Neural Coding and Auditory Perception

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Neural coding of sound in complex acoustic environments

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The long-term goal of this research is to understand the neural mechanisms that mediate the ability of normal-hearing people to understand speech and localize sounds in complex acoustic environments comprising reverberation and competing sound sources. In the past year, we continued work on two research projects: (1) Physiological studies of sound localization in reverberant environments; (2) Spatio-temporal representation of pitch in the auditory nerve and cochlear nucleus. We also started a new project on the dynamic range problem, which impacts all aspects of auditory perception.

Sound localization in reverberant environments

Most listening environments contain acoustically reflective boundary surfaces e.g., ground, walls, trees, and rocks. Listeners are thus faced with the task of localizing sound sources in the presence of interfering reflections and reverberation. Despite this interference, normal-hearing listeners localize sounds quite accurately in moderate reverberation. We showed previously that inferior-colliculus (IC) neurons sensitive to interaural time differences (ITD) are more robust to reverberation than predicted by current models of binaural processing based on interaural crosscorrelation [4]. This work was done in anesthetized animals, and focused on low-frequency IC neurons sensitive to ITDs in the fine time structure. In the past year, we extended these results by studying the effects of reverberation on ITD sensitivity across the entire tonotopic axis of the IC in awake rabbit, including high-frequency neurons sensitive to ITDs in the envelope.

We found that, in anechoic conditions, comparable rate-based information about ITD is available in both low and high frequency neurons. However, reverberation, leads to a frequency-dependent degradation in ITD-sensitivity, with more severe effects at higher frequencies. Model simulations suggest that the reduction in information at higher frequencies can be partially, but not entirely, accounted for by the differential effects of reverberation on stimulus fine-structure and envelopes.

While our results demonstrate that low-frequency ITD-sensitive IC neurons better encode ITD in reverberation than their high-frequency counterparts, there is significant variability in the effects of reverberation across the population of low-frequency neurons. Neurons in the IC also display a wide variety of temporal response patterns to tones and noise. Notably, many neurons fire more action potentials in the earlier portions of the stimulus than in later portions, a feature termed spike rate adaptation. Because reverberant energy builds up over time following the onset of a stimulus, we hypothesized that spike rate adaptation may enhance directional coding of reverberant sounds i.e. that units which adapt more rapidly to a sustained stimulus will more faithfully encode the true source ITD. This hypothesis was supported by the finding of a significant correlation between a measure of spike rate adaptation and the degree to which neural responses to reverberant stimuli deviate from predictions of a neuron model based on interaural correlation averaged over the entire stimulus duration [5].

Our finding that neural sensitivity to ITD in stimulus envelopes is degraded more by reverberation than sensitivity to ITD in stimulus fine structure has implications for bilateral cochlear implant processing strategies. Namely, current strategies that encode ITDs in the amplitude envelope of modulated pulse trains may provide listeners with relatively poor spatial information in natural listening environments. Improved spatial acuity in bilateral implantees may be achieved by developing strategies that encode ITDs in the fine-structure.

Spatio-temporal representation of the pitch of complex tones

We have previously shown that the auditory nerve (AN) contains spatio-temporal cues to the resolved harmonics of a complex tone that are more robust to variations in stimulus level than traditional rate-place cues and could potentially be used in pitch extraction [2]. To investigate whether these cues are extracted by central neurons, we recorded from single units in cochlear nucleus (CN) of anesthetized cats.

To characterize the spatio-temporal sensitivity of CN neurons, we used transient complex stimuli (“Huffman sequences”) designed to manipulate the relative timing between AN fibers tuned to neighboring frequencies [1]. CN neurons were said to be phase-sensitive (PS) if their rate response changed more with Huffman phase manipulations than do AN fibers at comparable stimulus levels. About one-third of our CN neurons were PS; a majority of these (consisting mostly of primary-like and chopper units) preferred the stimulus that excited AN fibers less coincidently. Five PS units (one primary-like-with notch, one onset, and three low-frequency phase-lockers) behaved as predicted for cross-frequency coincidence detectors.

We hypothesized that PS CN neurons would have rate representations of pitch similar to spatio-temporal representations in the AN if they extracted the spatio-temporal pitch cues. To test this hypothesis, we recorded responses of CN units to harmonic complex tones with missing fundamentals. We found a few CN units that maintained salient pitch cues at high stimulus levels. However, on average, the units that were not PS had more robust rate representations of pitch than AN fibers and PS units, contrary to our hypothesis. Thus, even though there exist CN units that better represent the pitch percept of complex tones than do AN fibers, there is no evidence for a correlation between spatio-temporal sensitivity and robust rate cues to pitch.

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 firing rates of most auditory neurons only change with sound level over a narrow dynamic range (20-40 dB). Recently, Dean et al. [3] have shown that rate responses of midbrain auditory neurons adapt to the distribution of levels in the stimulus by shifting their dynamic range towards the most frequently occurring levels. We investigated whether such dynamic range adaptation also occurs in primary auditory neurons.

We measured rate-level functions of auditory-nerve (AN) fibers in anesthetized cats using 50-ms tones and broadband noise presented with no inter-stimulus silent intervals. The distribution of stimulus levels always spanned 75 dB, but contained a 12-dB wide high-probability region (HPR, 80% probability) whose mean level was systematically varied. We found that the dynamic range of AN fibers shifts nearly linearly with the HPR mean level at a rate ranging from 0.1 to 0.5 dB/dB. However, the benefits of these dynamic range shifts for level coding were partially offset by decreases in both the maximum firing rates and the slopes of rate-level functions with increasing HPR mean level. In order to quantify the precision of level coding, we computed the Fisher information for our entire population of AN fibers in response to broadband noise. The maximum of the Fisher information (representing maximum level sensitivity) shifted nearly linearly with HPR mean level at a rate of 0.26 dB/dB, resulting in enhanced coding accuracy within the HPR.

We also investigated the dynamics of dynamic range adaptation by using sound stimuli whose HPR mean level alternates between two different values every 5 sec. The time constants of dynamic range adaptation ranged from 30 ms to 3 sec, and were about 3 times shorter when switching from low to high levels than vice-versa.

The observation of dynamic range adaptation in the auditory nerve demonstrates rapid adaptive processing in the auditory periphery that improves coding accuracy of the most relevant levels in the acoustic environment. These dynamic range shifts are nevertheless smaller than those observed in the midbrain, suggesting that additional adaptation may also occur at intermediate processing stages in the brainstem.

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Bilateral Cochlear Implants: Physiological and Psychophysical Studies

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Bilateral cochlear implantation is becoming increasingly common with the goal of restoring the functional benefits of binaural hearing, including accurate sound localization and improved speech reception in noise. While most wearers of bilateral cochlear implants benefit, they have difficulty processing interaural time differences (ITD), which provide the greatest binaural benefits in normal-hearing listeners. The overall goal of this project is to give a detailed, quantitative characterization of sensitivity to ITD with bilateral cochlear implants by means of closely-integrated psychophysical, neurophysiological and modeling studies. Over the past year, we developed a neuronal population model of ITD sensitivity with bilateral cochlear implants aimed at making predictions of psychophysical performance. We also initiated neurophysiological studies investigation the effect of binaural experience on ITD sensitivity.

Population model of inferior colliculus neurons

In normal hearing, ITD acuity for broadband stimuli is best on the midline (ITD = 0) and degrades as the reference ITD moves laterally. This trend is captured by a population model of ITD discrimination based on IC data from normal-hearing cats [1]. The model includes realistic distributions of best frequency and best ITD. In the model as in the data, the rising slopes of rate-ITD curves tend to align near the midline because the best ITD is correlated with the width of ITD tuning across the population [1]. This correlation is likely to be partly dependent on cochlear mechanics, which influences both sharpness of tuning and best ITD, through the effects of bandpass filtering and disparities in traveling wave delays, respectively. Since cochlear

processing is bypassed in cochlear implants, we hypothesized that the normal correlation between best ITD and tuning width would be disrupted, and with it the normal alignment of rate-ITD curves near the midline which leads to fine acuity.
To test this hypothesis, we modified our IC population model so that ITD tuning curves and distributions of best ITDs would match IC data from bilaterally implanted cats [2]. We also measured ITD JNDs as a function of reference ITD in two bilaterally-implanted human subjects. We found that JNDs increase as the reference ITD moves away from the midline as in normal hearing, although the mean JNDs are larger for electric hearing. A first version of the model in which best ITD and tuning widths were uncorrelated predicted nearly constant ITD acuity for all reference ITDs, consistent with our hypothesis but contrary to the psychophysical data. This failure led to a reanalysis of the IC data from bilaterally-implanted cats, which revealed that best ITD is in fact positively correlated with width of tuning, tending to position the steepest slopes of the rate-ITD curves on the midline. A modification of the model based on this new analysis brought predictions in line with the psychophysical data.

This work demonstrates that model predictions of psychophysical performance depend not only on the tuning characteristics of individual neurons (which were the same in both versions of the model) but also on the distributions of neuronal characteristics across the population. The correlation between best ITD and width of tuning observed in the IC of both normal-hearing and deafened cats may reflect an experience-dependent selection process occurring during development. If so, congenitally-deaf animals may lack this correlation. We plan to test this prediction in future experiments.

Effect of auditory experience on neural ITD sensitivity

We previously showed that ITD tuning for pulse train stimuli in the IC of deafened, bilaterally-implanted cats is similar to that found in normal hearing cats for broadband noise [2]. Yet, human wearers of bilateral cochlear implants have poorer ITD discrimination than normal-hearing subjects. A major difference between our animal model of bilateral cochlear implants and the human patients is binaural experience: While our cats have normal hearing until they are deafened just before the neurophysiological experiments, human patients often undergo long periods of deprivation of binaural experience before they receive their second implant. We hypothesized that such deprivation may degrade ITD sensitivity.

To test this hypothesis, we characterized neural ITD sensitivity in the IC of two groups of animals: (1) congenitally deaf white cats (DWC) who lose all hair cells before the onset of hearing, and therefore presumably never hear until they are bilaterally implanted; (2) acutely-deafened cats (ADC) who have normal hearing until just before the neural recordings. These two groups of animals represent the maximal contrast with respect to auditory experience.

We found sharp differences in the characteristics of IC neurons in the two groups of animals. Spontaneous activity was common in DWC, with some neurons reaching spontaneous rates as high as 60 spikes/s, whereas spontaneous activity is rare in ADC. More importantly, ITD sensitivity for low-rate pulse trains was less common and weaker in DWC than in ADC. Only 39% of neurons were considered ITD sensitive (by an ANOVA test) in DWC vs. over 80% in ADC. In some DWC neurons, each stimulus pulse produced a long lasting suppression of spontaneous activity, contrasting with the precisely timed excitatory response to each pulse typically found in ADC neurons. Nevertheless, ITD tuning in the minority of DWC neurons that were ITD sensitive could be as sharp as that found in ADC neurons.

These results support the hypothesis that deprivation of binaural experience (in this case including the neonatal period) can alter neural ITD sensitivity and suggest that the acutely deafened cats used in previous studies [2] may not provide a sufficiently realistic animal model of bilateral cochlear implants. Since DWC and ADC represent the maximum possible contrast in binaural experience, future studies need to examine the effect of timing and duration of binaural deprivation on neural ITD sensitivity.

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