

## Neurophysiologic Basis for Cochlear and Auditory Brainstem Implants

Aage R. Møller

*Callier Center for Communication Disorders, School of Human Development, University of Texas at Dallas*

The physiologic basis for cochlear and brainstem implants is discussed. It is concluded that the success of cochlear implants may be explained by assuming that the auditory system can adequately discriminate complex sounds, such as speech sounds, on the basis of their temporal structure when that is encoded in a few separate frequency bands to offer moderate separation of spectral components. The most important roles of the cochlea seems to be to prepare complex sounds for temporal analysis

and to create separate channels through which information in different frequency bands is transmitted separately to higher nervous centers for decoding of temporal information. It is then pertinent to ask how many channels are needed. Because speech discrimination is very important, it is probably sufficient to use enough channels to separate formants from each other.

**Key Words:** cochlear implants, brainstem implants, auditory physiology.

Cochlear implants were pioneered by Michelson (Michelson, 1971) and W. House (House & Urban, 1973). But before that, other investigators had shown that electrical signals applied to the ear or the auditory in deaf individuals could produce the sensation of sounds. Also notable was the work by Simmons (1966), who described how he placed a bipolar electrode on the auditory nerve of a person undergoing a neurosurgical operation (Simmons, Mongeon, Lewis, Huntington, 1964). Later, Simmons implanted a six-wire array in the cochlea and studied the patient for 16 months (Simmons, 1966). It was, however, Dr. William House who introduced cochlear implants as a means of providing hearing in deaf patients (House, 1976, 1985). This development was met with great skepticism by physiologists and others. This early cochlear implant stimulated parts of the cochlea with a single electrode to which an electrical signal from a microphone was applied through a simple electronic converter. It seemed unlikely that such a simple approach could provide any useful hearing.

Bilger (1977), who subjected 13 individuals with the House type of cochlear implants to an extensive battery of audiologic tests, found that these patients could identify 56.9% of 27 environmental sounds correctly with the implants working, but only 36.1% of these sounds could be identified with the implant off. The implants also aided in lip reading where the Craig lip-reading test showed that cochlear implants improved lip reading from a mean

score of 79.4% without activation of the prosthesis to a score of 87.2% with the prosthesis switched on.

Whereas it was true that these early cochlear implants did not provide speech discrimination in the way we normally understand it, they did indeed provide valuable sound awareness to people who were deaf. Dramatic improvements were made when cochlear implants that used multiple electrodes implanted in the cochlea were introduced. These devices stimulated different parts of the cochlea with electrical impulses derived from different frequency bands of sound. This major improvement, compared with the single-electrode implants, implied that the auditory system was better suited to process sounds when different frequency bands activated different populations of auditory nerve fibers. After that, more sophisticated processing of the sound was added. The results were clearly astonishing, even for those individuals who had great expectations. Therefore, modern cochlear implants provide more than 90% word recognition (Dorman, Loizou, Kemp, & Kirk, 2000) and correct identification of many environmental sounds.

Cochlear implants are now the most successful of all prostheses of the nervous system. The success of cochlear implants in providing useful hearing may still appear surprising because even multichannel cochlear implants cannot replicate the spectral analysis that occurs in the cochlea to a degree that can explain the acuity of the normal frequency discrimination in the auditory system. Brainstem implants that stimulate the cochlear nucleus are less

effective in restoring hearing, but their success is even more intriguing than that of cochlear implants.

Since it would require a very large number of filters and a very large number of electrodes to mimic the basilar membrane function of the normal cochlea, the success of cochlear implants must depend on the ability to provide information about frequency through temporal coding. The success of single- and multiple-channel cochlear implants, therefore, hinge on the ability to use temporal coding of frequency for frequency discrimination of complex sounds, such as vowels. The separation of sound spectra into a few discrete spectral bands, which occurs in multichannel cochlear implants, facilitates temporal analysis of complex sounds, such as speech sounds. It is insufficient, however, as a model for the place hypothesis of frequency discrimination.

The success of these prosthetics has not only provided the sensation of sound to individuals lacking hearing; it has initiated the study of the human auditory system from a new perspective.

Frequency discrimination is considered to be important for discrimination of complex sounds, such as speech sounds. There are two hypotheses for frequency discrimination: the place hypothesis and the temporal hypothesis. The place hypothesis states that frequency is coded according to the place that is activated along the basilar membrane. The temporal hypothesis states that the frequency is coded in the discharge patterns of neurons in the auditory nerve. The relevance of these hypotheses has long been debated within auditory physiology, and the development of cochlear prosthetics has recently brought this debate to a level of practical importance.

Yet, the improvement in perception from multichannel implants cannot be explained by the common models for frequency discrimination. Therefore, the roles of place and temporal coding for frequency discrimination need to be reexamined, taking into consideration results of physiological studies as well as the results obtained using cochlear prosthetics.

### ***Place or Temporal Coding for Frequency Discrimination?***

The ability of the auditory system to discriminate frequency is assumed to be of fundamental importance for speech discrimination, although the discrimination of changes in amplitude and duration of sounds and gaps between sounds are also important in discrimination of speech sounds. Much attention has therefore been devoted to finding the anatomical and physiological bases for such frequency discrimination. Two hypotheses for auditory frequency discrimination have prevailed: the place hypothesis and the temporal hypothesis. The frequency (or spectrum) of a sound can be determined equally well from the result of spectral analysis such as that performed by the cochlea or from analysis of the time pattern. This means that information about the frequency (or spectrum) of sounds can be derived from both of these two types of coding of sounds. There is ample evidence that frequency

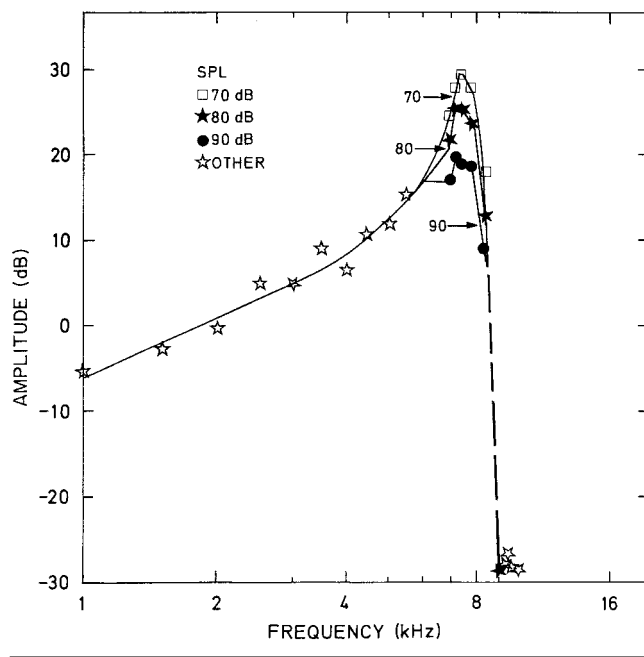
is normally coded in the discharge pattern of single auditory nerve fibers, both as a temporal and a place code. Less evident, however, is which of these two ways of coding frequency is used as a basis for frequency discrimination.

Frequency analysis in the cochlea is the basis for the place hypothesis, and coding of the temporal pattern of sounds in the discharge pattern of auditory nerve fibers is the basis for the temporal hypothesis (Licklider 1959, Langner 1992). The cochlea normally separates sounds into narrow frequency bands that activate different populations of hair cells and thereby different populations of auditory nerve fibers. Individual nerve fibers are tuned to different frequencies. Frequency tuning is a characteristic feature of nerve cells throughout the ascending classical auditory nervous system. Nerve cells in the ascending auditory pathways are organized according to the frequency to which they are tuned (tonotopical organization). This organization has been regarded to be the result of the tuning of the basilar membrane. However, recent studies (Leake, Snyder, Rebscher, Moore, & Vollmer, 2000) showed that tonotopic organization of the inferior colliculus is normal in neonatally deaf mice. Electrical stimulation of a single location of the cochlea could expand the response areas and degrade the cochleotropic organization. Competing stimulation of two locations on the basilar membrane, however, maintained the frequency representation of each sector of the inferior colliculus without expanding the response areas.

The fact that sounds of various kinds are coded according to these two principles and that the frequency can be extracted from both forms of coding (see e.g., Møller 2000), however, does not answer the question about which one of these two forms of coding is actually used by the central nervous system in providing the basis for frequency discrimination of complex sounds, such as speech sounds (Kral, 2000; Møller 1999; Zwislocki 1992).

The temporal hypothesis has earlier been regarded as less important than the place principle because it has been assumed that the time code could not be preserved in synaptic transmission and because it was not known how the temporal code could be decoded. The difficulties in explaining how the temporal code may be preserved in synaptic transmission and how it could be decoded, and the prominence of place representation in the cochlea, as well as in the auditory nervous system, have favored the place coding as the basis for frequency discrimination. Several recent studies have, however, presented evidence that makes it less likely that cochlear spectral analysis is important for speech discrimination. Some of the first studies that convincingly set the importance of the place code in doubt concerned coding of vowel sounds in single auditory nerve fibers. These were published by Sachs and co-workers. These investigators showed that the place code was much less robust than the temporal code (Young and Sachs 1979, Sachs and Young 1979). These investigators showed that coding of formant frequencies was preserved over a large range of stimulus intensities,

**FIGURE 1.** Amplitude of vibration of a single point on the basilar membrane of an anesthetized squirrel monkey for constant displacement amplitude of the malleus using the Mossbauer technique. The three solid curves show the vibration at three different sound intensities. The curves were shifted vertically so that they would coincide if the basilar membrane functioned in the way of a linear system (from Rhode, 1971).



including the physiological range. The place coding deteriorated when the stimulus intensity was increased, and it became insufficient to communicate information about formant frequencies at intensities above 50 dB SPL, thus within physiologic sound levels. Other studies have shown that the acuity of cochlear frequency selectivity decreased with increasing sound intensity (Rhode 1971; Figure 1). Studies of the tuning of the basilar membrane using recordings of the cochlear microphonic potential (Honrubia and Ward 1968) showed a considerable shift in the location of the maximal response. Other studies of the basilar membrane tuning have also found that the location of the maximal response shifts along the basilar membrane when the sound intensity is changed, although different studies have shown different magnitudes of that shift.

Studies of the tuning of auditory nerve fibers have shown that the frequency to which nerve fibers were tuned shifted and became broader when the sound intensity was increased from threshold levels to the physiologic range of sound intensities (Møller 1977, Møller 1983, Zwislocki 1992, Harrison and Evans 1982; Figure 2). Since the pitch of sounds changes little with sound intensity (Stevens 1935), the findings that the tuning of the basilar membrane depends on the sound intensity placed serious doubt on the place coding of frequency as a basis for frequency discrimination. Also, frequency discrimination of speech and musical sounds are known to change very little with sound intensity.

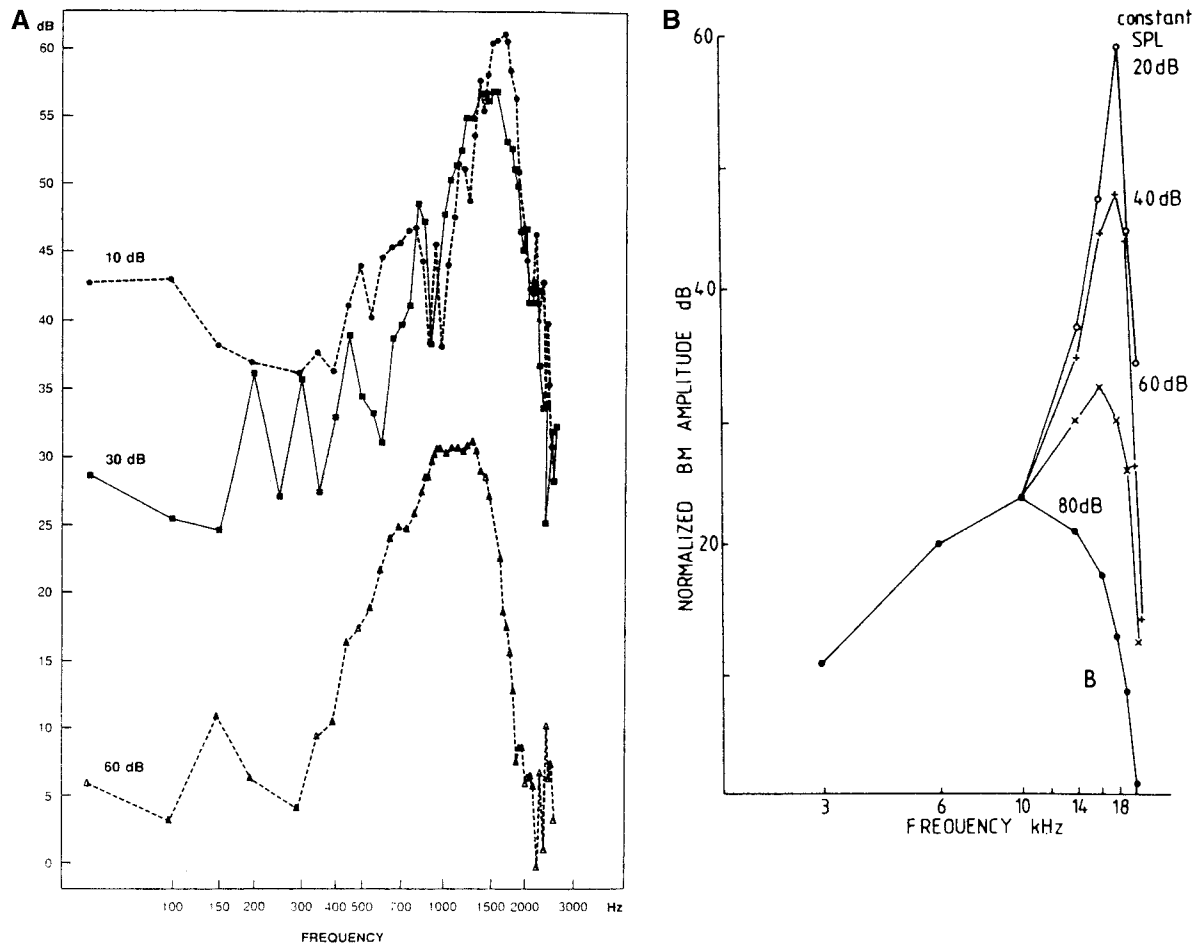
Studies by Sachs and Young (Sachs and Young 1979, Young and Sachs 1979) have provided additional support for the importance of the temporal code for speech discrimination, thus supporting the temporal hypothesis for frequency discrimination. Sachs, Young, & Miller (1983) have emphasized the importance of these findings in designing cochlear implants.

### *Temporal Analysis of Complex Sounds in the Auditory System*

Many experiments have shown that nerve impulses in the auditory nerve are phase locked to the waveform of the basilar membrane vibration, at least up to 5 kHz and probably higher (Arthur et al. 1971, Rose, Galambos, & Hughes, 1959, Møller 1977a, Møller 1983, see also Møller 2000; Figure 3). Hair cells respond to deflection of the hairs in only one direction: toward the basal body (Flock, 1965). As a first approximation, that corresponds to a deflection of the basilar membrane toward the scala vestibuli. However, the complex and viscoelastic coupling between the motion of the basilar membrane and the deflection of the stereocilia results in a more complicated relationship between the deflection of the basilar membrane and the excitation of the inner hair cells (Konishi and Nielsen 1973, Sokolich et al. 1976, Zwislocki and Sokolich 1973). Despite that, recordings from single auditory nerve fibers show distributions of nerve impulses that mainly replicate the half-wave rectified waveform of the vibration of the basilar membrane at the location of the individual inner hair cell that innervates the nerve fiber from which recordings are made (see e.g., Arthur et al. 1971, Rose, Hind, Anderson, & Brugge 1971; Figure 3). The (average) interval between nerve impulses can, therefore, be used as the basis for frequency discrimination according to the temporal hypothesis.

Phase locking of auditory nerve impulses to the waveform of complex sounds has also been demonstrated in experiments in which two tones were presented at the same time. The histograms of the distribution of nerve impulses to such sounds had the waveform of the half-wave rectified waveform of the sound (Rose et al. 1971; Figure 4). Auditory nerve fibers are normally not phase locked to all components of complex sounds, such as speech sound, because the basilar membrane functions as a series of band-pass filters that divides the spectrum of sounds into narrow bands. The discharges of individual nerve fibers are, therefore, phase locked to the waveform of band-pass filtered sounds. The temporal patterns of the discharges of different populations of nerve fibers, therefore, represent the periodicity of different parts of the spectrum of a broadband sound. Separating the spectrum in different bands makes it possible to adequately code the time pattern of complex sounds. The waveform of complex sounds, such as speech sounds, is too complex to be accurately coded in the discharge pattern of auditory nerve fibers. It would not be possible to extract the different frequency components of a complex sound from such a neural code. Early cochlear implants using a single electrode coded the raw waveform of complex sounds into

**FIGURE 2.** Comparison between the tuning of a single auditory nerve fiber in a rat (A) and that of the basilar membrane in a guinea pig (B). **A:** Estimates of frequency transfer function of a single auditory nerve fiber in a rat at different stimulus intensities (given in dB SPL), obtained by Fourier transforming cross-correlograms of the responses to low-pass-filtered pseudorandom noise (3400 Hz cutoff). The amplitude is normalized to show the ratio (in dB) between the Fourier transformed cross-correlograms and the sound pressure. The individual curves would have coincided if the cochlear filtering and neural conduction had been linear (From Møller 1999, modified from Møller 1983). **B:** Vibration amplitude at a single point of the basilar membrane of a guinea pig obtained using pure tones as test sounds at four different intensities. The amplitude scale is normalized, and the individual curves would have coincided if the basilar membrane motion had been linear (from Møller 1999, modified from Johnstone et al. 1986 and based on results from Sellick et al. 1982).



the discharge pattern of the auditory nerve fibers. The inadequacy of this code to communicate the information about the frequency of sounds is most likely the reason for the poor performance of the old cochlear implants.

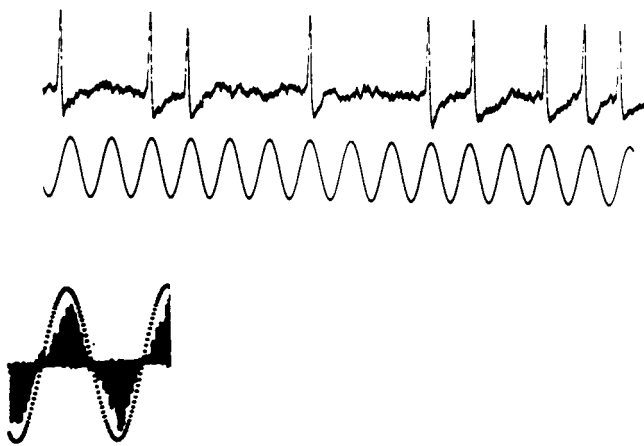
In the normal cochlea, the stimulus of individual hair cells is not the “raw” waveform of sound but rather band-pass filtered sounds that divide the spectrum of sound up into “slices,” each of which stimulates a different population of nerve fibers. The waveform of such band-pass-filtered sounds is much less complex than that of the unfiltered sounds. That means that discharges of single auditory nerve fibers become phase locked to a much less complex waveform than that of the sound wave that reaches the ear. Transmitting the temporal information in different frequency bands of complex sounds separately to higher CNS centers through different populations of auditory nerve fibers makes it possible to encode and decode

the time pattern of complex sounds accurately. By combining the information in different frequency bands in the CNS, information about the entire spectrum of the sound may then be reassembled.

### How Many Channels Are Needed?

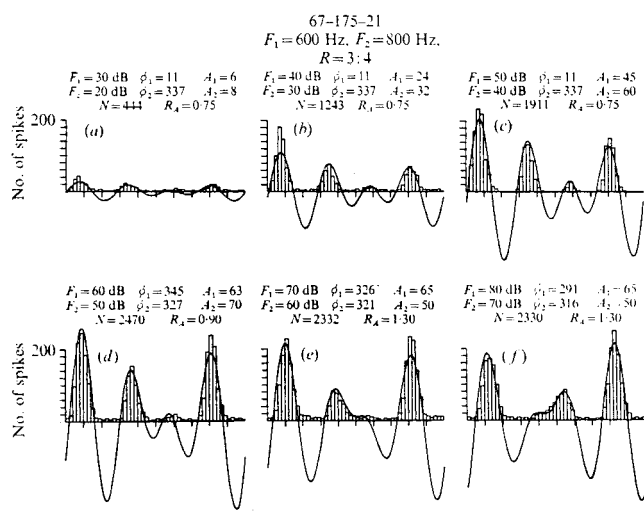
The question about how the speech spectrum should be divided before the temporal pattern is coded is important for design of cochlear implants. The advantages of performing temporal coding of complex sounds in separate frequency bands is to a great extent responsible for the improvement of the performance of cochlear implants that is represented by the modern multichannel cochlear implant compared with its single channel predecessor. Some of the advantages in coding the time pattern of vowels in

**FIGURE 3. Phase locking of discharges in a single guinea pig auditory nerve fiber to a low-frequency tone (300 Hz), near threshold (from Arthur et al. 1971).**



separate frequency bands can be illustrated by the analysis of vowel sounds shown in Figure 5. The waveform of a vowel is the sum of three or four damped oscillations (Figure 5; Fant 1959). The frequency of each of these damped oscillations is equal to each of the formants of a vowel. Vowels can be discriminated on the basis of the frequencies of their first three formants, and it is therefore assumed that proper coding and decoding of formant frequencies is important for the discrimination of vowels. The waveform of a vowel is complex, but separating the spectrum into frequency bands that only contain a single formant results in a single damped oscillation, the frequency of which is equal to that of the formant in question. That means that encoding the waveform of a

**FIGURE 4. Period histograms of discharges in a single auditory nerve fiber of a squirrel monkey to stimulation with two tones of different frequencies that were locked together with a frequency ratio of 3:4 and an amplitude ratio of 10 dB. The different histograms represent the responses to this sound when the intensity was varied over a 50-dB range (modified from Rose et al. 1971).**



damped sinusoid provides exact information about a formant's frequency (Figure 6). The cochlear filters normally perform such spectral separation and different nerve fibers code the frequency of formants (Figure 7). The different fibers of the auditory nerve, therefore, normally phase lock to the waveform of damped oscillations of formants providing exact information about the frequency of the different formants of vowels.

The effect of increasing the number of channels in cochlear implants was studied by Shannon and colleagues (Shannon et al., 1995). These investigators used speech in which the spectral information had been greatly reduced. The output of band-pass filters similar to those used in modern cochlear implants was half-wave rectified and then used to modulate broadband noise. The output from several band-pass filters was summed and used as test material. That processing removed (most of) the spectral characteristic of the signals but preserved the temporal pattern. Recognition<sup>1</sup> of consonants, vowels, and sentences processed in that way increased with the number of band-pass filters, but it reached nearly 100% for only three filters. Sentence recognition scores for one channel were close to zero. That shows that a small number of filters is sufficient for obtaining good speech discrimination with cochlear implants.

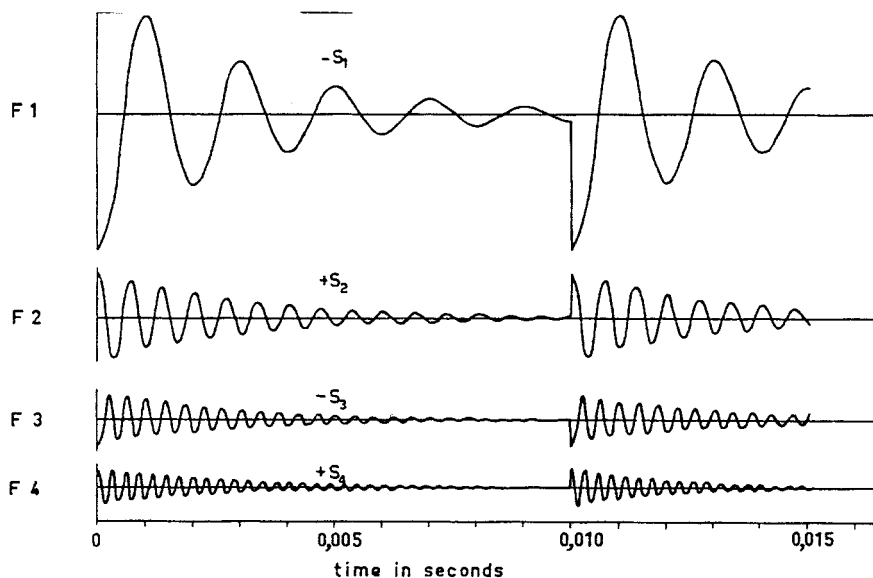
Dividing the spectrum of complex sounds into narrow bands, therefore, reduces the demand on the encoding of the waveform of complex sounds, such as speech sounds. It is likely that the main importance of the spectral selectivity of the basilar membrane is to facilitate the analysis of the temporal pattern of broadband sounds that occur in the nervous system by dividing the spectrum of sounds into bands that are suitable for temporal analysis. This is known as "synchrony capture."

With that in mind, it can be understood why increasing the number of spectral filters, and thus the number of electrodes of cochlear implants, resulted in dramatic improvements of speech discrimination compared with single-electrode cochlear implants. Assuming that a temporal code provides information about frequency, it also explains why it is not necessary to replicate the filtering function of the basilar membrane exactly, which would require a very large number of filters and the same large number of electrodes to be implanted in the cochlea.

The results obtained by Shannon et al. (1995) are slightly better than the results obtained in tests of cochlear implants. More than 90% sentence recognition was achieved with as few as four channels for speech presented in the quiet (Dorman, Loizou, & Rainey, 1997). Dorman et al. (2000) showed that children needed more channels than adults to recognize words. Adults obtained 99% correct word recognition with 10 channels, but children obtained only 92% correct with 12 channels. The number of amplitude channels in prostheses with 8 to 16

<sup>1</sup>For speech recognition, listeners were instructed to identify the presented vowels from a list of 8 vowels and consonants from a list of 16 consonants. The listeners were instructed to repeat as many words as they could from the presented sentences.

**FIGURE 5.** The waveform of vowels is the sum of damped oscillations, the frequencies of which are the formant frequencies (modified from Fant 1959).

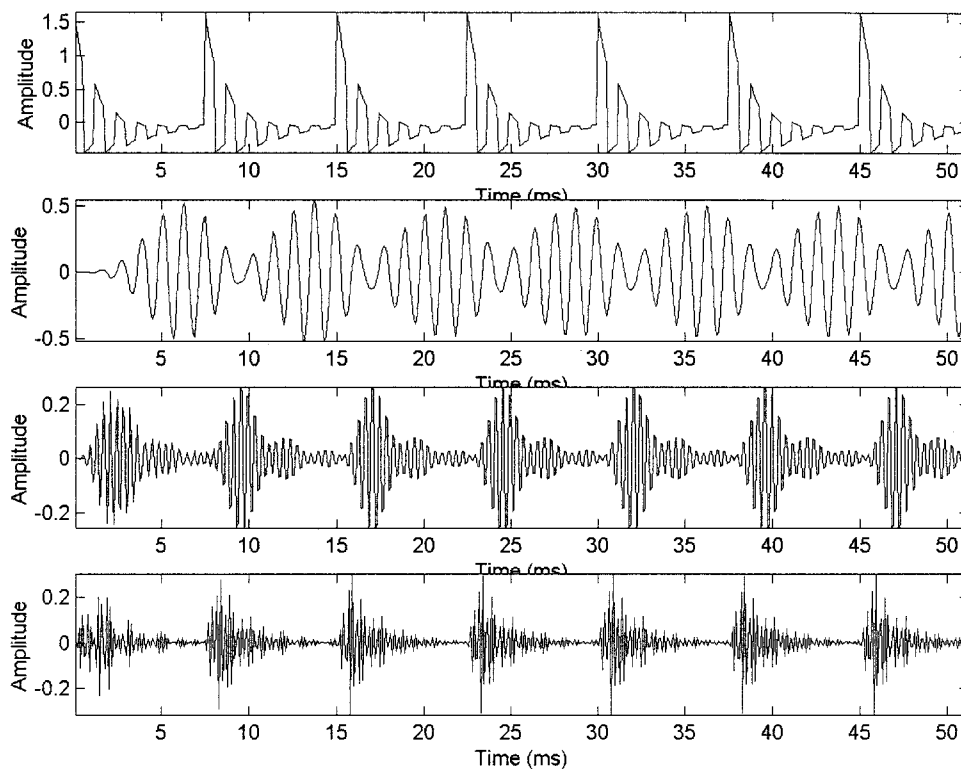


filters needed to obtain a certain speech recognition was higher when speech was presented in noise (Loizou, Dorman, Tu, & Fitzke 2000). The maximal performance was obtained with 12 amplitude channels, and 16 channels did not improve the results.

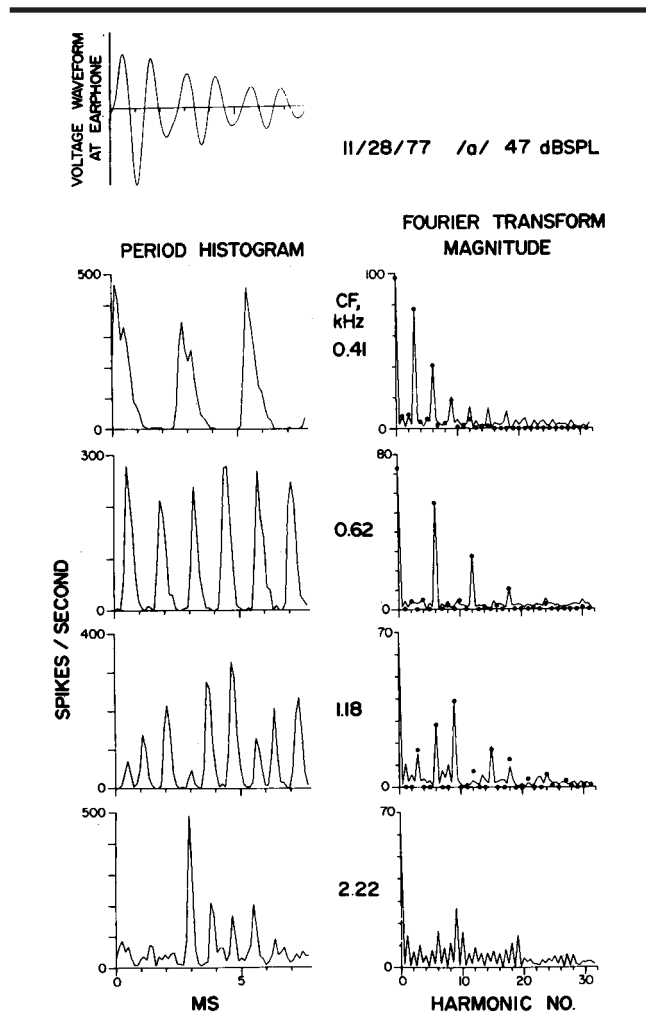
### *Preservation of the Temporal Code in the Nervous System*

To be the basis for frequency discrimination, the temporal code must be preserved as the information ascends

**FIGURE 6.** Band-pass filtering of a synthetic vowel. The center frequencies of the filters were equal to the formant frequencies (500, 1500, and 2500 Hz). Courtesy of Peter Assmann and Ginger Stickly.



**FIGURE 7. Temporal coding of the formant frequencies**  
(Young and Sachs, 1979)



toward the location where it is decoded. It has been assumed that the temporal code is degraded by synaptic transmission because of “synaptic jitter.” Synaptic jitter is a result of synaptic transmission using quanta of chemicals (transmitter substances), and that has been assumed to impair the precision of the temporal code. Impairment of temporal precision would affect high-frequency sounds and make it impossible to code the temporal pattern of sounds above a certain frequency.

However, several kinds of research have shown that the temporal code can indeed be preserved in synaptic transmission. Thus, many studies of binaural hearing have shown that the auditory system can detect differences in the time of arrival of sounds at the two ears of the order of 5 to 10  $\mu$ s (Tobias and Zerlin 1959). The information has to pass at least one synapse before it reaches the neurons that do the comparison of time of arrival. This means that timing of auditory information can be preserved through synaptic transmission with the accuracy of a few microseconds. The seeming controversy between the lack of precision in synaptic transmission and the fact

that the timing is preserved with extraordinary precision, through the first one or two synapses of the ascending auditory pathway, can be explained by the fact that some cells in the cochlear nucleus receive input from many auditory nerve fibers. They therefore act as spatial averagers that improve temporal precision similar to the way that signal averagers can improve the signal-to-noise ratio of evoked potentials. In the nervous system, the precision of timing is enhanced by many nerve fibers converging onto one nerve cell, whereas signal averaging is based on repeating the same stimulus and adding the responses.

Modeling studies have shown that synaptic transmission can decrease the temporal dispersion (increase temporal precision) of the input to neurons that receive many inputs (Burkitt and Clark, 1999). That would mean that cochlear nucleus cells can improve the precision of the timing of discharges of single auditory nerve fibers. That this is in fact the case has been supported by electrophysiologic studies that have shown that the temporal precision of the firing of some cells in the cochlear nucleus, in response to transient sound stimuli, is much greater than that of single auditory nerve fibers (Møller 1969).

This supports the hypothesis that these cells act as averagers of the neural activity in the cochlear nerve fibers and thereby improve the temporal precision of the firing of some cells in the cochlear nucleus.

### *Decoding of Temporal Information*

It is not known how temporal information of frequency is decoded. There is some evidence that similar neural circuits in the superior olivary complex of the ascending auditory pathways that decode binaural time differences (Yin and Chan 1990) also decode temporal information about the frequency of sounds. Some neurons in the superior olivary complex (probably the medial superior olivary nucleus [MSO]) are associated with detection of interaural time differences (Yin and Chan 1990). These neurons act as coincidence detectors. The path to these neurons from the two ears have different delays, and different neurons will thus fire for different delays between the arrival of sounds at the two ears corresponding to different azimuths to a sound source in accordance with the model of Jeffress (Jeffress 1948). It is a more complex task to detect the interval between waves of a sound than the difference in arrival time of sounds at the two ears. Convincing experimental evidence for the existence of such ability of the nervous system to detect time intervals between sound waves has not been published.

### *Amplitude Compression*

Another important function of the cochlea is that it provides amplitude compression, which makes it possible to code sounds within very large ranges of intensities in the discharge pattern of auditory nerve fibers. Cochlear implants mimic that function by appropriate electronic circuits that function relatively well.

## ***Functions that Are Not Covered by Modern Cochlear Implants***

Studies in animals have revealed that inhibitory bands surround the response areas of auditory nerve fibers (Sachs and Kiang 1968). This feature, known as two-tone inhibition, is a result of cochlear nonlinearity. It is not covered by modern cochlear implants. Two-tone inhibition resembles lateral inhibition and probably enhances the contrast between the energy in adjacent frequency bands. It may enhance responses to sounds with rapidly varying frequency. The normal cochlea also provides various forms of adaptation. The short-term (rapid) adaptation is important for processing of speech sounds, adding spatiotemporal contrast and extending the operating range of the cochlea (Smith, Brachman, & Goodman, 1983). Inclusion of such properties in cochlear implants may improve performance regarding speech discrimination.

Another feature of the cochlea that is not included in modern cochlear implants is the different travel times of the motion of the basilar membrane for sounds in different frequency ranges. Because the waves on the basilar membrane travel relatively slowly from the basal portion toward the apical portion of the basilar membrane, low-frequency components will normally activate nerve fibers later than high-frequency components. The importance of this effect is not known, but it could be studied in individuals with normal hearing using synthetic speech in which the timing of the different spectral components can be manipulated.

Auditory nerve fibers, as well as other neurons in the classical ascending auditory pathway, are organized according to the frequency to which they are tuned (tonotopic organization). Cochlear implants may not stimulate auditory nerve fibers according to the frequencies to which they are normally tuned. It is not known whether this tonotopic organization is important for processing the temporal code of frequency. For example, can neurons that are normally tuned to, for example, 2000 Hz adequately process the temporal code of sounds in the frequency region of 1000 Hz? Thus, can neurons process the temporal code of sound, independent of the frequency, to which they are normally tuned? Or must low-frequency sounds stimulate auditory nerve fibers in the apical part of the cochlea and high-frequency sounds stimulate fibers in the basal portion of the cochlea in order to provide the best basis for speech discrimination?

Perhaps the central processor not only identifies the neurons of the ascending auditory pathway by their anatomical connections to hair cells at different locations along the basilar membrane, but also by their "signature" firing pattern. Neurons may be "tagged" by the sounds that activate the neurons because stimulation with transient sounds gives rise to damped oscillations in the cochlear filter with a frequency that is the same as the frequency to which the neurons are tuned, thus creating a tonotopic organization that is independent of the location on the basilar membrane from which the fibers originate. That hypothesis could be studied in people with normal hearing using synthetic speech.

## ***Cochlear Nucleus Implants***

Cochlear nucleus implants, also known as brainstem implants, were introduced recently (Brackmann et al. 1993). Only a few individuals have had such implants. Consequently, much less is known about the success of cochlear nucleus implants compared with cochlear implants. Electrodes for stimulating the cochlear nucleus are placed in the lateral recess of the fourth ventricle through the foramen of Luschka, in a similar way that electrodes have been placed for recording evoked potentials from the cochlear nucleus in operations where the cerebello pontine angle is exposed (Møller and Jannetta 1983, Kuroki and Møller 1995). The cochlear nucleus has three main divisions: the dorsal cochlear nucleus, the anterior ventral cochlear nucleus, and the posterior ventral cochlear nucleus. The floor of the lateral recess of the fourth ventricle is shared by the surface of the ventral cochlear nucleus and that of the dorsal cochlear nucleus. The anterior ventral nucleus occupies the most rostral part of the cochlear nucleus (Kuroki and Møller 1995).

Electrically stimulating cochlear nucleus cells is more complex than stimulating auditory nerve fibers by electrodes placed in the cochlea. Not only is it more difficult to maintain a stable electrode placement in the brain than in the cochlea, but it is also more difficult to stimulate the optimal population of nerve cells. The cochlear nucleus includes a complex network of many different types of cells that are interconnected and that have excitatory and inhibitory influence on each other.

Parallel processing is prominent in the ascending auditory pathways, and each auditory nerve fiber innervates each of the three main divisions of the cochlear nucleus (for details, see Møller, 2000). Cochlear nucleus implants are likely to activate only one of these three divisions of the cochlear nucleus. Therefore, only one of the parallel pathways to higher nervous centers is activated by a cochlear nucleus implant. The implications of reduced parallel processing are unknown.

Although little evidence is available about which part of the cochlear nucleus should be stimulated to get the best results, it seems reasonable to assume that the best results can be obtained by stimulating the ventral cochlear nucleus. Cells in the ventral cochlear nucleus respond more precisely to the time pattern of sounds, and the ventral cochlear nucleus projects directly to the nuclei of the superior olivary complex, which may be involved in decoding temporal information. Some fibers from the ventral cochlear nucleus project directly to the inferior colliculus (see Møller 2000).

The electrical stimulation of the cochlear nucleus is a more complex task than that of the auditory nerve. Electrical stimulation of the auditory nerve in the cochlea activates most nerve fibers in the same way, depending only on the stimulus strength and the distance to the stimulating electrode. The situation is different in the cochlear nucleus, where the excitability of nerve cells depends on the size of the cells, their membrane potentials, and threshold, all of which vary considerably among cells.

That means that electrical stimulation will activate a selected proportion of nerve cells. A specific type of stimulation is, therefore, likely to stimulate a specific population of cochlear nucleus cells, whereas other types of stimulation may activate other types of cells.

Because it is not known precisely which kind of cells the cochlear nucleus implants stimulate, such stimulation may bypass some parts of the synaptic transmission that normally occur between auditory nerve fibers and cells in the cochlear nucleus and that may be important in transformation of the information.

Cochlear nucleus cells are known to respond to the envelope of sounds in ways that are different from that of auditory nerve fibers. The responses from different cochlear nucleus cells differ, whereas all auditory nerve fibers respond to the envelope of sounds in nearly the same way (Joris and Yin 1992, Møller 1976b). This means that different nerve cells in the cochlear nucleus perform different kinds of processing of the input from the auditory nerve. Many cochlear nucleus cells respond preferentially to small, rapid changes in the amplitude of sounds, which enhances the response to the envelope of amplitude-modulated sounds (Frisina, Smith, & Chamberlain, 1985, Frisina, Smith, & Chamberlain, 1990, Møller 1972, Møller 1976a, Møller 1974b). One- to two-decibel changes in the amplitude can cause more than 50% modulation of the period histograms of the responses to amplitude-modulated sounds. The sensitivity to amplitude-modulated sounds is greatest in the modulation frequency range from 20 to 400 Hz (Møller 1972). Many cells in the cochlear nucleus maintain that high sensitivity to amplitude modulation over a range of 50 to 70 dB SPL, covering the physiologic range of normal hearing (Møller 1976a). The envelope of vowels resembles amplitude-modulated sounds where the modulation frequency is the fundamental frequency, the range of which is 80 to 400 Hz. It is therefore similar to that which is best transmitted by cells in the cochlear nucleus (Møller 1972).

Some of these forms of neural processing may be bypassed when the auditory system is stimulated by cochlear nucleus implants if the stimulating electrodes activate cells in ways different from how they are normally activated by auditory nerve fibers.

The cochlear nucleus is tonotopically organized (Rose et al. 1959), but it is not known whether it is important to stimulate the cochlear nucleus cells according to this tonotopic organization. However, the orientation of the tonotopic maps is insufficiently known.

## Conclusion

The progress in the performance of cochlear implants during the past two or three decades has come about by combined efforts by physiologists, engineers, and clinicians who have been willing to implement these new devices in their patients. Whereas the design of cochlear implants will improve in the future, but at a less dramatic pace, the greatest progress can be expected in the field of applications. Such progress can only be achieved when

audiologists and other health professionals get more involved in the fitting of cochlear implants and in the rehabilitation that follows. It is therefore important that audiologists become knowledgeable about cochlear and brainstem implants, their function, and their possibilities.

## References

- Arthur, R. M., Pfeiffer, R. R., & Suga, N. (1971). Properties of "two tone inhibition" in primary auditory neurons. *Journal of Physiology (London)*, 212, 593–609.
- Bilger, R. C. (1977). Evaluation of subjects presently fitted with implanted auditory prostheses. *Annals of Otolaryngology, Rhinology and Laryngology*, 86(Suppl 38), 1–76.
- Brackmann, D. E., Hitselberger, W. E., Nelson, R. A., Moore, J., Waring, M. D., Portillo F., Shannon, R. V., & Telischi, F. F. (1993). Auditory brainstem implant: 1. Issues in surgical implantation. *Otolaryngology—Head and Neck Surgery*, 108, 624–633.
- Burkitt, A. N., & Clark, G. M. (1999). Analysis of integrate-and-fire neurons: Synchronization of synaptic input and spike output. *Neural Computation*, 11, 871–901.
- Dorman, M. F., Loizou, P. C., & Rainey, D. (1997). Speech intelligibility as a function of the number of channels of stimulation for signal processors using sine-wave and noise-band outputs. *Journal of the Acoustical Society of America*, 102, 2403–2411
- Dorman, M. F., Loizou, P. C., Kemp, L. L., & Kirk, K. I. (2000). Word recognition by children listening to speech processed into a small number of channels: Data from normal-hearing children and children with cochlear implants. *Ear and Hearing*, 21, 590–596.
- Fant, G. (1959). Acoustic analysis and synthesis of speech with applications to Swedish. *Ericsson Technics*, No 1.
- Flock, A. (1965). Transducing mechanisms in lateral line canal organ receptors. *Cold Spring Harbor Symposia on Quantitative Biology*, 30, 133–146.
- Frisina, R. D., Smith, R. L., & Chamberlain, S. C. (1985). Differential encoding of rapid changes in sound amplitude by second-order auditory neurons. *Experimental Brain Research*, 60, 417–422.
- Frisina, R. D., Smith, R. L., & Chamberlain, S. C. (1990). Encoding of amplitude modulation in the gerbil cochlear nucleus. II. Possible neural mechanisms. *Hearing Research*, 44, 123–142.
- Harrison, R.V., & Evans, E. F. (1982). Reverse correlation study of cochlear filtering in normal and pathological guinea-pig ears. *Hearing Research*, 6, 303–314.
- Honrubia, V., & Ward, P. H. (1968). Longitudinal distribution of the cochlear microphonics inside the cochlear duct (guinea pig). *Journal of the Acoustical Society of America*, 44, 951–958.
- House, W. H. (1976). Cochlear implants. *Annals of Otolaryngology, Rhinology and Laryngology*, 85(Suppl. 27), 3–91
- House, W. H. (1985). A personal perspective on cochlear implants. In R. A. Schindler, & M.M Merzenich (Eds.), *Cochlear Implants*. New York: Raven Press.
- House, W. F., & Urban, J. (1973). Long term results of electrode implantation and electrical stimulation of the cochlea in man. *Annals of Otolaryngology, Rhinology and Laryngology*, 82, 503–510.
- Jeffress, L. A. (1948). A place theory of sound localization. *Journal of Comparative Physiology*, 41, 35–39.
- Johnstone, B. M., Patuzzi, R., & Yates, G. K. (1986). Basilar membrane measurements and the travelling wave, *Hearing Research*, 22, 147–153.

- Joris P. X., & Yin T. C. T.** (1992). Responses to amplitude-modulated tones in the auditory nerve of the cat. *Journal of the Acoustical Society of America*, *91*, 215–232.
- Konishi, T., & Nielsen, D. W.** (1973). The temporal relationship between motion of the basilar membrane and initiation of nerve impulses in the auditory nerve fibers. *Journal of the Acoustical Society of America*, *53*, 325.
- Kral, A.** (2000). Temporal code and speech recognition. *Acta Oto-Laryngologica*, *120*, 529–530
- Kuroki, A., & Møller, A. R.** (1995). Microsurgical anatomy around the foramen of Luschka with reference to intraoperative recording of auditory evoked potentials from the cochlear nuclei. *Journal of Neurosurgery*, *82*, 933–939.
- Langner, G. A.** (1992). Review: Periodicity coding in the auditory system. *Hearing Research*, *60*, 115–142.
- Leake, P. A., Snyder, R. L., Rebscher, S. J., Moore, C. M., & Vollmer, M.** (2000). Plasticity in central representation in the inferior colliculus induced by chronic single- vs. two-channel electrical stimulation by cochlear implant after neonatal deafness. *Hearing Research*, *147*, 221–241
- Licklider, J. C. R.** (1959). Three auditory theories. In S. Koch (Ed.), *Psychology: A Study of a Science*. Vol. 1. New York: McGraw Hill.
- Loizou, P. C., Dorman, M. F., Tu, Z., & Fitzke, J.** (2000). Recognition of sentences in noise by normal-hearing listeners using simulations of speak-type cochlear implant signal processors. *Annals of Otology, Rhinology, and Laryngology. Supplement*, *185*, 67–68.
- Michelson, R. P.** (1971). Stimulation of the human cochlea. *Archives of Otolaryngology*, *93*, 317–323.
- Møller, A. R.** (1969). Unit responses in the rat cochlear nucleus to repetitive transient sounds. *Acta Physiologica Scandinavica*, *75*, 542–551.
- Møller, A. R.** (1972). Coding of amplitude and frequency modulated sounds in the cochlear nucleus of the rat. *Acta Physiologica Scandinavica*, *86*, 223–238.
- Møller, A. R.** (1974b). Responses of units in the cochlear nucleus to sinusoidally amplitude modulated tones. *Experimental Neurology*, *45*, 104–117.
- Møller, A. R.** (1976a). Dynamic properties of excitation and two-tone inhibition in the cochlear nucleus studied using amplitude modulated tones. *Experimental Brain Research*, *25*, 307–321.
- Møller, A. R.** (1976b). Dynamic properties of primary auditory fibers compared with cells in the cochlear nucleus. *Acta Physiologica Scandinavica*, *98*, 156–167.
- Møller, A. R.** (1977a). Frequency selectivity of single auditory-nerve fibers in response to broadband noise stimuli. *Journal of the Acoustical Society of America*, *62*, 135–142.
- Møller, A. R., & Jannetta, P. J.** (1983). Auditory evoked potentials recorded from the cochlear nucleus and its vicinity in man. *Journal of Neurosurgery*, *59*, 1013–1018.
- Møller, A. R.** (1983). Frequency selectivity of phase-locking of complex sounds in the auditory nerve of the rat. *Hearing Research*, *11*, 267–284.
- Møller, A. R.** (1999). Review of the roles of temporal and place coding of frequency in speech discrimination. *Acta Oto-Laryngologica*, *119*, 424–430.
- Møller, A. R.** (2000). *Hearing: Its Physiology and Pathophysiology*. San Diego: Academic Press.
- Rhode, W. S.** (1971). Observations of the vibration of the basilar membrane in squirrel monkeys using the Mossbauer technique. *Journal of the Acoustical Society of America*, *49*, 1218–1231.
- Rose, J. E., Galambos, R., & Hughes, J. R.** (1959). Micro-electrode studies of the cochlear nuclei in the cat. *Bulletin of the Johns Hopkins Hospital*, *104*, 211–251.
- Rose, J. E., Hind, J. E., Anderson, D. J., & Brugge, J. F.** (1971). Some effects of stimulus intensity on response of auditory fibers in the squirrel monkey. *Journal of Neurophysiology*, *34*, 685–699.
- Sachs MB and Kiang NYS.** (1968). Two-tone inhibition in auditory nerve fibers. *Journal of the Acoustical Society of America*, *43*, 1120–1128.
- Sachs, M. B., & Young, E. D.** (1979). Encoding of steady-state vowels in the auditory nerve: Representation in terms of discharge rate. *Journal of the Acoustical Society of America*, *66*, 470–479.
- Sachs, M. B., Young, E. D., & Miller, M. I.** (1983). Speech encoding in the auditory nerve: Implications for cochlear implants. In C. W. Parkins (Ed), *Cochlear Prostheses: An international Symposium. Annals of the New York Academy of Sciences*, Vol. 405 (pp. 94–113). New York: New York Academy of Sciences.
- Sellick, P. M., Patuzzi, R., & Johnstone, B. M.** (1982) Measurement of basilar membrane motion in the guinea pig using the Mossbauer technique. *Journal of the Acoustical Society of America*, *72*, 131–141.
- Shannon, R.V, Zeng, F-G., Kamath, V, Wygonski, J., & Ekelid, M.** (1995). Speech recognition with primarily temporal cues. *Science*, *270*, 303–304.
- Simmons FB, Mongeon CJ, Lewis WR, & Huntington, D. A.** (1964). Electrical stimulation of acoustic nerve and inferior colliculus. *Archives of Otolaryngology*, *79*, 559–567.
- Simmons, F. B.** (1966). Electrical stimulation of the auditory nerve in man. *Archives of Otolaryngology*, *84*, 22–76.
- Smith R. L., Brachman M. L., & Goodman D. A.** (1983). Adaptation in the auditory periphery. In C. W. Parkins (Ed.), *Cochlear Prostheses: An international Symposium. Annals of the New York Academy of Sciences*, Vol. 405 ( pp. 79–93). New York: New York Academy of Sciences.
- Sokolich, W. G., Hamernick, R. P., Zwislocki, J. J., & Schmiedt, R. A.** (1976). Inferred response polarities of cochlear hair cells. *Journal of the Acoustical Society of America*, *59*, 963–974.
- Stevens, S. S.** (1935). The relation of pitch to intensity. *Journal of the Acoustical Society of America*, *6*, 150–154.
- Tobias, J.V, & Zerlin, S.** (1959). Lateralization threshold as a function of stimulus duration. *Journal of the Acoustical Society of America*, *31*, 1591–1594.
- Yin, T. C. T., & Chan, J. C. K.** (1990). Interaural time sensitivity in medial superior olive of cat. *Journal of Neurophysiology*, *64*, 465–488.
- Young, E. D., & Sachs, M. B.** (1979). Representation of steady-state vowels in the temporal aspects of the discharge patterns of populations of auditory nerve fibers. *Journal of the Acoustical Society of America*, *66*, 1381–1403.
- Zwislocki, J. J.** (1992). What is the cochlear place code for pitch? *Acta Oto-Laryngologica*, *111*, 256–262.
- Zwislocki, J. J., & Sokolich, W. G.** (1973). Velocity and displacement responses in auditory nerve fibers. *Science*, *182*, 64–66.

Received March 6, 2001

Accepted September 7, 2001

First published (online) November 5, 2001

<http://journals.asha.org>

D.O.I: 10.1044/1059-0889 (2001/012)

Contact author: Aage R. Møller, Callier Center for Communication Disorders, School of Human Development, University of Texas at Dallas, Dallas, TX 75235. Email: amoller@UTDALLAS.EDU