

Signal Transmission in the Auditory System

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1 Middle and External Ear

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Project Staff

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1.1 Goals

Sound is received by vertebrates (except fish) through a common set of anatomical components, which have evolved into a variety of configurations in different taxonomic groups. Our goal is to understand the function of these structures in the hearing process and to apply this knowledge (a) to explanation of the evolutionary processes that produced this variety, (b) to interpretation of pathological processes (in humans) that interfere with sound reception, and (c) to guidance of reconstruction of damaged ears to restore hearing capabilities. Experimental work is carried out at the Eaton-Peabody Laboratory at the Massachusetts Eye and Ear Infirmary in Boston, in cooperation with Dr. Saumil N. Merchant of the Department of Otolaryngology.

1.2 Comparative Structure and Function in Mammalian Ears

The Mongolian gerbil is often used as an experimental animal for the study of the ear. Measurements of responses of the gerbil middle ear before and after modifying specific structures (the *pars flaccida* of the tympanic membrane and the middle-ear cavity) allow specification of the effects of these structures, but the results do not lead to simple connections with the hearing of the gerbil. Thus, the connection between the specialization in structure and specialization in function is complex. (Rosowski et al., 1999)¹

One well-identified cause of hearing loss in humans is exposure to high-intensity sound. Variations among individuals in sensitivity to “acoustic trauma” are substantial and their physiological basis is not known. Measurements in an inbred mouse strain (Yoshida et al., 2000)² demonstrate a resistance to noise-induced hearing loss; the physiological difference is apparently in the inner ear.

Some species have middle-ear cavities which are divided into multiple smaller cavities by bony laminae. The acoustic effect of these multiple spaces is generally to generate anti-resonances which reduce the response of the ear in narrow frequency regions. The evolutionary forces that might favor this configuration have been the subject of speculation. A recently suggested idea is that the creation of anti-resonances at relatively low frequencies (from Helmholtz resonances) avoids the occurrence of anti-resonances at higher frequencies (organ-pipe resonances) that might interfere with cues to sound-source localization that are known to occur at high frequencies. Measurements in cats with the bony septum removed demonstrate that the higher-frequency effects do occur, thus supporting the hypothesis (Rosowski, et al.).³

1.3 Abnormal Human Middle-Ear Function

In audiology departments hearing tests are usually conducted with earphones and it is assumed that the earphones generate the same sound pressure independent of the ear to which they are coupled. However, because some pathological ears have highly abnormal acoustic impedance, it is possible that the generated sound may also be abnormal. This problem has been investigated with measurement of sound pressures in the ear canals of normal and abnormal ears with two kinds of earphones, insert and supra-aural. The results show that specific pathologies which decrease the acoustic-impedance magnitude of the ear can cause sizeable reductions in the generated sound pressure and therefore sizable over estimates of the hearing loss of the ear (Voss et al., in press).⁴ The acoustic basis of the variations with earphone type and pathology type can be understood in terms of acoustic models related to the structural variations (Voss et al., 2000).⁵ This demonstration leads to the suggestion that audiometers used in clinics should include microphones that assess the sound pressure in each ear.

In otitis media, a common middle-ear malady, fluid may fill the middle-ear space that is normally air-filled. The mechanisms through which the fluid alters hearing sensitivity are not well understood. An experimental approach, in which controlled fluid injections are made in ears extracted from cadavers, has demonstrated that more than one mechanism is involved and that the effects can be separated (Ravicz et al., in press).⁶ This knowledge will allow physicians to assess how much of a patient's hearing loss results from the fluid and how much might be caused by other factors.

¹ J.J. Rosowski, M.E. Ravicz, S.W. Teoh, and D. Flandermeyer, “Measurements of middle-ear function in the Mongolian gerbil, a specialized mammalian ear,” *Audiol. Neurootol.*, 4: 129-138 (1999).

² N. Yoshida, J. Hequembourg, C.A. Atencio, J.J. Rosowski, and M.C. Liberman, “Acoustic injury in mice: 129/SvEv is exceptionally resistant to noise-induced hearing loss,” *Hearing Res.* 2000 (in press).

³ J.J. Rosowski, G.T. Huang, C.A. Atencio, and W.T. Peake, “Acoustic effects of multiple middle-ear air spaces”, *New Developments in Auditory Mechanisms*, H. Wada, Ed., Presented July 1999 in Sendai, Japan (in press).

⁴ S.E. Voss, J.J. Rosowski, S.N. Merchant, A.R. Thornton, C.A. Shera, and W.T. Peake, “Middle-ear pathology can affect the ear-canal sound pressure generated by audiologic earphones,” *Ear and Hearing* (in press)

⁵ S.E. Voss, J.J. Rosowski, C.A. Shera, and W.T. Peake, “Acoustic mechanisms that determine the ear-canal sound pressures generated by earphones,” *J. Acoust. Soc. Am.* 107: 1548-1565 (2000).

⁶ M.E. Ravicz, S.N. Merchant, and J.J. Rosowski, “Effects of middle-ear fluid on umbo motion in human ears. *New Developments in Auditory Mechanisms*, H. Wada, Ed., Presented July 1999 in Sendai, Japan (in press).

Measurement of mechanical responses in the ears of patients has always been a problem in diagnostic situations. Now new instruments (laser Doppler vibrometers) are available which can measure the velocity of the tympanic membrane in awake subjects. Preliminary measurements have been reported which test the robustness of the results obtained with this method (Whittemore et al., 2000).⁷

1.4 Middle-ear function across the cat family

We have chosen to focus on this family of mammals to search for structural and functional variations in the middle ears that might be related to ecological and ethological features of the species. A set of acoustic measurements in the external ears of anesthetized specimens (representing 11 of the 37 species in the family) have been analyzed (Huang, 1999)⁸ and prepared for publication (Huang et al., 2000).⁹ The results show that the acoustic admittance at the tympanic membrane tends to vary with the size of the animal (which varied from domestic cat size to tiger and jaguar). In essence, as the body size increases, the frequency dependence moves to lower frequencies. Some species deviate significantly from the family trend.

1.5 Publications

Journal Articles

Rosowski, J.J. , M.E. Ravicz, S.W. Teoh, and D. Flandermeyer. "Measurements of middle-ear function in the Mongolian gerbil, a specialized mammalian ear," *Audiol. Neurootol.*, 4: 129-138 (1999).

Yoshida, N., J. Hequembourg, C.A. Atencio, J.J. Rosowski, and M.C. Liberman. "Acoustic injury in mice: 129/SvEv is exceptionally resistant to noise-induced hearing loss," *Hearing Res.* 2000 (in press).

Huang, G.T., J.J. Rosowski, W.T. Peake, "Relating middle-ear acoustic performance to body size in the cat family: Measurements and models" *J. Comp. Physiol. A* (in press).

Voss, S.E., J.J. Rosowski, C.A. Shera, and W.T. Peake. "Acoustic mechanisms that determine the ear-canal sound pressures generated by earphones," *J. Acoust. Soc. Am.*, 107: 1548-1565 (2000).

Voss, S.E., J.J. Rosowski, S.N. Merchant, A.R. Thornton, C.A. Shera, and W.T. Peake. "Middle-ear pathology can effect the ear-canal sound pressure generated by audiologic earphones," *Ear and Hearing* (in press).

Dissertation

Huang, G. T. *Measurement of middle-ear acoustic function in intact ears: Application to size variation in the cat family*, Ph.D. Thesis, MIT Dept. of Electrical Engineering and Computer Science, February, 1999.

Meeting Papers

Ravicz, M.E., S.N. Merchant, and J.J. Rosowski, "Effects of middle-ear fluid on umbo motion in human ears," *New Development in Auditory Mechanisms*, H. Wada, Ed., Presented July, 1999 in Sendai, Japan (in press).

⁷ K.R. Whittemore, J.J. Rosowski, B.B. Poon, C.Y. Lee, and S.N. Merchant "Measurements of umbo velocity using a laser-Doppler vibrometer in live human subjects with normal hearing," *Abstracts of the 23rd Midwinter Meeting of the Association for Research in Otolaryngology*, Saint Petersburg Beach, Florida, February 20-24, 2000, p. 114.

⁸ G.T. Huang, *Measurement of middle-ear acoustic function in intact ears: Application to size variation in the cat family*, Ph.D. Thesis, MIT Dept. of Electrical Engineering and Computer Science, February, 1999.

⁹ G.T. Huang, J.J. Rosowski, and W.T. Peake, "Relating middle-ear acoustic performance to body size in the cat family: Measurements and models," *J. Comp. Physiol. A* (in press).

Rosowski, J.J., G.T. Huang, C.A. Atencio, and W.T. Peake. "Acoustic effects of multiple middle-ear air spaces," *New Developments in Auditory Mechanisms*, H. Wada, Ed., Presented July 1999 in Sendai, Japan (in press).

Whittemore, K.R., J.J. Rosowski, B.B. Poon, C.Y. Lee, and S.N. Merchant, "Measurements of umbo velocity using a laser-Doppler vibrometer in live human subjects with normal hearing" *Abstracts of the 23rd Midwinter Meeting of the Association for Research in Otolaryngology*, St. Petersburg Beach, Florida, February 20-24, 2000, p. 114.

2 Cochlear Mechanics

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2.1 Mechanical properties of the tectorial membrane (TM)

Although it is widely agreed that the TM plays a key role in delivering sound-induced mechanical stimuli to the hair bundles of hair cells, basic properties of the TM and its role in hearing remain unclear.

In many conceptions of cochlear micromechanics, the TM is assumed to be mechanically stiff, so that it moves as a rigid plate that is connected to other cochlear structures as a mechanical lever (see Abnet and Freeman, 2000). In other conceptions, mechanical properties of the TM contribute to the frequency selectivity of cochlear neurons. There is little agreement about some mechanical properties of the TM. For example, models of the thin (limbal) part of the TM that connects to the spiral limbus vary over the maximum possible range: from completely rigid to completely flexible and therefore mechanically unimportant. With only one important exception, effects of the TM are analyzed with 2D cross-sectional models that attribute two seemingly contradictory features to the thicker middle portion of the TM that overlies the hair cells: (1) its radial stiffness is taken to be so large that the middle zone of the TM moves as a rigid body, and (2) its longitudinal stiffness is taken to be so small that longitudinal coupling through the middle zone can be completely ignored.

Uncertainty about basic mechanical properties of the TM limits our understanding of its role in cochlear mechanics. For the most part, neither the generally accepted nor controversial assumptions about the mechanical properties of the TM have been tested experimentally.

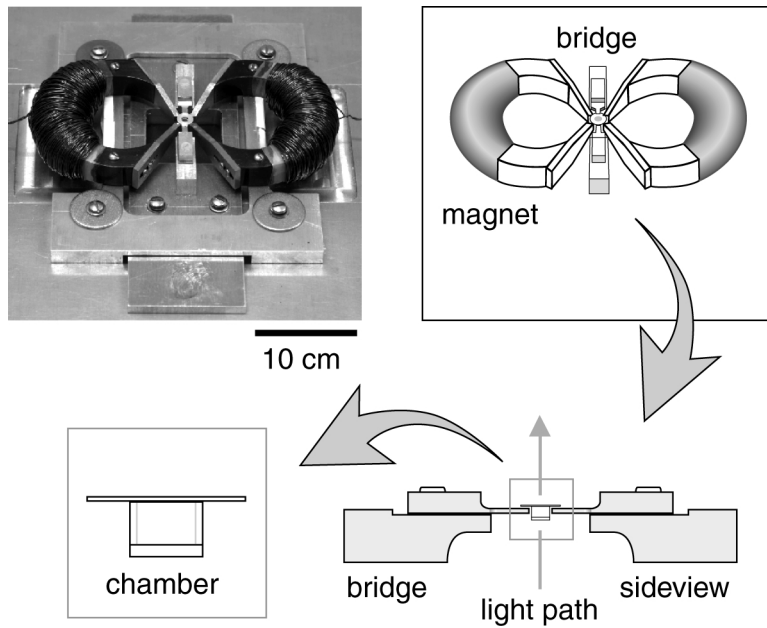


Figure 1: Magnetic bead method. Tectorial membranes were attached to the glass floor of an experimental chamber (lower left panel) shaped like an inverted top hat (5 mm inner diameter, 3 mm length). The chamber was supported on an aluminum bridge in the light path of an Axioplan microscope (Zeiss, Thornwood, NY). The bridge was oriented between two electromagnets (top left).

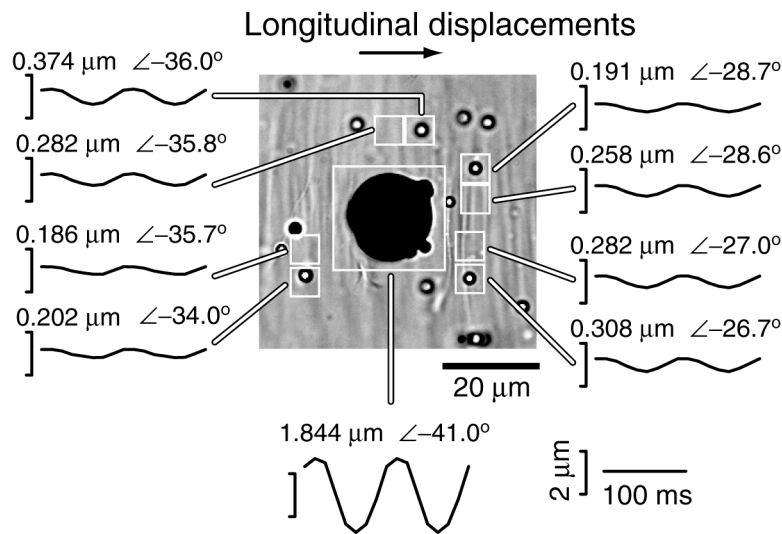


Figure 2: Motions of the magnetic bead and adjacent tissue. The image shows an isolated TM stimulated with a longitudinal (horizontal) magnetic force (≈ 40 nN) applied to the magnetic bead (large black circle). The smaller dots are non-magnetic marker beads attached to the free-surface of the TM and to the magnetic bead. Images acquired at 8 equally spaced phases of the 10 Hz stimulus were used to calculate displacement time waveforms. Two cycles of the waveform resulting for each region are shown in the surrounding plots. The numbers indicate the peak displacement and angle of the fundamental component of the time waveform. Analyzed regions (white boxes) include the magnetic bead plus 4 marker beads plus regions near the marker beads in which motions of the radial fibrillar structure of the TM are tracked.

We have prepared a manuscript (Abnet and Freeman, 2000)¹⁰ describing mechanical properties of the isolated mouse TM measured with a magnetic bead method (Figure 1). This method allowed measurements with submicrometer displacements, which are in the range of sound-induced motions and more than 100 times smaller than those in previous studies (Figure 2). Results show (1) **Viscoelasticity**: The frequency dependence of TM displacement lies between that of a purely viscous and purely elastic material, suggesting that both contribute to frequency selectivity of the material. (2) **Mechanical coupling**: Space constants on the order of 10–40 μm suggest that adjacent hair bundles are mechanically coupled via the TM. (3) **Anisotropy**: The mechanical impedance is approximately 3 times greater in the radial direction than it is in the longitudinal direction. This mechanical anisotropy correlates with anatomical anisotropies, such as the radially oriented fibrillar structure of the TM.

2.2 Publications

Journal Articles

Abnet, C. C., and D. M. Freeman. "Deformations of the isolated mouse tectorial membrane produced by oscillatory forces." *Hearing Research*, in revision (2000).

Meeting Papers

Aranyosi, A.J., and D. M. Freeman, "Media dependence of bleb growth in cochlear hair cells," *Abstracts of the 22nd Midwinter Meeting of the Association for Research in Otolaryngology*, St. Petersburg, Florida, February 13-18, 1999, pp. 159-160.

Theses

McAllister, A. R., *Measuring electrical properties of the tectorial membrane*, Masters Thesis, MIT Dept. of Electrical Engineering and Computer Science, February 1999.

3 Auditory Neural Coding of Speech

Sponsor:

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Project Staff:

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The long-term goal of this project is to understand neural mechanisms for the processing of speech, music, and other biologically-significant sounds. Efforts during the past year have focused on three different areas: (1) neural representation of musical consonance, (2) a mathematical model of onset neurons in the cochlear nucleus, (3) stimulus coding for cochlear implants.

3.1 Neural correlates of musical consonance

Musical consonance depends on the absence of *roughness*, the auditory percept associated with amplitude envelope fluctuations in the range of 30-300 Hz. Neurons in the auditory midbrain respond preferentially to

¹⁰ C.C. Abnet and D.M. Freeman, "Deformations of the isolated mouse tectorial membrane produced by oscillatory forces," *Hearing Res.*, in revision (2000).

modulation frequencies in that range, and are therefore likely to perform temporal processing relevant to musical consonance. To test this hypothesis, we recorded responses of single units in the inferior colliculus (IC, the principal auditory nucleus in the midbrain) of anesthetized cats to pairs of either pure or complex tones selected to form musical intervals varying in dissonance. Temporal properties of these neurons were characterized by their modulation transfer functions (MTFs).

For a majority of IC neurons, dissonant tone pairs gave rise to greater fluctuations in discharge rate than consonant pairs. Moreover, for a subset of neurons having onset response patterns to tones, average rates of discharge were higher for dissonant tone pairs than for consonant pairs. This situation contrasts with that in the auditory nerve, where there are no correlates of roughness in average discharge rates, and correlates in temporal discharge patterns are only revealed by additional bandpass filtering. The filtering, which is presumably performed in the brainstem, is consistent with the MTFs of IC neurons.

Together with our previous finding of neural correlates of musical pitch in interspike intervals of auditory-nerve fibers, these results indicate that music perception is constrained by neural processing in the auditory periphery, brainstem and midbrain, and that percepts such as roughness may be coded in specific temporal discharge patterns.

3.2 Mathematical model of onset neurons in the cochlear nucleus

Onset (On) neurons in the cochlear nucleus are characterized by a transient response at the onset of high-frequency (HF) tones and by entrainment (a spike on every cycle) to low-frequency (LF) tones up to 1000 Hz. These neurons are divided into three types based on the shape of their peri-stimulus time (PST) histograms for HF tone-bursts: On with chopping (On-C), On with late activity (On-L), and ideal On (On-I). To better understand the neuronal mechanisms underlying this diversity, we determine what a model must have to both entrain to LF tones and account for all three subtypes of On PST histograms.

First, we consider the simplest model that can produce On responses, an integrate-to-threshold model with a constant refractory period. Inputs to the model are from model auditory-nerve (AN) fibers acting via excitatory synapses. On-C PST histograms for HF tones and entrainment to LF tones are obtained when the integration time constant is sufficiently low (< 0.5 ms) and the number of inputs sufficiently large (> 400) for the model to act as a coincidence detector. However, this model cannot produce both entrainment and On-I/On-L PST histograms.

We developed a new model with a stimulus-dependent refractory state to meet the opposing constraints of preventing short interspike intervals which would lead to chopping, and allowing short intervals so as to entrain to LF tones. The model is an integrator-to-threshold, as above, but, after entering the refractory state following each spike, it does not exit this state until the membrane voltage hyperpolarizes past a transition voltage. The model entrains to LF tones because the membrane voltage drops below the transition voltage on every cycle when the AN inputs are phase-locked. Moreover, there is no chopping so long as the membrane voltage stays above the transition voltage. With relatively fewer inputs (~ 200), increased membrane voltage fluctuations produce some spikes during the later part of the stimulus, leading to On-L PST histograms.

These results suggest that On-I and On-L neurons differ from On-C neurons by their spike generator, whereas On-I neurons differ from On-L neurons by their larger number of AN inputs.

3.3 Stimulus coding for cochlear implants

Cochlear implants restore partial hearing to the deaf by electric stimulating the auditory nerve. With current devices, only 25% of the users achieve open sentence recognition. The overall goal of our research is to understand the deficiencies in current devices and to point to a way in which these deficiencies can be overcome. Our working hypothesis is that a successful device will produce activity on the auditory nerve that is similar to the sound-evoked activity in a healthy ear.

Many modern cochlear implants use sound processing strategies in which speech information is encoded by amplitude modulation of a periodic train of biphasic pulses. Rubinstein et al., (1999)¹¹ have proposed that neural representation of the modulator might be improved by addition of a constant, high-rate desynchronizing pulse train (DPT). One motivation for the DPT is to reintroduce spontaneous activity into the deaf cochlea. The goals of our experiments were (1) to compare responses of auditory nerve fibers elicited by electric pulse trains to spontaneous activity in a healthy cochlea, and (2) to determine whether the DPT is useful for better encoding of sinusoidal modulation. We recorded responses from auditory nerve fibers in acutely-deafened, anesthetized cats to both unmodulated and sinusoidally-modulated pulse trains delivered through an intracochlear electrode.

We found both similarities and some surprising differences between responses to unmodulated pulse trains and spontaneous activity. Response variability from presentation to presentation (as characterized by the pulse number distribution) was comparable to variability in spontaneous activity for all pulse rates. Interspike interval distribution for a 1.2-kpps pulse train had exponential envelopes, as for spontaneous activity. However, interval distributions for stimuli with pulse rates above 4.8 kpps often had a prominent mode near 5 msec and an exponentially-decaying tail, quite unlike spontaneous activity.

We also measured the sensitivity of auditory-nerve fibers to sinusoidal modulation of a 4.8-kpps biphasic pulse train. Using very small modulation depths (< 5%), we were able to obtain both period and interval histograms for sinusoidal modulation resembling responses to pure tones in a healthy ear. Such stimuli with very small modulation depths can be thought of as the superposition of an unmodulated DPT and a highly-modulated pulse train similar to those used in current processors. However, this similarity between the response to pure tones and that to modulated pulse trains only held over a narrow range of stimulus levels and modulation depths, suggesting that the DPT amplitude would have to be very precisely adjusted in real-life situations.

These results are encouraging, with some major caveats, about the prospect of using a desynchronizing pulse train to improve speech processors for cochlear implants. Future work will aim at further testing the DPT concept using more realistic and complex stimuli.

3.4 Publications

Journal Articles

McKinney, M.F. and B. Delgutte, "A possible neurophysiological basis of the octave enlargement effect," *J. Acoust. Soc. Am.* 106: 2679-2692 (1999).

Meeting Papers

Kalluri, S. and B. Delgutte, "Cellular properties of ventral cochlear nucleus onset units studied using a mathematical model," *Abstracts of the 22nd Midwinter Meeting of the Association for Research in Otolaryngology*, St. Petersburg, Florida, February 13-18, 1999, p. 144.

Kalluri, S. and B. Delgutte, "Models for the diversity of response properties of cochlear-nucleus onset neurons," *Abstracts of the 23rd Midwinter Meeting of the Association for Research in Otolaryngology*, St. Petersburg, Florida, February 20-24, 2000, p. 184.

Litvak, L.M., B. Delgutte, D.K. Eddington, and P.A. Cariani, "Auditory-nerve fiber responses to electric stimulation: Modulated and unmodulated pulse trains," *Asilomar Conference on Cochlear Implantable Auditory Prostheses*, August 1999.

McKinney, M.F. and B. Delgutte, "Neural correlates of roughness: A possible basis for musical dissonance," *Neural Information Processing Systems Workshop*, December 1999.

¹¹ J.T. Rubinstein, B.S. Wilson, C.C. Finley, and P.J. Abbas, "Pseudospontaneous activity: stochastic independence of auditory nerve fibers with electrical stimulation," *Hearing Res.*, 127: 108-118 (1999).

4 Neural Mechanisms of Spatial Hearing

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Project Staff

Dr. Bertrand Delgutte, Ruth Y. Litovsky, Courtney C. Lane

The long-term goal of this project is to understand the neural mechanisms for sound localization in noisy and reverberant environments. Such research might lead to hearing aids and auditory prostheses that would be more effective in noise and reverberation. Our efforts in the past year have focused on neural correlates of spatial release from masking, the phenomenon whereby a signal becomes more easily detected when spatially separated from a masker.

We recorded from single units in the inferior colliculus (IC) of anesthetized cats in response to a broadband signal (100-Hz click train or 40-Hz chirp train) in continuous broadband noise. Stimulus azimuth was simulated using a virtual space (VS) technique based on head-related transfer functions. VS stimulation allows us to digitally manipulate individual localization cues, thereby probing which localization cues give rise to spatial release from masking. We had previously shown that individual IC neurons show directionally-dependent masking in a virtual acoustic environment. The directional changes in masked threshold were commensurate with psychophysical observations. While responses of most neurons seem to depend only on interaural level differences, some neurons responses reflect changes in both interaural time and level differences. Recent results show that the directional pattern of masking in individual neurons is independent of signal azimuth. This finding contrasts with psychophysical results showing a complex dependence of masking on the locations of both signal and masker, thereby indicating that a correlate of spatial release from masking is not directly seen in responses of individual neurons. However, a neural correlate of spatial release might still be found by examining the responses of a population of IC neurons differing in their azimuth tuning.

We also examined the neural mechanisms underlying the directional masking of individual neurons. For two-thirds of the neurons, increasing the level of the masker caused the overall response to the signal to be reduced, indicating that masking reflects a suppressive mechanism such as synaptic inhibition. However, for those neurons which responded by spike discharges to the continuous masker, the most effective masking azimuth was highly correlated with the masker azimuth that produced the greatest excitation. These two results indicate that the suppression and the excitation produced by the masker have similar azimuth dependencies. Our findings suggest that models of spatial masking will have to incorporate not only directional and binaural mechanisms, but also the temporal properties of brainstem and midbrain auditory neurons.

4.1 Publications

Journal Articles

Delgutte, B., P.X. Joris, R.Y. Litovsky, and T.C.T. Yin, "Receptive fields and binaural interactions for virtual-space stimuli in the cat inferior colliculus." *J. Neurophysiol.* 81: 2833-2851 (1999).

Meeting Papers

Litovsky, R.Y., B. Delgutte, and T.C.T. Yin, "Physiological studies and neural mechanisms of echo suppression in the inferior colliculus of the cat," *J. Acoust. Soc. Am.* 105: 1150 (A) (1999).

Lane, C.C., B. Delgutte, R.Y. Litovsky, and M.C. Brown, "Spatial release from masking in the inferior colliculus," *Soc. Neurosci. Abstr.* 29: 667 (1999).