

## **Neural Coding and Auditory Perception**

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## **Neural coding of sound in complex acoustic environments**

### **Sponsor:**

NIH-NIDCD Grants DC02258 and DC05209

### **Project Staff:**

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The long-term goal of our research is to understand the neural mechanisms that mediate the ability of normal-hearing people to understand speech and localize sounds in everyday acoustic environments comprising reverberation and competing sound sources. In the past year, we continued work on three areas: (1) Physiological studies of sound localization in reverberant environments; (2) Spatio-temporal representation of pitch in the auditory nerve and cochlear nucleus; (3) Studies of dynamic range adaptation as a possible mechanism for alleviating the dynamic range problem, which impacts all aspects of auditory perception.

### ***Sound localization in reverberant environments***

In reverberant environments, acoustic reflections interfere with the direct sound arriving at a listener's ears, distorting the binaural cues for sound localization. Yet, normal-hearing listeners accurately localize sounds in everyday reverberant environments.

In order to identify neural correlates of robust localization in reverberation, we used virtual auditory space (VAS) techniques for studying the effects of reverberation on the directional rate responses of single units in the inferior colliculus (IC) of awake rabbits. We focused on neurons that are sensitive to interaural time differences (ITD) in broadband noise, including both low-frequency neurons sensitive to ITD in the fine time structure and high-frequency neurons sensitive to ITD in the amplitude envelope. We find that reverberation degrades the directional sensitivity of single neurons, although the amount of degradation depends on the characteristic frequency (CF) and the type of binaural cues available. When ITD is the only directional cue present in the VAS stimuli, low-CF cells maintain better directional sensitivity in reverberation than high-CF cells. Using recordings from primary auditory neurons, we show that this result can be attributed to the fact that reverberation degrades the directional information in envelope ITDs more so than in the fine time structure. On the other hand, when the VAS stimuli include interaural level differences (ILD) as well as ITDs, directional sensitivity is comparable throughout the tonotopic axis, suggesting that, at high frequencies, ILDs provide better directional information than envelope ITDs in reverberation. These results are in harmony with those of human psychophysical studies of sound localization in reverberant environments.

Rayleigh's duplex theory of sound localization stipulates that listeners use ITD at low frequencies and ILD at high frequencies. Our results suggest that, in the anechoic condition, sensitivity to envelope ITD in high frequency neurons can rival sensitivity to fine-structure ITD in low-frequency neurons. The low perceptual weight given to high-frequency envelope ITD cues in sound localization may result from the fact that these cues are less reliable than ILD cues in reverberant listening conditions.

### ***Spatio-temporal representation of the pitch of complex tones***

We have previously shown that the spatio-temporal pattern of auditory nerve (AN) fibers contains robust cues to the pitch of complex tones [2]. To investigate whether these cues are extracted centrally, we are evaluating whether cochlear nucleus (CN) neurons are sensitive to manipulations of the spatio-temporal pattern of AN activity. We recorded from single AN fibers and CN units in anesthetized cats and compared these responses to those of a peripheral auditory model [4]. We used Huffman stimuli, which have flat magnitude spectra and a  $2\pi$  phase transition around a frequency  $FT$ , to manipulate the relative timing of spikes between neighboring AN fibers without changing the overall firing rates [1].

We used the principle of cochlear scaling invariance to infer the spatio-temporal pattern of AN activity in response to a Huffman stimulus from the response of a single fiber. We first verified that responses of a single AN fiber to a set of Huffman stimuli with varying  $FT$  resembles the responses of an array of model fibers with different characteristic frequencies (CFs) to a fixed  $FT$  stimulus, as predicted by scaling invariance. In both the model and AN fibers, changing the steepness of the phase transition produced systematic changes in the spatio-temporal pattern of discharge. A broad phase transition excited fibers more coincidentally across CF at the response onset, while a sharp phase transition led to later coincident firings.

When  $FT$  was equal to the CF, AN fibers with low CF ( $<2$  kHz) tended to fire at  $1/CF$  intervals. In comparison, responses of CN units had fewer peaks and were shorter in duration. In particular, primary-like-with-notch and onset responders typically showed one peak for broad phase transition stimuli and two peaks for stimuli with sharp transitions. The extra later peak for stimuli that excite AN fibers more coincidentally later in their responses is consistent with the notion that these CN neurons act as cross-frequency coincidence detectors. Overall, our results suggest that the firing patterns of some CN neurons reflect processing of the spatio-temporal patterns of AN activity. This finding may explain some of the difficulties experienced by cochlear implant users because the spatio-temporal patterns of activity are highly abnormal with electric stimulation through cochlear implants.

### ***Rapid dynamic range adaptation to sound level statistics in the auditory nerve***

Human hearing covers a vast range of sound levels (100-120 dB) with nearly constant discrimination ability across the entire range. In contrast, the rate responses of most auditory neurons only change with sound level over a narrow dynamic range (20-40 dB), and saturate at low to moderate sound levels. To search for neural mechanisms that may help resolve the dynamic range problem, we have investigated whether dynamic range adaptation, a phenomenon previously observed in the auditory midbrain [3], already occurs in primary auditory neurons. Using continuous, dynamic stimuli whose level distributions contain a high-probability region (HPR), we found that the dynamic range of AN fibers shifts systematically toward the most probable sound level for both tone and noise stimuli. Using dynamic stimuli in which the mean sound level switches between two values every 5 s, we further found that dynamic range adaptation occurs rapidly, with time constants of only a few hundred milliseconds.

Dynamic range adaptation in the AN appears to be distinct from classic firing rate adaptation. Studies of firing rate adaptation in AN report that adaptation produces only a decrement in firing rate with no change in sensitivity or threshold, while dynamic range adaptation is fundamentally a

change in sensitivity or operating range. We find that, while there is substantial cross-fiber variability in both dynamic range shifts and rate decrements with HPR stimuli, the two metrics are not correlated. Furthermore the time constants of dynamic range adaptation estimated with switching HPR stimuli are not correlated with time constants of firing rate adaptation. These results suggest that the two forms of adaptation may be driven by distinct processes.

We quantitatively compared dynamic range adaptation in the AN and in the IC by using the same model to fit both our AN data and Dean et al.'s IC data. We found that dynamic range adaptation is weaker in the AN than in the IC. These findings suggest that rapid adaptive processing to the sound level distribution first occurs in the auditory periphery and is enhanced along the auditory pathway.

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#### Meeting Papers

S. Devore and B. Delgutte. "Spike-rate adaptation underlies robust neural encoding of sound source location in reverberation," Abstract 456.5, Society for Neuroscience, Washington, DC, November 2008.

S. Devore, A. Ihlefeld, B. Shinn-Cunningham and B. Delgutte. "Neural basis of spatial hearing in reverberant environments," Acoustical Society of America, Portland, OR, June 2009.

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### **Bilateral Cochlear Implants: Physiological and Psychophysical Studies**

#### **Sponsor:**

NIH-NIDCD Grants DC05775 and DC05209

#### **Project Staff:**

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The goal of this project is to identify the best stimulus configurations for effectively delivering binaural information with bilateral cochlear implants (CI) by means of complementary neurophysiological, psychophysical and theoretical studies. This year, physiological studies focused on characterizing the effect of binaural deprivation on sensitivity to interaural time differences (ITD) with bilateral implants by measuring the ITD tuning of midbrain auditory neurons in congenitally deaf cats. Psychophysical studies focused on studying the effects of electrode interactions on ITD sensitivity and developing methods for reducing these interactions. We also continued developing models of responses of auditory brainstem neurons to bilateral stimulation through CIs.

#### **Neurophysiology**

Human bilateral CI users do poorly on tasks involving ITD, a cue which provides important benefits to the normal hearing, especially in challenging acoustic environments. Yet the precision of neural ITD coding in acutely-deafened, bilaterally-implanted cats is essentially normal [2]. One possible explanation for this discrepancy is that the extended periods of binaural deprivation typically experienced by CI users degrade neural ITD sensitivity. To test this hypothesis, we recorded from single units in inferior colliculus (IC) of two groups of bilaterally-implanted, anesthetized cats: acutely-deafened cats, which had normal binaural hearing until experimentation, and congenitally deaf white cats, which received no auditory inputs until the experiment. In the congenitally deaf cats, the rate responses of only half as many neurons (42% vs. 82%) exhibited significant ITD sensitivity for low-rate periodic pulse trains compared to acutely deafened cats. The congenitally deaf cats also showed increased levels of spontaneous activity and increased prevalence of suppressive responses to electric stimulation compared to acutely-deafened cats. These results suggest that deprivation of auditory experience comprising the neonatal period has a major impact on the function of the brainstem circuits processing ITD. An important question is whether there is a critical period for the effects of deprivation or whether these effects also occur in animals deafened as adults (which would be a model for post-lingually deaf subjects). Another important question is whether the effects of deprivation can be reversed by appropriate electric stimulation of the binaural system.

Current CI processors deliver ITD information in the envelope of amplitude-modulated pulse trains. Psychophysical and physiological results suggest that ITD would be a more effective cue

if it were delivered in the fine time structure as well as in the envelope. However both behavioral and neural ITD sensitivities with electric pulse trains are poor for the high pulse rates used in today's CI processors. Inspired by the finding that introducing binaurally-coherent jitter improves behavioral ITD discrimination for high-rate pulse trains [1], we measured responses of IC neurons in anesthetized deaf cats as a function of pulse rate, pulse jitter, and ITD. For pulse rates above ~300 pps, jitter increased the firing rates of many IC neurons and gave these neurons ITD sensitivity comparable to that observed for low-rate periodic pulse trains. Thus, jitter appears to unmask neural ITD sensitivity by restoring sustained firing in IC neurons. These results may lead to new processing strategies that harness the effect of jitter to improve sound localization and speech reception in noise with bilateral CI.

### ***Psychophysics***

Simultaneous stimulation of multiple electrodes, as occurs when listening through a processor, may lead to interactions that influence ITD sensitivity with bilateral CI. Specifically, summation (integration) of information might occur when the same ITD is presented on two interaural electrode pairs. On the other hand, the presence of a fixed ITD on one interaural pair might degrade the ITD sensitivity for a second pair (interference). To test these hypotheses, ITD sensitivity was measured in two subjects using 50-pps unmodulated, biphasic pulse trains. An apical interaural electrode pair and a basal pair were selected from the left/right pairs used by the subject's sound processors. Both summation and interference were observed. For example, the just-noticeable difference in ITD (ITD JND) measured in one subject when both interaural pairs carried the same ITD, was half (70  $\mu$ s) the JND of the most sensitive interaural pair tested. In another subject, the ITD JND measured for one interaural pair increased from about 75  $\mu$ s when stimulated alone to 180  $\mu$ s when an interleaved pulse train was also presented with zero ITD to a second interaural pair. This relatively large interference is consistent with our hypothesis that electrode interactions may negatively impact the ability of CI to represent the ITD information from multiple sound sources.

In the hope of reducing electrode interactions that degrade ITD sensitivity, we implemented the method of van den Honert and Kelsall [3] for focusing intracochlear stimulation. In this method, all 16 electrodes in an intracochlear array are stimulated simultaneously, and the current at each electrode is adjusted to focus the stimulation at one or more sites along the electrode array. We conducted psychophysical measures in two subjects to determine whether this focusing technique reduces the degree to which a subthreshold stimulus delivered to an electrode influences the detection threshold for a neighboring test electrode. We found that, while the overall levels required to reach threshold were higher for focused stimulation than for monopolar stimulation, focused stimulation significantly reduced the interaction between electrodes. This is psychophysical evidence that current spread can be substantially reduced with focused stimulation. Such focused stimulation may improve the ability to represent multiple ITDs as would naturally occur in the presence of multiple sound sources.

These psychophysical results suggest that electrode interactions may limit the ability to individually represent the ITDs of multiple sound sources with bilateral CI. The current focusing technique offers hope of improving the ability of CI listeners to take advantage of binaural cues in noisy environments by reducing electrode interactions.

### ***Neurocomputation***

We continued to work on the modeling of auditory brainstem responses to bilateral CI stimulation. Specifically, we are developing a detailed model of the inputs to the IC, including a phenomenological model of auditory nerve responses to electrical stimulation, models of spherical bushy cells, and models of medial superior olivary (MSO) neurons. We have explored the effects of the model parameters in more detail, and we have looked at a wider set of stimulus conditions.

We find that ITD sensitivity in MSO model neurons is highly dependent on appropriate synaptic parameters for different input stimulation rates, so that, in order to achieve ongoing ITD sensitivity, the model parameters must be chosen for each specific rate. Generally, stronger excitatory synaptic inputs are required for the model neuron to be ITD-sensitive at high rates. When the model MSO cell is stimulated at a rate for which it is not tuned, the responses are limited to the onset or not sensitive to ITDs.

These modeling results suggest that the poor ITD sensitivity with bilateral CI may be due to a mismatch between the high stimulation rates used and the cellular properties of the binaural neurons stimulated by today's processors. Stimulation of the cochlear region below 1000 Hz might be required to achieve good ITD sensitivity at high stimulation rates. This hypothesis is consistent with the stimulation rate limitation observed in other tasks such as pitch perception.

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