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SUPERIOR OLIVE
This is the entire ascending auditory pathway with the location of the superior olive circled in yellow.
The location of the superior olivary nuclei in situ in the brainstem of the cat. MSO=medial superior olive; LSO= lateral superior olive; TB = trapezoid body; MNTB = medial nucleus of the trapezoid body; DMPO = dorsomedial periolivary nucleus.
Basic information to be learned about each major nucleus in the superior olive. One can approach almost any part of the brain in this manner.
Neurons (left) and axons (right) in Golgi stain.

Tsuchitani, 1978, Fig. 10
There are high degrees of specialization in the anatomy of the superior olive. Species like man and mouse are extremely specialized for low frequency and high frequency hearing, respectively, and this influences the size of the nuclei in the superior olive.
The first circuit is that of the MSO
MSO Principle Cells

- Fusiform
- Bipolar
- Disc-shaped
- Each dendrite innervated by a different side

[Diagram showing glutamate]
MSO cells use glutamate as a neurotransmitter. Note VGLUT2 expression. VGLUT1, VGLUT2, VIAAT are vesicular transporter proteins that load neurotransmitter into synaptic vesicles.
Few MSO cells express both VGLUT1 and 2
MSO cells form layers that are tonotopically organized. Low frequency dorsal and high frequency ventral. There is a low frequency bias since frequencies above 13 kHz are not represented (in the cat). Spherical bushy cells from the AVCN provide excitatory inputs. Axons tend to run along the length of the laminae. MNTB and VNTB provide inhibitory inputs.
ITD CODING

Unlike retinal targets, the cochlear nuclei contain maps of frequency, not location.

So how does the auditory system know 'where' a sound is coming from?

By comparing the interaural time differences (ITD) between the ears.

How is this accomplished?...
Postulated “delay lines” in MSO used for coding ITD. This interpretation is now controversial and alternative mechanisms are proposed. See Alan Palmer next week.

MSO neurons respond with excitation when inputs from the two sides converge. This is a peak response.
Peak responses can be from low frequency tones or the envelope of a high frequency sound.
MSO Summary

- Cytoarchitecture – Laminar stack
- Neuron types - glutamate
- Inputs – Spherical bushy AVCN
- Outputs – Inferior colliculus
- Synapses – Excitatory glutamate

- Basic Circuit – Coincidence detector for ITD
LSO circuit. Note that LSO projects to both sides of the brain. Inputs come from spherical bushy cells and from globular bushy cells that communicate via the MNTB.
LSO has a mix of neurons both glutamatergic and glycinergic.
In the medial nucleus of the trapezoid body. Largest axonal ending in the mammalian brain.
Bushy cells on the ipsilateral side excite the LSO and MNTB cells driven by the globular bushy cell on the contralateral side inhibits the LSO
Convergence in the LSO produces a reduced response, a trough.
Binaural Responses in Superior Olive

- **Low-freq. Neurons**
  - Pure Tone

- **High-freq. Neurons**
  - Sine AM

**Response**

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<tr>
<th>Peak-Type (MSO)</th>
<th>Trough-Type (LSO)</th>
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**Interaural Delay**
ILD CODING

ITDs work only for the low frequency components of sound
What about higher frequencies?

The sound shadow cast by the head produces interaural level differences
How is this comparison made?...
LSO neurons are driven when the sound is louder in the ipsilateral ear and suppressed when the sound is louder in the contralateral ear. MNTB cells are not ILD sensitive, that means that when they are driven by the contralateral ear, the activity in the ipsilateral ear has no effect.

Normalized interaural level difference functions for 10 MNTB cells and 8 representative LSO cells. Stimuli were tones at CF. For the MNTB cells, the contralateral stimulus was held constant at 20-30 dB above threshold while the level of the ipsilateral stimulus was varied. For the LSO cells, the opposite configuration was used. All LSO units were modulated by ILD while all MNTB units were not. The blue data point shows the LSO population mean half-maximal ILD +/- 95% confidence interval. The black and red ILD functions with the dots are from the LSO cell and MNTB cell, respectively, shown in Fig. 4.1B. Mean ILD function slope was significantly shallower than MNTB rate-level slope.
LSO Creates ILD Responses

- EI inputs to LSO
- When sound is louder in ipsilateral ear, LSO neurons fire action potentials
- When sound is louder in the contralateral ear, LSO neurons are inhibited
Output of SOC to IC

- pyramidal cell
- multipolar cell
- octopus cell
- spherical cell
- globular cell
- cochlear nerve fiber, left side
- right side, cochlear nerve fiber

MSO: medial superior olive; LSO: lateral superior olive
NTB: nucleus of trapezoid body; IC: inferior colliculus
LSO Summary

- Cytoarchitecture – S-shaped laminae
- Neuron types – glutamate or glycine
- Inputs –
  - Spherical bushy AVCN ipsilateral
  - MNTB principle cells driven by globular bushy cells contralateral
- Outputs – Bilateral inferior colliculus
- Synapses –
  - Excitatory glutamate from ipsilateral
  - Inhibitory glycine from MNTB
- Basic Circuit –
  - Coincidence detector for ILD and ITD
VIAAT predominates in the periolivary nucleus especially in the medial ones.
Inputs are from one side. Lateral to MSO inputs are from the ipsilateral ventral cochlear nucleus. Medial nuclei receive inputs from the contralateral side, mostly VCN.
Example of SPON circuitry from Saldana and Berrebi.
Important inputs to some periolivary nuclei come from higher levels of the auditory system especially the midbrain.
Periolivary Nuclei Summary

- Neurons use GABA, glycine, or acetylcholine
- Inputs from cochlear nucleus, one side only
- Monaural
- Output to
  - IC: SPON
  - Cochlear nucleus: VNTB & VLPO
  - Cochlea -medial OCB: VMPO & other
  - Cochlea -lateral OCB: VLPO & other