

## XIX. COMMUNICATIONS BIOPHYSICS

### A. Signal Transmission in the Auditory System

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William M. Siebert, William T. Peake, Thomas F. Weiss

Our broad objective is to understand the events that occur within the ear and brain during the process of hearing, and to apply knowledge obtained from these studies to clinically relevant issues.<sup>1</sup> Our methods are to obtain systematic and quantitative data on these events and to formulate mathematical models of signal transmission in the auditory system. We have focused primarily on the more peripheral stages of the system including the outer, middle, and inner ear, the auditory nerve, and the brain-stem nuclei. Specific goals include the development of a detailed model of signal transmission in the middle ear, understanding mechanical-to-neural transformations in the inner ear, determining the significance at the cellular level of radial and spiral innervation of the mammalian cochlea, formulating a theory of gross neural potentials in terms of the underlying activity of individual auditory-nerve fibers, understanding the sensorimotor middle-ear-muscle reflex, and determining input-output relations of cells in brain-stem nuclei. We plan to continue to collaborate with staff of the Massachusetts Eye and Ear Infirmary to develop diagnostic methods based on electrocochleographic recordings in humans. In collaboration with staff of the Neurological Service of the Massachusetts General Hospital we plan to investigate the use of auditory tests to diagnose the extent and location of brain-stem lesions.

Following is a brief summary of research completed during the past year.

#### 1. Middle Ear

In his study of the relationship of acoustic input impedance and signal transmission in the human middle ear, William M. Rabinowitz has measured the changes in these quantities associated with reflex contractions of middle-ear muscles, and changes in air pressure in the external ear canal. The measurements of acoustic impedance appear to be valid over a wider frequency range than previously reported. Interpretations of the results will be important for basic understanding of signal transmission in the middle ear and possibly for diagnostic procedures.

Thomas J. Lynch has extended his measurements of the acoustic input impedance in cats. From these measurements the impedance at the stapes can be resolved into one component associated with the stapes and another associated with the cochlea, and a network model of this portion of the middle ear has been formulated. Some issues still need to be resolved, but a manuscript based on the current results is in preparation.

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The results are useful for developing an accurate model of the middle ear in which elements of the network model can be identified with specific anatomical structures.

### 2. Inner Ear

#### a. Intracochlear Sound Pressure in the Cat

A comprehensive paper reporting a study of intracochlear sound pressure in scala tympani and scala vestibuli of the basal turn is being completed by Victor Nedzelnitsky.

#### b. Basilar Membrane Motion in the Alligator Lizard

Recordings from cochlear hair cells and auditory-nerve fibers in lizards give direct evidence of tonotopic organization at these levels, the apical region of the cochlea being more sensitive to low frequencies and the basal region to high frequencies. The basilar membrane in this animal is a simple structure without the systematic changes in dimensions from base to apex that are so evident in mammalian cochleas. In preliminary experiments using the Mössbauer technique we have not detected a difference in tuning of basilar membrane motion in the apical and basal regions that could account for the difference in tuning of apical and basal fibers. Further control experiments are necessary before this result can be regarded as established. If these results are confirmed, this raises the question of how the tuning of cochlear nerve fibers is related to basilar-membrane motion in this cochlea.

#### c. Cellular Mechanisms of Transduction in the Alligator Lizard

Electric responses to sound have been recorded intracellularly from hair cells and supporting cells in the cochlea of the alligator lizard. Properties of dc potentials in the lizard cochlea, including intracellular resting potentials and the endocochlear potential have been studied.<sup>2,3</sup> Results indicate that the average resting potential of supporting cells is more negative than that of hair cells. The endocochlear potential (EP) in the lizard ear has an average value of +14 mV, a finding that has implications for theories of ion transport in the lizard inner ear.

A study of intercellular junctions in the lizard cochlea, using transmission electron microscopy and freeze-fracture techniques, has been completed.<sup>4</sup> We have found that small gap junctions occur between hair cells and supporting cells, extensive gap junctions occur between the bases of adjacent supporting cells, and tight junctions occur between cells near the apical surfaces of the cells lining the cochlear duct. These findings have implications for the composition of the intercellular fluid in the receptor organ, transport of materials between the scalae, and the existence of functionally significant electrical connections between cells in the cochlea. The existence of gap junctions between cells is generally regarded as evidence for electrical connectivity between these cells. Hence our finding that responses to sound are recorded in supporting cells might be explained by the presence of gap junctions between hair cells and supporting cells. These junctions may also serve to connect electrically neighboring hair cells via intermediate supporting cells. In this view the auditory receptor organ would constitute a matrix of electrically connected transducer elements.

#### d. Cochlear Potentials in Cats

Electric responses of the cochlea to sound stimuli are mixtures of components, including cochlear microphonic (CM) and neural potentials. We have been able to infer the range over which the CM in response to tones is relatively free from neural contamination by comparing Fourier transforms of the averaged round-window response to clicks with the responses to tones.<sup>5</sup>

### 3. Auditory Nerve

#### a. Lizard

There are two populations of cochlear nerve fibers in the alligator lizard.<sup>6</sup> The fibers that innervate the apical region have sharp tuning curves, low CF, and exhibit "two-tone inhibition" (as is also seen in cat). The fibers that innervate the basal region have broad tuning curves, high CF, and do not exhibit "two-tone inhibition." The morphology of the apical region of the basilar papilla resembles that of the mammalian organ of Corti (e.g., a tectorial membrane and efferent endings on hair cells are both present). The morphology of the basal region differs from the mammalian organ of Corti (e.g., neither a tectorial membrane nor efferent endings on hair cells are present). These results may give clues to the structures in the mammalian organ of Corti that determine specific characteristics of auditory-nerve responses. They may also bear on theories concerning the evolution of the mammalian from the reptilian ear. We are now investigating the "two-tone inhibition" phenomenon in these fibers.

#### b. Cat

Studies of responses of fibers in pathological ears utilize cats injected with large doses of ototoxic drugs and cats that are acoustically traumatized with narrow-band noise stimuli. Consistent electrophysiological findings are beginning to emerge that aid in the interpretation of the recordings from normal animals and on the nature of the deficit in humans who have such cochlear pathology.

In order to establish whether the times of spontaneous discharges in auditory-nerve fibers are correlated, we have recorded simultaneously from pairs of fibers.<sup>7</sup> No statistically significant correlations were found for spikes in pairs of fibers, even when the characteristic frequencies of the fibers were essentially identical. This result is consistent with the view that spontaneous activity in fibers (even innervating the same region of the cochlea) is initiated by independent generators. This conclusion eliminates acoustic noise, including Brownian motion, at any stage preceding the cochlea as a source of spontaneous discharges.

### 4. Cochlear Nucleus

#### a. Association of Spike Patterns with Cell Types in AVCN

Terrance R. Bourk is completing a systematic analysis of single units in the anteroventral cochlear nucleus (AVCN). One of the main purposes of this survey, in a collaborative effort with Dr. D. K. Morest's laboratory in the Department of Anatomy at the Harvard Medical School, is to correlate physiological data with morphological features. The current work establishes that the "primarylike" single units in the cochlear nucleus with a complex spike waveform have a spatial distribution resembling that of bushy cells and are almost ubiquitous in region AA. The "chopper" units are divided into two subgroups, one with only a few peaks in the PST histogram to tone bursts and the second with many peaks. The first group is found in region AP, while the second group of more standard "chopper" units is found where the stellate neurons are located. We have described a new class of "on" units in the AVCN, which correspond presumably to a type of stellate neuron.

#### b. Intracellular Recording

A preliminary study has been initiated on intracellular recordings from the cochlear nucleus. In order to record from a relatively homogeneous population of closely packed neurons, the rostral AVCN was chosen as one of the locations from which to record.

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Thus far, it appears that "primarylike" units in this region do not exhibit a long-lasting synaptic potential, whereas many "chopper" units do. Some dye marking experiments are being attempted.

5. Superior Olivary Complex (Neural Pathways of the Middle-Ear Reflex)

Since barbiturate anesthetics depress the sound-evoked middle-ear reflex, procedures have been developed for doing experiments on unanesthetized, decerebrate cats. Preliminary experiments using electric stimulation to the brain stem indicate that the pathways for the reflexes may pass through the medial nucleus of the trapezoid body, and not through the medial superior olive.

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### B. Auditory Psychophysics

#### Academic and Research Staff

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#### 1. INTENSITY PERCEPTION AND LOUDNESS

National Institutes of Health (Grant 1 RO1 NS11153-01)

Louis D. Braida, Nathaniel I. Durlach, Jae S. Lim,  
Steven R. Purks, William M. Rabinowitz

This research is oriented toward the creation of a coherent, quantitative, and unified theory of intensity perception and loudness, and involves the construction and integration of models of decision making, sensory processes, short-term memory, and perceptual context effects, as well as extensive psychophysical experimentation.<sup>1-7</sup> Aside from providing greater insight into basic phenomena of intensity perception and loudness, we expect the results to be of value in the study of equivalent problems involving other stimulus dimensions and subjective attributes and other senses, in the study of memory processes involving more complex stimuli or more complex tasks, and in various applications such as the evaluation of annoyance in noise pollution and the interpretation of abnormal intensity perception and loudness in subjects with hearing impairments.

During the past year we have focused on the extension of our preliminary theory of intensity resolution<sup>1</sup> to include comparisons among different types of stimuli,<sup>6</sup> the design and performance of experiments to guide the development of the extended theory,<sup>6</sup> development of a revised model of context coding that is consistent with data on the resolution edge effect, and preparation of results for publication.

The extended theory is capable of interpreting results on mean loudness matches and the accuracy of loudness comparisons. It is also potentially applicable to cross-modality comparisons. According to the theory, two stimuli  $S_1$  and  $S_2$  at intensities  $I_1$  and  $I_2$  are matched in loudness if and only if the number of jnds between  $I_1$  and the absolute threshold for  $S_1$ , divided by the total number of jnds in the dynamic range for  $S_1$ , is equal to the number of jnds between  $I_2$  and the absolute threshold for  $S_2$ , divided by the total number of jnds in the dynamic range for  $S_2$  (the condition originally proposed by Riesz<sup>8</sup>). With regard to the accuracy of loudness comparisons, the theory is identical to the preliminary theory of intensity resolution except for the inclusion of an

additional variance term (the "transformation variance") in the trace mode, the magnitude of which depends on the similarity of the stimuli that are being compared.

The prediction for loudness matching has been found to be at least roughly consistent with available data on loudness matching for tone pulses of different frequency, for a tone in quiet against the same tone in noise, and for a tone presented to a normal ear against the same tone presented to a recruiting ear.

In order to guide further development of the theory, a new experiment has been conducted to determine the accuracy with which listeners compare the loudness of tone pulses of different frequencies.<sup>6</sup> The experimental paradigm was a two-interval, roving-level, loudness-discrimination paradigm in which the signals in the first and second intervals were of different frequencies ( $f_1$  and  $f_2$ ). The results of this experiment have been used to estimate the size of the transformation variance as a function of  $f_1/f_2$ .

The revised context-coding model is based on the notion that the extremes of the intensity range defining the context serve as perceptual anchors, and that a given intensity is coded by measuring the distances between the intensity and the anchors. The model assumes that the distances are measured by a counting process with a random step size  $S$ , where  $p(S) = \lambda \exp(-\lambda S)$  and the mean step size  $\lambda$  is proportional to the context width. The predictions of this model appear to be more consistent with the data than the predictions of either the preliminary model<sup>1</sup> or of our previous revised model.<sup>7</sup> In particular, the predictions of this model are at least roughly consistent with the dependence of average sensitivity on stimulus range, the resolution edge effect, and the shape of the receiver operating characteristics.

We have completed a paper on the effects of payoffs on sensitivity and bias in identification,<sup>5</sup> and nearly completed papers on the resolution and bias edge effects and on loudness comparisons. Other papers are being prepared on the effect of standards in identification, sequential effects in identification, and the revised context-coding model.

Future theoretical work will concentrate on further development of our revised model for the trace mode<sup>7</sup> and on the implications of the revisions in the trace mode and in the context-coding mode for the combined mode (in which the listener is assumed to make optimal use of the information from both modes) and for the theory of loudness comparisons. Future experimental work, as usual, will be directed primarily toward an evaluation of theoretical predictions.

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## 2. BINAURAL HEARING

National Institutes of Health (Grant 1 RO1 NS10916-01)

H. Steven Colburn, Robert H. Domnitz, Nathaniel I. Durlach,  
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The 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 is consistent with neurophysiological data on the auditory system.

During the past year, we have further developed our laboratory facilities, completed some experimental studies, continued to pursue the development of our theory, and prepared previous work for publication.<sup>1-6</sup> In our work on laboratory facilities, we have begun to develop an acoustic monitor-and-adjust system that may have important consequences for binaural experimentation. Binaural experiments have often been confounded by variability in the acoustic coupling of headphones. For example, experiments concerned with tradability and the dimensionality of the binaural image have probably underestimated the degree to which a single subjective position variable can describe the binaural image. As a first step toward eliminating the headphone-coupling problem, a simple and convenient system<sup>1</sup> has been devised for detecting and electrically compensating acoustic imbalances while the headphones are being worn by the listener. For example, using this system with 500-Hz tone stimuli, the experimenter can maintain interaural amplitude ratios within 0.1 dB of the desired value and interaural phases within 0.2° of the desired value. Without a compensating system, deviations up to 3 dB and 20° are not uncommon. Future work will focus on the development of a system that is automatic, operates continuously throughout the experimental runs, and is capable of handling broadband signals.

We have acquired a medium-scale computer (PDP-11/45) to support theoretical and experimental research on binaural hearing. This computer is equipped with a 32,000 word memory, 12-bit analog-to-digital and digital-to-analog converters, and crystal-controlled clock, together with 2.5 million word disk storage. We have begun to use this computer for theoretical computations and are in the process of developing a hardware/software system suitable for controlling experiments involving binaural signals. This system will permit complex signals with specified binaural disparity, including time delays of large time-bandwidth products, to be synthesized conveniently and will incorporate real-time monitoring of acoustic signals in the ear canal entrances as they are synthesized.

Experimentally, we have been measuring the degree to which it is possible to create perceptually indistinguishable binaural stimuli that have different values of interaural parameters. Combinations of small interaural time delays (15  $\mu$ s) and interaural amplitude differences were chosen to generate a stimulus localized at the midline, and the experimental paradigm was designed to eliminate differences in loudness and image width. We used the acoustic monitor-and-adjust system to improve stimulus control. The results from measurements on three subjects indicate that indistinguishable stimuli can be constructed. The results from measurements on the experimenter were different, in that he was able to perform significantly above the chance level for all tested

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stimulus pairs. It is not yet clear whether the difference was due to the additional listening experience of the experimenter or to some other factors; for example, the trading ratio of the experimenter is roughly twice as large as the trading ratios of the other subjects. Further work on this project is required.

A theoretical analysis was made of previous experimental results on lateral position judgments and interaural time and amplitude discrimination for 500-Hz tones.<sup>3</sup> Performance in the experiments was analyzed within the framework of a probabilistic subjective lateralization model in which internal noise is explicitly treated. The data are qualitatively consistent with the model, although there is close quantitative agreement for only one of three subjects. Calculated values of the internal noise of the subjective image position are in qualitative agreement with reports by observers of image diffuseness as a function of interaural parameters of the stimulus. Nontradability between large increments of interaural amplitude and time is implied by the experimental results, and can be interpreted in the model as discrimination between tones with equal position means but different position variances.

Our new model of binaural hearing<sup>4,7</sup> is being extended to predict and describe the subjective lateral position of binaural pure tones, as well as performance in binaural discrimination experiments. The subjective position predictions are obtained by non-optimally weighting the output of the central processor based on comparisons of auditory-nerve firing times.<sup>7</sup> The randomness of these firing patterns is the source of internal noise in the model. Discrimination predictions are based on the assumption that the subjective position is used as the sole decision variable. The predictions of the model are reasonably consistent with available data on lateralization scaling of 500-Hz pure tones, and the model predicts the form of results of interaural time and intensity discrimination experiments at that frequency more accurately than any previous model. At present, we are evaluating the predictions of the model for binaural detection experiments in an attempt to determine whether or not binaural detection and discrimination performance can be accounted for by a single decision variable.

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### 3. HEARING AIDS

[Part of this work is being carried out in collaboration with the Harvard-M. I. T. Rehabilitation Engineering Center, with support from the U. S. Department of Health, Education, and Welfare (Grant 23-P-55854).]

Lawrence G. Bahler, Ian M. Beguesse, Louis D. Braida, Nathaniel I. Durlach, David H. Gluss, Bruce L. Hicks, Richard P. Lippmann, Yvonne M. Perlmutter, William M. Rabinowitz, Charlotte M. Reed, Martin C. Schultz

The goal of this program is to develop improved signal-processing schemes to match acoustical signals to residual sensory capacity in people with nonconductive hearing impairments.

The research activities of this program are subdivided into three areas: signal enhancement, matching speech to residual auditory function, and tactile aids.

#### a. Signal Enhancement

Work has focused on the development of array processing schemes to improve the ability of a listener who has only one useful ear to understand speech signals coming from one direction in the presence of interfering signals from other directions, and on the development of comb-filtering techniques to improve a listener's ability to understand speech signals masked by other speech signals that arise from the same point in space but are created by another talker. Preliminary results on both projects suggest that significant enhancement is indeed possible. Present work is devoted to improving signal-processing schemes and to quantitative evaluation of the amount of enhancement that is provided by various schemes.

#### b. Matching Speech to Residual Auditory Function

We have focused on multiband amplitude compression and pitch-invariant frequency lowering. An extensive review of the literature on signal-processing for hearing aids, including amplitude compression and frequency lowering, is being prepared for publication. Work on amplitude compression included development of hardware and software for a 16-channel compression system, a headphone equalization system to restore the free-field-to-eardrum transfer function for a source straight ahead, a wide variety of recorded speech material to be used in experimental evaluation, and procedures for selecting the parameter values of the compression system to be tested on a given impaired listener. The work on pitch-invariant frequency lowering has progressed along two lines. In one project, we are comparing the ability of normal listeners to understand warped-lowered speech with their ability to understand lowpassed speech. Since our facilities do not permit us to perform the warped-lowering operation in real time, we make use of off-line processing. Work during the past year has been concentrated on the processing of various speech materials to be used in the experiments and on the development of computer-controlled testing and training procedures. In another project, we are exploring the ability of listeners to understand linearly lowered speech, using real-time processing. In these experiments pitch detection is based on the use of a throat accelerometer, and the training procedures include conversation among the subjects and experimenter using transformed speech. We are hopeful that significant experimental results on amplitude compression and frequency lowering will be obtained during the coming year.

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### c. Tactile Aids

Our work has progressed along three lines. In one project, we are developing a simple, wearable vibrotactile aid to provide a totally deaf user with a general awareness of acoustic signals and with the gross amplitude and temporal characteristics of these signals. A laboratory model of this aid has been completed and is undergoing tests to evaluate its usefulness in comparison with a standard bone-conduction hearing aid used as a vibrotactile aid. In a second project, we are developing a general-purpose, laboratory-based, computer-controlled, tactile display system for comparative study of different display strategies. At present, we are using the transducer portion of the Opticon as the transducer in this system. Present work involves development of appropriate software. Among the display strategies that will be explored during the coming year are one in which frequency is coded along one dimension and amplitude along the other, and one in which the frequency spectrum is continuously swept across the display in time. In a third project, we are initiating experiments to evaluate and to improve our understanding of the "vibration method" of speech perception used by certain deaf-blind subjects. We are now designing the proposed experiments and locating appropriate experimental subjects. We expect to complete preliminary experiments on one or two such subjects during the coming year.

## 4. MUSICAL PITCH

National Institutes of Health (Grant 1 RO1 NS11680-01)

Howard L. Golub, Adrian J. M. Houtsma, Roger W. Wicke

The objective of this project is to obtain a deeper understanding of the auditory processes that underlie the transformation of a complex sound containing more than one tone into a sensation of musical pitch.

### a. Pitch of Harmonic Two-Tone Complexes

Musical interval identification experiments have been conducted with harmonic two-tone complexes presented dichotically at low intensities. Confusion data were processed and compared with performance predicted by a stochastic model that utilizes optimal estimation.<sup>1, 2</sup> Similar experiments using complex tones of only successive odd harmonics indicate that in its present form the processor model is inadequate.

### b. Pitch of Interrupted White Noise

The musical interval identification paradigm has also been used to study the pitch of periodically interrupted wideband noise. The data obtained thus far support the use of a simple Gaussian decision model that permits computation of a sensation variable variance for these sounds. This variance was found generally to be larger than expected, based on earlier published results of experiments on interrupted noise. The pitch effect is quite weak and seems to be limited to an interruption rate between 100 Hz and 300 Hz.<sup>3</sup> Further experimental and theoretical work continues.

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5. MUSICAL ACOUSTICS

National Institutes of Health (Grant 1 RO1 NS11680-01)

Adrian J. M. Houtsma, Robert P. W. Boland, Nicholas B. Adler, Peter W. Siebert

The objective of this project is to develop a systematic approach to the design and construction of musical instruments. Thus far the project has been limited to stringed instruments. Acoustical performance criteria are developed by carefully comparing subjective evaluations of an instrument by professional musicians with physical performance data measured in the laboratory. Experimental methods are being developed to provide understanding and control of relevant physical parameters that determine acoustical performance. This should provide an instrument maker with the means to make an instrument meet certain performance criteria consistently.

a. Descriptive Model for Lute-type Instruments

A model has been developed to describe stringed instruments of the lute type which have a bridge on which the strings terminate. The model is composed of an ideal lossless string acting as the source, a nonlinear force transducer describing the action of the bridge, and a linear time-invariant filter describing soundboard, body, and radiation process. The radiation process was determined empirically by measuring frequency responses of a particular guitar with constant sinusoidal forces applied to the bridge normal to the soundboard and in the direction of the strings. The predicted relative levels of partials were compared with spectra obtained from actual tones played on the same guitar.<sup>1-3</sup> Agreement between theoretical predictions and observed data still leaves much to be desired; this could be attributed to random experimental error and oversimplified model assumptions. The model does explain, however, some well-known effects such as tone quality (spectral) change with intensity or direction of plucking the string. Further experimentation continues.

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

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Studies of vertebrate hair-cell mechanisms are basic to understanding the normal functioning of the auditory and vestibular organs and may contribute ultimately to understanding and treatment of pathological conditions in these systems. Our principal goal continues to be to understand transduction in hair cells with respect to cupula motion, ionic mechanisms, synaptic processes, and neural adaptation.

#### 1. STUDIES OF RECEPTOR POTENTIALS IN LATERAL LINE HAIR CELLS

National Institutes of Health (Grant 5 RO1 NS11080-02)

Lawrence S. Frishkopf, Charles M. Oman

We have recorded receptor potentials from cells of lateral line organs in the tail of the mudpuppy, Necturus maculosus, in response to cupula displacement. Such responses were observed in real time by averaging, using a DEC Lab 8/E computer. Histograms of spontaneous and evoked nerve activity were also obtained on-line and show characteristic patterns of interval and post-stimulus time activity. Responses were abolished by application of methylene blue, which indicated a physiological origin. Responses were small (less than 1 mV); intracellular dc potentials were rarely maintained for more than a few minutes. In the absence of more stable recording conditions we have been unable to stain cells or to make measurements of cell conductance changes. The cause of this instability has not yet been determined and needs to be explored before further progress can be made. Based on our previous work with this preparation,<sup>1</sup> there is reason to think that this difficulty can be overcome. A possible source is electrode motion caused by structural resonances in the support system. We intend to continue to record in individual hair cells and supporting cells, attempting to improve the stability of our preparation, with the purpose of measuring intracellular responses in identified cells and determining whether conductance changes occur during stimulation.

#### 2. ANALYSIS OF VERTEBRATE INNER-EAR FLUIDS

National Institutes of Health (Grant 5 RO1 NS11080-02)

M. I. T. Health Sciences Fund

Scott K. Peterson, Lawrence S. Frishkopf, Charles M. Oman

During the past year we have developed techniques to sample and analyze endolymph and perilymph in several species of vertebrates. This work is being carried out with the use of the facilities of the Biotechnology Resource in Electron Probe Microanalysis

at Harvard Medical School, in collaboration with Dr. C. Lechene, of Harvard Medical School, and Professor T. F. Weiss, of M. I. T. This method allows repeated nondestructive analysis of extremely small samples ( $10^{-11}$  -  $10^{-10}$  liter) for different elements. We are determining concentrations of 7 elements (Na, K, Cl, Ca, Mg, S, and P). Data have been obtained on three species (skate, alligator lizard, and cat) that span the vertebrate phylum; although preliminary, these results appear promising. The cat data agree closely with other recent findings for Na, K, and Cl obtained by different methods; the skate data are also in good agreement with previous results for these three ions, whereas there are no prior data on the lizard.<sup>2</sup> There are little consistent data for any species on the concentration of Ca and Mg, ions which appear to play an extremely important role in receptor and synaptic function in other systems. If, as we believe, the composition of endolymph and perilymph are important in hair-cell and synaptic transduction, such data on representative species of several vertebrate classes could provide useful insight and testable hypotheses. The analysis of skate endolymph and perilymph also provides control values for the study of the effects of various ionic environments on receptor mechanisms in the skate's semicircular canals.

We intend to refine our measurements of elemental concentrations in endolymph and perilymph in these three vertebrate species. The technique exists for determining intracellular concentrations of these elements too, and we would like to explore that possibility. It also would be extremely interesting to explore the effect of various experimental conditions such as stimulation on measured concentrations.

### 3. STUDIES OF TRANSDUCTION IN THE SEMICIRCULAR CANALS OF FISH

National Institutes of Health (Grant 5 RO1 NS11080-02)

M. I. T. Health Sciences Fund

National Aeronautics and Space Administration (Grant NSG-2032)

Charles M. Oman, Lawrence S. Frishkopf, Scott K. Peterson

We spent the summer at the Marine Biological Laboratory, Woods Hole, Massachusetts, where we continued our studies of the semicircular canal in the excised ear of the skate in collaboration with Professor M. H. Goldstein, of Johns Hopkins University. We explored the effect of varying ionic concentrations within the horizontal canal ampulla, using our recent data on the composition of skate endolymph as a starting point. While recording from the ampullary nerve of the horizontal canal, we cut the canal and cannulated it with a double pipette filled with artificial endolymph plus Alcian Blue (0.5-1%) on one side and with a test solution on the other. Alcian Blue stains the cupula and allowed us to observe the effect of hydraulically moving the cupula.

An alternative method of stimulation was available without cutting the canal by shining a light on the canal or ampulla (caloric method). In this case a small puncture was made through the wall of the ampulla and Alcian Blue in artificial endolymph was injected. We have explored the use of digestive enzymes to facilitate puncturing the canal wall. Under favorable conditions the system remains calorically sensitive after these procedures. Attempts are being made to measure the motion of the cupula resulting from a caloric stimulus in the almost-closed canal while monitoring the response of the nerve. Preliminary experiments show that large changes in afferent single-unit activity can result from cupula motions that are not observable under conditions permitting resolution of 5- $\mu$ m displacement. Improved techniques may permit a direct assessment of the magnitude of physiologic cupula motions and may also permit us to determine whether the cupula is attached to the wall of the ampulla. The study may provide some insight into the origin of neural adaptation that is observed in response to caloric stimuli. Furthermore, based on a comparison of our observations with the two methods, we are now convinced that the obvious methods of cutting and cannulating the canal easily traumatize the cupula.

(XIX. COMMUNICATIONS BIOPHYSICS)

It has been proposed recently that GABA is the afferent transmitter in hair-cell synapses.<sup>3</sup> In our summer work we explored the effects of certain drugs on the response of the ampullary nerve to caloric stimulation. Picrotoxin, known to block the postsynaptic effects of GABA in other systems, was ineffective in reducing this response in concentrations from  $10^{-6}$  to  $10^{-3}$  M. Thus our data do not support the hypothesis that GABA is the afferent transmitter. Attempts to establish acetylcholine as the (inhibitory) efferent transmitter were also unsuccessful. A variety of paradigms based on the known pharmacology of cholinergic synapses were employed in an attempt to establish an inhibitory action of ACh (and ACh analogs) either by direct application, or by producing conditions in which ACh release from the presynaptic terminals would be facilitated. Although some effects were observed, we were unable to reproduce them consistently.

We intend to continue physiological and pharmacological studies of the semicircular canals in the skate. We are attempting to measure the magnitude of cupula motion while recording responses to caloric stimulation from the ampullary nerve; implications of these results in terms of dynamics of the system will be explored. We shall continue to study the properties of adaptation in afferent nerves from the semicircular canals and attempt to use anatomical techniques (for example, tracers such as cobalt chloride) to identify peripheral sites of origin of fiber bundles from the crista which exhibit different dynamic properties. We shall also continue our attempt to identify the afferent transmitter and to establish ACh as the efferent transmitter.

References

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## XIX. COMMUNICATIONS BIOPHYSICS

### D. Development of Quantitative Vestibular Test Techniques

#### Academic Research Staff

Prof. Charles M. Oman

#### Graduate Students

John R. Tole

National Institutes of Health (Grant 5 TO1 GM01555-09)

Charles M. Oman, John R. Tole

Work continues on semiautomated stimulation equipment for clinical vestibular testing. Air caloric and galvanic stimulators have been developed, and standard procedures for their use have been determined in testing on normal subjects. Work is under way to delineate some of the sources of error in the caloric test, including day-by-day variation for an individual subject's response and a comparison of air and water as the thermal medium for the test.

We are also examining the test responses of patients with known pathologies of the peripheral vestibular system in an effort to determine the relative value of various response parameters in separating normal from abnormal populations. Work also continues on the use of automated nystagmus analysis techniques in the processing of the eye movement response records from these experiments. Among the parameters that are obtained are a running average of slow phase velocity and continuous estimates of fast phase frequency.

Two papers<sup>1,2</sup> have been published in connection with this work in the past six months.

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## XIX. COMMUNICATIONS BIOPHYSICS

### E. Biomedical Engineering

#### Academic and Research Staff

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#### Graduate Students

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Marvin S. Keshner	Victor Tom	Allen W. Wiegner

In July 1975, M. I. T. was awarded a grant from the National Institutes of Health (NIGMS) to establish a Biomedical Engineering Center for Clinical Instrumentation. This center is being administered through the Harvard-M. I. T. Program in Health Sciences and Technology (HST), and involves collaborative projects with several teaching hospitals. The Center has absorbed many of the faculty, staff, and students formerly associated with the biomedical engineering area of the Research Laboratory of Electronics. Although the professional communications remain as close as ever, the BME Center's activities are now administratively separate. The BME Center is focusing on the development of microprocessor-based medical instrumentation.

Several biomedical instrumentation activities continue to be pursued at R. L. E., M. I. T. Theodore L. Rhyne is completing his work in medical ultrasonics, and Allen W. Wiegner is continuing his research on cardiac muscle mechanics in collaboration with Dr. O. H. L. Bing at Beth Israel Hospital, in Boston.

### 1. ULTRASONIC CHARACTERIZATION OF THE LUNG SURFACE

Massachusetts General Hospital Purchase Order F63853

Theodore L. Rhyne

Within the last two years work has been undertaken in collaboration with several doctors at Massachusetts General Hospital, Boston (through the Noninvasive Diagnostics Laboratory) and with Prof. P. P. Lele, of the Mechanical Engineering Department, M. I. T., to characterize normal and diseased lungs using high-frequency sonar techniques (ultrasound) and communications analysis. An improved model for the loss and bandwidth of compressional wave ultrasonic transducers has been developed and applied to calibrated ultrasonic pulse-echo instrumentation involving real-time computer signal processing. A solution of the diffraction of a disk to a plane that permits a technique for the absolute calibration of transducer loss as a function of frequency has been produced. A stochastic model of the lung surface as a rough scattering surface with frequency-selective scattering and distinctive temporal modulation has been confirmed experimentally. Animal experiments have indicated pathologically induced alteration of the lung surface echoes in association with conditions of pulmonary edema and pulmonary embolism. It is anticipated that this model and instrumentation will be clinically useful in the detection of diseased lung states through techniques of optimal receiver design and classical detection. The immediate objective of this work is a doctoral dissertation anticipated to be submitted in January 1976.



2. RESEARCH IN CARDIAC MUSCLE MECHANICS

Boston City Hospital Purchase Order 4338-75431

Allen W. Wiegner

Recent work in cardiac muscle mechanics includes the study of isometric and isotonic relaxation in isolated cardiac muscle, and the study of the augmented inotropic state associated with physiologically sequenced relaxation of ventricular papillary muscle preparations. This work is being done in the Myocardial Physiology Laboratory at Beth Israel Hospital, in Boston, with the cooperation of Dr. O. H. L. Bing.

We are attempting to clamp the length of the "contractile element" of an isolated papillary or trabecular muscle preparation, in order to observe its length-force relation directly and to investigate the time course of force generation in the muscle. Work is also under way on a study that will simulate in an isolated preparation the loading conditions that are present in the midwall region of the intact ventricle. This project, utilizing real-time computer control, should provide a bridge linking isolated papillary muscle experiments, which historically have used nonphysiological loading conditions to elucidate the properties of cardiac muscle tissue, to the study of the intact heart, which now has primarily hemodynamic data to work with in attempting to determine the innate "contractile state" of the myocardium. A model will be developed relating midwall fiber shortening to midwall fiber stress as a function of various cardiac parameters. This will enable us to study the effects of muscle fiber length, load, and stimulation rate on ventricular efficiency.

