18. Communications Biophysics

A. Signal Transmission in The Auditory System

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18.1 Basic and Clinical Studies of the Auditory System

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Studies of signal transmission in the auditory system continue in cooperation with the Eaton-Peabody Laboratory for Auditory Physiology at the Massachusetts Eye and Ear Infirmary. The goals of this program are to determine the anatomical structures and physiological mechanisms that underlie vertebrate hearing and to apply that knowledge where possible to clinical problems. Studies of cochlear implants in humans continue in the Cochlear Implant Laboratory in a joint program with the Massachusetts Eye and Ear Infirmary. The ultimate goal of these devices is to provide speech communication for the deaf by using electrical stimulation of intracochlear electrodes to elicit patterns of auditory nerve fiber activity that the brain can learn to interpret.

18.1.1 Comparative Aspects of Middle-Ear Transmission

Darleen R. Ketten, William T. Peake, John J. Rosowski

Through study of the performance of ears of different species we work toward an understanding of how the functional capabilities of ears are related to their structural features. To compare among various ears we have defined three measures of performance related to the coupling of acoustic power from an incident sound wave into the inner ear.

1. The *power utilization ratio* (PUR) is a measure of the effectiveness of the ear as an

impedance matcher. It can be determined from knowledge of the acoustic input impedance of the middle ear at the tympanic membrane, Z_T, and the acoustic impedance looking out from the tympanic membrane through the external ear, Z_E.

2. The *effective area*, the ratio of the power absorbed by the middle ear to the incident power per unit area, is a measure of the ability of the ear to extract power from an incident wave. It can be determined from Z_T and the ratio of the pressure at the tympanic membrane to that of the incident wave.

3. The *efficiency* of the middle ear can be determined from its input and output impedance and its transfer ratio.

It has been possible to compute these measures from available measurements and acoustic models for three species: cat, guinea pig, and human.[1] Several interesting conclusions are suggested by the results. Since the PUR shows that in all of these species the impedances are far from "matched" over much of the frequency range of interest, the popular description of the middle ear as an "impedance matching device" seems inappropriate. In these three species the middle–ear efficiency deviates appreciably from unity over much of the frequency range, so that it is inaccurate to think of it as a lossless coupler of acoustic power. The frequency dependence of the effective area is similar across these species, but its magnitude varies with the size of the ear (and animal); i.e., it decreases from human to cat to guinea pig. This suggests that if smaller species are to hear as sensitively as larger ones, they must be more efficient in conveying the sound power to the receptor cells.

To study the effects of "size of ear" on sound receiving properties without the complication of species differences, we have initiated a new project to measure ear performance in one species across a wide range of sizes. We have chosen to start this with the alligator lizard since we have considerable experience with this species and we have developed a model of the middle ear[2] that relates structures to acoustic response; also these lizards can be obtained in a wide range of sizes.

18.1.2 Effects of Middle–Ear Muscle Contraction on Middle–Ear Transmission

Xiao–Dong Pang, William T. Peake

Our measurements of last year (in cat) had shown that the stapedius muscle of the middle ear, which plays an important role in reducing the sound transmission through the ear when sound intensity is very high, has a simple mechanical effect on the ossicular chain: it only moves the stapes and leaves the other ossicles stationary. This observation suggested that the muscle contractions must strain the annular ligament around the footplate of the stapes and thereby increase its impedance. Analysis of a model of the cat middle ear showed that the measured effects of stapedius contraction are consistent with previously measured changes in stapes impedance associated in static pressure differences across the footplate.[3] Further analysis showed that the measurements imply that both the stiffness and the resistance of the stapes must increase when the muscle contracts.[4]

18.1.3 Theoretical Studies of the Ear

Dennis M. Freeman, Robert C. Kidd, William T. Peake, John J. Rosowski, Thomas F. Weiss

We have developed a model of the ear of the alligator lizard that relates the sound pressure at the tympanic membrane to the receptor potential of hair cells with free-standing stereocilia.[5] The model contains stages to represent sound transmission through the middle and inner ear,[2] micromechanical properties of the hair-cell stereocilia,[6] mechanoelectric transduction,[7] and the electric properties of hair cells. This model accounts for most but not all of our measurements of hair-cell receptor potentials in response to sound.

We have continued theoretical studies of the mechanical stimulation of the stereocilia of hair cells. Our approach is to obtain solutions of the equations of motion for a Newtonian fluid to a succession of problems of increasing geometric complexity in order to isolate the role of the fluid load and of nearby boundaries (such as tectorial structures and the reticular lamina) on the mechanics of small structures (such as stereociliary tufts) immersed in fluids (representing the cochlear fluids). In the first study,[8] we examined the role of fluid inertia and viscosity on oscillating, isolated bodies of regular geometry. We found that both fluid inertial and viscous effects are important and that small bodies, of about the dimensions of stereociliary tufts, can resonate under water with a resonance frequency and quality of resonance that depends upon the geometry of the body. Stereociliary tufts are not isolated bodies but protrude from a vibrating surface (the reticular lamina) and in most ears are found near another vibrating surface (the tectorial membrane). Therefore, we next examined the motion of a small body, connected to a vibrating (basal) plate by a compliant hinge, in the presence of another (tectorial) plate. We simulate the mechanics of free-standing stereocilia by making the separation between the two parallel plates arbitrarily large, and simulate the mechanics of stereocilia that are not attached to but are surmounted by a tectorial membrane by making the interplate distance small. Robust analytical results have been obtained for the fluid motion and the motion of the hinged body in response to both very low and very high frequency vibration of the basal plate. These results can be summarized in terms of the transfer function, θ/U_p, which is the ratio of the angular displacement of the body, θ, to the basal plate velocity, U_p. For example, with the tectorial plate infinitely far away from the basal plate and for arbitrarily low frequencies, θ/U_p has a magnitude that is proportional to $f^{1/2}$ and an angle that approaches 45° , i.e., the body displacement is not proportional to the plate displacement, velocity or acceleration. In the presence of a nearby stationary tectorial plate, the angular displacement of the hinged body is proportional to the velocity of the basal plate at arbitrarily low frequencies. As distance to the tectorial plate increases, two distinct low frequency ranges emerge. At the lowest frequencies, for which the boundary layer thickness is large relative to both the body size and the plate separation, θ / U_p approaches a constant, i.e., angular displacement of the body is proportional to the plate velocity. At higher frequencies, for which the boundary layer thickness is large relative to the body dimensions but small relative to the plate separation, θ / U_p has a magnitude that is proportional to $f^{-1/2}$ and an angle that approaches 45°, i.e., a frequency dependence identical to that for a tectorial plate that is arbitrarily far away from the basal plate. At arbitrarily high frequencies, the body displacement is proportional to the displacement of the basal plate. The results at both low and high frequencies are relatively independent of the detailed geometry of the hinged body. Hence, they should apply to stereociliary tufts directly. To investigate fluid and body motion at intermediate frequencies, we have obtained numerical results for a specific body geometry — a rectangular flap hinged to a plate. Difference equations of motion were developed using a finite element approach and were solved on a VAX11/750 computer using a conjugate-gradient method. The numerical solutions and the analytical solutions validate each other at asymptotically low and high frequencies and the numerical solution gives results at intermediate frequencies where analytical solutions are not available. The numerical results demonstrate a passive mechanical resonance for flaps with dimensions as small as those of stereociliary tufts. Hence, stereociliary tuft mechanics may play a critical role in the frequency selective properties of hair cells.

18.1.4 Coding of Sounds into Discharges of Cochlear Nerve Fibers

Ruth Anne Eatock, Christopher Rose, Thomas F. Weiss

Systematic coordinated studies continue of hair cell receptor potentials and cochlear nerve fiber discharges in the alligator lizard ear. The goal is to determine which cochlear mechanisms and structures are involved in determining the encoding of sound stimuli into spike discharges.

We have completed a study of tone-induced synchronization of the discharges of cochlear neurons in the alligator lizard.[9] There are several results: (1) We have developed a new measure of the frequency dependence of neural synchronization that is independent of frequency selectivity. We measure the synchronization index at a constant average discharge rate. (2) The dependence of this measure on frequency has the form of a lowpass filter. This filter does not depend on the characteristic frequency of the fiber, and is the same for discharge rates of 20 and 40 spikes/sec (for free-standing fibers). (3) For the free-standing region of the alligator lizard cochlea, the high-frequency attenuation of this *neural* lowpass filter exceeds that found for the receptor potential of the hair cells so that synaptic and excitatory mechanisms at the hair-cell neuron junction must contribute appreciably to measured loss of synchronization at high frequency. (4) The corner frequency of the lowpass filter is lower for cochlear neurons innervating hair cells with free-standing stereocilia (free-standing nerve fibers) than for those innervating hair cells covered by a tectorial membrane (tectorial nerve fibers). It seems likely that differences in the synaptic transmission and nerve excitation are responsible for the differences in synchronization of these two populations of fibers.

We have investigated the coding of tones by the average discharge rate of cochlear nerve fibers by measuring the dependence of the driven discharge rate on sound-pressure level at the tympanic membrane, or rate-level function.[10] Our aim is to characterize this function for both free-standing and tectorial fibers. We have thus far examined both the rate of growth of the rate-level function at low levels and its behavior at high levels. At low levels, the rate-level function is approximated rather well as a power function, i.e., $(\Lambda_0)_d$ where $(\Lambda_0)_d = kP^n$ is the average driven discharge rate and P is the sound pressure at the tympanic membrane. At high levels, the rate-level function saturates; the saturated driven rate is $(\Lambda_0)_{sat}$. Our results indicate that: for free-standing fibers, n is near 2 at the characteristic frequency (CF) of the fiber, n does not change much as f/CF varies, and $(\Lambda_0)_{sat}$ is independent of frequency; for tectorial fibers, n is significantly larger than 2, n is lower for $f > CF$ than for $f \leq CF$, and $(\Lambda_0)_{sat}$ decreases as f increases. We are comparing these results with previous measurements of the receptor potential of hair cells in the free-standing region of the cochlea in an effort to draw conclusions about cochlear mechanisms. For example, the previous measurements showed that the saturated value of the DC component of the receptor potential is also independent of frequency although the saturated value of the AC component of the receptor potential depends upon frequency. Taken together, the results in hair cells and nerve fibers are compatible with the simple notion that the average discharge rate of a free-standing fiber is determined by the DC component of the receptor potential of the hair cell although these results alone do not specify the site of saturation of the nerve discharge rate.

18.1.5 Speech Coding in the Auditory Nerve

Bertrand Delgutte

Two-tone suppression in auditory-nerve fibers reflects nonlinear mechanisms that are likely to be important in the coding of complex stimuli such as speech. In order to characterize these nonlinearities, one needs to determine how suppression magnitude depends on the intensity and frequency of the suppressing stimulus.

The responses of auditory-nerve fibers to two-tone stimuli were measured in anesthetized cats.[11] One tone, the "excitor," was adjusted in level but was always at the fiber's characteristic frequency (CF), while the "suppressor" tone was varied in both frequency and intensity. For each suppressor setting, the level of the excitor tone that produced a criterion discharge rate (usually 60% of the dynamic range for a single tone at CF) was measured using an adaptive procedure.

Suppression (in dB) was defined as the excitor level that met criterion in the presence of the suppressor minus the excitor level at criterion without suppressor. The growth in suppression with suppressor level is well characterized by a straight line for sound levels exceeding the suppression threshold by 5–10 dB. The slope of this line (in dB–excitor/dB–suppressor) varies with suppressor frequency by as much as a factor of 10 in the same fiber. These slope differences are most pronounced for fibers with CF above 2 kHz, and are systematically related to position of the suppressor frequency relative to the fiber CF: suppressors below CF produce slopes ranging from 1 to 3 dB/dB, while the rates of growth of suppression above CF are between 0.15 and 0.7. This suggests that intense low-frequency stimuli such as the first formant of speech can suppress the responses of middle-CF fibers (2-6 kHz) more effectively than the high-frequency components of fricative stimuli, even though suppression thresholds are higher at low frequencies.

The finding that the rate of growth of suppression decreases with increasing frequency is reminiscent of similar trends in the frequency dependence of the rates of growth of basilar-membrane motion, hair-cell receptor potentials, and discharge rates of auditory-nerve fibers for single tones. In order to quantitatively examine these similarities, we have measured the slopes of rate-level functions in auditory-nerve fibers for single tones at stimulus levels near threshold. Specifically, the driven rate of discharge R_d (i.e., average discharge rate minus spontaneous rate) was fitted by a power function of the form $R_d = Kp^{\alpha}$, where p is the r.m.s. sound pressure, and α is an exponent characterizing the growth of the rate-level function. When the tone frequency is at the fiber CF, the exponent shows considerable scatter, varying between 1.3 and 5 from fiber to fiber. Mean values are greater for fibers with spontaneous discharge rates (SR) below 0.5 spike/s ($\bar{\alpha}$ = 2.8) than for fibers with SR above 18 spikes/s ($\bar{\alpha}$ = 1.8). Exponents for stimulus frequencies above CF are generally smaller than at and below CF. No evidence for correlation between the exponent of the rate-level function and the rate of growth of suppression was found, even though the two measures were obtained for the same frequencies and the same fibers. These detailed measurements provide constraints on models of the nonlinear responses properties of auditory-nerve fibers.

18.1.6 Afferent and Efferent Systems in the Mammalian Cochlea

M. Christian Brown

The mammalian cochlea contains an efferent as well as afferent neural innervation. Our goal is to understand the functional significance of these innervations, using electrophysiological and anatomical techniques. Micropipette recordings from the guinea pig spiral ganglion are used to sample the two physiological classes of units, designated as "afferent" and "efferent" classes.[12] Afferent units have physiological characteristics similar to those of afferent units recorded in the auditory branch of the eighth nerve, whereas efferent units have regular interspike intervals (for both spontaneous and sound-driven activity) and long latency to sound (5 to 100 msec). Five physiologically-characterized afferent units have been labeled with intracellular injections of horseradish peroxidase (HRP) and found to be type I ganglion cells with myelinated axons which innervate single inner hair cells. Three physiologically-characterized efferent units have been labeled and were found to innervate outer hair cells with thick, myelinated axons. Physiological and morphological characteristics of these efferent units were similar to those of efferent neurons of the medial brainstem group which have been recorded and labeled in the cat.[13] Since these efferent units can be divided into three groups which respond to sound in the ipsilateral, contralateral, or in both ears, they may play a role in binaural processes such as sound localization.

We are also studying the central projections of cochlear afferent neurons labeled with extracellular injections of HRP into the spiral ganglion. Although the projection of the more numerous type I spiral ganglion cells has been studied extensively in the past, the central projection of type II ganglion cells has proved more difficult to study. With extracellular injections of HRP into the peripheral axons, the ganglion cells can be morphologically sorted into two groups: 1) large cells with a high ratio of central to peripheral axon diameter (type I cells), and 2) smaller cells with a central to peripheral process ratio equal to about one (type II cells). Type I ganglion cells projected centrally into the auditory nerve and cochlear nucleus with thick, myelinated axons which bifurcated within the interstitial nucleus to form ascending and descending cochlear nucleus branches. Type II cells projected into the auditory nerve with thin, unmyelinated axons; most (14/15) followed the type I axons to the interstitial part of the cochlear nucleus. One of these fibers could be traced to a branch point, forming ascending and descending branches near the bifurcation of the type I axons. One other type II cell projected into the modiolus and branched extensively to form several branches which led back to the spiral ganglion. There was no obvious projection of this cell deep into the auditory nerve or to the cochlear nucleus.

18.1.7 Middle-Ear Muscle Reflex

John J. Guinan, Jr., James B. Kobler, Sylvette Vachet, Xiao-Dong Pang, Michael P.McCue

We aim to determine the structural and functional basis of the middle-ear reflexes. We have continued our work recording from single stapedius motoneurons and have now obtained data from both Ketamine-anesthetized and decerebrate cats. The data from both of these preparations indicate that stapedius motoneurons can be divided into four major groups: (1) "Binaural-Or" units respond to sound in either the left or the right ear and often show summation when both ears were stimulated simultaneously. (2) "Binaural-And" units respond only when both ears are stimulated. (3) "Ipsilateral" units respond selectively to ipsilateral stimuli (showing little or no responses to contralateral stimuli). (4) "Contralateral" units respond selectively to contralateral sounds. Ipsilateral and contralateral units frequently show lowered thresholds and higher discharge rates in response to binaural stimuli. All stapedius motoneurons have broad tuning curves and most are maximally sensitive to frequencies between 1 and 2 kHz. In Ketamine-anesthetized cats, most units usually have a lowest threshold of approximately 90 dB SPL. In contrast, in some decerebrate cats most units have a lowest threshold substantially lower than 90 dB SPL. Overall, the results indicate that the recruitment order of stapedius motoneurons will be strongly influenced by the spatial position and spectral characteristics of sounds eliciting the acoustic reflex. Manuscripts describing this work and related work are in preparation.

The cell bodies of stapedius motoneurons are located in four rather diffuse groups around the facial nucleus and near the facial nerve anterior to the lateral superior olivary nucleus. We have attempted to find possible correlations between these four anatomical groups and the four physiological groups outlined above. To do this we have developed techniques for injecting single, physiologically-characterized stapedius motoneurons with HRP and identifying their cells of origin in the brain. To date, only a few cells have been characterized and identified. More data are needed before correlations can be determined.

We have recently begun a project aimed at determining which auditory nerve fibers carry the signal that triggers the middle-ear muscle reflexes.

18.1.8 Cochlear Efferent System

John. J. Guinan, Jr.

Our aim is to understand the physiological effects produced by medial olivocochlear (MOC) efferents which terminate on outer hair cells. To do this we have measured the sound pressure in the ear canal generated by a volume velocity source, with and without electrical activation of MOC fibers. The pressure change induced by MOC activation gives an indirect measure of the MOC-induced change in cochlear mechanics. Originally we analyzed our measurements in terms of a change in the effective impedance at the eardrum, $\triangle Z_D$, and found that $\triangle Z_D$ was a strong, oscillatory, function of frequency. A simpler result is obtained, however, if ear-canal sound pressure is assumed to be the sum of a sound from the earphone and a sound which originates in the cochlea (which may be reflected incoming sound) and is transmitted backwards through the middle ear to the ear canal. The efferent-induced change in the ear-canal sound pressure, called P_{OC}, then represents a "sound of cochlear origin." The phase delay of P_{OC} was approximately a monotonically increasing function of frequency. Group delays, calculated from the slope of the angle of P_{OC} versus frequency, ranged from 0.5 to 7 ms with longer delays most often found at lower frequencies. Thus, the oscillatory nature of the $\triangle Z_D$ change is seen to be produced by P_{OC} alternately being in-phase and out-of-phase with the sound produced by the acoustic source. These data are consistent with P_{OC} being produced by a change (perhaps a reduction) in a "reflection" from a region of the basilar membrane which is more apical for lower frequencies. A preliminary report of ear-canal sound pressure changes in terms of P_{OC} has been given recently.[14]

In two publications, we have reviewed the evidence that the cochlear efferents can be divided into lateral and medial olivocochlear systems,[15] and have provided an integrated view of the effects of cochlear alterations including those caused by olivocochlear activity.[16]

18.1.9 Cochlear Implants

Donald K. Eddington, Gary Girzon

With the collaboration of Dr. Joseph Nadol at the Massachusetts Eye and Ear Infirmary, we have implanted arrays of 6 scala tympani electrodes in 5 subjects. The leads of these electrodes exit the body via a connector/pedestal assembly that is secured to the temporal bone just behind the pinna. Measures of electrode impedance, behavioral threshold and dynamic range over the past 6 months have remained stable. During the past 3 months, each of these subjects has been wearing a portable sound processor/stimulator. Initial results show that these subjects score higher on test of speech reading with the device than with speech reading alone (e.g., 98% vs. 61% on CID sentences for the highest scoring subject [HSS]; 92% vs. 68% for the lowest scoring subject [LSS]). Some subjects are also able to score significantly above chance on open-set material (e.g., 84% on Spondee words and 61% on CID sentences [HSS]; 2% and 0% [LSS]). Our aim during the next year is to characterize the information each of these subjects receives through his device using basic psychophysical and analytic speech measures. We expect such results will guide us in the development of better processing schemes that will be evaluated in these same subjects.

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B. Auditory Psychophysics and Aids for the Deaf

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18.2 Binaural Hearing

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H. Steven Colburn, Lorraine A. Delhorne, Nathaniel I. Durlach, Kaigham J. Gabriel, Gary Kline, Janet Koehnke, Carrin Passaro, Patrick M. Zurek

We are continuing our study of the binaural abilities of impaired listeners with measurements of performance on several binaural tasks. Specifically, we are measuring just-noticeable differences (JNDs) in interaural correlation (IC), interaural time delay (ITD), and interaural intensity difference (IID) for one-third octave noise bands centered at 500 Hz and at 4000 Hz. In addition, we are measuring NoSPi detection thresholds at the same two frequencies for a tone centered in a third-octave band of masking noise. The choices of levels at each ear are made such that the stimulus at each ear is clearly above monaural threshold, and the reference IID values are chosen to correspond to equal SPL, equal sensation level (20 dB SL), equal loudness (ABLB measurements), and a centered perception. Performance in the four binaural tasks is measured at reference interaural conditions that include all combinations of these IIDs with interaural time differences of –300, 0, and +300 us. JNDs and thresholds are estimated using a relatively crude adaptive method so that a complete set of measurements can be obtained quickly for each subject.

We have obtained a complete set of data for five impaired listeners: three with bilateral, moderate, flat losses; one with a bilateral, severe, flat loss; and one with a unilateral, severe, high-frequency loss. The performance of these subjects varies across tasks and does not appear to be dependent of the degree or type of hearing loss. For example, a listener with a bilateral, moderate, flat loss demonstrates no measureable binaural ability in any of our tests, while another listener with very similar patterns of hearing loss performs well on all the experiments (with some results comparable to the normal listeners and others somewhat elevated). Data for the other impaired listeners fall between the two just described, each demonstrating difficulty with one or more tasks for some or all interaural reference conditions. Like the data for normal listeners reported previously (Koehnke *et al.* 1986), the data for the impaired listeners and new normal listeners demonstrate that correlation thresholds (expressed as equivalent signal-to-noise ratios) closely approximate NoSpi thresholds for all interaural reference conditions. The ability to predict both of these tasks from ITD and IID discrimination data is being evaluated for various theoretical models.

We are also examining the influence of spectrally-remote masking sounds on interaural sensitivity. Specifically, we are measuring sensitivity to interaural delay in a target band when that band is presented along with a diotic spectral fringe (extending over the audio bandwidth). Both clicks and 100-msec noise bursts are being used as stimuli in which the target bandwidth is a constant proportion (40%) of its center frequency. Comparisons of interaural delay JNDs with and without the spectral fringe show that minimal degrading effects of the fringe are obtained in the octave between 0.5 and 1.0 kHz. With the target band centered at frequencies greater than about 1.5 kHz the effect of adding the fringe is to make any interaural target delay of naturally-occurring magnitude (up to 1.0 msec) undetectable. Expanding the target bandwidth beyond 40% of the center frequency helps little in increasing sensitivity until the band extends into the low-frequency ($<$ 1.5 kHz) region. It appears that the binaural system, even though it is sensitive to interaural delay of high-frequency sounds, makes little use of information in that frequency region when binaural information is also present in the low-frequency region.

We are continuing our work on the development of simple binaural interaction models for neural structures that can be related to available results from the lateral and medial superior olivary regions. The modeling results continue to give insights when compared to available physiological data.

We are applying our psychophysical model to the trial-by-trial results with frozen noise waveforms as reported by Gilkey and others. We believe that an analysis on this level will lead to a more precise model and give us insights into binaural perception that are difficult to achieve in more traditional psychophysical experiments. From the analysis so far, it appears that the model shows greater variability from waveform to waveform than observed experimentally, even when the temporal smoothing of interaural parameter variations is considered.

Finally, we have developed our experimental facilities. The digital-to-analog converter section of the PDP-11/23 has been replaced by a more sophisticated subsystem which uses a bit-slice microprocessor to control signal output. The new subsystem is capable of performing waveform scaling and time shifting, provides much more flexibility, and is faster than the original system. We have also interfaced a similar subsystem to the VAX-11/750 so that the VAX is now able to control another experimental facility while serving other users at the same time.

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18.3 Discrimination of Spectral Shape

National Institutes of Health (Grant 1 RO1 NS16917)

Louis D. Braida, Lorraine A. Delhorne, Nathaniel I. Durlach, Yoshiko Ito, Charlotte M. Reed, John Swartz

This research is concerned with the ability of listeners with both normal and impaired hearing to discriminate broadband continuous spectra on the basis of spectral shape.

Results

Experimental results have been obtained for broadband noises whose spectral shapes are modeled after prototypical shapes of the spectra observed in the production of unvoiced fricative and plosive sounds. Discriminability was measured as a function of signal-to-background noise ratio using a two-interval paradigm in which loudness cues were eliminated by roving the overall stimulus level between observation intervals. Discriminability was studied as a function of intensity rove-width, stimulus duration, and stimulus pair in both normal and hearing-impaired listeners (Farrar *et al.*, 1986; Reed *et al.*, 1985).

Work in the theoretical area has been concerned with modeling the results of our spectral-shape experiments (as well as other, more traditional, psychophysical measurements) using a conventional model which assumes that resolution is limited by peripheral internal noise that is statistically independent across channels (Durlach *et al.*, 1986; Farrar *et al.*, 1986). In addition, work is being conducted to extend this model in a number of directions. For example, computations have been made concerning the effects of interchannel correlation and central noise on the sensitivity index d' for discrimination of overall level and discrimination of spectral shape (Durlach *et al.*, 1986) and on optimum performance in roving-level spectral-shape discrimination (Braida, 1986). In close connection with the development of the theory, experiments are underway to check predictions that are consequences of assumptions made about internal-noise structure, criterion-noise structure, and central processing (Ito, 1986).

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18.4 Role of Anchors in Perception

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This research seeks to provide a unified theory for identification and discrimination of stimuli which are perceptually one-dimensional [e.g., sounds differing only in intensity, (Braida and Durlach, 1986)]. During this period, we have i) made quantitative predictions for the effect of standards and anchors on sensitivity, and ii) measured sensitivity using synthetic-speech continua.

i) Our current theory of intensity perception (Braida *et al.*, 1984) postulates perceptual anchors near the extremes of the stimulus range. Observers identify stimuli by measuring the perceptual distance from a sensation to the anchors and achieve improved resolution for stimuli near the anchors [particularly when the stimulus range (measured in jnds) is large]. Explicit anchors can be introduced in the interior of a stimulus range by the presentation of standards (Berliner *et al.* 1978). Generally, the presentation of a standard stimulus on each trial of an identification experiment improves sensitivity in the neighborhood of the standard when the standard is in the middle of the stimulus range, but not when it coincides with one of the edges of the range (where the internal anchors are presumed to exist).

We have made quantitative predictions for the effect of such standards on sensitivity in identification experiments by assuming that the presentation of a standard creates an anchor, and that observers make use of this anchor, together with the nearer edge anchor, in identifying stimuli. These predictions were made using a Monte Carlo simulation technique for efficiency. Simulation results for the no-standard case were essentially identical to those obtained by using a numerical integration technique (Braida *et al.* 1984). Simulation results indicate that presentation of the standard increases sensitivity. When the stimulus range is large, the increase is nonuniform, being largest in the vicinity of the standard (except when the standard coincides with a stimulus at the edge of the range, when the standard has very little effect) and independent of the extent to which the anchor corresponding to the standard is correlated with the anchors at the edge of the range. When the stimulus range is small, the increase is essentially uniform over the range, but dependent upon anchor correlation (with the greatest increase occurring in the uncorrelated case). A relatively good account of the large-range identification measurements reported results from assuming the variance of the anchor associated with the standard is about four times sensory variance (Berliner *et al.* 1978).

ii) For many continua, especially those which are "categorically" perceived, sensitivity reaches a peak in the interior of the stimulus range. It has been argued that at least some of these peaks are likely to result from the use of perceptual anchors interior to the stimulus range (Macmillan 1984). If such peaks reflect regions of natural high sensitivity, all resolution tasks, including fixed discrimination, should exhibit a peak. If instead they reflect interior anchors, identification and roving discrimination tasks should show sharper peaks than fixed discrimination. Further, the presentation of a fixed standard in identification tasks should increase the sharpness of the peak in the first case, but not in the latter (if the standard coincides with an interior anchor).

We have explored these notions using two synthetic-speech continua: steady-state vowels in the range /i-I-ae/ and stop-consonants differing in voicing along the range /ba/-/pa/. Resolution was measured in four discrimination conditions (two-interval forced-choice and same-different, fixed-level and roving-level discrimination), and in identification conditions with and without a standard. Three subjects participated in the vowel experiment, and four in the consonant experiment. Roughly similar results were obtained from all subjects. These indicated that the trace mode is used more in the discrimination of vowels than consonants, and that possible anchor sites are at the middle of the vowel continuum, and at the /pa/ end of the consonant continuum. Anchor locations could not be identified precisely, and the use of standards improved sensitivity only slightly at best. According to the quantitative analysis reported above, the results on anchors and standards are consistent with the small size of the stimulus range measured for these continua: 6-7 jnds, so that resolution was primarily limited by sensory rather than memory factors. Thus the sensitivity peaks observed for these stimuli reflect primarily patterns of natural sensitivity rather than the effects of perceptual anchors. Further details are available (Goldberg 1985).

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18.5 Hearing Aid Research

National Institutes of Health (Grant 5 RO1 NS12846)

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This research is directed toward improving hearing aids for persons with sensorineural hearing impairments. We intend to develop improved aids and to obtain fundamental understanding of the limitations on such aids. The work includes studies of i) effects of noise on intelligibility; ii) amplitude compression, iii) frequency lowering; and iv) clear speech.

i) The goal of this study is to determine the extent to which the difficulty experienced by impaired listeners in understanding noisy speech may be explained merely on the basis of elevated detection thresholds. Twenty impaired ears of fourteen subjects, spanning a variety of audiometric configurations with average hearing losses to 75 dB, have been tested for reception of consonants in a speech-spectrum noise. Speech level, noise level, and the frequency-gain characteristic were varied to generate a range of listening conditions. For comparison, normal-hearing listeners were also tested under the same conditions with extra noise added to approximate the impaired listeners' thresholds. Although there are a few exceptions, the conclusion based on this sample of moderate-to-severe hearing losses is that, when compared to normals listening under similar conditions of threshold shift, hearing-impaired listeners exhibit little or no additional handicap in speech reception.

ii) Many sensorineural hearing impairments are characterized by reduced dynamic range and abnormally rapid growth of loudness. Multiband amplitude compression has been suggested to improve speech reception for listeners with such impairments, but the intelligibility advantages associated with multiband compression are limited by distortion of speech cues associated with the short term spectrum (De Gennaro *et al.*, 1985). To overcome this problem we are studying amplitude compression based on a principal-component (PC) decomposition of the short-term speech spectrum. In this decomposition, the first and second principal components (PC1 and

PC2) of the short-term speech spectrum are representative of overall level and spectral tilt, respectively. Thus, compression of PC1 roughly tends to equalize consonant and vowel energy while compression of PC2 provides time-varying high frequency emphasis. Two principal-component compression systems, one which compressed PC1 and one which compressed PC1 and PC2 were compared to linear amplification, wideband compression (WC) and independent compression of multiple bands (MBC). Systems were evaluated in terms of both physical and perceptual measurements.

Physical measurements consisted of critical-band level distributions and principal-component coefficient distributions. These measures showed that PC1 compression and WC provide comparable reductions in band level variation relative to linear amplification. PC1 and PC2 compression and MBC provide further reductions in level variations. With regard to spectral shape modification, MBC has the largest effect.

Perceptual comparisons were made on the basis of the intelligibility of CVC nonsense syllables and Harvard sentences with four hearing impaired listeners. The subjects had moderately-severe to severe sensorineural hearing losses and had roughly flat audiometric configurations. With the nonsense syllables, compression of overall level as provided by compression of PC1 and wideband compression improved intelligibility (3–6 %) over the 10 dB range of input levels relative to linear amplification. With the Harvard sentences, the improvements obtained with WC (roughly 25 points for three subjects and 6 points for one subject) were greater than those with PC1 compression (roughly 20 points for two subjects and 3 points for two subjects). Multiband compression, although beneficial in some cases, generally provided scores poorer than with wideband compression. Compression of spectral tilt did not benefit but rather degraded performance relative to linear processing. Error analyses and band level measurements indicated that the highest intelligibility was obtained when audibility was improved and the relative spectral shapes of different speech sounds were preserved relative to linearly processed speech. Further details are available (Bustamante 1985).

iii) Frequency-lowering is a form of signal processing intended to make high-frequency speech cues available to persons with high-frequency hearing loss. We have been investigating the intelligibility of artificially coded speech whose spectrum is confined to frequencies below 500 Hz.

The strategy of our current research in this area is to develop artificial speech codes (using waveforms that represent low-frequency scaled abstractions of natural speech sounds) and to study the intelligibility of the coded sounds as a function of lowpass cutoff frequency (F). This strategy assumes a two-component processing scheme with a speech-recognition system (that has spoken speech as input and written phonemic representation as output) and an auditory coder (that has phoneme representation as input and sound as output). We have constructed codes for 24 artificial consonants (C) and 15 artificial vowels (V) by specifying various abstract properties of speech sounds using frequency, bandwidth, intensity, and duration of noises and tones as the building blocks for these sounds.

Performance on the coded sounds is compared to that obtained on natural speech utterances lowpass filtered to equivalent values of F. Filtering studies of natural speech indicate that performance is affected by the number of utterances or speech tokens used to represent each speech segment in a given experiment (Dubois, 1984). In comparing performance on the two types of sounds (coded or lowpass filtered natural speech), we rely on results obtained from single-token studies of lowpass filtered natural speech.

Identification of coded Cs and Vs has been examined for F = 500 and 300 Hz (see Foss, 1983 and Power, 1985). For a set of 24 consonants in C–/a/ context, performance on coded sounds averaged 90% correct for F = 500 Hz and 74% for F = 300 Hz, compared to 76% and 45% for lowpass filtered speech. For a set of 15 vowels in /b/–V–/t/ context, performance on coded sounds averaged 88% at both values of F, compared to 88% and 56% for the lowpass filtered sounds. The overall results thus indicate that it is possible to construct low-frequency codes which provide better performance than lowpass filtered natural sounds with the same cutoff frequency (at least for the case in which each phoneme is represented by a single token). Furthermore, for the specific codes considered, the coding advantage is greater for consonants than vowels (in the sense that it is retained at higher cutoff frequencies).

We have also begun to investigate the ability of subjects to comprehend streams of coded consonants and vowels. Results have been obtained at F = 500 Hz for a CV indentification experiment in which C was chosen at random from a set of 24 Cs and V was chosen at random from a set of 15 Vs. Performance averaged across two subjects indicated a C identification score of 67% correct and a V identification score of 71% when the subject was asked to respond to both C and V. Similar scores were obtained when the subject was required to respond only to the C or to the V in a randomly selected CV syllable. The percentage of syllables in which both C and V were identified correctly averaged 50%.

iv) The ultimate goal of our research on clear speech is the development of improved signal-processing schemes for hearing aids. The ability of naturally produced clear speech has been demonstrated to increase intelligibility for both normal and hearing impaired listeners (Picheny 1985, 1986, and Chen 1980). Current research has two major components: characterization of the acoustic differences between conversational and clear speech, and determination of which acoustic properties are responsible for the improved intelligibility.

Detailed durational measurements have been made of speech segments in 50 sentences spoken conversationally and clearly by three speakers. Durational differences can be large (greater than 50%) and are dependent on the sound class (e.g., vowel, plosive, fricative, etc.). An additional 1200 sentences are in the process of being analyzed.

Since durational differences between conversational and clear speech are both large and nonuniform, we are attempting to determine the extent to which such differences contribute to the increased intelligibility of clear speech. Stimuli are processed to control durational differences at the speech segment level using an iterative algorithm developed by Griffin and Lim 1984. Several hundred sentences will be used in perceptual evaluations. Four processing conditions will be tested: naturally produced conversational sentences, naturally produced clear sentences, clear speech processed to have segment durations characteristic of conversational speech, and conversational speech processed to have segment durations characteristic of clear speech.

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18.6 Multimicrophone Monaural Aids for the Hearing-Impaired

National Institutes of Health (Grant 5 RO1 NS21322)

Cathleen R. Corbett, Nathaniel I. Durlach, Daniel A. Frost, Michael V. McConnell, Patrick M. Peterson, William M. Rabinowitz, Patrick M. Zurek

The goal of this work is the development of systems that sample the acoustic environment at multiple points in space to form a single-channel output providing enhanced speech intelligibility for the hearing-impaired. Work in the past year has focused on studies of i) a head-worn microphone array to provide a fixed directional beam pattern; ii) adaptive processing schemes; iii) nonlinear processing schemes; and iv) coding of multiple messages for monaural presentation.

i) In the area of fixed-weight linear arrays, a theoretical analysis was undertaken to determine relationships among array geometry (number and spacing of sensors), array gain (zero-degree output against that of diffuse-field noise), and array noise sensitivity (zero-degree output against that of uncorrelated sensor noise) for linear arrays situated in a free, uniform plane-wave field. The approach (after Cox, Zeskind, and Kooij, 1985) provides a unified framework that spans the limits imposed by classical beamforming and supergain. Results indicate that a four-sensor array, with a length of 4.1 cm and configured as a second-order gradient system, achieves a free-field array gain of 8.5 dB with acceptable noise sensitivity. Such an array can be constructed simply using a pair of first-order hearing-aid directional microphones (Rabinowitz, Frost, and Peterson, 1985). Current efforts are directed toward achieving this performance with the array placed near the head, where diffraction modifies the free-field inputs to the sensor array.

ii) Adaptive processing schemes vary the complex weightings applied to the microphone signals so that the beam pattern tracks changes in the acoustic environment. Initial tests of an adaptive LMS beamforming algorithm (Griffiths and Jim, 1982; Widrow and Stearn, 1985) indicate that this simple algorithm can reduce interference in slowly-changing environments that are anechoic or moderately reverberant. Effort continues to characterize the performance of this algorithm as a function of algorithm parameters and environment complexity. In addition, faster-adapting algorithms are being developed for testing in the near future. Our work on algorithms has been accelerated by the ISPUD signal processing package, which was developed in our laboratory over the past year and has proven useful in a wide range of signal processing problems.

iii) Nonlinear processing schemes are motivated by an understanding of normal binaural hearing. Two variants of a nonlinear processing system first proposed by Kaiser and David (1960) were evaluated for enhanced intelligibility (McConnell, 1985; McConnell *et al.*, 1985). In both systems the running cross-correlation between two microphone signals is used to derive a time-varying gating signal that multiplies the sum of the microphone signals to form a monaural stimulus. With a target source straight-ahead and an interference source off-axis, this processing results in an output that is increasingly attenuated with decreasing target-to-interference ratio. In the first system this processing was applied to the wideband inputs and in the second it was applied independently in four octave bands. With the latter system three degrees of processing (determined by the function relating output attenuation to crossed-correlation) were investigated. Intelligibility tests were conducted using sentences as the straight-ahead target and continuous discourse as the off-axis (90° azimuth) interference. Contrary to expectations based on the report of Kaiser and David, in no case was speech intelligibility improved as a result of processing. Apparently, the benefits of removing remote interference (temporal and spectral) do not outweigh degradations of the target signal.

iv) If directional channels can be built, then we must face the problem of how to code the multiple simultaneous signals into a monaural signal that facilitates attention to each of the individual messages. We have begun a study of filtering as a means of coding two or four sentence-length messages. The question is whether by presenting individual messages in separate spectral regions the joint intelligibility of all messages is greater than it is when the wideband messages are simply summed. With only two messages the simplest filtering scheme consists of lowpass and highpass filters with the same cutoff frequency. Results show that the cutoff frequency that divides the spectrum into equal halves, in terms of intelligibility, is about 1100 Hz, considerably lower than the 1900 Hz found by other investigators using consonant-vowel-consonant test material. Further, intelligibility with this split-spectrum filtering scheme is poorer than with wideband summation of the two messages.

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C. Transduction Mechanisms in Hair Cell Organs

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The overall objective of this project is to study the sequence of steps by which mechanical stimuli excite receptor organs in the phylogenetically related auditory, vestibular, and lateral-line organs. The receptor cells in these organs are ciliated hair cells. Specific goals include the characterization of the motion of the structures involved, particularly the hair cell stereocilia; study of the nature and origin of the electrical responses to mechanical stimuli in hair cells; and investigation of the role of these responses in synaptic and neural excitation.

18.7 Micromechanical Basis of Neural Frequency Analysis and Tonotopic Organization in the Cochlea of the Alligator Lizard

National Institutes of Health (Grant 5 RO1 NS 11080)

Lawrence S. Frishkopf

We have measured the motion of hair cell stereocilia in relation to the underlying basilar membrane in the alligator lizard cochlea; in the basal region of the cochlea, where cilia are freestanding, a ciliary (micromechanical) basis for frequency analysis and tonotopic organization (observed in hair cells and nerve fibers) has been established.[1,2,3] Preliminary studies are underway of the mechanical response of the stereocilia and overlying tectorial membrane in the apical region of the cochlea, where more complex frequency-dependent phenomena appear in nerve fiber responses.

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