

## XXIV. COMMUNICATIONS BIOPHYSICS

### A. Signal Transmission in the Auditory System

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#### 1. BASIC AND CLINICAL STUDIES OF THE AUDITORY SYSTEM

National Institutes of Health (Grants 5 PO1 NS13126 and 5 KO4 NS00113,  
and Training Grant 5 T32 NS07047)

Nelson Y. S. Kiang, William T. Peake, Thomas F. Weiss

Research on signal transmission in the ear and auditory nervous system continues jointly with the Eaton-Peabody Laboratory at the Massachusetts Eye and Ear Infirmary. The mechano-electric transduction system of the inner ear has been investigated through studies of the mechanical responses of the basilar membrane,<sup>6</sup> the intracellular responses in the receptor organ,<sup>1</sup> and the chemical environment of the inner ear.<sup>7</sup> Characteristics of auditory nerve-fiber responses to acoustic stimuli have been described in normal<sup>2-4</sup> and in pathological<sup>5</sup> ears. The expanding clinical use of compound action potentials from the auditory nerve for diagnostic purposes has made it important to determine how these responses are related to responses of nerve fibers from different regions of the inner ear.<sup>8,9</sup> An anatomical study has led to a description of the organization of the "feedback" system from the brain stem to the inner ear, which is substantially different from the previous conceptions.<sup>10</sup>

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B. Auditory Psychophysics and Aids for the Deaf

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1. INTENSITY PERCEPTION AND LOUDNESS

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National Science Foundation (Grant BNS77-16861)

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This research continues to be concerned with the development of a unified, quantitative theory of intensity perception and loudness, and involves the construction and integration of models of sensory processes, short-term memory, perceptual context effects, and decision making, as well as extensive psychophysical experimentation. During the past year, work has been conducted in four areas: (i) the relation of intensity resolution to auditory-nerve firing patterns, (ii) the relation of intensity discrimination to loudness matching, (iii) the dependence of intensity identification on stimulus presentation frequency, and (iv) intensity resolution and loudness in listeners with hearing impairments.

(i) A study of the relation between intensity discrimination and the coding of intensity in auditory-nerve firing patterns has been initiated using an approach introduced by Siebert<sup>1,2</sup> that is based on optimum processing of average-rate information on

auditory-nerve fibers. Recent research results in both psychoacoustics and auditory physiology now differ sufficiently from older ideas that it appears worth while to rework Siebert's formulation. For example, psychoacoustic studies<sup>3</sup> indicate that Weber's Law does not hold for tones at intensities above roughly 40 dB SPL, but rather that intensity resolution improves systematically above this level. In addition, recent physiological data differ, for example, from the description of rate-intensity functions and threshold distributions used by Siebert. Unfortunately, initial indications are that performance predicted by optimum use of average-rate information on auditory-nerve fibers is very sensitive to details of the auditory-nerve description, and that the available physiological data are not sufficiently complete to specify these details. During the coming year we plan to prepare a discussion of this work for publication.

(ii) According to a recent extension of our theory of intensity perception,<sup>4</sup> two stimuli are matched in loudness if and only if their intensities divide the respective dynamic ranges proportionally in terms of just-noticeable differences. To test this prediction we have conducted a series of intensity discrimination and loudness-matching experiments using a common set of listeners with normal hearing. Data were obtained over essentially the entire dynamic range for three types of sound stimuli: 1000-Hz tone in quiet, 1000-Hz tone partially masked by a two-octave wide noise band, and spectrally flat wide-band noise. Of the five listeners tested, only three produced results that had sufficient internal consistency to be useful for testing the prediction. For these three subjects, the data and theory were found to be reasonably consistent. Furthermore, these data were found to be strongly inconsistent with predictions based on Fechner's classical theory. Further details of this research have been submitted for publication.<sup>5</sup>

(iii) Identification experiments using 13 tone-pulse stimuli (1000 Hz, 500 msec) spaced by equal decibel increments from 48 to 90 dB SPL were conducted under three different presentation probability conditions: EQ, in which all stimuli were equally likely; MF, in which the middle intensity was presented on roughly 1/3 of the trials; and EF, in which each of the two extreme intensities was presented on roughly 1/5 of the trials. No correct response feedback was provided. The results were analyzed in terms of sensitivity and bias in accordance with the preliminary theory of intensity resolution<sup>6</sup> using a maximum-likelihood procedure.<sup>7</sup> The listeners generally shifted their decision criteria for MF and EF conditions in the directions required to increase correct identification performance, but no significant changes in sensitivity were observed relative to the EQ condition. These results are consistent with the predictions of the preliminary theory of intensity resolution and the results of Lippmann<sup>7</sup> on the effects of payoff variation, but are at variance with those of Cuddy<sup>8</sup> on the effects of presentation probability variation on tone-frequency identification. Further details of these results are available in Bugnacki.<sup>9</sup>

(iv) Experiments currently under way with hearing-impaired listeners are concerned with the measurement of basic intensity resolution over the dynamic range of selected pure-tone frequencies, and with the determination of loudness matches at a given frequency between the normal ear and the impaired ear (for listeners with unilateral impairments) or between different frequencies in the same ear (for listeners with high-frequency loss). In addition, we are beginning a series of measurements of the variability of loudness comparisons between the normal ear and the impaired ear in order to obtain a quantitative measure of signal distortion in the impaired ear. This program includes listeners with a wide variety of type and severity of hearing loss, and is undertaken both to provide insights into the perceptual abnormalities associated with hearing impairments and to check the validity of our theoretical models. During the coming year we plan to prepare the results of these measurements for publication.

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2. BINAURAL HEARING

National Institutes of Health (Grant 5 RO1 NS10916)

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The primary objective of this research continues to be the development of a unified quantitative theory of binaural interaction that is applicable to a wide variety of binaural phenomena and that is consistent with neurophysiological data.<sup>1-5</sup> A secondary objective is to apply our understanding of binaural interaction to the problems of the hearing-impaired. During the past year, significant progress has been made in a variety of projects, including studies of both normal and impaired hearing.

In one project, we have completed two binaural detection experiments with pseudo-random noise maskers to examine the relative contributions to the variability of the decision variable from the randomness of the stimulus (external noise) and from the stochastic nature of the internal processing (internal noise).<sup>6</sup> The first experiment compares detection performance measured in a two-interval, temporal forced-choice paradigm for two conditions: the same noise waveforms in both intervals of a trial versus statistically independent samples of noise in the two intervals of a trial. The second, one-interval, experiment compares performance differences among ten samples of noise waveforms, each used for about 1000 trials. Two interaural configurations were studied. In the first, the stimuli at the two ears were identical. In the second, the target tone was inverted at one ear, although the noises at the two ears were identical. In the first configuration (NOSO), internal noise dominates external noise, and in the second (NOS $\pi$ ), the variance of the external noise is comparable to the variance of the internal noise. These results are surprising to us and will be pursued further with additional experiments.

In a second project, we are testing binaural hearing models that use subjective lateral position as the sole decision variable.<sup>7</sup> We measured the just-noticeable difference (jnd) in interaural time delay for several values of the reference interaural time delay for tone stimuli.<sup>8</sup> We concentrated our research in the region between one-fourth and one-half the period of the tone because the model predicts very large jnds in this region. Our results and our subjects' reports of their impressions cast serious doubt on the validity of the position model. We found no large interaural time jnds, even for values of interaural time delay for which the position model predicts the largest jnds. Furthermore, the subjects report that the perceived lateral position of a binaural tone is not a single, well-defined image as assumed by the position model, and that cues other than lateral position are often used in interaural time discrimination for large time

delays when the position-based cue is not helpful.

In a third project, we are investigating the effect of a masking noise on interaural time discrimination. The jnd in interaural time delay for a narrow-band noise signal was measured for several different interaural conditions of a wide-band masking noise. The narrow-band signal is a  $1/3$ -octave Gaussian noise band centered at 500 Hz with an overall level of approximately 56 dB SPL, the same at each ear. The masking signal is a Gaussian noise including frequencies from 250 Hz to 1500 Hz, also presented at an overall level of 56 dB SPL. The interaural conditions of the masker include the interaurally identical case (NO), the interaurally inverted case ( $N\pi$ ), and the interaurally uncorrelated case (NU). We also used maskers with an interaural delay of  $\tau = 100 \mu\text{s}$  ( $N\tau$ ), with an interaural attenuation of  $a$  dB ( $N\alpha$ ), or with both delay and attenuation ( $N\tau, a$ ), where  $a$  is realized by attenuating one ear and is chosen to center the masker when both  $\tau$  and  $a$  are present. Several relations held consistently for all four subjects. First, the masked jnds were always larger than the jnds measured with no masking. Second, the progression of increasing difficulty (increasing jnds) was NO, NU, and  $N\pi$ . Note that this progression is exactly opposite to that expected from detectability results. Third, the  $N\tau, a$  case is more difficult than  $N\tau$  or  $N\alpha$ . Note that this is consistent with the notion that the jnd task is easier when the lateral positions of the masker and target are separated within the perceptual space; however, this notion was not applicable consistently for the rest of the conditions measured. We are continuing to test some of these conditions.

In a fourth project, we are investigating the jnd in the interaural correlation of Gaussian noise. We are measuring the dependence of the jnd on bandwidth at two reference correlations, +1 and 0. Gaussian noise waveforms with eight different bandwidths from 3 Hz to 4500 Hz were synthesized with the narrow-band cases centered at 500 Hz. For seven of the bandwidths, waveforms were synthesized via sums of random-amplitude, random-phase cosines, one every three Hertz. For the 4.5-kHz low-pass case, waveforms were generated from Gaussian-distributed random numbers. At each bandwidth, waveforms were randomly chosen for each representation from an available set of 64 waveforms. In measurements so far, jnds from a reference correlation of +1 have been determined for three subjects. The jnds obtained are about 0.04 for the wide-band waveforms (greater than  $1/3$  octave) and decrease to 0.004 for the narrow-band waveforms (less than  $1/3$  octave). These results, together with results from a reference correlation of zero, will enable us to answer questions about the spectral characteristics of our correlation processors and help us to interpret binaural detection performance for narrow-band stimuli.

In a fifth project, we are investigating the discrimination of interaural time delay of the envelopes (onset and offset) of tone-burst stimuli. We are measuring the jnd in the interaural delay of the envelope with no ongoing delay. This jnd has been determined

for three rise times (5, 50, and 150 ms) and two frequencies (500 and 4000 Hz) for four subjects at 74 dB SPL. Also, the level dependence of the jnd at 500 Hz was measured for two of the subjects. The jnds are a few hundred microseconds for all subjects at 4000 Hz, with only a slight dependence on the rise time. At 500 Hz, except for one subject, jnds increase from a few hundred microseconds to about a millisecond when the rise time increases from 5 ms to 150 ms. One subject shows exceptional results at 500 Hz; his jnds are 2 ms, 20 ms, and 35 ms for the three rise times measured. (His audiogram was normal and the results were repeatable.) For the two subjects tested at various levels, the measurements show very large increases in the jnd as the level decreases. For example, the jnd at 14 dB SPL is 90 ms. The jnd is approximately inversely proportional to the pressure in dynes/cm<sup>2</sup> for low and moderate levels and asymptotes to a constant value at high levels.

In a sixth project, conducted in cooperation with the Eaton-Peabody Laboratory of the Massachusetts Eye and Ear Infirmary, we have made relatively crude but reliable measurements of spatial resolution and interaural discrimination in a number of persons with hearing impairments and in a group with multiple sclerosis, in addition to a normal control group. Measurements include: the minimum audible angle (MAA) in the vertical median plane, the MAA in the horizontal plane at eight reference locations around the head, the jnd in interaural time delay, and the jnd in interaural amplitude ratio. The standard stimulus was a pair of broadband (250 Hz-10 kHz) noise bursts of one-sec duration separated by one second, although additional measurements with other stimuli were occasionally performed. Subjects with several types of hearing impairments were used, including unilateral and bilateral conductive losses, bilaterally symmetric sensorineural losses, unilateral Meniere-type losses, acoustic neuromas (all surgically confirmed vestibular schwannomas), and unilateral dead ears. The bilateral sensorineural group was divided into two categories according to their performances on speech-discrimination tests. Results were relatively uniform within each category with the exception of the acoustic neuroma category, which showed large intersubject differences in all measurements. Results are generally consistent with the notion that there are separate processors for interaural timing information, interaural level information, and spectral information. Each of these types of information can be interfered with separately. For example, conductive losses, which degrade all three types of information, resulted in the poorest performance, and subjects with bilateral sensorineural losses and poor speech-discrimination performance showed poor use of spectral information (as reflected in the vertical MAA and the horizontal MAA on the sides) but relatively normal use of time and intensity information (as reflected in the jnds and the horizontal MAA ahead or behind). In subjects with multiple sclerosis and with audiometrically normal hearing, it was found that the ability to use each of the types of information could be compromised independently.



A seventh project is concerned with more careful measurements of binaural interaction in individuals with well-defined hearing losses of various types. Much of our work to date has been concerned with the development of a set of programs which permits the measurement of jnds for either time or intensity. One program constructs sets of narrow-band noise waveforms with specified bandwidths, center frequencies, and relative delays. The others control experiments in a very flexible way, including the option of substantial interaction between the experimenter and the subject. The experimenter can, for example, present stimuli at equal SPL to the two ears, preset the attenuation to each ear, or present the stimuli under subject control for ABLB or "centering" adjustment. Using the selected signal levels, the experimenter can test sensitivity to either interaural time or interaural intensity. The experimenter can choose to present a set of stimuli at a selected level, in which case the program displays the cumulative percent correct after each trial and a summary of the run including  $d'$  at the end of each block of trials. Alternatively, he can select a "PEST" adaptive procedure to obtain an estimate of the jnd, or he can elect to present single trials at selected stimulus parameters so that he can train the subject and/or make a subjective estimate of the jnd. The program is now being used in an extensive study of a subject with a suspected acoustic neuroma. Since this subject is available only a short time before surgery, the flexibility of the program has proved very helpful and the interactive features have been especially important by allowing efficient selection of parameters.

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3. HEARING AID RESEARCH

National Institutes of Health (Grant 5 RO1 NS12846)

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This research is concerned with the development of improved speech-reception aids for persons suffering from hearing loss and of fundamental understanding on the limitations of such aids. During the past year, our work in this area has continued to focus on the problem of matching speech to residual auditory function. The work in this area is directed toward improved signal-processing schemes for people with sensorineural impairments, and includes the study of linear amplification, amplitude compression, and frequency lowering.

Our research on linear amplification is concerned with modelling the dependence of speech-reception performance on the speech materials, the background interference, the listener, and the linear-amplification system. Initial work on this project focused on the extent to which Articulation Theory<sup>1-5</sup> can be used to predict the dependence of word intelligibility on frequency-gain characteristics and presentation level for listeners with specified audiometric configurations. In general, the theory was found to yield relatively good predictions for a group of listeners with steeply sloping, high-frequency hearing loss, although it was necessary to assign a single number, the proficiency factor, to each listener in order to derate performance relative to that for listeners with normal hearing. Further details of these results are available in Dugal.<sup>6</sup> Future work on this project will be concerned with evaluating the theory for listeners with a wider variety of audiometric configurations, with the determination of optimum linear-amplification systems for specified configurations, and with the development of a model for the proficiency factor.

Research on amplitude compression for listeners with reduced dynamic range has been primarily concerned with obtaining further insight into the negative results obtained in our initial study of the effects of multiband amplitude compression on speech intelligibility for persons with sensorineural losses.<sup>7</sup> We have duplicated the critical portions of our initial study on listeners with normal hearing, employing spectrally shaped noise to simulate the losses (in terms of elevated threshold, reduced dynamic range, and recruitment) of the listeners with genuine impairments tested in the initial study. Roughly speaking, the results of this study show that, although the normals with simulated losses

generally obtained higher scores than the impaired listeners, the relative performance of the various signal-processing transformations tested was independent of whether the loss was genuine or simulated. Specifically, the results for the normals, like the results for the impaired, showed no advantage for compression over linear amplification with appropriate high-frequency emphasis. Further details of these results are available in DeGennaro.<sup>8</sup>

Our research on frequency lowering for listeners with negligible hearing at high frequencies employs a pitch-synchronous time-dilation technique with warping of short-term spectra<sup>9</sup> and has included three major projects: (i) a study of the effects of training on the perception of frequency-lowered consonants, (ii) a study of the effects of lowering and warping parameters on the discriminability of frequency-lowered consonants, and (iii) a study of the perception of frequency-lowered vowels.

(i) Naive listeners with normal hearing were trained to identify a set of 72-CV nonsense syllables processed by frequency lowering or low-pass filtering to bandwidths of 1000 and 1667 Hz. Pre- and post-training identification tests indicated that, although substantial increases in performance occurred for both processing conditions, greater improvements were obtained for the frequency-lowered condition. In the post-training tests, subjects were generally better able to identify the filtered materials than the lowered materials, but achieved higher scores for the 1667-Hz bandwidth condition in a noisy background when frequency lowering was used. Analysis of identification errors suggests that the relatively good performance obtained in quiet-background tests for the filtered materials may have been due to weak low-frequency cues less resistant to additive noise than the recoded high-frequency cues introduced by frequency lowering.

(ii) Discriminability measurements were made on 89 pairs of consonants (in CV nonsense syllables), including contrasts of voicing, manner, and place, for a variety of lowering, warping, and filtering conditions. In general, for a given bandwidth, overall performance for lowering was roughly equivalent to that for filtering for those warping conditions which left low-frequency components relatively intact. Warping conditions which altered low-frequency components (such as linear lowering – proportional frequency reduction) resulted in overall performance inferior to that for low-pass filtering. The ranking of the various processing conditions on the phonetic contrast categories of voicing and manner was similar to that for overall performance, although the discriminability of specific types of manner contrasts was different for filtering and lowering. For example, for contrasts of affricates with plosives and fricatives, performance was better for lowering than for filtering, while for contrasts of nasals with semivowels the opposite was true. Performance on place contrasts, which was generally inferior to that for voicing and manner contrasts for all processing conditions, exhibited the same characteristic. For example, higher performance was obtained on filtered materials for place contrasts within semivowel and nasal sounds, but on lowered materials for

place contrasts of fricative sounds. The results of this discrimination experiment are roughly similar to the consonant identification experiment described above.

(iii) Discrimination and identification tests of filtered and lowered vowels in /b/-V-/t/ contexts were conducted using naive normal-hearing listeners. Discriminability was found to be high for materials processed to a 1000-Hz bandwidth either by low-pass filtering or lowering with warping adjusted to minimize change in low-frequency elements. The naive listeners used in this study were, however, able to achieve much higher identification scores for the 1000-Hz bandwidth condition on the filtered materials than on lowered materials. Furthermore, both warped lowering by a factor of 5 and linear lowering by a factor of 2 yielded similar overall performance – although different patterns of errors – in this test. In general, the confusions exhibited by the listeners used in this study tended to relate to changes in formant frequency induced by frequency lowering: features related to first-formant frequency were better perceived than those related to second-formant frequency for the warped-lowering condition (which altered high frequencies proportionally more than low frequencies), while both types of features were degraded for linear lowering (which lowers all frequencies the same relative amount). Further details of this study are available in Picheny.<sup>10</sup>

In general, the results obtained in our initial studies of both amplitude compression and frequency lowering have been disappointingly negative. In future work, we plan to conduct further analytical studies to achieve basic understanding of the results obtained and to develop insight into fundamental limitations on these techniques. We believe that such efforts are essential. Not only may further study lead to results which are more positive, but also it is extremely difficult to build on such results unless they are clearly understood.

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#### 4. TACTILE COMMUNICATION OF SPEECH

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Nathaniel I. Durlach, Douglas R. Mook, Charlotte M. Reed, Steven I. Rubin,  
Martin J. Schultz

The goal of this project is to develop tactile speech communication aids for the deaf and deaf-blind. Our research has been directed toward evaluating two basic types of tactile communication systems, one based on spectral displays of the speech waveform and the other based on the natural articulatory display present on the face during speech.

The spectral displays have been realized using an Optacon transducer system interfaced to a PDP-11 computer.<sup>1,2</sup> In these displays, frequency is coded in the 24 rows of the transducer while either amplitude or time is coded in the six columns. At present, subjects with normal sight and hearing are evaluating these displays with respect to discrimination and identification of short speech segments. One study has concerned the ability of subjects to identify a set of 12 consonants in CV nonsense syllables spoken by four speakers. An Optacon-based tactile display (spectral amplitude versus frequency) was compared to a visual analog driven by the same information. After training, the users of the tactile display performed much as listeners at a -12 dB S/N ratio, while the users of the visual display were equivalent to listeners at a -6 dB S/N ratio. For both displays performance was best on the feature voicing and poorest on place, which was most degraded by the use of multiple talker and vowel contexts. Additional details are available in Mook.<sup>3</sup> The second study concerned the discriminability of vowels (in isolation as well as /b/-V-/t/ contexts) displayed on the Optacon in amplitude-frequency and time-frequency modes. In general, very similar results were obtained on the two systems, although average scores were slightly higher for the amplitude-frequency

display. An analysis of results in terms of articulatory features indicated that the most salient cues were concerned with vowel amplitude, duration, and first-formant frequency, with less importance associated with the separation between first- and second-formant frequencies. Further details are available in Clements.<sup>4</sup>

Research on articulatory displays of speech has focused on the Tadoma method of speechreading. We are studying the performance of both deaf-blind individuals highly trained in the Tadoma method<sup>5</sup> and also inexperienced subjects.<sup>6</sup> Current work with an experienced Tadoma user is directed toward (a) increasing our understanding of the cues involved in speech perception through Tadoma by determining how error patterns for consonants and vowels change as a function of hand position; (b) exploring linguistic competence using standardized language tests as well as tests designed to examine more specific linguistic features; and (c) analyzing the subject's speech production through measurements of durational, prosodic, and articulatory aspects of speech recordings. Work with normal subjects<sup>6, 7</sup> (in which blindfolds and masking noise are used to eliminate visual and auditory cues) includes testing the ability of these subjects to discriminate speech elements, to learn to identify isolated phonetic units, and to learn to decode words in isolation and in connected speech.

Although it is already evident that the speech reception performance of certain experienced Tadoma users is substantially superior to the performance that has been achieved with artificial tactile displays, the reasons for this are not yet clear. It is possible that superiority arises because the experienced users have unusual tactile or cognitive abilities, the display itself is inherently advantageous (because it is a rich, multidimensional display and/or a display that is directly related to the speech-production process) or the opportunity afforded these experienced users to learn the Tadoma display greatly exceeds that afforded those subjects who were trained on artificial displays. A major portion of our research program is concerned with determining the extent to which each of these factors contributes to Tadoma's superiority.

Our future work will include comparative studies of Tadoma and various spectral displays using subjects with comparable amounts of training on the different displays. In addition, we plan to develop a "Synthetic Tadoma System" for use as a research tool. This system will involve a sensor array to be placed on the talker's face and an "artificial face" to be used as a display. Aspects of this display will be varied to determine their effects on speech-perception performance. Work is also in progress to build a new transducer system for spectral tactile displays. This device (modelled after a device developed by Sherrick at Princeton University) will consist of a rectangular array of piezoelectric bimorph vibrators appreciably larger in area than the Optacon. We are currently investigating such issues as the size and density of the vibrators in the array, appropriate interface hardware, and control algorithms.

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## 5. MUSICAL PITCH

National Institutes of Health (Grant 2 RO1 NS11680 and Fellowship 5 F32 NS05327)

Edward M. Burns, Adrian J. M. Houtsma

The overall objective of this research is to gain understanding of the auditory processes that underlie musical-pitch sensations arising from complex stimuli. Research effort has been devoted to three projects.

## a. Pitch Perception of Harmonic Tone Complexes

Musical-interval identification experiments were conducted using dichotic two-tone complexes of frequencies  $nf_0$  and  $(n+m)f_0$ , where  $f_0$  is the fundamental (note) frequency,  $n$  is a random integer between 1 and 10, and  $m$  is a fixed integer between 1 and 4. The results of these experiments were compared with theoretical results derived from three modern pitch theories. The optimum-processor theory<sup>1</sup> was used to derive best and worst performance bounds by computer simulation, where best performance is obtained if the range of expected fundamental frequencies is known to the processor, and worst performance results if the processor scans the entire fundamental frequency range. The virtual pitch theory<sup>2</sup> and the pattern-transformation theory<sup>3</sup> were augmented with additional specific assumptions which made it possible to derive quantitative performance bounds predicted for our experiments. It was shown that the predictions of the

optimum-processor and virtual pitch theories are very similar and quite different from predictions made by the pattern-transformation theory. The former two are much better supported by the data than the latter one.<sup>4</sup> Significant discrepancies between data and all theories were found in some instances, however, which seem to indicate the presence of a so-called "analytic" pitch mode in which the listener fails to hear the pitch of the missing fundamental, but, instead, hears pitches of individual tone components. This hearing mode is not included in any of the current theories, but is found to have significant effects on pitch or melody recognition data obtained with complex tones.

#### b. Pitch Perception of Amplitude-Modulated Noise

We are conducting a theoretical analysis of pitch perception of amplitude-modulated noise. In an earlier experimental study<sup>5</sup> it was shown that if white noise is first low-pass filtered (cutoff frequency  $f_{co}$ ) and subsequently modulated (100% AM) with a periodic signal (sine, square, or pulse) of fundamental frequency  $f_o$ , the sound evokes a pitch sensation of  $f_o$  when  $f_{co} \ll f_o$ . When  $f_{co}$  approaches  $f_o$ , there is no measurable pitch sensation for the pulse-modulated noise, but for the sine- and square-wave modulated noise, the pitch sensation increases again with increasing noise bandwidth. Traditionally, amplitude-modulated noise has been regarded as being devoid of spectral clues, and all pitch properties of these signals were therefore explained by temporal auditory processing. We are currently doing quantitative investigation of a pitch theory recently suggested by Pierce et al.<sup>6</sup> in which pitch clues are extracted from the short-term power spectrum. This formal model is similar to the classical "energy-detector model" in that it comprises a bank of parallel filters, square-law devices, and "leaky" integrators. It differs in the sense that it does not look at the temporal variation of the energy at each channel, but looks at any instant of time across all channel outputs, performing a running "spectral" autocorrelation. Qualitatively the theory can account for the experimental results described above.<sup>5</sup> Quantitative details are still being worked out.

#### c. Binaural Diplacusis

We have completed two projects concerned with the study of binaural diplacusis, the phenomenon in which a pure tone evokes a different pitch when presented to one ear compared to the other. In persons with normal hearing, the pitch differences in binaural diplacusis are very small; in pathological cases, however, this pitch difference can be large (e.g., 10%), and is often found at frequencies where the detection threshold curve shows abrupt changes. In one project, monaural and binaural pitch matches were made to the cubic difference tone (CDT)  $2f_1 - f_2$  by a subject who showed a significant amount of diplacusis over some frequency range. This range was made to coincide with either the CDT or with the primary tones. These experiments shed some light on the question of whether or not the CDT is coupled to the basilar membrane at the characteristic place



of the CDT frequency.<sup>7</sup> In another project, the effect of intensity on binaural diplacusis was investigated. Results from preliminary experiments seem to indicate that, at any given frequency, the diplacusis function of intensity is given by the difference between the monaural pitch-intensity functions measured at that frequency for the two ears.

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## XXIV. COMMUNICATIONS BIOPHYSICS

### C. Transduction Mechanisms in Lateral Line and Vestibular Organs

#### Academic Research Staff

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National Institutes of Health (Grant 2 RO1 NS11080)

Lawrence S. Frishkopf, Charles M. Oman

Our overall objective is to understand the changes that occur in receptor cells of the phylogenetically related auditory, vestibular, and lateral-line systems in response to mechanical stimuli. Under investigation are the processes of mechanical-to-electrical transduction, membrane depolarization, synaptic transmission, and neural excitation in hair-cell organs. The two organ systems that we are studying were chosen because of their relative accessibility and simplicity: free-standing lateral-line organs in amphibians and elasmobranch vestibular organs.

Goals during the past year have been (1) to characterize the mechanical properties and motion of hair-cell cilia in response to controlled mechanical stimuli; and (2) to estimate through theoretical models the magnitude of cupula motion in semicircular canals of different species during normal head movements.

#### 1. MECHANICAL PROPERTIES OF HAIR-CELL CILIA

Lawrence S. Frishkopf, Richard D. Kunin

The mechanical properties of hair-cell cilia may determine, in part, the frequency response of hair-cell organs, particularly of auditory organs. Certain frequency-related properties such as sharpness of neural tuning, tone-on-tone interactions, and nonlinear response characteristics are not well accounted for by observed basilar membrane motion, leading to a postulated second stage of filtering. It is possible that the hair-cell cilia which couple the overlying tectoral membrane to the hair cells within the organ of Corti may be the site of such nonlinear processes.

With this in mind, we have begun to study the motion of hair-cell cilia in the isolated crista of the semicircular canal of the skate using the Nomarski interference contrast microscope. Fine probes have been used to contact and displace cilia in order to observe their mechanical properties. Stereocilia appear to be stiff and brittle whereas kinocilia are flexible and may, under appropriate conditions, "beat" spontaneously. Rapid return of the stereocilia after displacement suggests a high-frequency response characteristic. Results are preliminary.

## 2. THEORETICAL MODEL FOR SEMICIRCULAR CUPULA MOTION

Charles M. Oman

In 1972, Oman and Young theoretically estimated the magnitude of human semicircular canal cupula motion. To provide a basis for comparison of our more recent experimental results on cupula motion in the skate (Oman, Frishkopf, and Goldstein, 1979) with the observations of McLaren and Hillman (1976) in the frog, a mathematical model for semicircular canal fluid flow was developed which specifically accounts for intercanal and interspecies differences in the large radius and cross-section shape of the membranous duct. Body temperature dependent differences in endolymph viscosity were also taken into account. Differences in the length and width of the utricle were included by extending an analytical approach originally suggested by Van Buskirk (1977) to a more general case. The analysis shows that the canal short time constant (associated with the development of steady flow in the canal duct) is probably a factor of four shorter than some previous estimates. The short time constant should be significantly influenced by the ellipticity of the duct cross section, but independent of utricular shape. The volume of endolymph displaced during cupula deformation is expected to be proportional to the short time constant of endolymph flow, and also to the length of the utricular segment. Cupula volume displacement, however, is normally relatively independent of utricular cross-sectional area. Based on estimates of cupula area in different species, cupula midpoint displacement for a swinging door or shearing mode displacement of the cupula, in millimicrons per degree per second of head velocity, is estimated to be 15-20 in man; 20-40 in the frog; and 85-300 in the skate. The range in these estimates results directly from known differences between the horizontal, anterior, and posterior canal morphology.

To interpret the above results, it is necessary to estimate the dynamic range of head angular velocities. The latter is poorly known, except in man. In the human, although head velocities not uncommonly exceed 1000 degrees per second, most normal head motions involve stimuli in the range from 2-200 degrees/second in yaw. It seems likely, therefore, that most head movements in man are associated with cupula displacements below the range of light microscopy. Although it may be possible to visualize cupula motion in animals using large stimuli (cf. McLaren and Hillman, 1976; McLaren, 1977; Oman, Frishkopf, and Goldstein, 1976), such results should be interpreted cautiously, particularly since the bending mode of cupula deformation is likely to be amplitude-dependent.

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XXIV. COMMUNICATIONS BIOPHYSICS

D. Biomedical Engineering

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Included under this heading are a variety of topics in biophysics, physiology, and medical engineering. Many of these are individual projects of students supported by a training grant from the National Institutes of Health.

