

## HST.723J/9.285J - Neural Coding and Perception of Sound

Spring 2005

### Macpherson & Middlebrooks (2002)

It has been known for over a century that the auditory system uses both timing and intensity differences between the two ears to calculate the location of a sound. This paper uses the more modern head-related transfer function technique (or directional transfer functions - DTFs) to simulate sounds in space. Timing or level cues are manipulated independently to see which cue is dominant in which spectral regions. The results confirm the dominance of timing and low frequencies and level at high frequencies for much more complicated (and realistic) stimuli than were possible in the days of Lord Rayleigh.

### Tollin & Yin (2003)

The precedence effect refers to the perceptual suppression of echoes, and is thought to be an important part of our ability to function in reverberant environments such as classrooms. There have been a number of physiological studies into the possible neural bases of the precedence effect but there was very little evidence that the animals used in the physiological studies really perceived things in the same way as humans. This paper addresses the question using a number of neat behavioral tasks in cats to map out some of the most important aspects of the precedence effect, including summing localization (also used in stereo reproduction), localization dominance, and the echo threshold.

### Freyman et al. (2001)

It is intuitive that separating a target from a masker in space makes the target easier to hear, but why is that? Earlier work using noise maskers had shown that this release from masking can be predicted based on known binaural cues, involving level and timing differences between the ears. This study shows that things become more complicated when the masker shares some similarities with the target. The precedence effect (see the Tollin and Yin paper) is used to shift the perceived location of the masker without substantially changing the simple detection cues available to listeners. This is found to have no effect for noise maskers, but a substantial effect for speech maskers. Various manipulations are used to narrow the range of potential "similarities" between the target and masker that might be responsible for the effect.

### Reyes et al. (1996)

- This paper uses an *in vitro* brain slice preparation to study the characteristics of binaural coincidence detector cells in *nucleus laminaris* (NL), the avian homolog of the mammalian MSO. Slice preparation are very popular in neurobiology

because they allow stable intracellular recordings from anatomically-identified cells for long periods of time, and they also make it possible to deliver chemicals with known concentration to either the extracellular medium or, via a patch micropipette, to the intracellular space as well. Here, the slice preparation is primarily used to study the intrinsic electrical properties of the neural membrane of NL cells.

- An original feature of this paper is the use of the *conductance clamp* technique, whereby currents are injected intracellularly to mimic the effects of the changes in membrane conductance produced by synaptic inputs from the cochlear nuclei (called *nucleus magnocellularis*, NM, in birds). This involves both intracellular measurements of the instantaneous membrane voltage and a mathematical model to compute the current to mimic a desired change in membrane conductance.
- Results show that high firing rates and good phase locking in NL cells at high frequencies are best achieved by having a small number of large synaptic inputs from NM. On the other hand, sensitivity to differences in arrival times of the NM inputs from the two sides (to mimic ITD) is best when there is a large number of small synaptic inputs. The authors propose a hypothesis to reconcile these somewhat conflicting requirements.
- An important finding is that only cells containing a low-threshold, outward-rectifying K<sup>+</sup> conductance show good phase locking and ITD sensitivity at high frequencies.
- How does the width of the "ITD" tuning curves *in vitro* compare with the physiological range of ITDs for the chick (less than 200 μsec)? Think about what aspects of the normal cell function *in vivo* might not be adequately mimicked by the *in vitro* stimulation protocol.

### **Brand et al. (2002)**

- This paper addresses the role of inhibitory inputs to the MSO in ITD processing. The animal model is the Mongolian gerbil, a small rodent with good low-frequency hearing.
- The first part of the paper replicates for the gerbil MSO the finding McAlpine et al. (2001) made in the guinea-pig IC, specifically the systematic dependence of best ITD on CF. This suggests that this dependence is neither created at the level of the IC nor idiosyncratic to the guinea pig.
- The second (and more interesting) part shows that glycinergic inhibition affects ITD tuning of MSO neurons, by shifting the best ITD away from the midline. Note that the most informative results were obtained by local application of strychnine, an antagonist to the neurotransmitter glycine, rather than by application of glycine itself. This is often the case in pharmacological studies. How solid is the result on the effect of strychnine?
- Also presented are simulation results using a point neuron model of MSO cells. For the model to work at 1000 Hz, the time constants of the inhibitory PSCs had to be extremely short (0.1 msec). How plausible is this?
- Can you think of a mechanism other than inhibition that could explain the systematic shift in best ITD with pure-tone frequency as shown in Fig. 1b and 4b?

## Zhou et al. (2005)

- Brand et al found that inhibition shifts the best ITDs of MSO neurons in the gerbil. To explain this finding, they use a point neuron model to show that brief, precisely timed inhibition preceding contralateral excitation can produce the observed shift in best ITD.
- The present paper by Zhou et al argues that the mechanism proposed by Brand et al. can only work if the inhibition is extremely brief, so brief that it is inconsistent with *in vitro* physiological observations from MSO neurons. They propose an alternative mechanism for ITD tuning based on an anatomical asymmetry observed in most MSO neurons, that the axon originates on the dendrite that receives AVCN inputs from the ipsilateral side. They use a compartmental model of MSO neurons to show that this structural asymmetry can create a best ITD of about 200  $\mu$ sec. This best ITD can be modulated by two opposing forces, inhibition and activation of sodium channels. Their model predicts the results of Brand et al., while being consistent with the known anatomy and physiology of MSO neurons.
- An important implication of the Zhou et al model is that, rather than being hard-wired, ITD tuning in MSO can be dynamically modulated, possibly under central control.
- You can skip the sections entitled "Linear cable properties" and "Additional simulations", as well as the text associated with Fig. 3, 10 and 12.