Section 3 Auditory Physiology

Chapter 1 Signal Transmission in the Auditory System

Chapter 1. Signal Transmission in the Auditory System

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1.1 Middle and External Ear

Sponsors

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1.1.1 Goals

Our aim is to determine how the structure of normal and pathological external and middle ears affects their acoustic and mechanical function. We measure the workings of ears of various animals as well as normal and pathological human middle ears. These acoustic and mechanical measurements are combined with structural measurements to generate testable quantitative models of external and middle-ear function. This knowledge is then applied to practical issues such as providing specifications for reconstructive surgery of the human ears and more basic issues such as whether the anatomical specializations of animal ears are related to the environment that the animals live in.

The work we performed this year includes an expansion of our collaboration with ear surgeons at the Massachusetts Eye and Ear Infirmary: this collaboration is leading to a better understanding of the mechanical effects of ear disease on the hearing process. Of special note this year is the work of Ms. Voss on how perforations of the tympanic membrane affect hearing function. This year's progress also includes a continuation of our work on (1) the middle-ear specializations in a Mongolian gerbil—an animal that is highly adapted to desert life, and (2) the analysis of the middle ear of different cat species to help us understand the effects of ear size on middle-ear function. The progress in the later project this year included a publication of some of our results from post-mortem zoo-cat specimens and an as yet unpublished series of acoustic measurements made on live cats of seven different species at the Cincinnati Zoo.

1.1.2 Publications

Journal Articles

Gopen, Q., J.J. Rosowski and S.N. Merchant. "Anatomy of the Normal Human Cochlear Aqueduct with Functional Implications." *Hear. Res.* 107: 9-22 (1997).

Huang, G.T., J.J. Rosowski, D.T. Flandermeyer, T.J. Lynch III, and W.T. Peake. "The Middle Ear of a Lion: Comparison of Structure and Function to Domestic Cat." *J. Acoust. Soc. Am.* 101: 1532-49 (1997).

Merchant, S.N., M.E. Ravicz, and J.J. Rosowski. "Experimental Investigations of the Mechanics of Type IV Tympanoplasty." *Ann. Otol. Rhinol. Laryngol.* 106: 49-60 (1997).

Merchant, S.N., M.E. Ravicz, S. Puria, S.E. Voss, K.R. Whittemore, W.T. Peake, and J.J. Rosowski. "Analysis of Middle-ear Mechanics and Application to Diseased and Reconstructed Ear." *Am. J. Otol.* 18: 139-54 (1997).

Puria, S., W.T. Peake, and J.J. Rosowski. "Sound-Pressure Measurements in the Cochlear Vestibule of Human Cadavers." *J. Acoust. Soc. Am.* 101: 2754-70 (1997).

Ravicz, M.E., and J.J. Rosowski. "Sound-power Collection by the Auditory Periphery of the Mongolian Gerbil *Meriones unguiculatus*: III. Effect of Variations of Middle-ear Volume on Power Collection." *J. Acoust. Soc. Am.* 101: 2135-47 (1997).

Teoh, S.W., D.T. Flandermeyer, and J.J. Rosowski. "Effect of *pars flaccida* on Peripheral Sound Conduction of Mongolian Gerbil: Evidence from Acoustical and Anatomical Measurements." *Hear. Res.* 106: 39-65 (1997).

Chapter in a Book

Peake, W.T., and J.J. Rosowski. "Acoustic Properties of the Middle Ear." In *Encyclopedia of Acoustics*, vol 3. Ed. M.J. Crocker. New York: Wiley, 1997, pp. 1337-46.

Published Conference Papers

Merchant, S.N., M.E. Ravicz, S.E. Voss, S. Puria, W.T. Peake, and J.J. Rosowski. "Middle-ear Mechanics in Normal, Diseased and Reconstructed Ears." In *Middle Ear Mechanics in Research and Otosurgery.* Ed. K.-B. Huttenbrink, Dresden, Germany: Dresden University of Technology, 1997, pp. 175-82.

Peake, W.T., and J.J. Rosowski. "Middle-ear Structural and Functional Dependence on Animal Size." In *Diversity in Auditory Mechanics.* Eds. E.R. Lewis, G.R. Long, R.F. Lyon, P.M. Narins, C.R. Steele, and E Hecht-Poinar. Singapore: World Scientific, 1997, pp. 3-10.

Puria, S., and J.J. Rosowski. "Measurements of Reverse Transmission in the Human Middle Ear." In *Diversity in Auditory Mechanics.* Eds. E.R. Lewis, G.R. Long, R.F. Lyon, P.M. Narins, C.R. Steele, and E. Hecht-Poinar. Singapore: World Scientific, 1997, pp. 151-57.

Rosowski, J.J., S.W. Teoh, and D.T. Flandermeyer. "The Effect of *pars flaccida* on the Sensitivity to Sound." In *Diversity in Auditory Mechanics.* Eds. E.R. Lewis, G.R. Long, R.F. Lyon, P.M. Narins, C.R. Steele, and E. Hecht-Poinar. Singapore: World Scientific, 1997, pp. 129-35.

Rosowski, J.J., S.N. Merchant, M.E. Ravicz, S.E. Voss, M. Caradonna, M.J. Cunningham, and W.T. Peake. "Analyses of Acoustic Mechanisms in Middle-ear Pathology and Reconstruction." In *Middle Ear Mechanics in Research and Otosurgery.* Ed. K.-B. Huttenbrink. Dresden, Germany: Dresden University of Technology, 1997, pp 183-89.

Conference Papers Presented

Cherukupally, S.R., S.N. Merchant, and J.J. Rosowski. "Correlations between Stapes Pathology and Conductive Hearing Loss in Otosclerosis." *Abstracts of the 20th Midwinter Research Meeting of the Association for Research in Otolaryngology,* St. Petersburg Beach, Florida, February 2-6, 1997, p. 66.

Huang, G.T., J.J. Rosowski, B.R. Cranston, and W.T. Peake. "Middle-ear Cavity Structure and Function in Bobcat (*Lynx rufus*)." *Abstracts of the Twentieth Midwinter Research Meeting of the Association for Research in Otolaryngology,* St. Petersburg Beach, Florida, February 2-6, 1997, p. 140.

Rosowski, J.J., S.W. Teoh, M.E. Ravicz, and D.T. Flandermeyer. "Measurements of Ossicular Velocity in Gerbil Middle Ears." *Abstracts of the Twentieth Midwinter Research Meeting of the Association for Research in Otolaryngology,* St. Petersburg Beach, Florida, February 2-6, 1997, p. 60.

Voss, S.E., J.J. Rosowski, S.N. Merchant, and W.T. Peake. "How Do Tympanic Membrane Perforations Affect Human Middle-ear Sound Transmission?" *Abstracts of the Twentieth Midwinter Research Meeting of the Association for Research in Otolaryngology,* St. Petersburg Beach, Florida, February 2-6, 1997, p. 49.

1.2 Cochlear Mechanisms

Sponsors

W.M. Keck Foundation
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John F. and Virginia B. Taplin Award in Health
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1.2.1 Osmotic Properties of the Tectorial Membrane

The tectorial membrane (TM) is a gelatinous structure that overlies the mechanically sensitive hair bundles of hair cells in the inner ear. This strategic position suggests that the TM plays a key role in cochlear micromechanics. However, little is known about the physicochemical properties of this tissue. The structure and biochemical composition of the TM suggest that it is a polyelectrolyte gel. Approximately 97 percent of the mass of TM is water. The dry weight consists of a matrix of proteins and polysaccharides. This matrix contains ionizable charge groups that attract mobile counterions from the bath to achieve macroscopic electroneutrality. These mobile counterions contribute to the osmotic pressure in the tissue which induces osmotic water influx. The resulting tissue swelling is opposed by the mechanical rigidity of the matrix. We have developed a mathematical model of these molecular mechanisms, and we have analyzed the model to determine relations between the osmotic, electrical, and mechanical properties of the TM.[1]

To test the model, we have measured changes in the size and structure of the isolated TM of the mouse in response to changes in the pH of the surrounding artificial endolymph solution.[2] Changes in the pH of the bath changes the ionization of charge groups in the TM. We incorporated knowledge of the prevalent charge groups (e.g., amino, carboxyl, and sulfate groups) into the gel model and compared theoretical predictions of the model with the experimental results.[3] There was generally good agreement for the range of pH from 5 to 11.

1.2.2 Mechanical Properties of the Tectorial Membrane

All current cochlear models include effects of the TM, and the mechanical properties of the TM are generally taken to be anisotropic: (1) Longitudinal stiffness is generally assumed to be small so that the TM introduces little coupling of adjacent longitudinal sections. (2) Radial stiffness is generally assumed to be large for the thick part of the TM that overlies inner and outer hair cells, so that the thick part of the TM moves as a rigid plate when viewed in radial cross-section. (3) Radial stiffness for the thinner part of the TM that forms its attachment to the spiral ligament is assumed to be small in models that predict mechanical resonance of the TM. These anisotropies are based almost entirely on functional interpretations of anatomy. There are few experimental measurements to support these ideas. As a step toward understanding the mechanical properties of the TM, we have applied the magnetic bead method reported in last year's *Progress Report*[4] to measure force-displacement relations in isolated TM preparations from 12 mice.

Cochlea were dissected from adult male mice and placed in an artificial endolymph solution. An apical portion of the TM was removed from the cochlea and attached to the glass bottom of an experiment chamber using a cell adhesive. A single magnetizable

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[1] T.F. Weiss and D.M. Freeman. "Equilibrium Behavior of an Isotropic Polyelectrolyte Gel Model of the Tectorial Membrane: The Role of Fixed Charges." *Aud. Neurosci.* 3: 351-61 (1997a).

[2] D.M. Freeman, S.M. Hattangadi, and T.F. Weiss. "Osmotic Responses of the Isolated Mouse Tectorial Membrane to Changes in pH." *Aud. Neurosci.* 3: 363-75 (1997).

[3] T.F. Weiss and D.M. Freeman. "Equilibrium Behavior of an Isotropic Polyelectrolyte Gel Model of the Tectorial Membrane: Effect of pH." *Hear. Res.* 111: 55-64 (1997).

[4] T.F. Weiss et al. *RLE Progress Report* 139: 409-25 (1997).

bead (10-20 µm diameter) was attached to the free surface of the TM with tissue adhesive. The preparation was placed between two computer-controlled electromagnets, which produced a sinusoidally modulated force on the magnetizable bead. Motions of the magnetizable bead and surrounding tissue were measured using video microscopy.

Amplitude Dependence

Application of forces from 1 to 100 nN caused displacements of the magnetizable bead from approximately 0.01 to 1 µm (Figure 1). This range is important since the mechanical properties of connective tissues are typically nonlinear: stiffness tends to increase as the magnitude of the displacements increases. The range of displacements in this study is similar to the range that would result during exposure to loud sounds and is more than 100 times smaller than those used in previous studies of the TM.[5] For applied forces from 5 to 100 nN, the magnitude of the displacement was nearly proportional to the magnitude of the applied force.

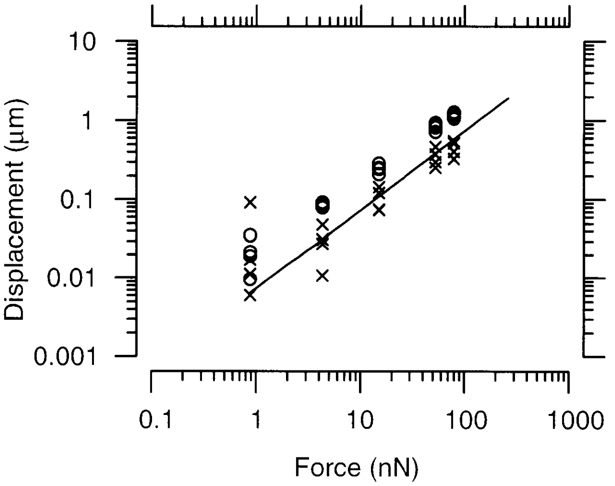

Figure 1. Level dependence of TM motion. Sinusoidal forces (10 Hz) with amplitudes from 1 to 100 nN were applied to a magnetizable bead and the magnitude of the resulting displacement was measured. Radial displacements resulting from radial forces are shown by x symbols; longitudinal displacements resulting from longitudinal forces are shown by circles. The solid line has a slope of 1.

Longitudinal forces produce larger displacements than radial forces of the same magnitude (Figure 2). Thus the TM is mechanically anisotropic. Regression analysis suggests that longitudinal displacements are approximately three times greater than radial displacements for the same stimulus condition. The TM contains prominent, radially oriented collagen fibers. The measured mechanical anisotropy correlates with this structural anisotropy, suggesting that the radially oriented collagen fibers add radial stiffness. These measurements support the idea that the TM is not isotropic. However, the difference between longitudinal and radial properties measured in these studies is smaller than the difference that is typically assumed in cochlear models.

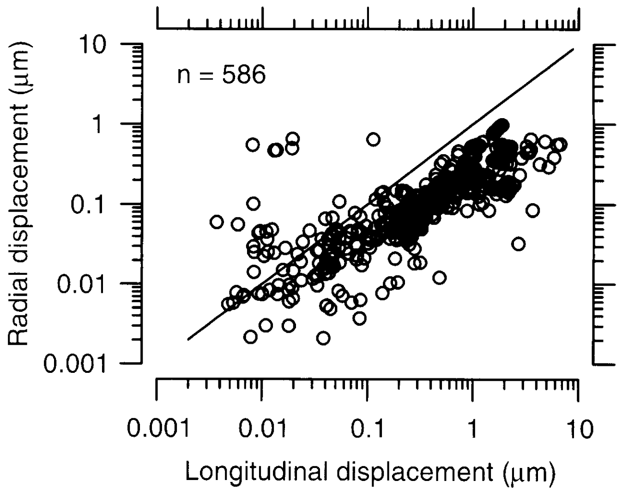

Figure 2. Comparison of radial and longitudinal displacements. Forces with equal amplitude and frequency were applied radially to measure radial displacement (ordinate) and longitudinally to measure longitudinal displacement (abscissa). Results are pooled for 5 force amplitudes in 12 preparations. The solid line has a slope of 1.

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[5] J.J. Zwislocki and L.K. Cefaratti. "Tectorial Membrane II: Stiffness Measurements *in vivo*." *Hear. Res.* 42: 211-27 (1988); G. von Bekesy. *Experiments in Hearing.* (New York: McGraw-Hill, 1953); G. von Bekesy. "Description of Some Mechanical Properties of the Organ of Corti," *J. Acoust. Soc. Am.* 25: 770-85 (1960).

Frequency Dependence

Measurements for frequencies from 10 to 100 Hz show that the magnitudes of the measured bead displacements tend to decrease with increasing frequency—displacements for radial forces decrease by 8 dB/decade and for longitudinal forces by 10 dB/ decade (Figure 3). There was a consistent phase lag (approximately 45 degrees) between the applied force and resulting displacement. This lag suggests that both viscous and elastic material properties are important. Elastic behavior is consistent with the presence of TM macromolecules such as collagen. Viscous behavior is consistent with the fact that the TM is 97% water. However, the frequency responses are not similar to those of a simple spring or dashpot.

Spatial Dependence

Motion of the magnetizable bead produces displacements of the surrounding tissue (Figure 4). Measured space constants for longitudinal forces were 13 μm and 15 μm in the longitudinal and radial directions, respectively. Motions of the TM resulting from radially applied forces (right) were much smaller than those for longitudinal forces (left). The radial displacements approach the limit of resolvable motions. Experiments with different force magnitudes (1 to 100 nN) and frequencies (10 to 100 Hz) gave similar space constants.

Motion of the magnetizable bead induces motions in parts of the TM more than 30 μm from the bead. These distances are large compared to the distances between neighboring hair cells (typically 10 μm), supporting the notion that the TM would tend to mechanically couple nearby hair bundles.

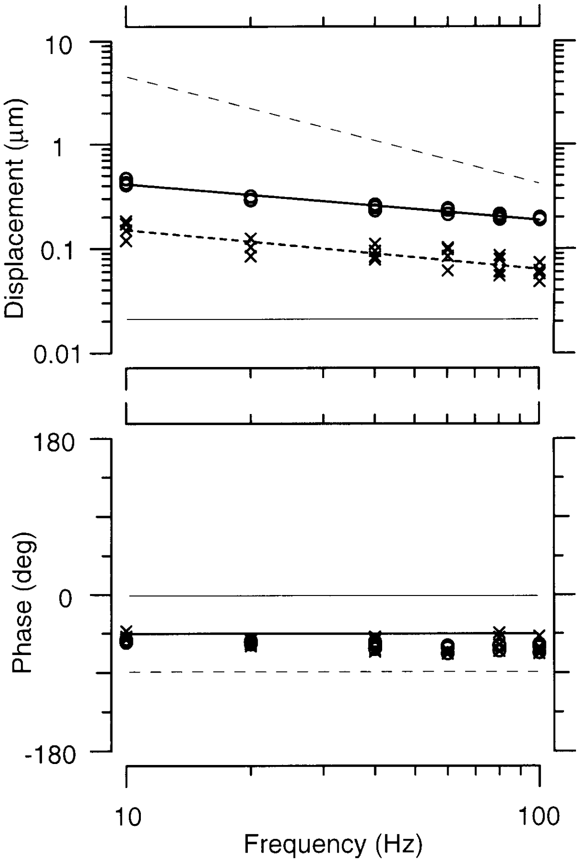

Figure 3. Frequency dependence of TM displacements. Displacements were measured from 10 to 100 Hz for an 80 nN force. The magnitude (top) and phase (bottom) of bead displacements are shown for longitudinal (o symbol) and radial (x symbol) forces. The thick lines are least squares fits to the data. The thin solid lines represent the response of a spring that obeys Hooke's law (force proportional to displacement). The thin dashed lines represent the response of a viscous dashpot (force proportional to velocity).

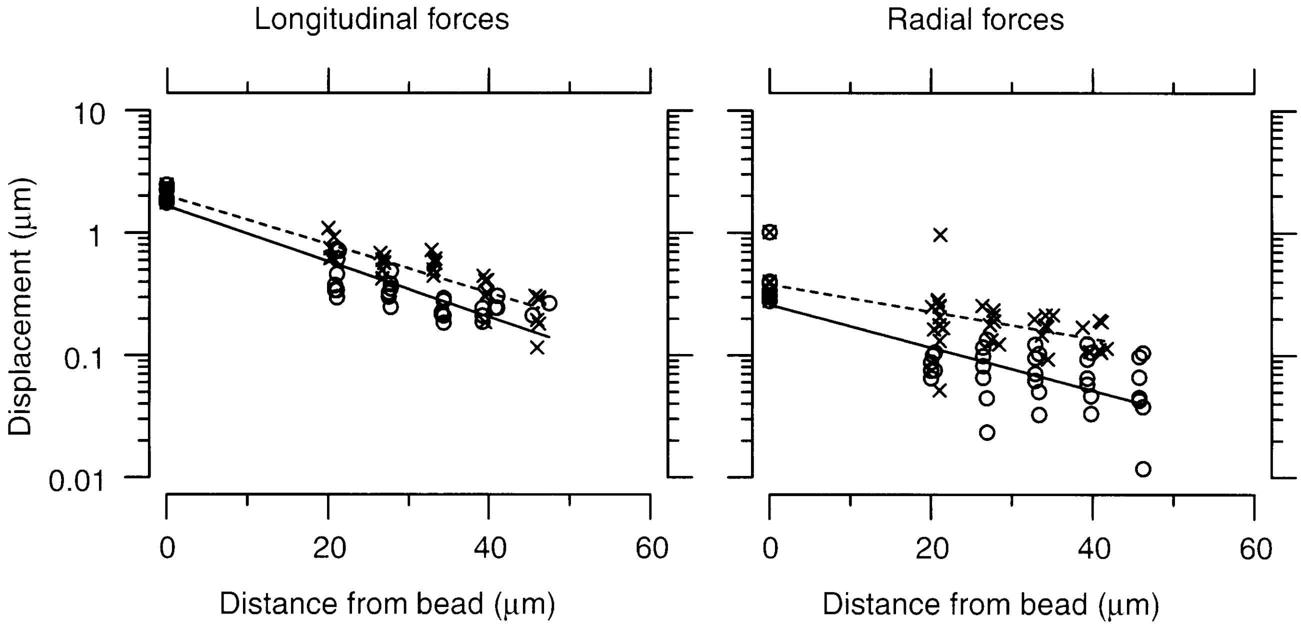

Figure 4. Mechanical coupling through the TM. Displacements at locations on the TM surface extending in the radial (x symbol) and longitudinal (o symbol) directions were measured for forces (100 nN at 10 Hz) applied in the longitudinal (left) and radial (right) directions. An exponential function was fit to the data and is represented here by a straight line on semilog coordinates. The slope of the line is used to estimate the space constant, which is the distance over which the displacement magnitude decreases by a factor of e.

1.2.3 Sound-induced Motions of Cochlear Structures

We are interested in measuring the micromechanical motions of structures in the cochlea: that is, how structures such as the tectorial membrane (TM), reticular lamina (RL), and tips of hair bundles move in response to sound, and what the mechanical relationships among these structures are. To that end, our group has developed an *in vitro* preparation of the cochlea of the alligator lizard as well as video microscopic methods to measure sound-induced motions. The preparation and measurement techniques have been described in previous issues of the *Progress Report*. During the past year, we have examined relationships among micromechanical structures for 140 hair bundles in nine cochleae. We summarize our findings below.

There are several prevalent theories for how motions of the reticular lamina (RL) induce motions of the tectorial membrane (TM). Early theories suggested that the motions are determined kinematically and that the ratio of TM displacement to RL displacement would not depend on frequency. More recently, it has been suggested that motion of the TM is resonant and that the ratio of TM displacement to RL displacement will exceed 1 at its best frequency. Although there is much scatter in our measurements (Figure 5), there is little support for sharp frequency selectivity of TM motion. The ratio of TM displacement to RL displacement is roughly constant and slightly smaller than 1 from 40 Hz to 4 kHz. Displacements of the TM and RL are nearly in phase.

The effective stimulus for the sensory (hair) cells is the shearing motions of the TM relative to the RL. To quantify shear, we measure the displacement of the TM relative to that of the RL, i.e., TM displacement minus RL displacement. Kinematic models of the TM predict that this ratio should be independent of frequency. By contrast, recent models have suggested that the TM provides an inertial load. At low frequencies, the TM should move with the RL and provide no shearing excitation. As frequency increases, TM motion should decrease and the shearing excitations will increase. Our results (Figure 6) show a slight increase in shearing drive with frequency.

It has been suggested that the efficacy of cochlear micromechanics depends critically on the disposition of the TM. If hair bundles are attached to the TM, then the displacements of hair bundles should be proportional to TM shearing displacements. However, if hair bundles are not attached, then hair bundle motion will be driven by viscous fluid forces, and the resulting hair bundle displacement will be proportional to the TM shearing velocities. Our results (Figure 7) show great variability. However, there is little evidence to suggest that higher frequencies produce greater hair bundle displacements than low frequencies. In summary, we examined micromechanical relations in nine cochleae, and none of the micromechanical relations showed sharp frequency selectivity. These are the first measurements of sound-induced motions of the reticular lamina, tectorial membrane, and hair bundles in any cochlea. However, no electrical responses to sound were detected from these excised cochleae. It is possible that damage during our surgical preparation led to the loss of electrical responses and that the damage also affected mechanical responses. Consequently, these results must be considered preliminary at this time.

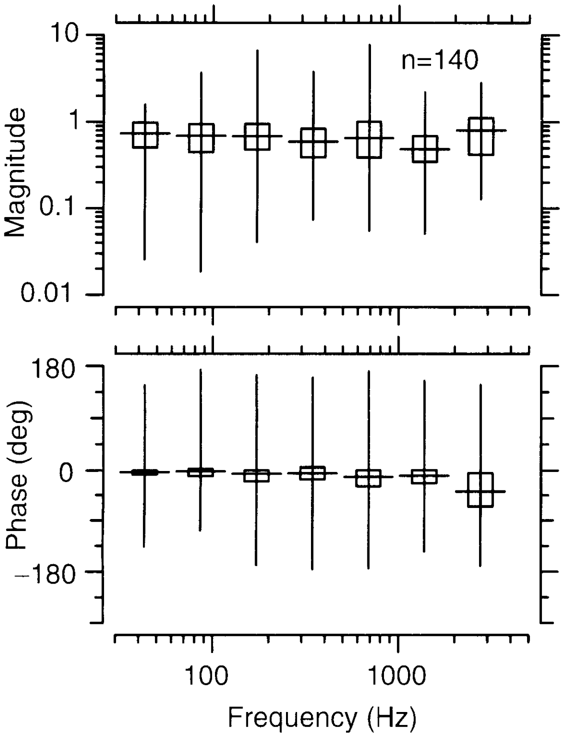

Figure 5. Ratio of TM displacement to RL displacement. RL motion was measured at the base of a hair bundle, and TM motion was measured at the top surface of the part of the TM directly overlying the hair bundle. The ratio of TM displacement to RL displacement is shown versus frequency. The range of results and the median are indicated by the vertical and horizontal lines, respectively. The box encloses the interquartile range.

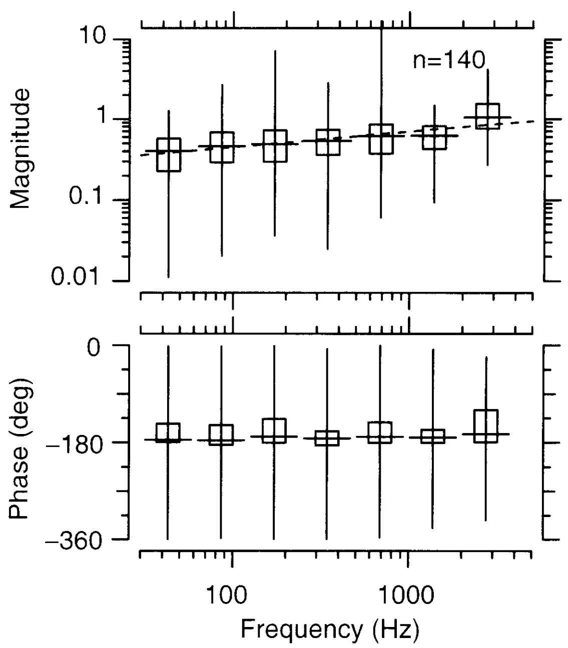

Figure 6. Dependence of TM shear on RL displacement. TM shear is taken as the difference between the displacements of the TM and RL. The plots illustrate the magnitude and phase of the ratio of TM shear to RL displacement. Other aspects of this figure are as in Figure 5.

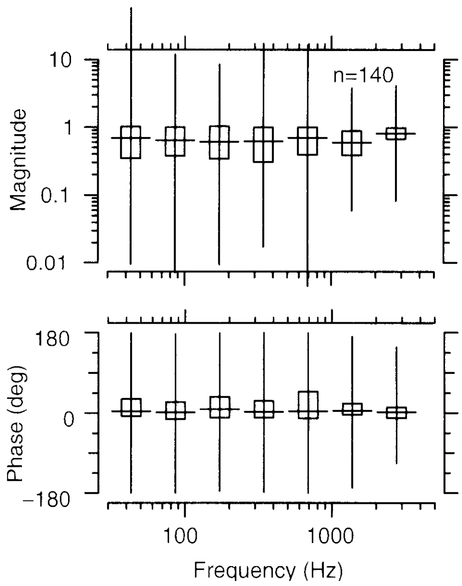

Figure 7. Relation between shearing motions of the TM and rotation of hair bundles. TM shear is taken as the difference between the displacements of the TM and RL. Rotation of hair bundles is proportional to the difference between displacements of the tips and bases of hair bundles. This figure summarizes the ratio of the latter to the former.

1.2.4 Publications

Journal Articles

Freeman, D.M., S.M. Hattangadi, and T.F. Weiss. "Osmotic Responses of the Isolated Mouse Tectorial Membrane to Changes in pH." *Aud. Neurosci.* 3: 363-75 (1997).

Weiss, T.F., and D.M. Freeman. "Equilibrium Behavior of an Isotropic Polyelectrolyte Gel Model of the Tectorial Membrane: The Role of Fixed Charges." *Aud. Neurosci.* 3: 351-61 (1997).

Weiss, T.F., and D.M. Freeman. "Equilibrium Behavior of an Isotropic Polyelectrolyte Gel Model of the Tectorial Membrane: Effect of pH." *Hear. Res.* 111: 55-64 (1997).

Conference Papers

Abnet, C.C., and D.M. Freeman. "Deformations of the Isolated Mouse Tectorial Membrane Produced by Calibrated Oscillatory Forces." *Abstracts of the Twenty-First Midwinter Research Meeting of the Association for Research in Otolaryngology,* St. Petersburg Beach, Florida, February 15-19, 1998, p. 183.

Aranyosi, A.J., C.Q. Davis, and D.M. Freeman. "Experimental Measurements of Micromechanical Transfer Functions in the Alligator Lizard Cochlea." *Abstracts of the Twenty-First Midwinter Research Meeting of the Association for Research in Otolaryngology,* St. Petersburg Beach, Florida, February 15-19, 1998, p. 183.

Theses

Abnet, C.C. *Measuring Mechanical Properties of the Tectorial Membrane with a Magnetizable Bead.* Ph.D. diss., Department of Mechanical Engineering, MIT, February 1998.

Davis, C.Q. *Measuring Nanometer, Three-dimensional Motions with Light Microscopy.* Ph.D. diss., Department of Electrical Engineering and Computer Science, MIT, June 1997.

Patire, A.D. *Measuring the Point Spread Function of a Light Microscope.* B.S. thesis, Department of Electrical Engineering and Computer Science, MIT, February 1997.

Rouf, R. *Effect of Metal Ions on the Isolated Tectorial Membrane of the Mouse.* B.S. thesis, Department of Electrical Engineering and Computer Science, MIT, September 1997.

1.3 Auditory Neural Coding of Speech

Sponsor

National Institutes of Health/National Institute of Deafness and Other Communication Disorders

Project Staff

Dr. Bertrand Delgutte, Sridhar Kalluri, Martin F. McKinney

1.3.1 Goals

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

1.3.2 Temporal Interactions for Speech and Nonspeech Stimuli in the Auditory Midbrain

Speech perception is context-dependent in that the phonetic identity of a given acoustic segment depends on segments that precede and follow it. Likewise, auditory neurons exhibit temporal interactions, whereby the response to a given "probe" stimulus can be altered by a preceding "conditioning" stimulus. To investigate the role of temporal interactions in the neural representation of speech, we recorded from single units in the inferior colliculus (IC) of anesthetized cats for diotically-presented stimuli designed to reveal these interactions. We constructed synthetic speech continua in which the phonetic identity of a constant probe was altered by varying the preceding conditioning stimulus. For example, we created a [sa]-[sta] continuum by varying the duration of a silent interval between a conditioning [s] and a constant [da] probe. Similarly, we created a [da]-[na] continuum by varying the amplitude of a conditioning [n] preceding a constant [da]. We also created parallel nonspeech continua with tones and noise in which the same parameters were varied as for speech continua.

For a majority of cells in the IC, the response to the probe was suppressed when preceded by a conditioning stimulus. As for auditory-nerve adaptation, suppression generally increased with the duration and intensity of the conditioner, and decreased with increasing delay between probe and conditioner. However, unlike the auditory nerve, probe responses in the IC could be suppressed by conditioners that produced little or no spike discharges, suggesting that suppression was due to long-lasting inhibition rather than adaptation. Suppression was strongest at the onset of the probe, and, in some cases, the main effect of the conditioner was to desynchronize the burst of activity at probe onset without greatly altering the number of spike discharges. In general, temporal interactions for speech stimuli were consistent with those for tones and noise. These results show that temporal interactions occur on the time scales of phonemes and syllables in speech (100-300 msec) and can profoundly influence the neural representation of speech. The similarity in temporal interactions for speech and nonspeech stimuli suggests that very general neural mechanisms may underlie context dependence in the perception of speech and other auditory objects.

1.3.3 Functional Model of Onset Cells in the Cochlear Nucleus

We are continuing to develop a simple mathematical model of onset neurons in the ventral cochlear nucleus (VCN). This model, which is based on well-characterized responses to tones and noise, will be used to examine the representation of complex stimuli such as speech in the populations of onset neurons.

The model is a single-node electrical circuit that receives statistically-independent model auditory nerve inputs via identical excitatory synapses. The membrane model, inspired by the work of Hill, is a leaky integrator with a voltage dependent resistance and a time-varying threshold.

By using simplified representations of the electrical current that flows into an onset neuron during acoustic stimulation, we have analytically examined the model response as a function of its parameters. These analytic results allow us to state parameter constraints for modeling the onset response. For example, we find that the time constant of the leaky integrator must be at least three times smaller than the previously reported 1-ms time constant of octopus cells in order to explain the onset response to both low and high frequency tones. More recent measurements of membrane time constants from octopus cells using improved techniques are within the theoretically imposed limit. Another significant result from analytic and numerical examination of the model is that most VCN response types are achievable with this model structure.

This model of onset cells provides important constraints on biophysical mechanisms for generating VCN onset responses. Furthermore, there may be a simple, unifying mathematical description of all major VCN response types. We are now in a position to use this model for evaluating hypotheses concerning the coding of speech and correlates of psychoacoustical phenomena in the VCN neuron populations.

1.3.4 Neural Representation of Pitch

We are using the octave enlargment effect (the tendency for listeners to prefer octave ratios slightly greater than 2:1) to constrain models for the neural representation of pitch. We have previously shown that interspike intervals (ISIs) of auditory-nerve fibers for pure-tone stimuli show systematic deviations from stimulus periods and that these deviations can quantitatively account for psychophysical measures of octave enlargement. Recent work has focused on possible physiological mechanisms underlying these deviations.

Although auditory-nerve (AN) responses to low-frequency pure-tones are phase-locked to the stimulus, short (<4 ms) ISIs in response to frequencies above 400 Hz are slightly larger than multiples of the stimulus period. This deviation has been attributed to the refractory properties of the fiber. To test this idea, we employed a statistical model (nonhomogeneous Poisson process with dead time) for AN excitation which accounts for a wide variety of physiological data.[6] We found that the model predicts ISI deviations, but the predicted deviations are much smaller than those in the physiological data. This result suggests that either the model does not accurately represent the refractory properties of AN fibers or that there is some other cause besides refractoriness for the ISI deviation. In a study of discharge-history effects in the AN in response to pure-tones,[7] conditioned period histograms on the time since the last

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[6] D. Johnson and A. Swami, "The Transmission of Signals by Auditory-nerve Fiber Discharge Patterns," *J. Acoust. Soc. Am.* 74: 493-501 (1983).

[7] R. Gaumond, D. Kim, and C. Molnar, "Response of Cochlear Nerve Fibers to Brief Acoustic Stimuli: Role of Discharge-history Effects," *J. Acoust. Soc. Am.* 74: 1392-98 (1983).

spike and revealed a positive phase shift in probability of discharge for short ISIs (<3 msec). This phase shift is inconsistent with the afore-mentioned model and is a possible source for the ISI deviation. A modification of the model to include the phase shift and test this hypothesis is underway.

These findings suggest that computational models of pitch and other auditory forms based on interspike intervals may have to simulate detailed statistical discharge characteristics of auditory neurons in order to correctly predict psychophysical effects such as the octave enlargement.

1.3.5 Publications

Chapters in Books

Delgutte, B. "Auditory Neural Processing of Speech." In *Handbook of Phonetic Sciences.* Eds. W.J. Hardcastle and J. Laver. Oxford, England: Blackwell, 1997, pp. 507-38.

Delgutte, B., B.M. Hammond, and P.A. Cariani. "Neural Coding of the Temporal Envelope of speech: Relation to Modulation Transfer Functions." In *Psychophysical and Physiological Advances in Hearing.* Eds. A.R. Palmer, A. Reese, A.Q Summerfield, and R. Meddis. London: Whurr. Forthcoming.

Delgutte, B., B.M. Hammond, and P.A. Cariani. "Neural Coding of the Temporal Envelope of Speech." In *Listening to Speech. Eds.* W.A. Ainsworth and S. Greenberg. Oxford, England: Oxford University Press. Forthcoming.

Journal Article

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Conference Papers

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1.4 Neural Mechanisms of Spatial Hearing

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The long-term goal of this project is to understand the neural mechanisms for sound localization in noisy and reverberant environments. Our efforts in the past year have focused on studying neural correlates of the precedence effect (PE) in the inferior colliculus. The PE is an auditory illusion that allows accurate sound localization in the presence of acoustic reflections. Recent studies have identified physiological correlates of the PE in the responses of single units in the inferior colliculus (IC). In these experiments, two brief sounds are presented from different locations, one simulating the direct sound and the other one, delayed, simulating a reflection. For most cells, the response to the lagging click is suppressed at short delays and recovers with increasing delay.

Suppression depends on the locations of the leading and lagging clicks. Although this directionality of suppression is thought to depend primarily on interaural time differences (ITD), other localization cues could also play a role, and the relative importance of these cues is unknown.

To address this issue, we recorded from single units in the IC of anesthetized cats for "virtual space" (VS) click stimuli synthesized from head-related transfer functions. These stimuli contain multiple localization cues (ITD, interaural level differences (ILD), and spectrum) as in free field, and allow selective manipulation of individual cues. We measured the response to a fixed lagging click as a function of the azimuth of a leading click. Suppression for these stimuli was consistent with findings in free field; it occurred at the same range of delays (2-100 ms) and, for most cells, was maximum when the leading click was at the neuron's best (most effective) azimuth. For some cells, however, suppression was omnidirectional, even though the response to the leading click was strongly directional. These findings confirm the validity of the VS technique for investigating neural correlates of the PE. We then measured suppression for modified VS stimuli such that some localization cues in the leading click were held constant while others were varied with azimuth as in free field. For many cells, ILD was the most potent cue for the directionality of both the leading-click response and echo suppression. However, for some low-frequency cells ITD was the most potent cue.

In conclusion, for some cells, directional responses to the leading click and suppression are strongly correlated, and may be mediated by common neural mechanisms. Other cells show dissociations between the response to the leading click and suppression, suggesting that different mechanisms may be involved. Further experiments may elucidate which aspects of suppression reflect general properties of the nervous system, and which ones specifically play a role in the PE.

1.4.1 Publiccation

Abstract

Litovsky, R.Y., B.R. Cranston, and B. Delgutte. "Neural Correlates of the Precedence Effect in the Inferior Colliculus: Effect of Localization Cues." *Abstracts of the Twenty-First Midwinter Research Meeting of the Association for Research in Otolaryngology,* St. Petersburg Beach, Florida, February 15-19, 1998, p. 40.