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 RO1 NS11000-03 and 1 PO1 NS13126-01) William T. Peake, William M. Siebert, Thomas F. Weiss, Nelson Y. S. Kiang

In recent years we have found opportunities to apply results of our basic research to clinical problems. Interaction with clinical investigators in such projects is an important part of a new program supported by the National Institutes of Health in which a consortium of four institutions (Massachusetts Institute of Technology, Massachusetts Eye and Ear Infirmary, Harvard Medical School, and Massachusetts General Hospital) is cooperating on basic and clinical studies of the auditory system. Specific clinical problem areas are those involving pathologies of the ear and of the brain. In cooperation with otologists at Massachusetts Eye and Ear Infirmary we are working on the interpretation of auditory nerve action potentials recorded from patients who appear to have hearing defects. Methods for localizing abnormal regions in the brain are also being developed, including the use of electric responses of the lower brain centers and the characteristics of the acoustic middle-ear muscle reflex. These clinical components will complement continuing basic studies on the processes of hearing.

We have made progress during the past year in the following studies:

a. Middle Ear

Using physical and psychophysical methods, William M. Rabinowitz has measured changes in the input impedance and the transmission of the middle ear that occur during the acoustic reflex. The dependence of these changes on the frequency and on the level of the eliciting stimulus can be interpreted in terms of a change in stiffness of elements in the middle ear. The growth of the reflex effect with increases in eliciting stimulus level indicates that the neural system involved in the reflex has frequency-dependent

characteristics.¹

We have completed measurements of the input impedance of the inner ear in cats,² and have demonstrated that variations in cerebrospinal fluid pressure can affect the acoustic compliance of middle-ear ligaments.

b. Inner Ear

(i) Cellular Mechanisms of Transduction in the Alligator Lizard

The dc potentials in the cochlea, the intracellular resting potential and the extracellular endolymphatic potential are thought to be important for the generation of responses to sound in the receptor cells. We have described properties of these potentials.³

A paper describing intercellular junctional complexes using transmission electron microscopy and freeze-fractured preparations has been accepted for publication. 4

Within the past year we have concentrated our efforts on the use of new techniques for intracellular recording. The combined use of new facilities at the Massachusetts Eye and Ear Infirmary and the use of a mechanical micropipet drive has enabled us to record stable intracellular potentials for longer time intervals than has been possible previously. By using beveled, double-barreled micropipets we have been able to record intracellular potentials from one barrel while passing current through the second barrel. Such techniques will be employed in investigating the mechanisms of mechanoelectric transduction in hair cells and perhaps in measuring the electrical characteristics of supporting and hair cells.

(ii) Cochlear Potentials in Lizards

Both cochlear microphonic (CM) and neural response components can be recorded by means of a gross wire electrode placed near the round window. In response to clicks the two components are partially separable in time. In response to tones, the resultant wave shape is a complex composite of such components. In order to isolate these components, we used a potent neurotoxin, tetrodotoxin, to attempt to eliminate the component attributable to action potentials in cochlear nerve fibers.⁵ Results showed that the apparently complex dependence of the N_1 component of the response to clicks on the stimulus parameters in an intact ear probably results from the interaction of a neural component with a low-frequency CM component.

c. Auditory Nerve

(i) Lizard

Since it is feasible to study intracellular responses in the lizard basilar papilla, it is essential to determine whether results obtained in this preparation have general validity for sensory transduction in vertebrate auditory organs. Therefore we studied responses of cochlear nerve fibers in this animal and compared our results with those obtained by using the same techniques in the cat. Thus far, we have systematically studied the frequency tuning properties,⁶ the spontaneous activity,⁷ and the phenomenon of two-tone rate suppression and we have observed responses to clicks and tone bursts. We find characteristic differences in the response properties of apical and basal fibers that go to morphologically different regions of the basilar papilla. The response properties of apical fibers resemble those of mammalian fibers more closely than do those of basal fibers.

(ii) Cat

The spontaneous activity of auditory-nerve fibers in the absence of acoustic stimuli was studied by recording simultaneously from pairs of fibers. The discharges were shown to be statistically independent even when the characteristic frequencies of the fibers were essentially identical. This result indicates that acoustic noise, including Brownian motion, is not the dominant source of spontaneous discharges.⁸

Studies of acoustically traumatized and "normal" cats suggest that cochlear abnormalities exist even in "normal" animals.⁹ To obtain baseline data from animals known to be free from previous exposure to high-level environmental sound, kittens are being raised in a "sound-proofed" room. The study of cats subjected to acoustic trauma has demonstrated several correlations between abnormal single-fiber responses and the condition of hair cells and neurons in the cochlea observed with the light microscope.¹⁰ These findings are of interest not only because of their implications for interpretation of the damage resulting from high-intensity sounds but also for the light they shed on normal cochlear mechanisms. For instance, the fact that some abnormal fibers exhibit a supernormal sensitivity to certain acoustic stimuli suggests an interaction of excitatory processes in the normal cochlea.

d. Cochlear Nucleus

(i) Signal Transformations of AVCN Neurons

A survey has been completed of the physiological properties of single units in the anteroventral cochlear nucleus (AVCN) of the cat, based on spike responses recorded extracellularly.¹¹ Localization of extracellularly recorded spikes has made it possible to compare various categories of spike responses with descriptions of cell morphology. The spatial distribution of "primarylike" units strongly suggests their correlation with the bushy cells, particularly in the most rostral subdivision of the AVCN where both predominate. The complex spike waveforms consistently found for "primarylike" units are interpreted as a physiological correlate of the presence of very large synaptic

endings (end-bulbs of Held) on the bushy cells. In posterior AVCN where the end-bulbs are smaller, the complex waveform is less prominent. The two other major categories of units in the AVCN, "chopper" and "on", presumably correspond to stellate cells. Since at least two subcategories of "chopper" units were found to be differentially distributed within the AVCN and the "on" units showed a range of characteristics, we expect that subsequent anatomical studies will reveal further distinctions among the stellate neurons.

(ii) Synaptic Mechanisms

To understand the cellular processes involved in the signal transformations, we have worked on methods for recording responses intracellularly and are preparing results from an initial study for publication. The current effort is concentrated on technical improvements aimed at extending the intracellular recording time and introducing sets of stimulating electrodes to allow antrodomic activation and stimulation of efferent pathways.

e. Superior Olivary Complex: Neural Pathways of the Middle-Ear Reflex

Experiments on unanesthetized decerebrate cats in which electric stimuli have been used have indicated that the pathways of the middle-ear reflex involve neurons that are in the vicinity of the ventral and medial nuclei of the trapezoid body but do not go through the medial superior-olivary nuclei as had been suggested previously. These electric stimulation experiments do not give precise locations for the neurons that are involved. Therefore we have begun injecting the enzyme horseradish peroxidase (HRP) into the VIIth motor nuclei (through which the stapedius reflex is known to pass). The HRP should be transported along the nerve fibers in retrograde direction and should make the cell bodies of the neurons that innervate the VIIth motor nuclei histologically detectable.

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B. Auditory Psychophysics

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1. INTENSITY PERCEPTION AND LOUDNESS

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

Louis D. Braida, Nathaniel I. Durlach, Adrian J. M. Houtsma, Jae S. Lim, 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.¹⁻⁸ We expect the results to provide greater insight into basic phenomena of intensity perception and loudness, and 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, our funds for this project have been extremely limited and our efforts have been confined primarily to preparation of a new grant proposal, preparation of previous results for publication,^{7,8} and further testing of our theory of loudness matching.^{7,9}

The work on loudness matching has been directed toward an experimental evaluation of the theory's prediction that two stimuli S_1 and S_2 at intensities I_1 and I_2 are matched in loudness if and only if I_1 and I_2 divide the dynamic ranges of S_1 and S_2 proportionately

in terms of number of just-noticeable differences (jnds) in intensity. The stimulus pairs considered were a tone signal vs the same tone signal in a background of noise, and a tone signal vs a noise signal. The results of these experiments, although very preliminary, tend to support the theory.

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2. BINAURAL HEARING

National Institutes of Health (Grant 2 RO1 NS10916-02)

H. Steven Colburn, Nathaniel I. Durlach, Philip W. Herman, Jr., Allen W. Mills, William M. Siebert, Ronald A. Siegel, Richard M. Stern, Jr.

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 continued to pursue the formulation of our theory, further developed our laboratory facilities, and conducted several experimental studies.

Theoretical work has continued to focus on the development of our theory of binaural interaction based on auditory-nerve data.^{1, 2} This theory incorporates explicitly the transformation from acoustic stimulus to auditory-nerve firing patterns and postulates that decisions are made on the basis of an optimum linear combination of outputs from

a binaural displayer that processes the time structure of the firing patterns on fibers from the two ears. This model describes essentially all of our data on the binaural detection of tones in noise,² but is unable to describe the dependence of the just-noticeable difference (jnd) in interaural time delay on the interaural phase and amplitude difference of a tone.³

We have modified our theory by restricting the information that is available for making decisions within the model.⁴ Whereas earlier versions of the model postulate that the displayer outputs are combined optimally, the modified version postulates that the displayer outputs are processed nonoptimally to give a decision variable that is related to subjective lateral position and that represents the only information available, aside from pitch and loudness information. This model has been evaluated for 500-Hz tonal stimuli and describes the lateral-position-matching data of Domnitz,⁵ as well as most interaural discrimination results. The only cases for which the predictions of this model are inconsistent with discrimination results are those for both stimuli in the discrimination task. For example, predictions are inconsistent with interaural time jnds when the graph of mean lateral position vs interaural time delay has zero slope. In these cases, empirical data are generally quite variable within and among subjects, but some subjects, with training, can perform significantly better than predicted.

When the predictions of the modified model are compared with binaural detection results, only a subset of the data can be described.⁶ In particular, the dependence of thresholds on the interaural parameters of the masking noise cannot be described, although the model seems adequate to describe detection situations with interaurally identical masking noise. To encompass all detection cases within the domain of the modified model, we have postulated a decision variable in addition to the one related to lateral position (and in addition to the implicit pitch and energy-based loudness variables). The model that assumes optimum use of these two variables in binaural situations makes use of considerably less information than the original model that uses the optimum linear combination of displayer outputs, and this modified model is consistent with most of the data from lateralization, discrimination, and detection experiments with 500-Hz tones.⁶ Further information on this work is available in the doctoral thesis of R. M. Stern, Jr.⁷

We have also pursued the extension of our binaural interaction model to high frequencies for which the auditory-nerve patterns are not synchronized to the detailed time structure of the stimulus.⁸ All of our work is consistent with the hypothesis that the only differences between high- and low-frequency processing reside in the peripheral transformation from acoustic waveform to firing patterns on the auditory nerve fibers. The processing of the information in the patterns would thus be described by a mechanism that gives equivalent treatment to all fibers whether they are primarily sensitive to high or low frequencies.

We have expanded our laboratory facilities by developing a computer-controlled acoustic monitor-and-adjust system.⁹ (We had previously determined the need for a monitor-and-adjust procedure for certain binaural experiments and developed a manual monitor system.¹⁰) The new system synthesizes a pair of waveforms with the desired interaural relationships, monitors acoustically the stimuli presented at the ear canals of the subject during each stimulus presentation of an experiment, computes the corrections that are required to remove deviations from the desired interaural relationships, and makes the computed corrections on the next stimulus presentation (which is also monitored, etc.). The system has been evaluated for tone-burst stimuli, in which the problems of synthesis and estimation of interaural phase and amplitude parameters are relatively simple. In order to use the system for wideband stimuli, a more complex interaural parameter estimation scheme such as the fast Fourier transform would have to be used.

Experimentally, we completed a project on the discrimination of interaural time delay for 500-Hz tonal stimuli.¹¹ Interaural time jnd measurements were made on several subjects using parameter values near points of perceptual ambiguity, specifically at time delays in the neighborhood of 750 μ s. Results in this region show large differences from subject to subject and large training effects for some subjects. Also, we have initiated projects on interaural adaptation effects, tradeability of interaural time and amplitude differences, and localization of tones in a background of masking noise. All of these projects are being continued.

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3. HEARING AIDS

National Institutes of Health (Grant 1 RO1 NS12846-01)

[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).]

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The goal of this program is to develop improved signal-processing and display 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

In this work we are seeking to develop preprocessing schemes to assist hard-ofhearing listeners in noisy and reverberant environments. A speech intelligibility enhancement system¹ based on adaptive comb filtering has been implemented and evaluated quantitatively for listeners with normal hearing. Sentences spoken by males and females were used as both targets and maskers. Tests were conducted with various combinations of system parameters (duration of filter impulse response, treatment of unvoiced segments), talkers, and target-to-masker amplitude ratios. Baseline tests were conducted for processed materials in the absence of interference, as well as for unprocessed materials at various target-to-masker ratios. The results indicate that comb filtering attenuates the masker amplitude 2-10 dB, and that greater attenuation corresponds to longer filter impulse-response durations and to male-female speaker combinations. The processing also degrades the intelligibility of targets presented in the absence of maskers, particularly for the longer filter impulse responses. Adaptive comb filtering failed to increase intelligibility in the presence of interference; in fact, in all of these cases scores were inferior to those for unprocessed materials. Further work in this area is required to understand these results. In addition, the comb-filtering system will be evaluated for maskers consisting of broadband random noise. Further details are available in the Master's thesis of Yvonne M. Perlmutter.²

b. Matching Speech to Residual Auditory Function

We are continuing to focus on multiband amplitude compression for listeners with reduced dynamic range and on frequency lowering for listeners with negligible hearing at high frequencies.

Our present work on multiband amplitude compression is directed toward comparative evaluation of a multiband compression system adjusted to restore normal loudness function for tones and several linear amplification systems. In these studies we employ a small number of listeners with sensorineural impairments characterized by reduced dynamic range and recruitment. Performance of the systems is being studied for male and female speakers in both quiet and reverberant noisy environments.

Our work on frequency lowering is directed toward evaluating pitch-invariant processing techniques, including both lowering and warping.³ In initial studies we are comparing the ability of listeners who have normal hearing to understand warpedlowered speech with their ability to understand lowpass filtered speech. The results of preliminary tests of CV nonsense syllable identification have indicated the need for including multiple tokens of test items to prevent artifacts from providing reliable cues. Since our facilities do not permit us to perform the warping-lowering operation in real time, we have had to provide for random-access storage of a large vocabulary of preprocessed test materials. This has taken a little extra time, but we hope that significant results will soon be obtained.

We have prepared a series of three detailed articles on signal processing for hearing aids, including linear amplification, 4 amplitude compression, 5 and frequency lowering.

c. Tactile Aids

We are working on the development of a simple, wearable, vibrotactile aid to provide the profoundly deaf with a general awareness of acoustical signals and with the gross amplitude and temporal characteristics of these signals. In one such aid now being considered,⁷ the envelope of the acoustical signal is used to modulate the amplitude of a 250-Hz tone. The circuit design also includes preemphasis of high frequencies and automatic gain control. Preliminary psychophysical tests involving detection of tones in silence and in background noise and recognition of environmental sounds and sentences in closed sets indicate that this device is superior to a simple linear amplification system.

We are also exploring different encoding and display schemes for the tactile perception of speech using the Optacon transducer system. Among the schemes that are being compared are a unidimensional frequency display, a two-dimensional frequencyamplitude display, and a two-dimensional time-swept frequency display. The software for this project, which makes use of a computer system for processing and control, has been completed and experiments concerned with the discriminability of selected pairs of speech elements are now under way.

An evaluation is being made of tactile speech communication using the Tadoma method, in which the "reader" monitors the articulatory features of speech directly by placing his hand on the talker's face. Preliminary experiments with a deaf-blind, experienced Tadoma user⁸ have included tests of the discriminability of speech elements, recognition of words in isolation and in sentences, and perception and comprehension of syntactic and prosodic features of speech. Preliminary experiments with comparatively inexperienced normal subjects (for whom deafness and blindness are simulated) have focused on the discriminability of speech elements. In general, the results of these various experiments have not only demonstrated that good tactile perception of speech is indeed possible but also have documented the types of errors made in Tadoma and have provided insight into the perceptual cues used in Tadoma.

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4. MUSICAL PITCH

National Institutes of Health (Grant 1 RO1 NS11680-01) Howard L. Golub, Adrian J. M. Houtsma, Afarin Ordubadi, Roger W. Wicke

The objective of this project is to obtain a better understanding of the auditory processes that underlie the transformation of a complex sound into a sensation of musical pitch.

a. Pitch of Harmonic Two-Tone Complexes

Musical interval identification experiments were conducted with dichotically presented two-tone complexes of nonsuccessive harmonic numbers. As expected, we found that for complexes of harmonics n, n+2 identification performance is identical to that for successive harmonics of twice the fundamental frequency when n is even. When n is odd, fundamental tracking is worse than for successive harmonics, although it is still significant. For n, n+3 complexes, no significant evidence for fundamental tracking was found. These last two results cannot be explained by any currently available model on pitch processing.¹⁻³

b. Pitch of Amplitude-Modulated Noise

The musical interval identification paradigm was also used to study the pitch of square-wave, sine-wave, and pulse-modulated wideband noise. The noise was lowpass filtered before modulation, and the lowpass cutoff frequency served to control the amount of statistical correlation between successive periodic noise samples. Results seem to indicate that there are two different and independent pitch mechanisms at work, one of which may be spectral, the other almost certainly temporal.⁴

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- 5. MUSICAL ACOUSTICS

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

Adrian J. M. Houtsma, Ernest J. Perevoski

We are seeking to understand the physical behavior of musical instruments, particularly stringed instruments.

a. An Electronic Pickup System for the Classical Guitar

When an acoustically weak instrument such as the classical guitar is played in a symphony orchestra concert, the intensity unbalance makes electronic amplification of the guitar necessary. The conventional technique of amplifying a near-field microphone recording, typically a few inches from the sound hole, gives a less than optimal representation of the far-field acoustic spectrum of the instrument. We are trying to find a limited array of point pickups that by linear mixing can provide a close approximation of the acoustic far field measured in a flat-response reverberant chamber.

We have made aural comparisons of white noise driven inputs at the bridge and of actually played instruments. Results thus far indicate that best matches can be obtained through a linear combination of an acoustic air-pressure signal taken at the sound hole and the integrated output of an accelerometer placed on the bridge that represents the velocity of the string termination point.²

b. Development of a "Melograph"

In folk music the musicologist is faced with the problem of charting the exact timing and pitch structure of actually performed melodies. This is often accomplished with a device called a melograph that charts pitch vs time. Problems are encountered with currently available equipment when musical signals are measured that are largely upper harmonics or that have more than one major peak per period, since this equipment usually works through filtering and fundamental-frequency tracking or through peak detection.¹ Various hardware and software schemes are being investigated to find an efficient means of tracking the pitch of fast-changing periodic or quasi-periodic sounds, irrespective of their harmonic nature.

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C. Transduction Mechanisms in Lateral Line and Vestibular Organs

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Our broad goal is to understand the mechanisms of transduction in the receptor organs of the acustico-lateralis system of vertebrates. Study of the mechanical, electrical, and synaptic events in hair cell organs and their relation to nerve activity is basic to such understanding. In pursuit of these goals we have during the past year: (i) determined the composition of the inner-ear fluids in representative species of several classes of vertebrates; (ii) estimated experimentally an upper bound on the magnitude of cupula motion in the ampulla of the semicircular canal of the skate in response to maintained caloric stimulation and begun to measure afferent response characteristics of ampullary nerve fibers in this preparation; and (iii) continued our effort to identify the hair cell afferent synaptic transmitter.

1. ANALYSIS OF VERTEBRATE INNER-EAR FLUIDS

National Institutes of Health (Grant 5 RO1 NS11080-03) M.I.T. Health Sciences Fund (Grant 76-07) Scott K. Peterson, Lawrence S. Frishkopf, Charles M. Oman

Vertebrate hair cells – the receptor cells of the auditory, vestibular, and lateral line systems – are part of an epithelial membrane that separates fluids of different compositions. These fluids, called endolymph and perilymph, bathe the apical hair-bearing and basal synaptic portions of the hair cells, respectively; tight junctions between cells at the epithelial surface appear to present an effective barrier to ionic movement across the membrane. Ions present in endolymph and perilymph may play a significant role in mechanical-to-electrical transduction and synaptic and neural transmission in these receptor organs. Therefore a knowledge of their concentrations could be important in understanding these processes. Much is already known of the composition of the inner-ear lymphs.^{1, 2}

In collaboration with Professor Thomas F. Weiss of the Communications Biophysics Group, RLE and Dr. Claude Lechene of Harvard Medical School, we have obtained Table XXII-1. Summary of composition measurements.

CONCENTRATIONS ARE IN MILLIMOLES PER LITER MEAN = MEAN OF ANIMAL MEANS SEM = STANDARD ERROR OF THE MEAN NA = NUMBER OF ANIMALS NS = NUMBER OF SAMPLES NA CL CA MG P 5 К _____ CAT PERILYMPH NA = 3; N5 = 83, 196 154, 8 165, 7 1, 883 0, 7556 0, 6244 1, 128 MEAN 0.6031 9.806 13.37 0.2205 0.0973 0.0296 0.4311 SEM CAT ENDOLYMPH NA = 3; N5 = 6191.6 0.9983 208.4 0.3939 0.0022 0.5028 1.174 MEAN 0.4994 4.062 0.0056 0.0022 0.0255 0.6311 SEM 1.72 LIZARD PERILYMPH NA = 17; N5 = 42172.2 MEAN 2.873 160.2 1.745 1.065 0.4469 2.029 0.1133 3.597 4.806 0.0737 0.0522 0.0814 0.2791 SEM SKATE PERILYMPH NA = 5 ; N5 = 184.324 173 230.7 3.964 3.36 0.5887 19.84 19.99 0.5945 1.17 MERN 6.404 3.36 1.625 SEM 0.253 0.974 SKATE ENDOLYMPH NA = 5 ; NS = 13 91.64 MERN 248.3 408.1 3.786 0.4866 0.6845 1.56 SEM 8.733 24,02 27.21 0.3557 0.1042 0.1051 0.4377 SKATE CEREBROSPINAL FLUID NR = 4; NS = 43.217 MERN 180.3 226, 9 2,725 1,562 1,527 8.33 SEM 0.3657 23.81 28.6 0.3774 0.4417 0.2633 3.472 SER WATER NA = 4 ; NS = 8MEAN 8.165 330.5 451.7 8,905 40.82 0.7725 25.73 SEM 0,4081 24,82 20.55 0.3967 1.019 0.1797 1.273

Because of the difficulty of obtaining endolymph in the lizard and the high variability in the data, no estimates for this fluid have been included in the table.

samples of endolymph and perilymph by micropuncture of the inner ears of three vertebrate species, skate, alligator lizard, and cat. These samples have been analyzed for concentrations of seven elements (Na, K, Cl, Ca, Mg, S, P), using the technique of electron probe microanalysis.³ Some of the results of this study are shown in Table XXII-1. The skate data form the basis of formulations of artificial endolymph and perilymph that we have used in physiological experiments on the excised inner ear of this species, as described in Section XXII-C. 2.

Two aspects of this study seem unique: first, it provides a comparison of inner-ear lymph concentrations of representative species of several vertebrate classes, by using a single technique; second, for the first time data have been obtained in these species on the concentrations of Ca and Mg, elements whose significance in the functioning of nerve, muscle and receptor cells, and of synapses is well documented. Ca⁺⁺ appears to play a significant role in hair cell transduction.⁴ Limited data on Ca and Mg concentrations in inner-ear fluids have been available previously for only a few species.^{1, 5}

We have measured element concentrations in endolymph from the ampulla of the skate's semicircular canal before and after prolonged excitatory or inhibitory stimulation. Preliminary results indicate a significant increase in concentrations of four elements (Na, K, Cl, and Ca) during excitation and a significant decrease during inhibition. Although of variable magnitude from preparation to preparation, the direction of these changes was consistent under a variety of stimulus conditions.

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2. STUDIES OF CUPULA MOTION IN THE SKATE SEMICIRCULAR CANAL

M. I. T. Health Sciences Fund (Grant 76-07) National Institutes of Health (Grant 5 RO1 NS11080-03)

Charles M. Oman, Lawrence S. Frishkopf

During the past year, we determined experimentally an upper bound on the physiological range of cupula motion in the skate semicircular canal, and have begun to study the response characteristics of different types of afferent units in the ampullary nerve.

The question of what constitutes the naturally occurring magnitude and mechanical mode of cupula motion is one of the oldest problems in vestibular physiology, one that cannot be satisfactorily resolved purely on the basis of anatomical studies. Investigators have therefore attempted to answer the question by means of observations in vivo. Experimental studies¹⁻⁴ have reported cupula motions well in excess of 5 μ m. Theoretical considerations,⁵ however, led us to question whether physiological cupula motions, in fact, are large enough to be visualized when looking through the wall of the ampulla, and whether earlier workers imposed traumatically large stimuli on the semicircular canal ampulla.

Working in the isolated labyrinth of the skate <u>Raja erinacea</u>, we visualized the cupula by puncturing the ampullary wall with a sharpened glass pipette and by staining local regions by slow infusion of small amounts of Alcian blue dye. Single and multiunit activity in the ampullary nerve was monitored while caloric stimulation was applied with a spot of light focused on the canal duct. Caloric stimuli that more than doubled the level of afferent activity and recruited many previously silent units were found to produce no detectable motion of stained regions of the cupula as monitored visually through the ampullary wall. If the cupula was first visibly displaced by rapid dye injection, however, motion of the top of the cupula was thereafter observed in response to an identical caloric stimulus. The basis of this traumatic change in the mechanical stiffness of the cupula resulting from rapid dye injection could not be determined.

We concluded that the physiologic range of cupula motion in this animal is probably less than the resolution of our optical method, which we conservatively estimate as $3-5 \ \mu m$. Experimentally observed motions of the cupula an order of magnitude larger are probably not physiological, and may result from trauma-induced changes in the mechanical characteristics. These results were presented at the 6th Annual Meeting of the Society for Neuroscience in Toronto, Canada,⁶ and a detailed report is being prepared for publication.

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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 training grants from the National Institutes of Health.