similarly if they share a common synaptic input’) and the other from stimulus-induced correlations (‘two neurons with the same BF should respond to the same stimulus in similar ways’):
  \[
  R_S = I(\text{Cell}_i, \ldots, \text{Cell}_N | S) - I(\text{Cell}_i, \ldots, \text{Cell}_N)
  \]
- The first contribution can be assessed only for simultaneously recorded neurons, and is often small. In other cases, we can assume that the neurons are independent except for the stimulus-induced correlations, in which case the RS measure is always negative (‘redundancy’).
Mutual information between stimuli and responses

Redundancy in pairs of conditionally independent neurons…
Transformations of Stimulus Representation Along the Ascending Auditory System

... and in triplets

Effect of BF difference on redundancy
Effect of BF difference on redundancy

Quantifying the relationships between acoustic content and response

Stimuli are cut into frames which are then clustered to a small number of representatives.

This allows to investigate the information residing in single spikes.
Transformations of Stimulus Representation Along the Ascending Auditory System

Mutual information between groups of neurons and acoustic content

Measuring similarity between responses to different stimuli
Case study 2: Responses to weak tones in naturalistic noise

An auditory scene...
Background and foreground sounds in auditory scenes

Many separable sounds have significant amplitude fluctuations
Comodulation Masking Release (CMR)

Modulated - Unmodulated Difference (MUD)
Responses of a cortical neuron to noise bands with and without fluctuations

![Graphs showing firing rate vs. time for noise bands with and without fluctuations.]

CMR actors: tones and noise bands, fluctuating and not

![Heatmaps illustrating frequency response areas and noise bandwidths.]

Dr. Eli Nelken, Hebrew University (ITP Neurodynamics Program 10/29/01)
Responses of a cortical neuron to noise bands with a weak tone added

Auditory cortex neurons show correlates of Comodulation Masking Release
Transformations of Stimulus Representation Along the Ascending Auditory System

And more examples...

Mechanisms?
Intracellular responses to narrow and wide noise bands

Low-level tones suppress envelope-following intracellularly
Depolarizing the neurons does not uncover ‘silent inhibition’

Wideband noise responses have some inhibitory components…
But the tones suppress both excitatory and inhibitory components!

Envelope following in MGB is much stronger than in cortex
MGB neurons already have suppression of envelope following by weak tones

Case study 3: Splitting of the tuning curve by rare stimuli
Stimulus-specific adaptation in AI

Population results
Effect of probability

A VCN neuron
But at the input stage to the cortex…

Multiple time constants of adaptation
Conclusions

- Responses in AI can be interpreted in terms of auditory source separation
- Formally, this is related to redundancy reduction (neurons with the same BF listen to different things in the stimulus)
- Responses in primary auditory cortex depend on more than just the nature of the stimuli – rare stimuli are emphasized
- All of these results require processing of sounds going beyond blob summation of spectro-temporal energy distributions
- These properties are created gradually, some of them are already apparent in MGB (and maybe IC), others are not.