Neural mechanisms of sound localization

How the brain calculates interaural time and intensity differences

Bottom line

Calculation of interaural differences in the brain depends on "wiring" and a balance between neural excitation and inhibition.

An overview of the auditory pathway

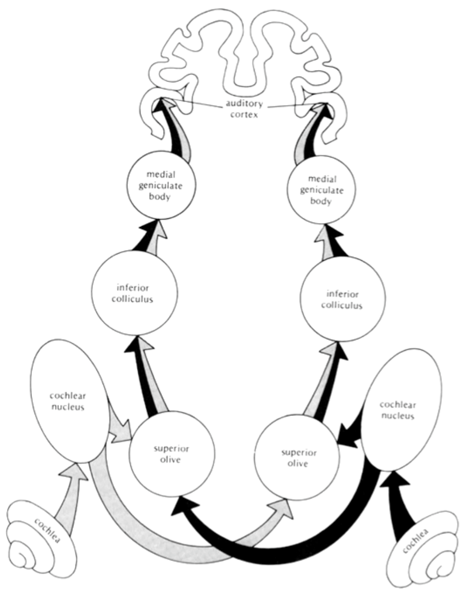
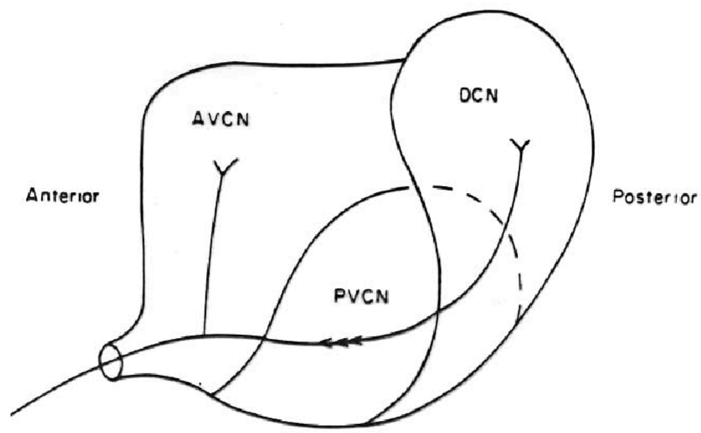


FIGURE 16.2 Highly schematic diagram of the bilateral central auditory system; the main pathways and nuclei are shown for both cochleas. Bilateral representation from binaural stimulation occurs at the superior olive and in all regions above. Based on a similar diagram by Lindsay and Norman (1972).

This is a highly schematic representation of the auditory pathways. The auditory nerve projects from the ear to the cochlear nucleus. The cochlear nucleus projects to the superior olive, on both the ipsilateral (same) and contralateral (opposite) side of the brain. Notice that information from both ears is carried along the pathway beginning with the superior olive. The superior olive projects to the inferior colliculus which projects to the medial geniculate body, or nucleus. The MGB projects to the auditory cortex, in the temporal lobe of the brain.

The circuit for sound localization starts in the cochlear nucleus



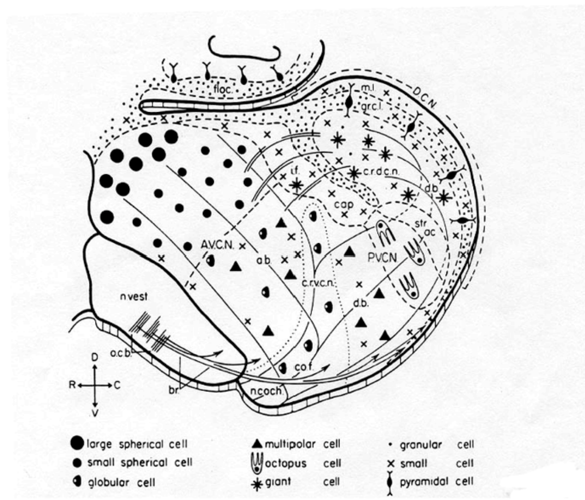
From Pickles (1988)

AVCN = anteroventral cochlear nucleus

PVCN = posteroventral cochlear nucleus

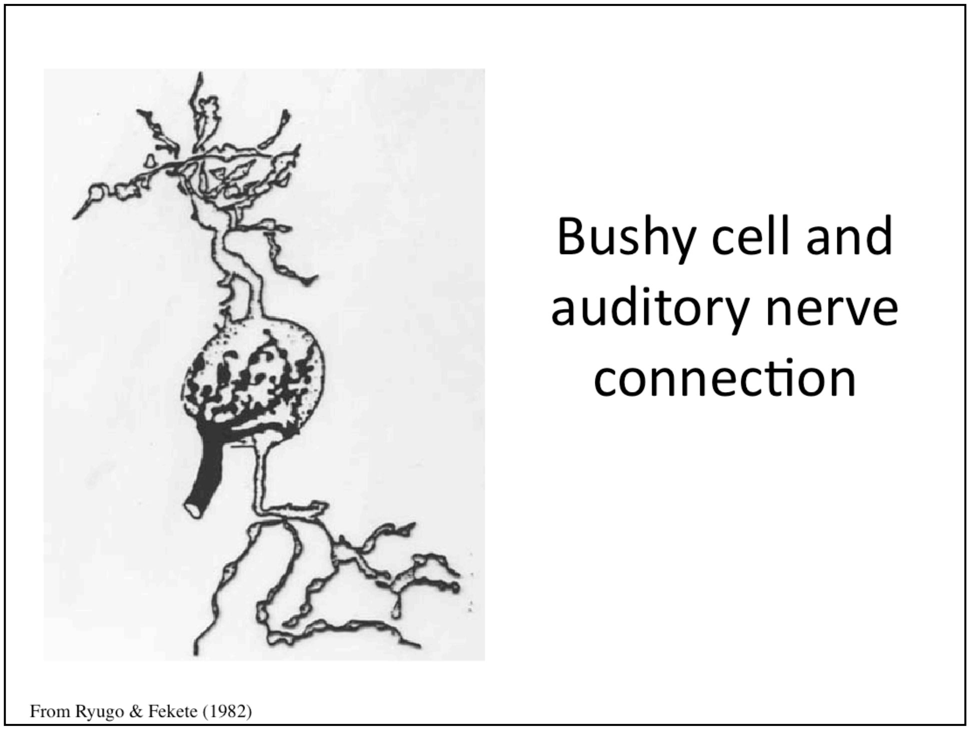
DCN = dorsal cochlear nucleus

Principal cells of the AVCN are spherical or bushy cells



From Pickles (1988)

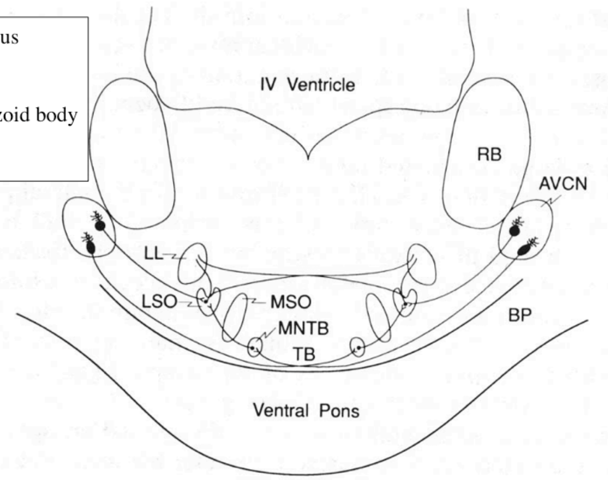
AVCN neurons respond like auditory nerve fibers do. We call them primarylike for that reason. AVCN is tonotopically organized.



Auditory nerve fibers make a large number of contacts with bushy cells, directly on the cell body. This connection is called an endbulb of Held, and it is what is called a secure connection. The bushy cell will fire each time the auditory nerve fiber fires.

Nuclei involved in interaural intensity comparisons

AVCN = anteroventral cochlear nucleus
LL = lateral lemniscus
LSO = lateral superior olive
MNTB = medial nucleus of the trapezoid body
MSO = medial superior olive
TB = trapezoid body



From Webster (1992)

Neurons in the AVCN project to the ipsilateral LSO and the contralateral MNTB. The MNTB projects to the ipsilateral LSO. So essentially, AVCN projects to LSO on both sides, but the contralateral projection makes a stop in MNTB. AVCN neurons respond like auditory nerve fibers do. We call them primarylike for that reason. AVCN is tonotopically organized.

Lateral superior olive (LSO)

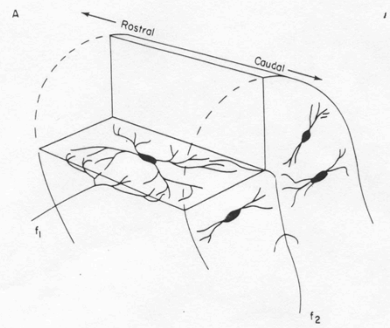
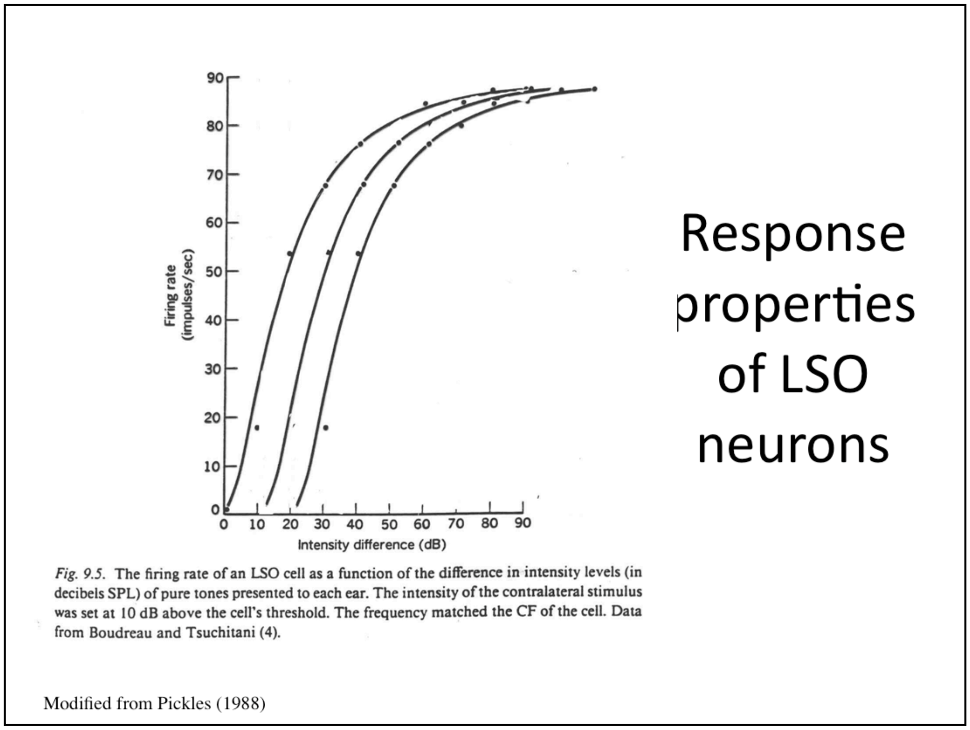


Fig. 6.11 (A) The neural organization of the LSO. f_1, f_2, afferent fibres. Adapted from Scheibel and Scheibel (1974).

EI
(Excitatory- Inhibitory)
Response

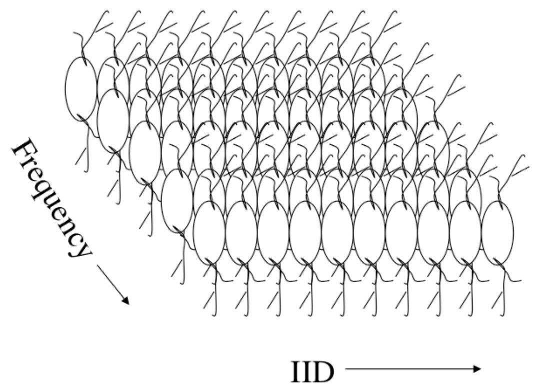
From Pickles (1988)

Neurons in the LSO have dendrites arrayed in two directions. They receive inputs from one set of (ipsilateral) fibers on the dendrites on one side, and inputs from another set of (contralateral via MNTB) fibers on the other side. Nerve fibers don't cross over to the other set of dendrites. LSO neurons seem to be structured to make comparisons across ears. The neurons are tonotopically organized. Neurons are excited by ipsilateral inputs and inhibited by contralateral inputs.



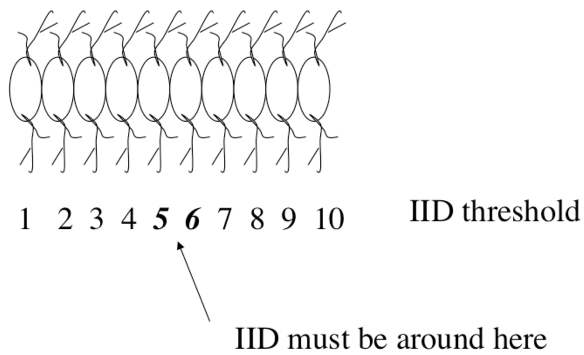
LSO neurons respond to intensity differences between the ears. Neurons start to respond at different IIDs and increase their response rate as the IID increases over a range of about 40 dB. By seeing which neurons are responding, a code for IID could be obtained.

Layout of LSO (rolled out)



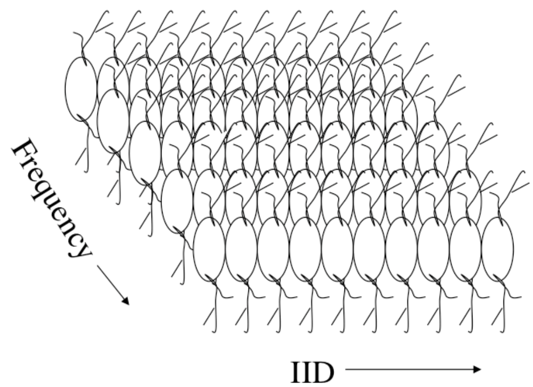
We can think of LSO as a sheet of cells. All the neurons in one row respond to the same frequency. All the neurons in one column respond to the same IID.

One frequency row in LSO



So as you move along one row, each neuron responds over a slightly different range of IIDs. In this picture, if the IID is 5 dB, the neurons with IID thresholds of 5 dB or less will respond, but the ones with higher IID thresholds won’t.

Pattern of activity gives IID across the spectrum

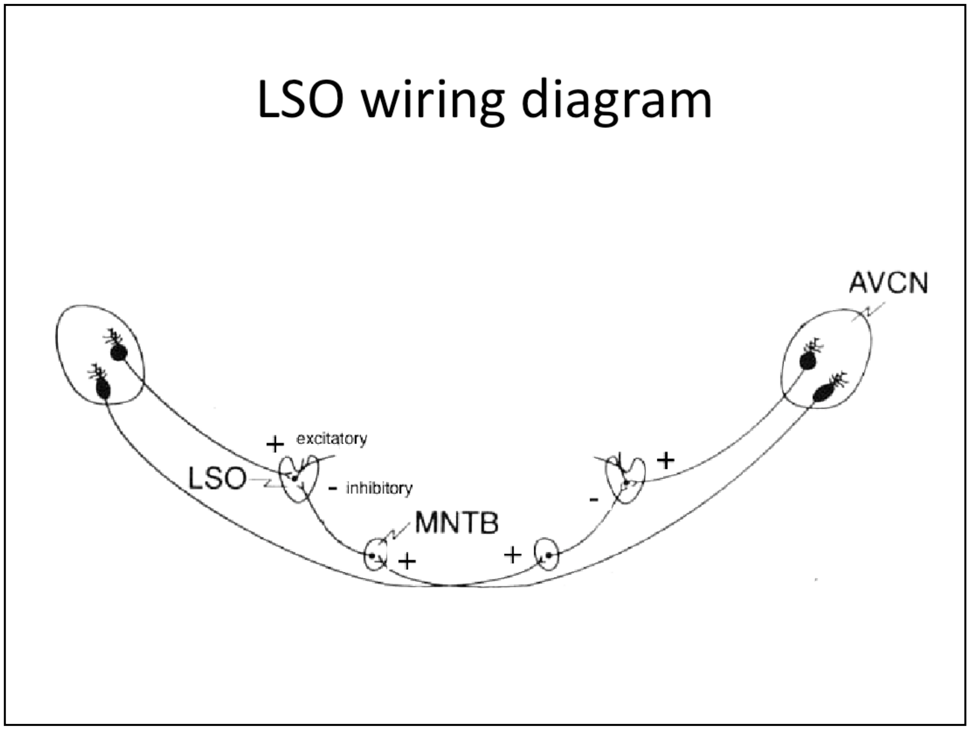


So LSO neurons form a sort of graph or chart that tells what the IID is across the range of frequencies.

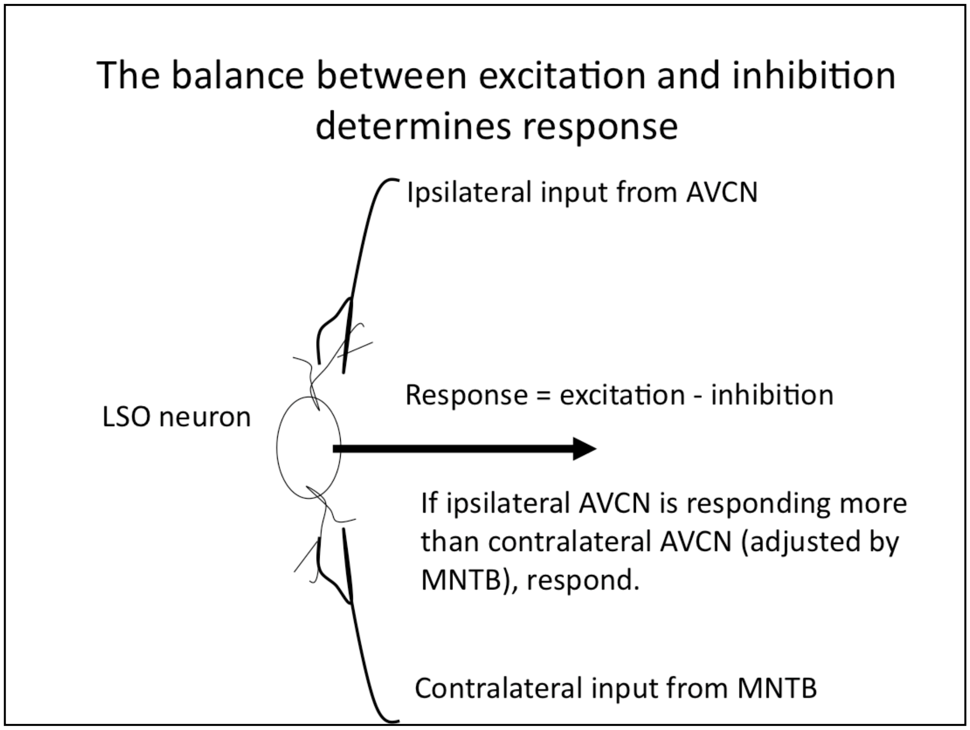
If the LSO were a graph, and the x-axis is frequency, then the y-axis is

- Intensity
- Spectral shape
- Interaural intensity difference
- Interaural time difference

How does response in LSO become specific for IID?



The output of AVCN is exitatory, but the output of MNTB is inhibitory. When AVCN excites MNTB, MNTB inhibits LSO.



This picture illustrates the inputs to one LSO neuron.

The LSO calculates IID by subtracting the response of the contralateral ear from the response of the ipsilateral ear using inhibition.

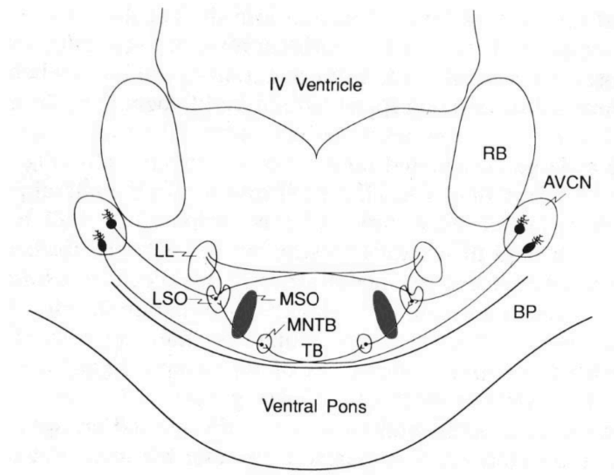
By adjusting the amount of inhibition delivered by MNTB, can make different LSO neurons respond over different ranges of IIDs.

This excitation/inhibition mechanism is a good example of how the auditory nervous system derives information from the code carried by the auditory nerve.

If the sound source is close to the right ear, then the LSO neurons on the left side of the brain

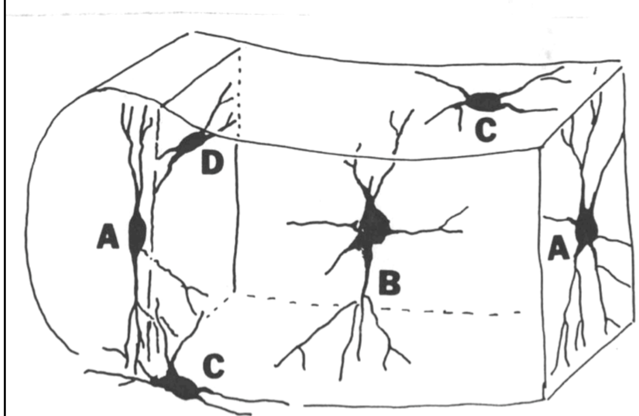
- respond a lot
- respond a little
- don't respond at all

How about MSO?



From Webster (1992)

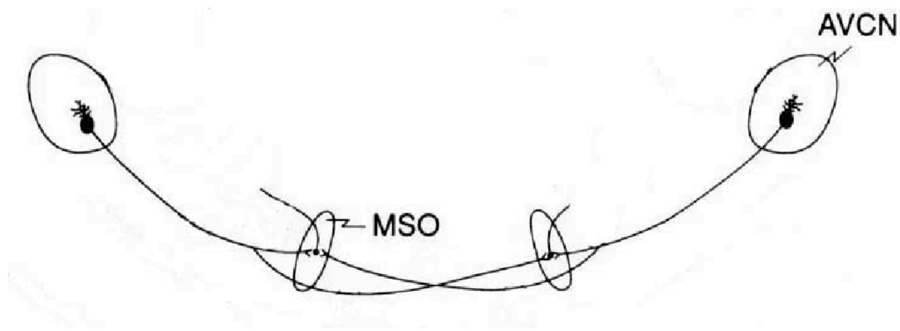
Like LSO neurons, MSO neurons look like they make comparisons



EE
(Excitatory-Excitatory)
Response

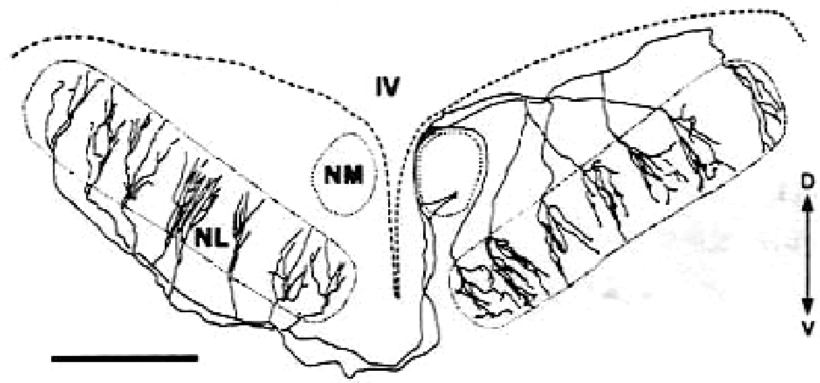
From Pickles (1988)

MSO neurons receive inputs from both AVCNs.



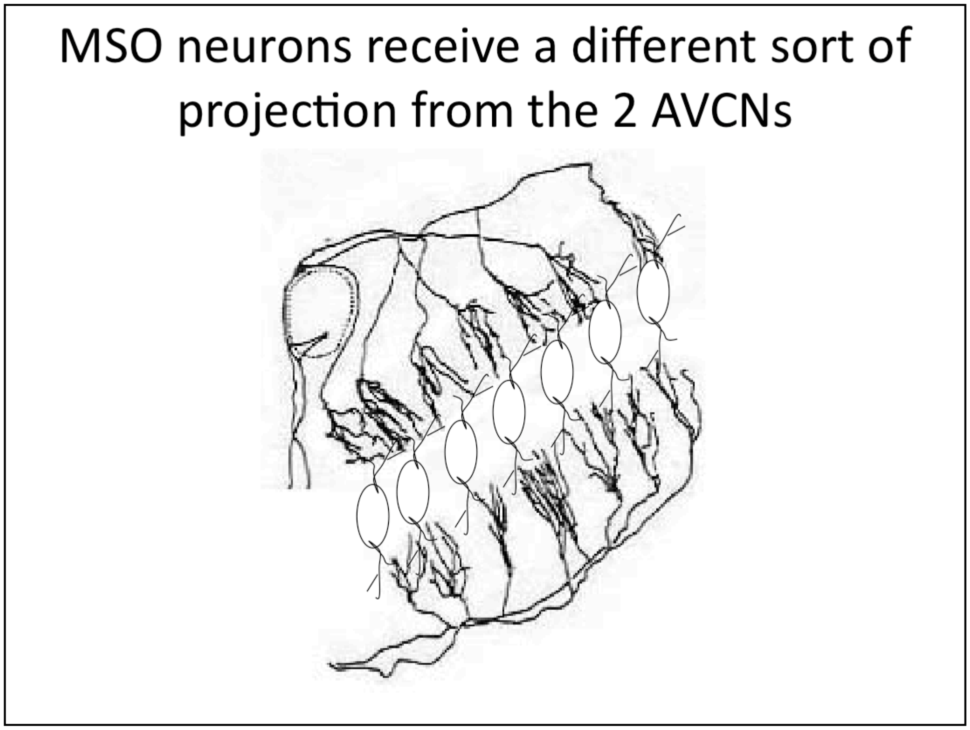
Each AVCN axon splits and sends a branch to the MSO on each side.

Branching pattern of AVCN axons is different on ipsilateral and contralateral sides

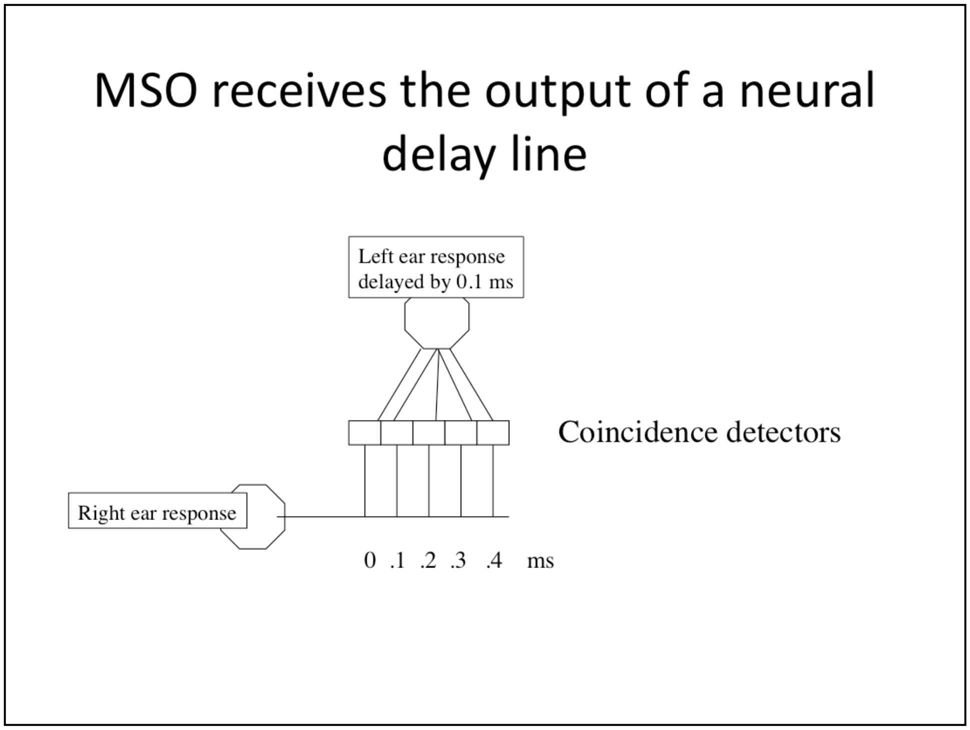


From Sullivan & Konishi (1986)

The branches of the axons on the ipsilateral side are all around the same distance from the branch point. On the contralateral side, a main axon branch extends along the nucleus, sending off a branch every so often. This drawing was made in an owl. NM is nucleus magnocellularis, which is homologus to the AVCN in mammals.



The neurons in each MSO, represented by the shaded ovals, will have one sort of branching pattern approaching them from the ipsilateral side and the other sort approaching them from the contralateral side. Remember that the input to the MSO is the phase-locked response of AVCN neurons.



The boxes in the center of the diagram are coincidence detectors. A box lights up when it receives two inputs simultaneously. The time it takes an input to travel from the right ear to the coincidence detectors is longer for the "later" branches, so the .4 ms box will receive right ear inputs .4 of a ms later than the 0 ms box does. The inputs from the left ear travel along equal length branches, so they all arrive at all the coincidence detectors at the same time. Now if the message from the left ear arrives a little later than the message from the right, then the message from the left ear will arrive at all the boxes at the same time as the message from the right ear arrives at one of the boxes, determined by the interaural delay. The action potentials from each ear are phase-locked to the same frequency-- so the delay we're talking about is the time between action potentials coming from the two ears. If the sound continues, then after a time coincidence detectors for longer delays will respond, but no coincidence detectors for shorter delays will respond.

MSO calculates ITDs by detecting coincident inputs from a delay line constructed from the axons of AVCN neurons.

IIDs are useful for localizing ____-frequency sounds; ITDs are useful for localizing ____-frequency sounds.

- high, high
- high, low
- low, high
- low, low

The tonotopic organization of the parts of the SOC matches the interaural calculations performed

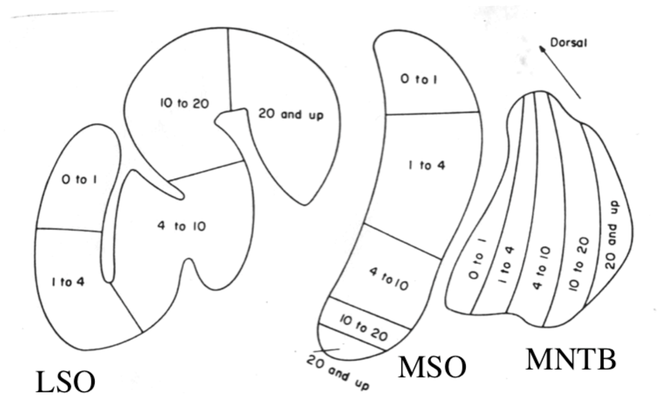


FIGURE 4.6. Tonotopic organization of the cat SOC from Figure 21, Guinan, Norris, and Guinan (1972), reprinted with permission of Gordon and Breach Science Publishers Ltd.

From Pickles (1988)

Most neural space in LSO is devoted to high frequencies--the frequencies where IIDs occur in nature. By contrast, most neural space in MSO is devoted to low frequenices--the frequenciees for which ITD can be calculated unambiguously. MNTB's tonotopic organization matches that of LSO, as expected.

Conclusions

- The neurons of the superior olive calculate interaural differences in intensity and time.
- The LSO uses a balance of inhibition and excitation to calculate IIDs.
- The MSO uses a circuit established by the axons of AVCN neurons to calculate ITDs.

Text sources

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