

Section 3 Auditory Physiology

Chapter 1 Signal Transmission in the Auditory System.

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Academic and Research Staff

Professor Lawrence S. Frishkopf, Professor Nelson Y.S. Kiang, Professor William T. Peake, Professor William M. Siebert, Professor Thomas F. Weiss, Dr. Robin A. Davis, Dr. Bertrand Delgutte, Dr. Donald K. Eddington, Dr. Dennis M. Freeman, Dr. Jill C. Gardner, Dr. John J. Guinan, Jr., Dr. James B. Kobler, Dr. Harlan Lane, Dr. Joseph S. Perkell, Dr. William M. Rabinowitz, Dr. John J. Rosowski, Dr. Xiao Dong Pang, Robert M. Brown, Debra S. Louison, Frank J. Stefanov-Wagner, David A. Steffens, Sylvette R. Vacher

Graduate Students

Kathleen M. Donahue, Scott B.C. Dynes, Farzad Ehsani, Donna K. Hendrix, Michael P. McCue, Jennifer R. Melcher

1.1 Basic and Clinical Studies of the Auditory System

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

1.2 Signal Transmission in the External- and Middle-Ear

Project Staff

Kathleen M. Donahue, Professor William T. Peake, Dr. John J. Rosowski

During the past year, the work of Professor William T. Peake and Dr. John J. Rosowski has focused on four issues: 1) a description of external-ear function in cat ears, 2) measurements of middle-ear function in human cadaver ears, 3) the effect of ear size on auditory function and 4) estimates of the auditory capabilities of the earliest mammals. These foci are linked by the common goal of understanding how the structure of the external and middle ears of various animals relates to the function of their auditory systems. Significant results include:

1. A description of the acoustics of the cat external ear.¹

¹ J.J. Rosowski, L.H. Carney, and W.T. Peake, "The Radiation Impedance of the External Ear of the Cat: Measurements and Applications," *J. Acoust. Soc. Am.* 84:1695-1709 (1988).

2. A comparison of human middle-ear function in living and cadaver ears which show that the latter are useful tools for further studies.²
3. Data which suggest that the inner and middle ears of the alligator lizard grow at different rates and that growth causes changes in the middle-ear mechanics.³
4. A description of middle- and inner-ear structures of the earliest known mammal which points out similarities between these ears and the ears of present day mice and bats.⁴

These results can influence the development of middle- and external-ear reconstructive procedures used by clinicians and also our conception of both the life style of the earliest mammals and the environmental pressures which led to the evolution of mammals.

1.3 Cochlear Mechanisms

Project Staff

Dr. Dennis M. Freeman, Farzad Ehsani, Professor Lawrence S. Frishkopf, Donna K. Hendrix, Professor Thomas F. Weiss

We have published three papers that analyze the degradation of timing information in the cochlea⁵ and have substantially completed a manuscript that describes a theoretical study

of the role of calcium processes in the degradation of timing information in the cochlea. Results of this study suggest that three hair-cell processes, each acting as a first-order lowpass filter process, contribute to the degradation of timing information in the cochlea. These are: 1) the charging of the membrane capacitance, 2) the kinetics of opening of calcium channels, and 3) the time course of accumulation of calcium in intracellular compartments.

We have continued theoretical studies of the mechanical stimulation of the hair bundles of hair cells. Our approach is to obtain solutions of the equations of motion for a Newtonian fluid to a succession of problems of increasing geometric complexity in order to isolate the role of the fluid load and of nearby boundaries (such as tectorial structures and the reticular lamina) on the mechanics of small structures (such as hair bundles) immersed in fluids (representing the cochlear fluids). We have published a paper that gives a non-mathematical overview of our principal results⁶ and have finished papers that more completely describe these results.

We have developed an *in vitro* preparation of the cochlear duct of the alligator lizard. The technique is to rapidly remove the duct (in under five minutes) and place it in an artificial endolymph solution. The vestibular membrane is opened and a cement (derived

² S.N. Merchant, P.J. Davis, J.J. Rosowski, and M.D. Coltrera, "Normality of the Input Immittance of Middle Ears from Human Cadavers," *Abstracts of the Eleventh Midwinter Meeting of the Association for Research in Otolaryngology*, 1988.

³ J.J. Rosowski, D.K. Ketten, and W.T. Peake, "Allometric Correlations of Middle-Ear Structure and Function in One Species: The Alligator Lizard," *Abstracts of the Eleventh Midwinter Meeting of the Association for Research in Otolaryngology*, 1988.

⁴ A. Graybeal, J.J. Rosowski, D.R. Ketten, and A.W. Crompton, "The Inner-ear Structure of Morganucodon, an Early Jurassic Mammal," *Zool. J. Linn. Soc.*, in press; J.J. Rosowski and A. Graybeal, "What Did Morganucodon Hear?," submitted to *Zool. J. Linn. Soc.*

⁵ C. Rose and T.F. Weiss, "Frequency Dependence of Synchronization of Cochlear Nerve Fibers in the Alligator Lizard: Evidence for a Cochlear Origin of Timing and Non-Timing Neural Pathways," *Hear. Res.* 33:151-166 (1988); T.F. Weiss and C. Rose, "Stages of Degradation of Timing Information in the Cochlea: A Comparison of Hair-Cell and Nerve-Fiber Responses in the Alligator Lizard," *Hear. Res.* 33:167-174 (1988); T.F. Weiss and C. Rose, "A Comparison of Synchronization Filters in Different Auditory Receptor Organs," *Hear. Res.* 33:175-180 (1988).

⁶ D.M. Freeman and T.F. Weiss, "The Role of Fluid Inertia and Viscosity in Mechanical Stimulation of Hair Cells," *Hear. Res.* 35:201-208 (1988).

from mussels) is used to attach the duct to a glass slide at the bottom of a chamber. The chamber is normally perfused with artificial endolymph, but test solutions of different composition are also used. The duct is observed under a compound microscope using Nomarski optics. In order to assess the sensitivity of the tissue to the composition of the artificial endolymph, we have varied the composition and measured the changes in the positions of microscopic particles (either titanium dioxide or polystyrene) that have been allowed to settle on various inner-ear structures. The results should have implications for the physical-chemical properties of inner-ear structures such as the tectorial membrane.

1.4 Membrane Properties of Auditory Neurons

Project Staff

Dr. Robin A. Davis

What do VIIIth nerve fibers contribute to signal transmission in the auditory system? We have begun to investigate specific aspects of this broad question during the past year. Individual VIIIth nerve fibers were studied *in vitro*, thus permitting the membrane properties of the cells to be examined independent of extrinsic complications such as afferent and efferent synaptic events or hormonal modulation.⁷

Since different types of K⁺ channels contribute to the unique patterns of neuronal activity, we studied how these channel types regulate the firing characteristics of auditory neurons. We have begun to categorize K⁺ channel properties with single channel recordings from the cell body membrane using the cell-attached configuration of the patch clamp technique.⁸ A compilation of the

K⁺ channel conductance measurements made under similar recording conditions showed that conductances fell into five distinct groups (approximately 25, 47, 83, 142 and 220 pS). These divisions may reflect different categories of K⁺ channels located in the perikaryal membrane.

In conjunction with single channel measurements, intracellular voltage recordings taken from isolated auditory neurons revealed spontaneous bursting properties that may be related to the activity of the different types of K⁺ channels described above. Additional experiments will be carried out to: 1) examine the voltage dependent and pharmacological characteristics of the fast spikes and slow oscillations observed in intracellular recordings and 2) to determine the channel types underlying this activity.

Thus, goldfish auditory neurons demonstrated physiological properties, such as the multiplicity of K⁺ channel types and distinctive firing properties, which could play a role in regulating signal transmission.

1.5 Stimulus Coding in the Auditory Nerve

Project Staff

Dr. Bertrand Delgutte

During the past year, a series of experiments on physiological mechanisms underlying psychophysical masking was completed, and a preliminary report of these experiments was published.⁹

In these experiments, masked thresholds of auditory-nerve fibers in anesthetized cats were measured for both simultaneous and nonsimultaneous presentations of the signal and the masker. The difference between

⁷ R.L. Davis, E.A. Mroz, and W.F. Sewell, "Isolated Auditory Neurons in Culture," *Abstracts of the Association of Research for Otolaryngology* 11:240 (1988).

⁸ R.L. Davis, E.A. Mroz, and W.F. Sewell, "Single Channel Properties of Goldfish (*Carassius auratus*) Auditory Neurons *in vitro*," *Soc. Neurosci. Abstr.* 14(2):798 (1988).

⁹ B. Delgutte, "Physiological Mechanisms of Masking." In *Basic Issues in Hearing*, eds. H. Duifhuis, J.W. Horst, and H.P. Wit, 204-214. London: Academic, 1988.

simultaneous and nonsimultaneous masked thresholds is a measure of the contribution of suppression to masking because suppression occurs only when two stimuli overlap in time. Results for a 1 kHz tone masker show that suppression strongly contributes to masking when the masker level is above 40 dB SPL and signal frequency is well above the masker. In particular, the rapid growth of masking with masker level (which is often called "upward spread of masking") is primarily due to the growth of suppression. In contrast, for low masker levels and signal frequencies near and below the masker, masking is not due to suppression, but to spread of the excitation produced by the masker to the place of the signal along the cochlea. These experiments further showed that the auditory-nerve fibers that have the lowest masked thresholds are not those that are tuned to the signal frequency, but those whose characteristic frequency is slightly on the opposite of the masker frequency with respect to the signal frequency. This finding is a physiological correlate of the phenomenon of "off-frequency listening" in psychophysics.

While suppression of the response to the signal by the masker contributes to masking, suppression of the response to the masker by the signal might help signal detection. Our results show that this phenomenon does occur, and that, for certain fibers, signal thresholds are lower in the presence of the 1-kHz masker than in quiet, justifying the term "unmasking." However, these unmasking thresholds were always higher than the masked thresholds of fibers tuned to the signal frequency, suggesting that suppression of the masker by the signal is not essential for psychophysical signal detection in the presence of tone maskers. Unmasking is likely to be more important for multiple-component maskers.

1.6 Middle-Ear Muscle Reflex

Project Staff

Dr. John J. Guinan, Dr. James B. Kobler, Sylvette Vacher, Dr. Xiao Dong Pang, Michael P. McCue

We are aiming to determine the structural and functional basis of the reflex contractions of the middle-ear muscles in response to high intensity sound. Two papers were completed describing the anatomical foundation for our previous physiological results.¹⁰ Stapedius motoneuron axons and cell bodies were labeled by injecting stapedius muscles with horseradish peroxidase in normal cats and in cats in which the middle segment of the internal facial genu had been cut. We divided stapedius motoneurons into two groups: "Perifacial" and "Accessory." Perifacial stapedius motoneurons have cell bodies located around the motor nucleus of the facial nerve and axons which follow the classical course of facial motor axons through the internal genu of the facial nerve. Accessory stapedius motoneurons have cell bodies near the descending facial motor root and axons which ascend to the rostral tip of the internal facial genu, abruptly reverse direction, and then join the descending facial motor root. Our present results,¹¹ with the physiologic effects of similar lesions described last year and now published,¹² demonstrate that cats have two groups of stapedius motoneurons, perifacial and accessory, which can be separated anatomically by the locations of their cell bodies or the courses of their axons, and which, on the average, have different response properties. In particular, the more rostral group, the accessory stapedius

¹⁰ M.P. McCue, J.J. Guinan, Jr., "Anatomical and Functional Segregation in the Stapedius Motoneuron Pool of the Cat," *J. Neurophysiol.* 60:1160-1180 (1988); J.J. Guinan, Jr., M.P. Joseph, and B.E. Norris, "Brainstem Facial-Motor Pathways from Two Distinct Groups of Stapedius Motoneurons in the Cat," submitted to *J. Comp. Neurol.*

¹¹ M.P. McCue, J.J. Guinan, Jr., "Anatomical and Functional Segregation in the Stapedius Motoneuron Pool of the Cat," *J. Neurophysiol.* 60:1160-1180 (1988).

¹² J.J. Guinan, Jr., M.P. Joseph, and B.E. Norris, "Brainstem Facial-Motor Pathways from Two Distinct Groups of Stapedius Motoneurons in the Cat," submitted to *J. Comp. Neurol.*

motoneurons, respond predominantly to ipsilateral sound.

During the past year, we completed the data analysis to determine in more detail how the locations of stapedius-motoneuron cell bodies are correlated with their responses to sound.¹³ Single unit recordings and injections of horseradish peroxidase were made in axons of stapedius motoneurons in the fascicles which go from the facial nerve to the stapedius muscle in the cat. Single units were characterized physiologically by their responses to ipsilateral, contralateral and binaural sounds. Labeled cell bodies (N = 28) were found in all of the brainstem regions previously identified as containing stapedius motoneurons. Motoneurons characterized as having similar response properties had cell bodies in relatively circumscribed locations. Most (eight of twelve) motoneurons excited by sound in either ear had cell bodies in a narrow band around the facial nucleus. Most (seven of eight) motoneurons excited by ipsilateral but not contralateral sound had cell bodies in the cleft between the superior olivary complex and the facial nucleus. All four motoneurons excited by contralateral, but not by ipsilateral sound, had cell bodies located ventromedial to the facial nucleus. The three motoneurons excited only by binaural sound had cell bodies located dorsal to the superior olivary complex. The cell body of the one motoneuron which shows activity in the absence of sound stimulation with similar electrophysiologic properties tends to have similar locations in the brainstem. The results are consistent with the idea that the stapedius motoneuron pool is divided into subgroups that are spatially segregated in terms of their patterns of input from the two ears.

During the past year, a thesis was completed¹⁴ and a talk was presented¹⁵ on

our project to determine the effects of the stapedius-muscle contractions on the responses of single auditory-nerve fibers. We are concentrating on the effects of the stapedius in reducing masking. Because of the nonlinear properties of the cochlea, intense sounds at low-frequencies are particularly effective in reducing (masking) responses to sounds at higher frequencies. Contractions of the stapedius muscle reduce sound transmission primarily at low sound frequencies. Our experiments show that stapedius contractions reduce the masking of high-frequency sounds by low-frequency sounds. We block normal sound-evoked contractions with a barbiturate anesthesia and elicit controlled stapedius contractions with direct shocks. Our results show that:

1. The attenuation of middle-ear transmission produced by a given amplitude of stapedius contraction does not depend on sound level.
2. The stapedius-induced reduction of masking can be much larger than the attenuation of low-frequency sound, due to the rapid growth of the masking of high-frequency tones by low-frequency noise which averaged 2 dB/dB. Unmasking effects up to 40 dB were observed; the data suggest that unmasking up to 75 dB might occur in some fibers.
3. The observed unmasking effects can be completely explained by a model which predicts the unmasking based only on the (linear) stapedius-produced attenuation of the sound and the (nonlinear) growth-rate of masking for a particular auditory-nerve fiber.

We conclude that this reduction of masking is probably one of the most important functions of the stapedius muscle.

¹³ S.R. Vacher, J.J. Guinan, Jr., and J.B. Kobler, "Intracellularly Labeled Stapedius-Motoneuron Cell Bodies in the Cat are Spatially Organized According to Their Physiologic Responses," submitted to *J. Comp. Neurol.*

¹⁴ X.D. Pang, *Effects of Stapedius-Muscle Contractions on Masking of Tone Responses in the Auditory Nerve*. Ph.D. diss., Dept. Electr. Eng. & Comp. Sci., MIT, 1988.

¹⁵ X.D. Pang and J.J. Guinan, Jr., "Effects of Stapedius Contractions on the Masking of Cat Auditory-Nerve-Fiber Responses to Tones," Association for Research in Otolaryngology, *Abstracts* 12(A): 1989.

An invited review of the anatomy and physiology of the stapedius muscle reflex was delivered to the Association for Research in Otolaryngology.¹⁶

1.7 Cochlear Efferent System

Project Staff

Dr. John J. Guinan, Jr.

Our aim is to understand the physiological effects produced by medial olivocochlear (MOC) efferents which terminate on outer hair cells. During the past year, our efforts have focused on data analysis and publishing of our work on the effects of electrical stimulation of medial olivocochlear efferents on single auditory-nerve fibers. This work has led to three papers; two of these, which were almost completed during the last reporting period, were described in last year's report, and have since been published¹⁷ The third paper¹⁸ is described below.

Tuning curves, or similar measures of threshold, were obtained from auditory-nerve fibers in the presence or absence of electrical stimulation of medial olivocochlear (MOC) efferents. Efferent stimulation raised the thresholds of fibers for tones at the characteristic frequency (CF) by an amount which varied with the spontaneous rate (SR) of the auditory-nerve fiber. On the average, high-SR fibers had the smallest threshold shifts, and low-SR fibers had the largest threshold shifts. Within the high-SR or medium-SR groups, the fibers with the lowest thresholds had the largest threshold shifts. The distribution of threshold shifts as a function of CF peaked at CFs of 3 to 8 kHz

for high-SR and medium-SR fibers but appeared to peak at higher CFs for low-SR fibers. The distribution of high-SR threshold shifts versus CF appears to be displaced apically in the cochlea compared to the distribution of MOC endings on outer hair cells. This can be understood in terms of efferent activity depressing basilar membrane motion and affecting regions at, and apical to, the activated efferent synapses. An additional way in which efferent activity inhibits responses appears to be required to explain the low-SR threshold shifts. The data are consistent with one function of the medial efferents being to raise the thresholds of auditory-nerve fibers, and thereby adjust the effective range of the auditory system.

During the past year, a previously submitted paper which reviews the physiology of olivocochlear efferents was published.¹⁹

1.8 Sources of the Brainstem Auditory Evoked Potential

Project Staff

Jennifer Melcher, Professor Nelson Y.S. Kiang

The brainstem auditory evoked potential (BAEP) is a time-varying voltage that can be recorded from electrode pairs on the surface of the head in the 10 msec immediately following the delivery of a punctate acoustic stimulus to the ear. Because it is generated by cells in the auditory nerve and brainstem, the BAEP has proven useful as a non-invasive monitor of neural activity in the auditory system. Its usefulness, however, is limited since exactly which cell groups con-

¹⁶ J.J. Guinan, Jr., "Recent Advances in Our Understanding of Middle-Ear Muscle Efferents," Association for Research in Otolaryngology, *Abstracts* 12(A):1989.

¹⁷ J.J. Guinan, Jr. and M.L. Gifford, "Effects of Electrical Stimulation of Efferent Olivocochlear Neurons on Cat Auditory-Nerve Fibers. I. Rate Versus Sound Level Functions," *Hear. Res.* 33:97-114 (1988); J.J. Guinan, Jr. and M.L. Gifford, "Effects of Electrical Stimulation of Efferent Olivocochlear Neurons on Cat Auditory-Nerve Fibers. II. Spontaneous Rate," *Hear. Res.* 33:115-128 (1988).

¹⁸ J.J. Guinan, Jr. and M.L. Gifford, "Effects of Electrical Stimulation of Efferent Olivocochlear Neurons on Cat Auditory-Nerve Fibers. III. Tuning Curves and Threshold at CF," *Hear. Res.* 37:29-46 (1988).

¹⁹ J.J. Guinan, Jr., "Physiology of the Olivocochlear Efferents." In *Auditory Pathway - Structure and Function*, eds. J. Syka and R.B. Masterton, 253-267. New York: Plenum, 1988.

tribute to the BAEP is largely unknown. Our first goal is to determine which cell groups contribute to the BAEP and to determine the latency and, in some cases, waveform of their contribution. A second goal is to understand why particular cell groups contribute to the BAEP at the latency and with the waveform that they do.

A series of lesion experiments is being performed in the cat to achieve the first goal. Kainic acid, a neurotoxin, is injected into the brainstem to eliminate particular cell populations. The resulting changes in the BAEP are connected with the cells eliminated.

To meet the second goal, a model for the cat BAEP is being developed. The BAEP is written as the sum of the potentials produced by particular populations in the auditory brainstem. The potential produced by particular cell populations is calculated using two types of quantities. The first are called unitary potentials. A unitary potential is the potential produced at the BAEP recording electrodes when a particular cell fires an action potential. These potentials are determined theoretically. The second type of quantity is derived from previous measurements of the rate at which cells fire in response to the BAEP stimulus.

Unitary potentials are calculated in two steps. First, the transmembrane current that flows on a cell when it fires an action potential is calculated using a core conductor model. Unitary potentials are then calculated from the transmembrane currents assuming a model for the extracellular medium. At this point, only the simplest possible model has been considered; the extracellular medium is modeled as an infinite, homogeneous conductor. Eventually, more realistic head models will be considered.

1.9 Cochlear Implants

1.9.1 Current Spread During Electrical Stimulation of the Human Cochlea

Project Staff

Dr. Donald K. Eddington

The basic function of a cochlear prosthesis is to elicit patterns of activity on the array of surviving auditory nerve fibers by stimulating electrodes that are placed in and/or around the cochlea. By modulating these patterns of neural activity, these devices attempt to present information that the implanted subject can learn to interpret. The spike activity patterns elicited by electrical stimulation depend on several factors: the structure of the cochlea (three-dimensional, electrically heterogeneous), the geometry and placement of the stimulating electrodes, the stimulus waveform, and the distribution of excitable auditory nerve fibers. An understanding of how these factors interact to determine the activity patterns is fundamental to designing better devices and interpreting the results of experiments involving intracochlear stimulation of animal and human subjects. As a first step towards this understanding, the goal of this project is to construct a software model of the cochlea that predicts the patterns of current flow produced by the stimulation of arbitrarily placed, intracochlear electrodes.

As reported last year, a three-dimensional, finite element model of the human cochlea has been developed that predicts the potential distribution produced in this structure by electrical stimulation of model electrodes of arbitrary position and geometry. For a scala tympani/far-field electrode pair, the model predicts that potential along the scala tympani falls monotonically from the electrode toward the base; while, from the electrode to the apex, the potential falls initially, and then plateaus. These potential distributions indicate that current spreads more toward the base than toward the apex. Measurements of potential at unstimulated electrodes made in the initial five human subjects implanted with intracochlear electrodes confirmed the asymmetric poten-

tial distributions predicted by the model in all five subjects.

This year, we collected psychophysical measures of current interaction to determine if the pattern of interaction between simultaneously stimulated electrodes would exhibit the same asymmetries as the potential distributions. That is, a subthreshold stimulus at the base of the cochlea should not alter threshold measured using a more apical electrode as much as an apical subthreshold stimulus alters threshold measured using a more basal electrode. This has been confirmed in five subjects.

1.9.2 Psychophysical Measures and Their Correlation With Speech Reception

Project Staff

Dr. Donald K. Eddington

One striking aspect of speech reception measurements made with subjects using cochlear implants is the wide range of performance. This project identifies basic psychophysical measures that correlate with the subject's speech reception ability. Three correlations should help us to: 1) identify basic performance deficits that might be overcome with alternative processing schemes and 2) relate correlations found between pathology and psychophysical measures in experimental animals to their potential effect on speech reception.

We now have preliminary analyses for the correlation of speech reception with four psychophysical measures in as many as ten subjects. The speech reception test used in these analyses is the Initial Consonant identification test of the Minimal Auditory Capabilities Test Battery. Comparison of these speech reception scores have been made with four psychophysical measures: amplitude (current) threshold, dynamic range, electrode interaction, and discrimination of electrode place using pitch.

Amplitude threshold was measured using an adaptive, three-alternative, forced-choice procedure with 200 Hz, biphasic pulsatile stimuli delivered to each of the scala tympani electrodes (using a common ground

electrode located in the temporalis muscle). Thresholds measured at basal electrodes tend to be higher than those measured at the more apical electrodes. Average threshold (average of the individual thresholds measured at the four most apical electrodes used by the subject's portable processor) ranged from 40 to 180 μA (peak-to-peak) across the subjects tested. When threshold and speech reception data are compared for all ten of our subjects, the correlation is not very strong ($r = -0.48$). When the one subject who is not using the implant (for what we suspect are psycho/social reasons) is not included, the correlation is very strong ($r = -0.80$). Comparison of speech reception and measures of dynamic range also shows a significant correlation ($r = 0.78$).

Threshold interaction between two electrodes was measured by comparing the threshold measured for a test stimulus at one electrode to thresholds measured at that same electrode while a subthreshold stimulus (both in and out of phase with the test stimulus) was applied at a second electrode. An interaction measure was computed for each subject by: 1) subtracting the threshold measured when the two stimuli were in phase from the threshold measured when they were out of phase and 2) dividing the result by the subthreshold stimulus amplitude. Comparison of speech reception scores and an averaged (using the four most apical electrodes) interaction measure for each subject demonstrated a significant correlation ($r = -0.90$).

The ability to discriminate relative electrode position (e.g., whether one electrode is more basal than another) when two electrodes are stimulated sequentially with the same stimulus has been measured in five subjects. These measures are made by stimulating a pair of electrodes in sequence (e.g., first the most apical electrode; then the most basal electrode). The subject's task is to declare which sound was higher in pitch. If the sound produced by the more basal electrode was judged higher, the answer is considered to be correct. We presented all possible combinations of the six intracochlear electrodes taken two at a time. Each combination was presented ten times in random order. The amplitude of each stimulus was randomly picked from three possibilities for

each electrode: 1) a level selected to match the resulting precept's loudness to a reference, 2) a level significantly louder than the reference, and 3) a level significantly softer than the reference. Comparison of speech reception scores and the overall score (percentage correct) from the electrode place discrimination task shows a significant correlation ($r = 0.83$).

1.9.3 Speech Production in Cochlear-Implant Patients

Project Staff

Dr. Joseph S. Perkell, Dr. Harlan Lane

Work is continuing on the study of the speech of post-lingually-deafened cochlear implant patients. Longitudinal recordings and signal processing of those recordings have continued; and analysis of patterns of respiration are in progress. A new computer system and new software for signal processing, data extraction, plotting and statistical analysis have been brought on line. Efficient algorithms and procedures have been developed for the processing of our multi-bandwidth, multi-channel signals and extraction of respiratory data from those signals. Our original longitudinal measurements of respiration patterns (from our old data processing system) have been repeated on the new system for validation of our techniques. Work is in progress on the development of procedures for the extraction of acoustic and other physiological data from processed signals.

1.9.4 Responses of Auditory-Nerve Fibers to Electrical Stimulation

Project Staff

Dr. Bertrand Delgutte, Scott B.C. Dynes

Psychophysical studies from several laborato-

ries have shown that cochlear-implant patients poorly discriminate loudness-balanced tones applied through a single electrode pair for frequencies above 1 kHz. To determine whether this poor performance is due to a lack of phase-locking information in the auditory nerve, the activity of auditory-nerve fibers was recorded in anesthetized cats in response to electric sine wave stimuli applied through a bipolar electrode pair inserted about 5 mm into the cochlea through the round window. The two stimulating electrodes were separated by 2 to 3 mm. The synchronization index was calculated from period histograms for frequencies ranging from 2 to 17 kHz. The stimulus artifact was considerably reduced through the use of an adaptive digital filter and "differential" micropipettes.²⁰

Measured synchronization indices were many times larger than the indices that would have resulted from the residual stimulus artifact according to a model developed by Johnson.²¹ Synchronization indices of single fibers did not vary systematically with intensity for stimuli that produced discharge rates exceeding ten spikes/s. Synchronization indices at each stimulus frequency varied considerably from fiber to fiber. This variability was not obviously correlated with spontaneous discharge rate or electric threshold. In about 25 to 30 percent of the fibers, synchronization index varied nonmonotonically with frequency. However, the average synchronization index for many fibers decreased with frequency at a rate of 6 dB/octave for frequencies above 4 kHz. This average electric synchrony was nevertheless greater than the average acoustic synchrony measured by Johnson²² for frequencies above 4 kHz, suggesting that acoustic phase locking is not limited by jitter of spike conduction in auditory-nerve fibers, but by more peripheral stages of processing. The finding of significant synchrony to electrical stimuli well above 1 kHz suggests that the poor performance of single-channel cochlear implant

²⁰ Van den Honert and Stypulkowsky, *Hearing Res.* 14:225-243 (1984).

²¹ *Biophys. J.* 22:413-430 (1978).

²² *J. Acoust. Soc. Am.* 68:1115-1122 (1980).

patients in frequency discrimination above this frequency is due to the inefficiency of

the central processor in making use of phase-locking information.²³

²³ S.B.C. Dynes and B. Delgutte, "Phase-Locking of Auditory-Nerve Fiber Responses to Electric Sinusoidal Stimulation of the Cochlea," Association for Research in Otolaryngology, *Abstracts of the Twelfth Midwinter Research Meeting* p. 269 (1989).