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CHAPTER 9

Neural Basis of Audition

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INTRODUCTION

The nervous system's ability to detect, analyze, and segregate dynamic acoustic stimuli in complex environments surpasses the signal-processing powers of even the most sophisticated machines and algorithms in existence. The auditory system is as fast as it is complex, a quality necessitated by the fleeting nature of auditory information. The goal of this chapter is to provide an introduction to the physiology of the auditory pathway. The level of detail is intended to be accessible to students and researchers new to the field of audition as well as to those familiar with the psychology of audition but not with its physiology. This review provides a relatively comprehensive overview of the entire auditory pathway, but the emphasis is on topics that have received significant attention and yielded interesting results in recent years, especially since the last publication of this handbook.

The review starts with an introduction to the structure of the auditory pathway followed by a description of the physiology. This review focuses on basic neuroanatomy and on neurophysiology at the extracellular level. Biophysical descriptions of cells in the various auditory nuclei, as well as descriptions of the neurochemical properties of these cells, are beyond the scope of this review. Comprehensive book-length reviews of the anatomy (Webster, Popper, & Fay, 1992) and physiology (Popper & Fay, 1992) provide much more detailed descriptions of the auditory pathway. Other reviews that are specific to certain topics will be referenced later.

A primary function of the auditory system is to encode the frequency spectrum of a sound, that is, the level of energy at each frequency within a stimulus. The physical dimensions of frequency and sound level convey most of the important information in sounds. Studies of frequency and level coding have traditionally focused on pure-tone stimuli, and the responses to these simple stimuli are considered first. Then, the encoding of information in more realistic sounds that are made up of more than one tone, or so-called complex sounds, is presented. The representation of complex sounds in the auditory system is not related in a simple way to the representation of pure tones because the auditory system is not linear. Complex sounds that are discussed include sounds with noise maskers and amplitude-modulated sounds. The other major dimension of sound is its spatial location; this chapter concludes with a discussion of the physiology of spatial hearing.

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Because a large body of literature in this field is based on experimental work in different species, some introduction to the general structure of the auditory pathway across species is provided. Although space does not allow a comprehensive overview of the comparative anatomy, interesting specializations in a few species are pointed out, as these often play a role in the interpretation of physiological results. Comprehensive reviews of comparative anatomy and physiology of the auditory system have been provided by Manley (1990) and Popper and Fay (1980). In this review, description is limited to species with an auditory periphery that is characterized by a basilar membrane or papilla, which includes mammals, birds, and reptiles (Manley, 1990).

THE AUDITORY PERIPHERY

External and Middle Ears

In the auditory periphery, sound is transduced from mechanical energy (sound pressure) into a neural signal, resulting in a pattern of neural activity in the fibers of the auditory nerve (Figure 9.1).

Sound reaches the ear as a pressure wave, having traveled through either air or water to reach the tympanic membrane, which serves to couple the pressure wave into motion of the bones of the middle ear, or the ossicles. The ossicles are coupled directly to the inner ear, and their motion is translated into a pressure wave in the fluid-filled inner ear. The efficiency with which energy in the environment is transmitted from one part of the ear to

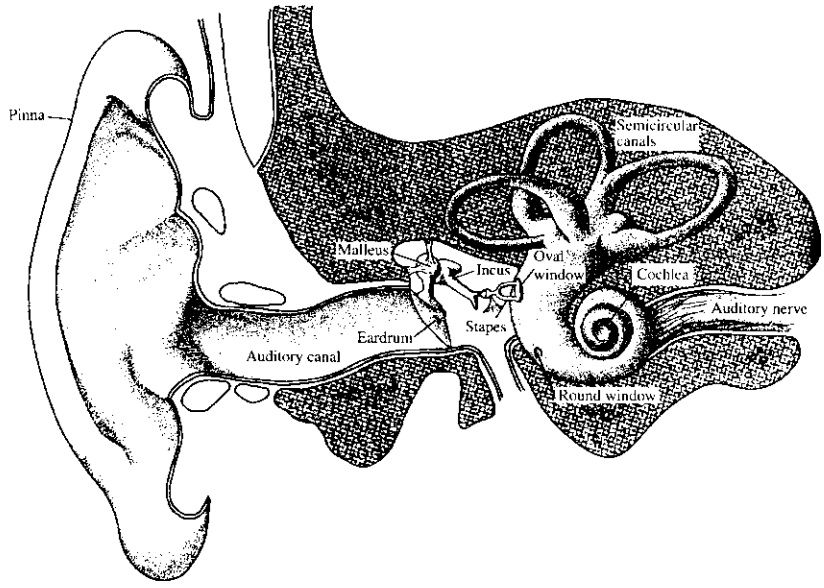

Figure 9.1 Drawing of the peripheral auditory system in human.
NOTE: The external ear consists of the pinna and auditory canal. The middle ear is the air-filled space between the tympanic membrane (eardrum) and the inner ear (cochlea); the motion of the tympanic membrane is coupled to the inner ear by three small bones, the ossicles (malleus, incus, and stapes). The primary afferent fibers of the auditory nerve each innervate a single sensory receptor cell located at a place along the cochlea.
SOURCE: Figure from *Human Information Processing: An Introduction to Psychology,* Second Edition by Peter Lindsay and Donald Norman. Copyright © 1977 by Harcourt College Publishers. Reproduced by permission of the publisher.

the next, before it is finally transduced into a neural signal, depends on the matching of the acoustical impedances at each interface between media and tissues (i.e., the difference in acoustical properties between air and cochlear fluid presents an impedance mismatch). Thus, the middle ear is often described in terms of the degree to which it successfully matches the radiation and input impedances. The lever action of the ossicles and the ratio of the sizes of the tympanic membrane and the oval window contribute to the middle ear's ability to match these impedances. A perfect match would result in optimal transfer of energy. The radiation impedance (the acoustic impedance looking outward from just outside the tympanic membrane) is dominated by the external ear and the atmosphere through which the sound travels. The input impedance (the acoustic impedance looking inward from just outside the tympanic membrane) is dominated by the properties of the middle and inner ears (Hemila, Nummela, & Rueter, 1995; Peake & Rosowski, 1991; Rosowski, 1996).

The sound waves that reach the two ears are influenced by many factors, including the acoustical environment (e.g., nearby surfaces or objects that may reflect, refract, or absorb the sound waves), as well as by the presence of the head and torso. The physical and acoustical properties of the external and middle ears differ dramatically from species to species (mammals: Huang, Rosowski, & Peake, 2000; birds and reptiles: Manley, 1990). For example, the mammalian middle ear is characterized by three ossicles forming a chain between the tympanic membrane and the cochlea, whereas the middle ear of birds and reptiles contains a single ossicle (Manley, 1990). The mechanical and acoustical properties of the auditory periphery influence the sound that reaches the inner ear and play an important role in determining the frequency range and sensitivity of hearing (for a review of external and middle ear function, see Rosowski, 1996).

The Inner Ear

The mechanical properties of the inner ear further shape the detailed properties of the effective stimulus for each neural element in the auditory periphery. The cochlea is often described as performing a mechanical frequency analysis that results in a sharply tuned and very sensitive input to the neural transduction elements, or hair cells. The mechanical resonant frequency of the basilar membrane changes systematically along the length of the cochlea because of a combination of systematic gradients of the stiffness, structural dimensions, and tissue properties along the length of the basilar membrane (Figure 9.2; von Békésy & Rosenblith, 1951;

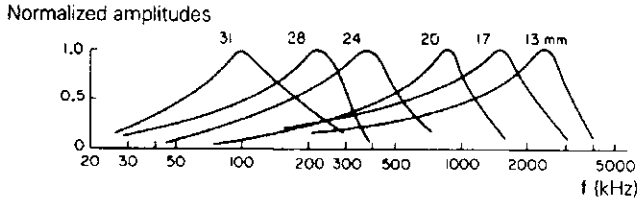

Figure 9.2 Illustration of the response amplitudes of six places along the length of the cochlea (location identified by numbers at top) to tones at different frequencies.
NOTE: Each place along the cochlea is tuned, or most responsive, to a particular frequency. This frequency tuning is a result of systematic changes in the mechanical properties of the cochlea along its length.
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von Békésy, 1960; Naidu & Mountain, 1998). Von Békésy's influential studies of basilar membrane motion date to 1942, when he first used stroboscopic illumination of the cochlea in the human cadaver in response to extremely high level stimuli (approximately 140 dB SPL). Since then, improved techniques have allowed measurements at lower sound levels, and these have transformed our understanding of the mechanics of the cochlea (e.g., Rhode, 1971; Ruggero, Rich, Recio, Narayan, & Robles, 1997; reviews by Zwislocki, 1986; de Boer, 1991; Ruggero, 1992b).

A pure-tone stimulus causes a maximal mechanical vibration at the place along the cochlear partition that is tuned to the stimulus frequency, as well as a spread of excitation to neighboring areas, depending on the sound level of the tone. In the mammalian cochlea, the pattern of excitation, or vibration, in response to a stimulus propagates along the length of the spiral-shaped cochlea in what is referred to as the traveling wave (von Békésy, 1960; Johnstone et al., 1986; de Boer, 1991). Figure 9.3 illustrates a cross-section of one turn of the spiral-shaped mammalian inner ear. The vibration of the cochlear partition results in excitation of the hair cells, whose stereocilia are deflected by means of the shear forces set up by the relative motion of the basilar membrane and tectorial membrane (reviewed by de Boer, 1991; Ruggero, 1992b).

There are two types of hair cells in the mammalian ear (Figure 9.4). The inner hair cells (IHCs) provide the major afferent input to the brainstem via the type I auditory-nerve (AN) fibers, which make up approximately 95% of the auditory nerve (reviewed by Ryugo, 1992). (See Table 9.1 for list of abbreviations used in the text.) The outer hair cells (OHCs), which are larger and outnumber the inner hair cells by a 3:1 ratio, are contacted by the relatively small number of type II AN fibers (5% of AN fibers; Ryugo, 1992). OHCs

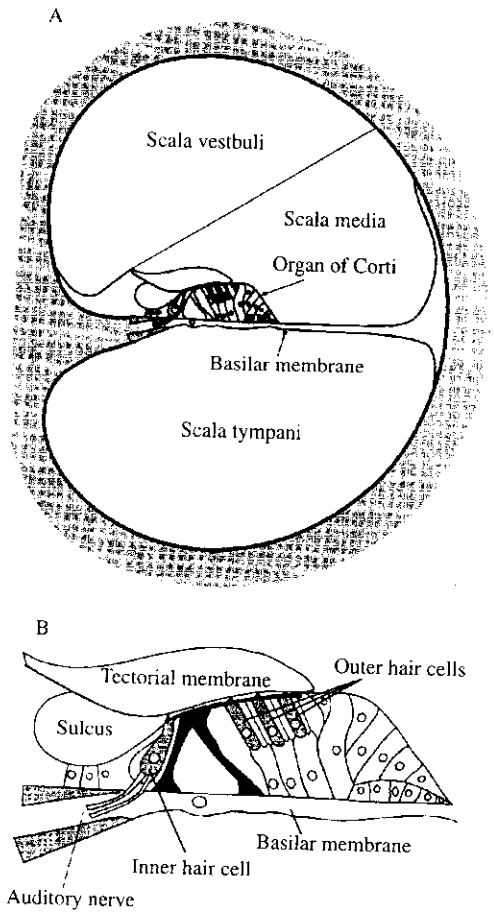

Figure 9.3 Schematic diagram of the key structures in the mammalian inner ear.
NOTE: A) Cross section of the cochlea shows the three major fluid-filled chambers, or scalae, and the organ of Corti, which lies on top of the basilar membrane. B) The organ of Corti includes the inner and outer hair cells, a large number of supporting cells and tissues, and the gelatinous tectorial membrane that overlies the stereocilia of the hair cells.
SOURCE: Reprinted from *Trends in Neurosciences, 15*, G. K. Yates, B. M. Johnstone, R. B. Patuzzi, & D. Robertson, "Mechanical preprocessing in the mammalian cochlea," pp. 57–61. Copyright © 1992, with permission from Elsevier Science.

are thought to be involved primarily in modifying the mechanical response of the basilar membrane itself (discussed later). It has become clear in recent years that essentially all major features of the responses of mammalian

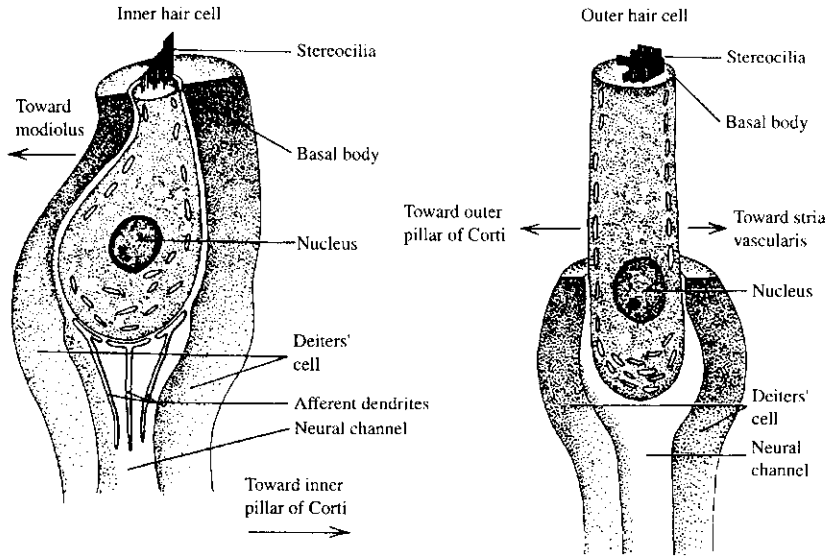

Figure 9.4 Drawing of the major features of mammalian inner and outer hair cells.
SOURCE: From *Hearing: Physiology and Psychophysics* by W. Lawrence Gulick, R. Frisina, & G. Gescheider, copyright © 1971 by Oxford University Press, Inc. Used by permission of Oxford University Press, Inc.

AN fibers (e.g., the sharpness of tuning, sensitivity, and nonlinear response features such as compression and two-tone suppression) can be observed in mechanical responses of the cochlea (e.g., Ruggero, Robles, & Rich, 1992; Cooper, 1996).

In nonmammalian species, frequency analysis in the inner ear takes advantage of different mechanical and electrical mechanisms (reviewed by Fettiplace & Fuchs, 1999). The ultimate result of this analysis, as in the mammalian cochlea, is that individual hair cells and the AN fibers that innervate them are tuned in frequency. However, the mechanisms by which this tuning is achieved vary significantly. For example, in the ear of the alligator lizard, systematic differences in length of the stereocilia result in different passive resonant frequencies along the length of the basilar papilla (Freeman & Weiss, 1990). In the turtle cochlea, electrical resonances set up by different ionic conductances through the hair cells contribute to frequency tuning (Crawford & Fettiplace, 1981; Art, Crawford, & Fettiplace, 1986).

The sensory hair cells (Figure 9.4) transduce mechanical vibration into an electrical signal, the receptor potential, by means of transduction channels associated with the stereocilia (reviewed by Fettiplace & Fuchs, 1999). The mechanisms by which motion of the basilar membrane, the surrounding fluids and tissues, or both results in the motion of the stereocilia of the hair cells differs from species to species, and in some cases from region to region within the ear (depending upon the presence of accessory structures, such as the tectorial membrane, shown in Figure 9.3, or tectorial sallets, reviewed by Manley, 1990, and Fettiplace & Fuchs, 1999). A common property of hair-cell transduction is a receptor potential consisting of both AC and DC components. At low frequencies (below about 1000 Hz, as discussed later), the AC component dominates and the receptor potential follows the fine temporal details of the

Table 9.1 List of Abbreviations

Anatomical Terms	
AN	auditory nerve
IHC	inner hair cell
OHC	outer hair cell
CN	cochlear nuclear complex
AVCN	anteroventral cochlear nucleus
PVCN	posteroventral cochlear nucleus
DCN	dorsal cochlear nucleus
NM	nucleus magnocellularis
NA	nucleus angularis
SOC	superior olivary complex
MSO	medial superior olive
LSO	lateral superior olive
TB	trapezoid body
MNTB	medial nucleus of the trapezoid body
LNTB	lateral nucleus of the trapezoid body
VNTB	ventral nucleus of the trapezoid body
NL	nucleus laminaris
SON	superior olivary nucleus
COCB	crossed olivocochlear bundle
LL	lateral lemniscus
VNLL	ventral nucleus of the lateral lemniscus
DNLL	dorsal nucleus of the lateral lemniscus
INLL	intermediate nucleus of the lateral lemniscus
IC	inferior colliculus
ICC	central nucleus of the inferior calculus
LN or lCx	lateral nucleus, or external nucleus, of the inferior calculus
DN	dorsomedial nucleus of inferior calculus
SC	superior colliculus
MGB	medial geniculate body
Auditory Cortex	
AI	primary auditory cortex
AII	secondary auditory cortex
EP	posterior ectosylvian region
SS	suprasylvian fringe
A or AAF	anterior field
P	posterior field
V	ventral field
VP	ventralposterior field
Periolivary regions	
VNTB	ventral nucleus of the trapezoid body
AVPO	anteroventral periolivary nucleus
ALPO	anterior lateral periolivary nucleus
DPO	dorsal periolivary nucleus
PPO	posterior periolivary nucleus
DMPO	dorsomedial periolivary nucleus
Stimulus-related Terms	
dB SPL	decibels sound pressure level
ITD	interaural time difference
ILD	interaural level difference
HRTF	head-related transfer function
AM	amplitude modulated
Physiological Terms	
CF	characteristic frequency
SR	spontaneous rate
PST	peri-stimulus time histogram
EE	cells that are excited by stimuli delivered to either ear
IE	cells that are inhibited by stimuli to the contralateral ear and excited by stimuli to the ipsilateral ear
EI	cells that are inhibited by stimuli to the ipsilateral ear and excited by stimuli to the contralateral ear
MTF	modulation transfer function

stimulus waveform. At higher frequencies, the low-pass filtering introduced by the capacitance and resistance associated with the hair-cell membrane attenuate the AC component, and the DC component dominates, resulting in a response to the envelope of the sound (e.g., Palmer & Russell, 1986).

The sensitivity and frequency tuning in the mammalian ear are not caused simply by passive mechanics of the inner ear but are strongly influenced by what has been called an active process or "cochlear amplifier" (Davis, 1983), which refers to an enhancement of the mechanical response of the inner ear. Responses of the healthy basilar membrane to a low-level sound input are larger in amplitude, because of this enhancement or amplification, than are responses of the ear in the presence of ototoxic drugs (which block transduction by the hair cells) or after death (e.g., Ruggero & Rich, 1991). Although the details of the neural, electrical, and mechanical mechanisms by which this amplification occurs are not completely understood, there is a body of evidence suggesting that in mammals the OHCs are involved, possibly by means of length changes of these cells in response to sound (Figure 9.5; first reported by Brownell, Bader, Bertrand, & de Ribaupierre, 1985; see the review by Yates, Johnstone, Patuzzi, & Robertson, 1992). The length changes of the OHCs are believed to provide forces that enhance (or "amplify") the mechanical vibration on a cycle-by-cycle basis (Dallos & Evans, 1995; Frank, Hemmert, & Gummer, 1999; reviewed by Ashmore & Geleoc, 1999). A protein that is abundant in the membranes of OHCs has recently been proposed to be the motor protein associated with OHC motility (Zheng et al., 2000). An alternative mechanism for OHC motility based on membrane biophysics (flexoelectricity) has also been recently proposed (Raphael, Popel, & Brownell, 2000). Further, an alternative mechanism for the cochlear amplifier based on active movements of the OHC stereocilia, rather than on length changes of the cell body, has also been proposed (reviewed by Yates, 1995).

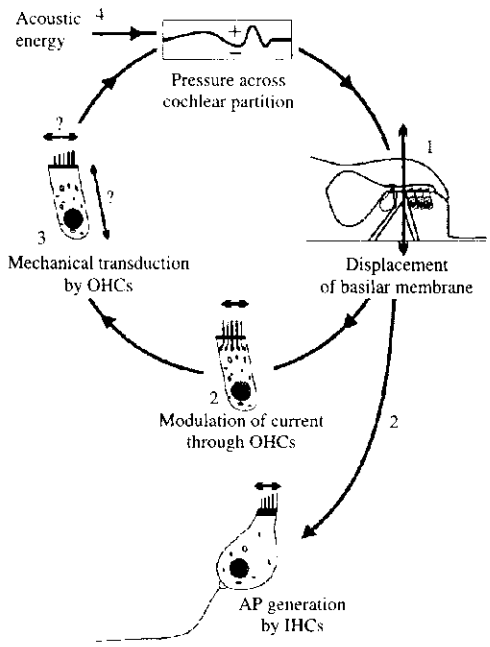

Figure 9.5 How the motile response or active process is thought to operate as a positive feedback loop within the cochlea.

NOTE: (1) Acoustic stimulation produces pressure fluctuations in scala vestibuli, causing the basilar membrane to vibrate. (2) The resulting shearing between the tectorial membrane and the tops of the hair cells modulates the standing current, driven by a K^+ electrochemical gradient. (3) The resulting receptor potential within the outer hair cells triggers the active process, causing some form of mechanical activity in the outer hair cell. (4) This in turn feeds pressure fluctuations back into the scala vestibuli to complete the loop. The receptor potential within the hair cell leads to transmitter release across the afferent synapse.

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It is worth noting that species that do not have OHCs also exhibit an active process in the inner ear (Manley & Koppl, 1998).

There appear to be a number of different electrical, mechanical, and molecular mechanisms involved in the sensitive responses of the inner ear to sounds that vary across and within species, as well as across frequency (e.g., active motion of stereocilia: Crawford & Fettiplace, 1985; Martin & Hudspeth, 1999; molecular aspects of electrical tuning in the turtle: Ricci, Gray-Keller, & Fettiplace, 2000; reviewed by Fettiplace & Fuchs, 1999).

The active process can be conceptualized as a level-dependent amplifier: It amplifies low-level sounds by up to 50 dB to 60 dB, and its amplification decreases at middle to high sound levels. It has been hypothesized that the amplification is driven by a mechanism that saturates, which would explain the systematic drop in amplification (often referred to as compression) as level increases (Mountain, Hubbard, & McMullen, 1983). Because the properties of the amplifier change with sound level, the overall response of the cochlea (and thus of the IHCs and AN fibers) is quite nonlinear; that is, responses to stimuli at one sound level do not necessarily provide a prediction of responses at other levels, and responses to simple stimuli do not provide predictions for complex sounds. In particular, the nonlinear properties of the inner ear cause complex interactions between components of sounds that are important for understanding physiological responses to complex sounds.

The active process is also associated with the generation of vibrations in the inner ear, which are then conducted back along the basilar partition and through the middle and outer ear, where they can be measured as acoustic signals in the ear canal (Kemp, 1978; reviewed by Lonsbury-Martin, Martin, McCoy, & Whitehead, 1995). These otoacoustic emissions may be spontaneous, or they may be evoked by auditory stimuli in an ear with a healthy auditory periphery. These emissions have been studied extensively as a tool for understanding cochlear function (e.g., Shera & Guinan, 1999), as well as for a noninvasive and objective diagnostic tool for audiologists.

The electrical, mechanical, and molecular basis of the active process, and the differences in mechanisms across species, is the topic of much current work. One goal of this research is to understand how the brains of different species achieve the exquisite sensitivity and discrimination ability that is generally believed to depend on the active process. In addition, the active process is typically described as a fragile process that is present in the healthy ear, and reduced or absent in the impaired ear (e.g., Patuzzi, Yates, & Johnstone, 1989). Thus, a better understanding of how the nonlinear properties of the active process influence the responses of the AN population should provide a better understanding of how the input to the central nervous system is altered in common forms of hearing impairment.

THE STRUCTURE OF THE AUDITORY PATHWAY

Ascending Pathways in the Central Nervous System

The auditory central nervous system is typically described in terms of ascending and descending pathways. Currently, much more is known about the ascending pathways than about the descending pathways. In general, the pathways of most species are characterized by a similar series of monaural, then binaural, nuclei along the ascending auditory pathway (Figure 9.6). Above the first level of binaural processing at the brainstem level, the anatomical and neurochemical pathways set up a general representation of acoustical stimuli arising from the contralateral hemifield on either side of the brain, as is true for the central representations of other sensory modalities.

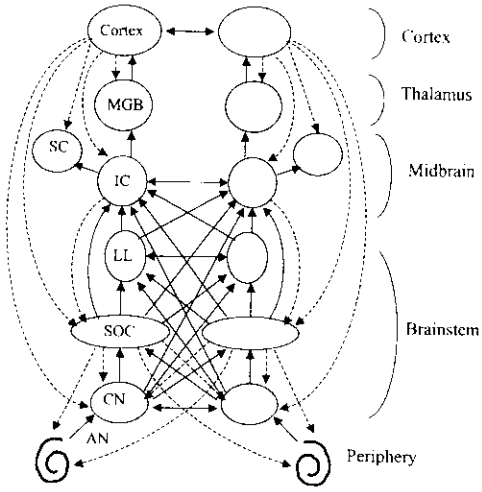

Figure 9.6 Schematic diagram of the mammalian auditory pathway showing the major ascending (solid arrows) and descending (dotted arrows) pathways.
NOTE: The details of the connections of individual nuclei are not shown, but rather the general scheme of connectivity across the two sides of the brain and across levels in the pathway. Abbreviations: auditory nerve (AN), cochlear nucleus (CN), superior olivary complex (SOC), lateral lemniscus (LL), inferior colliculus (IC), superior colliculus (SC), and medial geniculate body (MGB).

(Note that this is not strictly accurate for the auditory system because there are neurons with panoramic receptive fields, especially at the higher levels of the pathway.) The key features of each level along these pathways are briefly reviewed in the next sections.

First Level of Brainstem Processing

The first level of processing in all species is the projection of the auditory nerve to a brainstem region where distinct groups of cells receive excitatory inputs from AN fibers (Figure 9.7). In the mammal, this region is the cochlear nuclear (CN) complex, which consists of three regions: the anteroventral (AVCN), posteroventral (PVCN), and dorsal cochlear nuclei (DCN; reviewed by Cant, 1992). Each AN fiber bifurcates as it enters the CN and sends projections into all three regions of the CN (Figure 9.7). In general, there appear to be parallel representations of stimulus features in the responses of different cell groups in the CN (discussed later), and these cells project to different regions of the brainstem and midbrain (Figure 9.8).

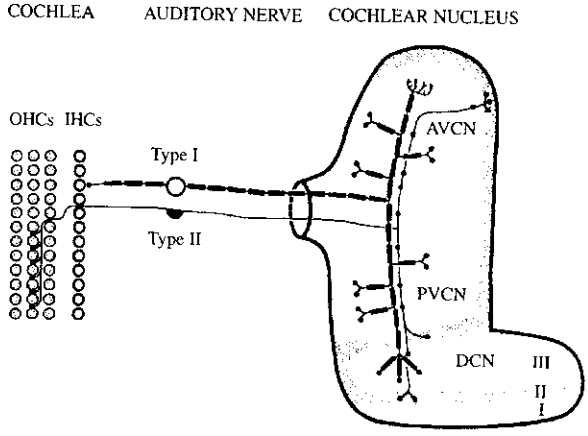

Figure 9.7 Schematic illustration of the projections of auditory nerve fibers in mammal showing their pattern of inputs from the inner and outer hair cells and the bifurcation of the AN fibers as they project into the cochlear nuclear complex.
SOURCE: From Ryugo (1992). Reprinted with permission.

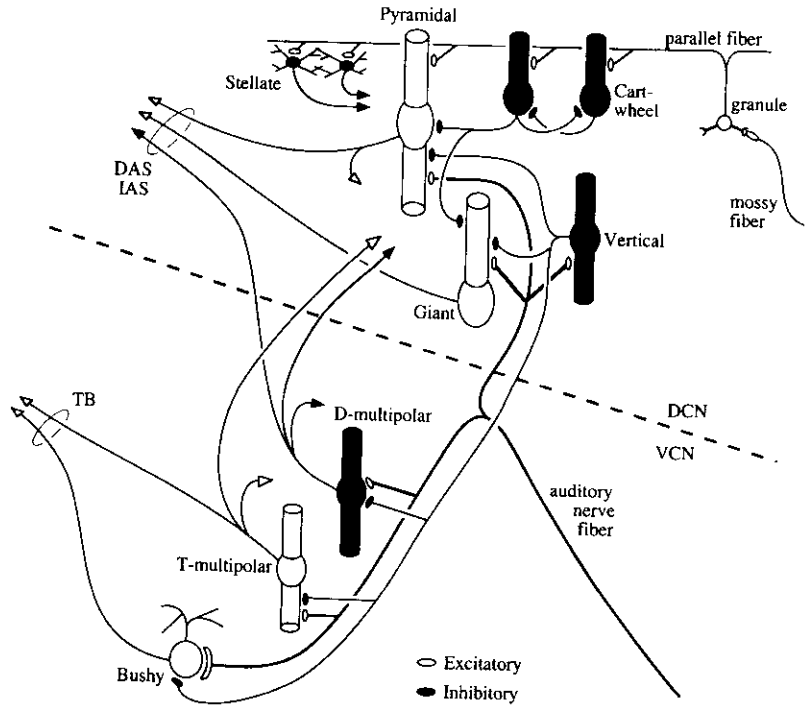

Figure 9.8 Schematic illustration of the major cell types in the cochlear nuclear complex in mammal and their primary projections.

NOTE: The VCN contains two major cell types: bushy cells, which send excitatory projections to the ipsilateral medial and lateral superior olives (MSO and LSO), and multipolar cells, which project to the inferior colliculus (IC) with collaterals to other brainstem and lemniscal nuclei. The DCN contains two major types of projection neurons, the pyramidal and giant cells, which project to the IC, and several types of interneurons, including cartwheel, vertical, stellate, and granule cells. The output pathways from the cochlear nucleus form three bundles, the trapezoid body (TB), which heads toward the superior olivary complex, and the dorsal (DAS) and intermediate (IAS) acoustic striae, which coarse through the lateral lemniscus toward the IC (reviewed by Osen, 1969; Harrison & Feldman, 1970; Osen & Mugnaini, 1981; Cant, 1992).

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The first level of processing in the brainstem is typically described as monaural, and responses are certainly dominated by the stimulus to the ipsilateral ear; however, connections between the two cochlear nuclei have been identified (e.g., Schofield & Cant 1996).

The avian brain, particularly that of the barn owl or chick, has also been a popular model for studies of binaural processing (reviewed by Knudsen, 1987; Takahashi, 1989). In avian species, the first level of brainstem processing occurs in two regions, the nucleus magnocellularis (NM) and the nucleus angularis (NA; Figure 9.9). NM cells have morphologies, connections, and response properties similar to that of the bushy cells in the mammalian AVCN, and the cells in NA are most similar to the stellate cells in the AVCN (e.g., Carr & Konishi, 1990; Hausler, Sullivan, Soares, & Carr, 1999; Sullivan, 1985; Warchol & Dallos, 1990).

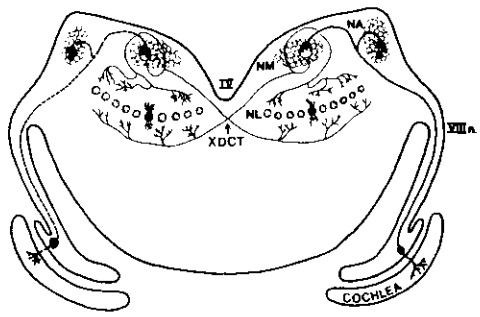

Figure 9.9 Anatomy of the chick brainstem illustrating the projections of the AN to the first level of brainstem processing, the nucleus magnocellularis and nucleus angularis.
NOTE: The nucleus magnocellularis in turn projects to the first major binaural brainstem region, the nucleus laminaris.
SOURCE: From Rubel, Born, Deitch, & Durham (1984).

Binaural Nuclei in the Brainstem

The first major binaural convergence takes place at the second stage of processing in the brainstem (Figure 9.6). There are two major binaural response types in the auditory brainstem: cells that are excited by stimuli delivered to either ear (EE), and those that are inhibited by stimuli to the contralateral ear and excited by stimuli to ipsilateral ear (IE). In the mammal the AVCN provides the major inputs to the first level of binaural processing, which occurs in the superior olivary complex (SOC; Figure 9.10; Cant & Casseday, 1986; Harrison & Feldman, 1970). The medial superior olive (MSO) receives inputs from the spherical bushy cells in both cochlear nuclei and is characterized by EE responses. The morphologies of the excitatory inputs from the contralateral side resemble delay lines (Beckius, Batra, & Oliver, 1999; Smith, Joris, & Yin, 1993), as was hypothesized in models for binaural hearing (Jeffress, 1948; discussed later). The lateral superior olive (LSO) receives excitatory inputs from spherical bushy cells in the ipsilateral cochlear nucleus and inhibitory inputs from the ipsilateral medial nucleus of the trapezoid body (MNTB) and is characterized by IE responses. The MNTB receives excitatory inputs from the contralateral AVCN. Although they are typically described as EE, cells in the MSO also receive inhibitory inputs from the ipsilateral lateral nucleus of the trapezoid body (LNTB; Cant & Hyson, 1992) and from the contralateral side, via the ipsilateral MNTB (Adams & Mugnaini, 1990). Furthermore, the LSO receives ipsilateral inhibition in addition to its classical IE inputs (Wu & Kelly, 1994). The SOC also contains a number of so-called periolivary regions (Figure 9.10) that are

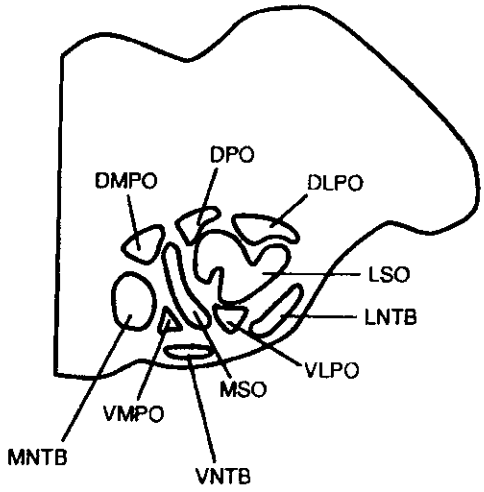

Figure 9.10 Drawing of a cross section of the mammalian brainstem at the level of the superior olivary complex (SOC).
NOTE: The three largest cell groups in this complex are the two major olivary nuclei, the medial superior olive (MSO) and lateral superior olive (LSO), and the medial nucleus of the trapezoid body (MNTB). Two other cell groups located in the trapezoid body (the bundle of fibers that arises in the cochlear nuclei) are the lateral and ventral nuclei of the trapezoid body (LNTB, VNTB). The major periolivary groups are shown: The dorsomedial, dorsal, and dorsolateral periolivary nuclei (DMPO, DPO and DLPO) span the dorsal extent of the SOC, and the ventromedial (VMPO) and ventrolateral (VLPO) periolivary nuclei lie ventral to the major nuclei in the SOC.
SOURCE: From Schwartz (1992). Reprinted with permission.

involved in both the ascending and (especially) in the descending pathways (discussed later; J. K. Moore, 1987; reviewed by Schwartz, 1992).

In the avian brainstem, the first primary site of binaural interaction is the nucleus laminaris (NL), which receives excitatory inputs from both sides of the brainstem. The inputs from the contralateral side have morphologies that resemble delay lines (Carr & Konishi, 1990; Overholt, Rubel, & Hyson, 1992). The NL is often described as a homologue to the mammalian MSO. Like the MSO, the NL receives not only binaural excitation but also inhibitory inputs from other cells in the brainstem (the avian superior olivary nucleus, or SON; Yang, Monsivais, & Rubel, 1999). The inhibitory inputs to the NL have been proposed to play a role in gain control for the binaural circuitry involved in spatial localization (Yang et al., 1999).

Nuclei of the Lateral Lemniscus

The major pathway for auditory nuclei from the brainstem to the midbrain is the lateral lemniscus (LL; Figure 9.11; reviewed by Schwartz, 1992). Two major cell groups lie in the LL: the ventral nucleus of the lateral lemniscus (VNLL) and the dorsal nucleus of the lateral lemniscus (DNLL). (An additional group, the intermediate nucleus of the lateral lemniscus, or INLL, has similar properties to and an indistinct boundary with the VNLL.) The VNLL is predominantly monaural, receiving inputs from spherical and globular bushy cells and octopus cells in the contralateral cochlear nucleus and the ipsilateral MNTB; the VNLL projects to the ipsilateral inferior colliculus and the medial geniculate body (Adams, 1997; Schofield & Cant, 1997). The DNLL is predominantly binaural, receiving bilateral inputs from the CN, LSO, MSO,

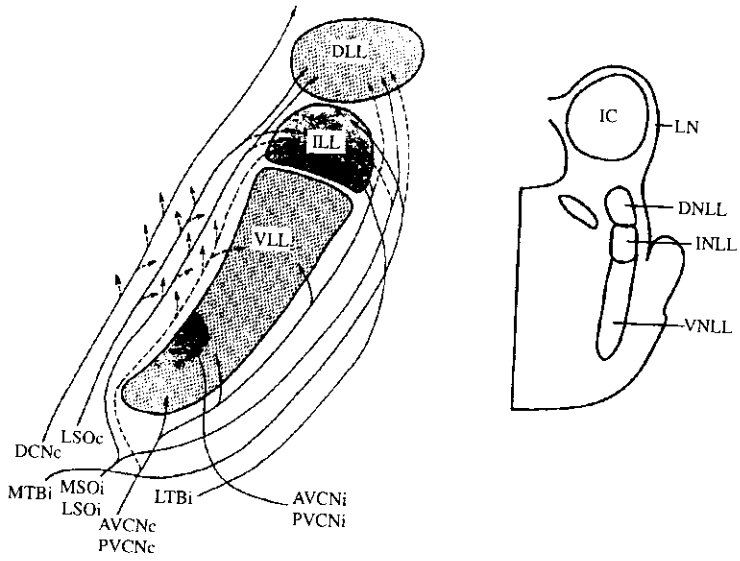

Figure 9.11 The nuclei of the lateral lemniscus, which lie along the major ascending pathway from the auditory brainstem to the auditory midbrain.
NOTE: The left-hand drawing shows the orientation and major inputs of the three lemniscal nuclei: the ventral, intermediate, and dorsal nuclei of the lateral lemniscus (VNLL, INLL, and DNLL). The right-hand drawing shows their orientation with respect to the inferior colliculus (IC) in the coronal plane.
SOURCE: From Schwartz (1992). Reprinted with permission.

and from the contralateral DNLL. The DNLL projects to both inferior colliculi, as well as to the contralateral DNLL (Kelly, 1997).

The Auditory Midbrain: Inferior Colliculus and Superior Colliculus

The next major level in the ascending pathway is in the midbrain of most species, where there is convergence of inputs from monaural brainstem regions, binaural nuclei, and the lemniscal nuclei. In mammals this midbrain region is the inferior colliculus (IC; Figure 9.12; reviewed by Oliver & Huerta, 1992); the homologous region in birds and reptiles is the torus semicircularis (G. E. Meredith, 1988). The pattern of inputs from the brainstem to the midbrain sets up the contralateral representation of auditory space, which predominates at all levels above the brainstem. A combination of crossed projections (which effectively convert EI responses—i.e., from cells that are excited by stimuli to the contralateral ear and inhibited by stimuli to the ipsilateral ear—to IE responses) and neurochemical sign changes (i.e., inhibitory projections to ipsilateral targets) is involved in this process, which is referred to as the acoustic chiasm (e.g., Glendenning, Baker, Hutson, & Masterton, 1992).

The main projections in the acoustic chiasm are as follows: The MSO, which is already dominated by stimuli in the contralateral field (Yin & Chan, 1990; discussed later), sends an excitatory projection to the ipsilateral IC. The high-frequency region of the LSO, which is IE, sends an excitatory projection to the contralateral IC; thus, high-frequency cells in the IC have EI responses and are excited by stimuli on the contralateral side. The low-frequency limb of the LSO is monaural and is excited by ipsilateral stimuli; this limb sends an inhibitory projection to the ipsilateral IC (Glendenning et al., 1992).

The IC has several divisions that are distinguished by different cell types and connections (Figure 9.12; Morest & Oliver, 1984;

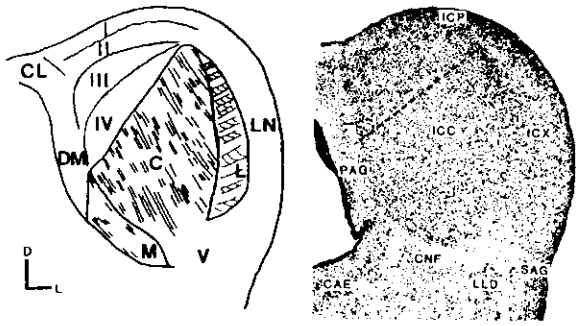

Figure 9.12 Drawings of coronal sections through the inferior colliculus in cat showing the two parceling schemes that have been proposed for the IC.

NOTE: The left-hand drawing shows the divisions of Morest & Oliver (1984). The central nucleus of the ICC is divided into several subdivisions: the pars centralis (C), pars medialis (M), pars lateralis (L), and pars ventralis (V). The dorsal cortex is indicated by the four layers, I–IV. Other labeled regions are the central nucleus of the commissure (CL), dorsomedial nucleus (DM), and lateral nucleus (LN). The right-hand drawing shows the traditional divisions (e.g., Rockel and Jones, 1973a, 1973b). Abbreviations: central nucleus (ICC), pericentral nucleus (ICP), external nucleus (ICX), periaqueductal gray (PAG), nucleus caeruleus (CAE), cuneiform nucleus (CNF), dorsal nucleus of lateral lemniscus (LLD), and sagulum (SAG).

SOURCE: Left-hand drawing from Oliver and Huerta (1992). Reprinted with permission. Right-hand drawing from Irvine (1986). Copyright ©1986 by Springer-Verlag. Reprinted with permission.

Rockel & Jones, 1973a, 1973b; reviewed by Oliver & Huerta, 1992). The largest region of the IC is the central nucleus, or ICC, which receives tonotopic inputs from the contralateral cochlear nucleus and the ipsilateral MSO and VNLL, and bilaterally from the LSO (discussed earlier) and DNLL. The ICC also receives a diffuse, nontonotopic input from the periolivary nuclei (Adams, 1983; Henkel & Spangler, 1983). The dorsal cortex of the IC (layers I–IV, based on cytoarchitecture; Figure 9.12) receives its major input from the auditory cortex (Morest & Oliver, 1984). The lateral nucleus (LN), or the external nucleus (ICx; Rockel & Jones, 1973b), receives inputs from the ICC as well as from a large number of other sources, such as somatosensory regions, the dorsal column nuclei, and possibly the auditory cortex (Oliver & Huerta, 1992). The dorsomedial nucleus (DN) receives inputs from the LL as well as the auditory cortex (Morest & Oliver, 1984).

There are two major ascending targets of the IC: One is the superior colliculus (SC), which integrates sensory and motor information and is involved in the control of reflexive movements of the eyes, pinnae, head, and body (Huerta & Harting, 1984). In birds and reptiles the homologous region is the optic tectum. The SC is a layered structure (Figure 9.13); the superficial layer has both inputs and outputs that are restricted to the visual system (Oliver & Huerta, 1992). The deep SC receives ascending auditory inputs from the IC, the dorsomedial periolivary nucleus, the nuclei of the trapezoid body, and the VNLL (Edwards, Ginsburg, Henkel, & Stein, 1979) and descending inputs from the auditory cortex (M. A. Meredith & Clemo, 1989). The somatosensory system also projects to the deep SC from the spinal cord, the dorsal column nuclei, trigeminal nuclei, and cortex. Topographic maps of the different modalities have been reported to be approximately in register with each other (discussed later; e.g., Middlebrooks & Knudsen, 1987; Stein, Magalhaes-Castro, & Kruger, 1976; Wise & Irvine, 1985).

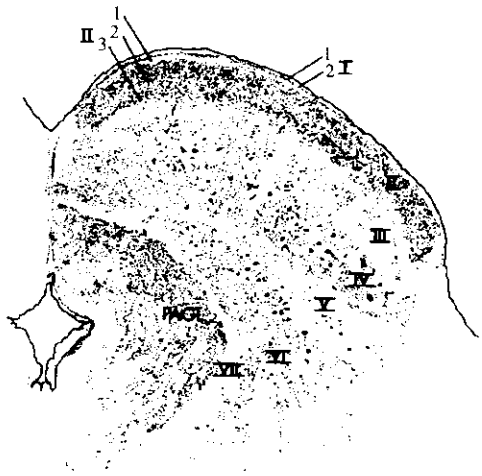

Figure 9.13 Cross section of the superior colliculus (SC) in cat.
NOTE: Layers I, II, and III comprise the superficial SC; layers IV–VII are the deep layers of the SC.
SOURCE: From Kanaseki & Sprague (1974). Reprinted by permission of McGraw-Hill.

Auditory Thalamus

The other major target of the IC is the auditory region of the thalamus. In mammals the auditory thalamus is the medial geniculate body (MGB); birds and reptiles also have auditory regions of thalamus, which are comparable to the MGB in terms of their connectivity to auditory regions in the midbrain and telencephelon. The mammalian MGB has been parceled into two (Rioch, 1929; Rose & Woolsey, 1949) or three (Winer, 1992) regions, based on the anatomical properties of cells and fibers in the MGB, their connectivity to the auditory cortex, physiological properties, neuropharmacology, and development. The three regions in the more recent description are the ventral, dorsal, and medial divisions (Figure 9.14); the earlier parceling scheme grouped the ventral and dorsal divisions into a single division.

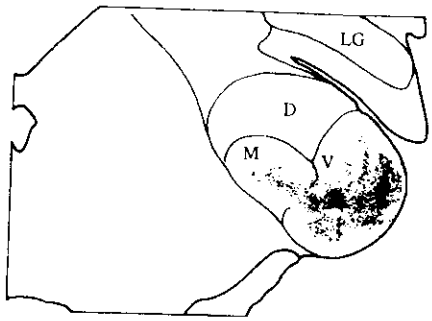

Figure 9.14 Coronal section through the medial geniculate body (MGB) in cat.
NOTE: The MGB is the auditory region of the mammalian thalamus. The three major divisions of the MGB are indicated: ventral (V), dorsal (D), and medial (M). The stippled areas represent regions that were labeled by an injection of tritiated leucine into the central nucleus of the IC. This labeling indicates locations in the MGB that receive inputs from the ICC.
SOURCE: From Kudo & Niimi (1980). Copyright © 1980 John Wiley & Sons, Inc. Reprinted by permission of McGraw-Hill.

The ventral division is a heterogeneous group of cells that receives its primary input from the ipsilateral ICC (R. A. Anderson, Knight, & Merzenich, 1980; Roullier & de Ribaupierre, 1985); this division receives input also from the thalamic reticular nucleus, a property common to the other sensory regions of the thalamus (reviewed by Winer, 1992; Rouiller, 1997). The dorsal division, also heterogeneous in terms of cellular morphologies, receives inputs from a vast number of auditory regions, including ICC, SC, and auditory cortex. The dorsal division receives inputs also from a number of nonauditory regions, including limbic areas, nonauditory areas of cortex, and regions of the basal ganglia, suggesting that this division plays a role in sensory-motor processing (reviewed by Winer, 1992). The medial division of the MGB is a heterogeneous group of cells that receives nontopographic input from diverse, predominantly nonauditory regions of the brainstem and midbrain.

The projections of the three divisions of MGB reflect the nature of their inputs. The ventral division has topographic and highly reciprocal connections with auditory cortex; the dorsal division has more diverse and less regular reciprocal connections with a wider range of cortical regions; and the medial division has a very diverse set of cortical targets, many of which are outside the classical auditory regions (see Winer, 1992, for a detailed review).

Auditory Cortex

The final stage in the ascending pathway is the projection from the thalamus to the cortex. The mammalian auditory cortex is typically described in terms of four major regions, which are distinguished by their physiological response properties and cytoarchitectures. Primary auditory cortex, AI, was the first to be described in terms of its tonotopic arrangement (Woolsey & Walzl, 1942). Rose (1949) described four regions of cortex based on cytoarchitecture: AI, AII, which is located ventral to AI, the posterior ectosylvian region (EP), and the suprasylvian fringe (ss; Figure 9.15). Rose and Woolsey (1949) also described the essential and orderly connectivity between auditory thalamus and area AI, with sustaining projections from the thalamus to the other cortical regions. Woolsey (1961) described complete tonotopic maps in each of these four central areas, plus an additional five peripheral regions.

Woolsey's map has been refined over time by additional mapping studies, but it has generally served as the standard map for subsequent studies (Goldstein & Knight, 1980). Detailed mapping studies have proposed that there are regions in the band around AI that also contain tonotopic maps, receive thalamic input, and have sharply tuned neurons (e.g., Reale & Imig, 1980). Thus, the auditory cortex cannot be thought of as one primary tonotopically mapped region (AI) that

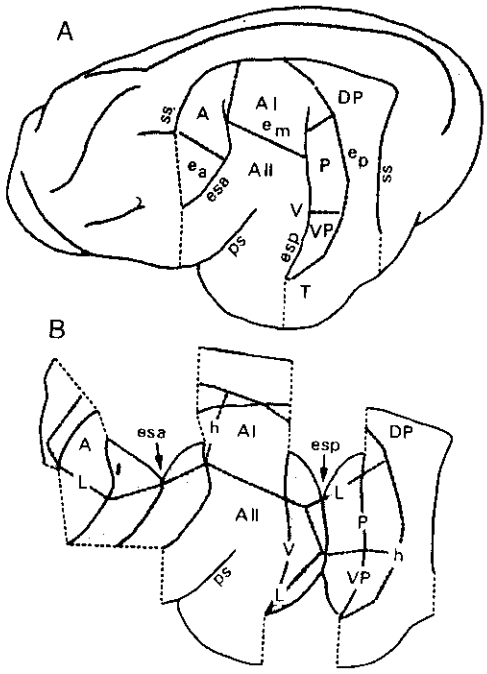

Figure 9.15 Major areas of the auditory cortex. NOTE: A) Drawing of the auditory cortex in cats showing the location of the auditory areas (left temporal cortex is shown). Four regions have clear tonotopic arrangements: anterior, primary, posterior, and ventral posterior areas (A, AI, P, VP). Other abbreviations: suprasylvian fissure (ss); anterior, medial, and posterior ectosylvian gyrus (e_a, e_m, e_p); anterior and posterior ectosylvian (esa, esp); dorsal posterior, temporal, ventral and secondary areas (DP, T, V, AII). B) "Flattened" representation of the cortical regions, showing the areas that lie within the fissures (shown in gray). The tonotopic arrangements of the major areas are indicated by "L" for low-frequency regions, and "h" for high-frequency regions.
SOURCE: From Buser & Imbert (1992), after Reale & Imig (1980). Copyright © 1980 by the MIT Press. Reprinted with permission.

then projects to other regions for higher processing (Goldstein & Knight, 1980).

A detailed review of the cytoarchitecture and neurochemistry associated with each of the cortical layers of the different regions of auditory cortex is provided by Winer (1992). The layered structure of the auditory cortex is generally similar to that of other sensory cortical regions, despite the fact that the basic pattern of connectivity of the auditory cortex differs significantly from that of other sensory areas, especially in terms of the interconnections between auditory fields and hemispheres (reviewed by Winer, 1992; Rouiller, 1997). Detailed descriptions of the laminar sources of input—as well as targets of projections—for AI are available but are not described here (reviewed by Winer, 1992).

Descending Pathways

The ascending pathways describe only half of the auditory nervous system. Although much less is known about the descending pathways, they have received increasing attention in recent years. The bias toward study of the ascending system stems probably from the fact that responses at higher levels of the auditory pathway, and thus the descending signals, are increasingly sensitive to anesthesia. Work in awake, and in some cases behaving, animals may be necessary to understand the interplay between ascending and descending systems. The descending pathways are implicated in a diverse set of roles, including attention, gating of ascending signals, modulation of intensity and frequency selectivity, spatial localization, and protection of the auditory periphery (see reviews by Huffman & Henson, 1990; Rouiller, 1997; Spangler & Warr, 1991).

Several anatomical studies have mapped out the substrate for the descending system. The classic studies of Rose and Woolsey (1949) mapped out the corticothalamic projections, which largely reflect the thalamocortical pattern of connectivity (discussed earlier; reviewed by Winer, 1992). Nearly all fields in the auditory cortex (except A, P, and VP) have strong projections from layer V (Kelly & Wong, 1981) to more than one area of the inferior colliculus; these cortical inputs do not terminate in the central

nucleus of the IC (except possibly from AII; Diamond, Jones, & Powell, 1969) but rather target the paracentral regions, such as LN (also referred to as the external nucleus; discussed earlier; Aitkin, Dickhaus, Schult, & Zimmerman, 1978). Auditory cortical fields also project to several other regions, including superior colliculus (M. A. Meredith & Clemo, 1989), cochlear nucleus (Feliciano, Saldaña, & Mugnaini, 1995; Weedman & Ryugo, 1996), pons, basal ganglia, and limbic regions (reviewed by Harrison & Howe, 1974; Huffman & Henson, 1990; Rouiller, 1997; Winer, 1992). The MGB does not play a significant role in the descending pathway; although it receives a strong ascending projection from the IC (discussed earlier), its projections are primarily to auditory cortex, which then projects directly down to the level of the IC.

The IC has a large number of descending projections to the superior olivary complex, primarily to the periolivary regions, which have descending projections to the cochlear nuclei. The two periolivary regions that receive the strongest collicular inputs are the ventral nucleus of the trapezoid body (VNTB) and anteroventral periolivary nucleus (AVPO); these regions project to all three regions of both contralateral and ipsilateral cochlear nuclei (Schofield & Cant, 1999). The IC also projects directly to the dorsal cochlear nucleus and granule cell area of the CN (Saldaña, 1993).

The periolivary nuclei of the SOC send a large number of projections to the cochlear nuclei. The lateral/dorsal periolivary regions (anterior lateral (ALPO), dorsal (DPO), posterior (PPO), and lateral nucleus of the trapezoid body (LNTB) have a strong projection to the ipsilateral CN, and a relatively weak projection to contralateral CN (Spangler, Cant, Henkel, Farley, and Warr, 1987). The medial regions (dorsomedial periolivary region, or DMPO, and the medial and ventral nuclei of the trapezoid body, or MNTB and VNTB, respectively) project more strongly to the contralateral than to ipsilateral CN (Spangler et al., 1987). The terminals of these projections are widespread throughout the regions of the CN, and they are tonotopic in some cases (Spangler et al., 1987).

The descending pathway extends to the cochlea. Two systems of fibers project from the periolivary regions of the superior olive to the cochlea, where they synapse directly on the OHCs or on the AN fibers underneath the IHCs (reviewed by Warr, Guinan, & White, 1986; Warr, 1992). The two olivocochlear systems are illustrated in Figure 9.16. The lateral olivocochlear neurons arise from lateral periolivary regions and project mainly to the IHC region of the ipsilateral cochlea. The medial olivocochlear system arises from medial periolivary regions and projects mainly to the OHCs of the contralateral cochlea (reviewed by Warr et al., 1986; Warr, 1992).

Comparison of Brainstem Regions across Species

Several interesting species have auditory specializations that are apparent in the anatomy of the auditory periphery, central pathway, or both (Figure 9.17; Glendenning & Masterton, 1998; J. K. Moore & Moore, 1971). Animals that are most sensitive to or communicate with high-frequency sounds have correspondingly enlarged high-frequency brainstem nuclei (e.g., the MNTB and LSO). Animals that are most sensitive to or communicate with low-frequency sounds have larger MSOs. For example, extreme biases in the anatomy are seen for echo-locating bats, which have a magnified region in their tonotopic maps, beginning in the inner ear and persisting at higher levels of the auditory pathway, that is tuned to the frequencies that dominate their vocalizations and thus their echoes (reviewed by Simmons et al., 1996). Also note that the

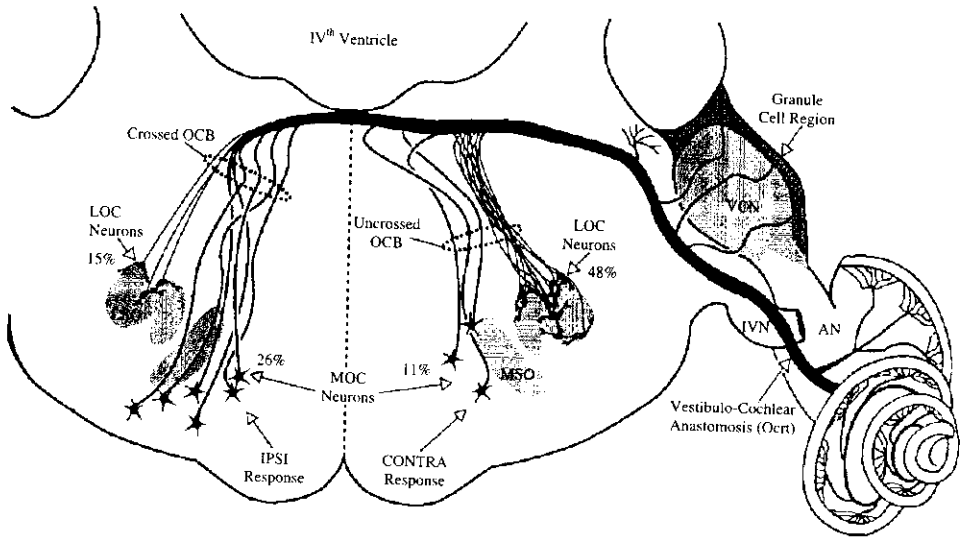

Figure 9.16 Major projections associated with the olivocochlear system, which arises from cells groups in the periolivary regions of the superior olivary complex and projects directly to the cochlea.
NOTE: The olivocochlear bundles (OCB) comprise two subsystems: the medial olivocochlear (MOC) and lateral olivocochlear (LOC) systems.
SOURCE: From Warr (1992). Reprinted by permission of McGraw-Hill.

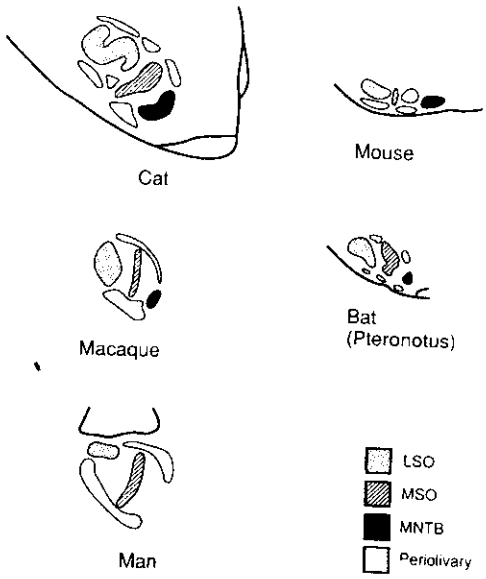

Figure 9.17 Diagram of typical cross sections through the brainstem for several different species, showing the relative sizes of different regions.
SOURCE: From Schwartz (1992). Reprinted with permission. Cat, mouse, monkey, and human data are from J. K. Moore & Moore (1971). Bat drawing based on Zook & Casseday (1982).

human brainstem has no MNTB and a relatively small LSO; although researchers have identified a few cells that have characteristics similar to those of the MNTB, they are not organized into a well-defined nucleus in human (Richter, Norris, Fullerton, Levine, & Kiang, 1983). These variations in the basic structure of the auditory pathways must be kept in mind when generalizing physiological results across species, for example, to relate physiology in nonhuman species to psychoacoustical performance in humans.

ACOUSTIC STIMULI

Before reviewing physiological responses, this section briefly reviews the units of measurement and important parameters of acoustic stimuli. Sounds can be either simple stimuli, which consist of a sinusoid (or tone) at a single frequency, or complex stimuli, which refer to all other sounds. Simple stimuli can be described completely in terms of

their frequency, amplitude, and starting phase, as well as duration and onset/offset ramp shapes. Complex sounds can be represented as combinations of multiple sinusoids of different frequencies by using the Fourier transform. Descriptions of complex sounds must contain the amplitudes and phases of all component frequencies (i.e., the spectral magnitudes and phases), in addition to duration and onset/offset ramp shapes.

Sound waves are pressures that propagate through a medium, typically air or water. (Note that sound can also be conducted by bone or other solid materials.) The amplitudes of acoustic stimuli are typically measured as sound pressure in units of Pascals (1 Pa = 1 Newton of force per square meter of area) or as intensity in units of Watts. Logarithmic units are typically used to describe sound amplitudes because the auditory system is sensitive to changes in stimuli over a wide range of amplitudes and because log units seem to provide a representation that makes sense in terms of many physiological and psychophysical response properties. The standard reference pressure that is used for acoustic stimuli is 20 μPa, which is approximately the threshold of hearing at 1000 Hz for human listeners (Sivian & White, 1933). Sounds represented in terms of dB SPL (sound pressure level) are referenced to this standard pressure; that is, the level in dB SPL = 20 log(P/P_0), where P_0 is 20 μPa. Note that the amplitude of air particle motion associated with sounds at the threshold of hearing is similar to the dimensions of a hydrogen atom.

The description of stimuli in three-dimensional space requires additional parameters, and these parameters are of interest in experiments that explore binaural processing (such as how the information that arrives to the two ears is combined to improve detection of signals in a noisy environment) and sound localization. The physical dimensions of sounds that arrive at the two ears differ because of the different path lengths from a sound source to the ears located on each side of the head and because of the presence of the head between the two ears. There are three major cues for binaural processing: (a) differences in time between the stimuli to the two ears (both at the onset of a stimulus and during ongoing differences in the phases of the two stimuli due to a delay to one side), (b) differences in the sound levels at the two ears due to different distances to the target from the two ears as well as to head-shadowing effects, and (c) spectral cues introduced by the anatomical structure of the external ear that are sensitive to the angle of incidence of the sound.

The importance of each cue for binaural processing varies according to the stimulus frequency. At low frequencies (below about 2000 Hz in humans) the size of the head is small compared to a wavelength of the stimulus, so the presence of the head does not have a large effect on the propagation of sound waves. Therefore, at low frequencies the predominant binaural cue is simply the difference in arrival time of sounds to the two ears, or interaural time difference (ITD), which is caused primarily by the different distances to the two ears from sources located at nonzero azimuths (zero azimuth conventionally refers to the location straight ahead). At high frequencies, the size of the head is large with respect to the wavelength of sound, and head-shadow effects are significant. The head-shadow effect refers to the increase in pressure caused by reflection of sound from the side of the head nearer to the source, in addition to the reduction in pressure at the side of the head that is farthest from the source. Both of these effects contribute to significant interaural level differences (ILDs) for sounds that are located at nonzero azimuths.

These differences in the physical cues that dominate at low and high frequencies are reflected in both physiology and psychophysics.

For example, at low frequencies the phase differences of sounds arriving at the two ears from different locations are well encoded by the temporal response properties of auditory neurons, whereas at high frequencies fine temporal details of pure tone stimuli are not as well encoded (discussed later). Psychophysically, localization of pure tones is relatively good at low frequencies (below approximately 1500 Hz), relatively poor at middle frequencies (approximately 2000 Hz), and relatively good at higher frequencies (e.g., Mills, 1972; reviewed by Blauert, 1997; Durlach & Colburn, 1978). The different cues and mechanisms that dominate at different frequencies have led to what is called the duplex theory of sound localization (Lord Rayleigh, 1907; reviewed by Kuhn, 1987; physiological aspects reviewed by Kuwada & Yin, 1987). Note that complex sounds are typically rich in combinations of dynamic temporal and level cues across all frequencies, so it is not reasonable, for example, to ignore temporal information when considering the encoding of high-frequency complex sounds.

The third type of cue for localization is the so-called spectral cue, which refers to the complex spectral shapes that are associated with sounds arriving from different angles of incidence (Figure 9.18). Spectral cues are often described by head-related transfer functions (HRTFs), which show the effect of the reflections in the pinna and ear canal as a function of frequency (e.g., Batteau, 1967; Blauert, 1969; reviewed by Blauert, 1997; Kuhn, 1987; Shaw, 1982). The reflections in the pinna that result in spectral cues essentially impose these spectral shapes upon the spectrum of the acoustic source. (Note that the strong notches and peaks associated with spectral cues are at high frequencies, so they do not interfere with the low-frequency spectrum of sounds.) Spectral cues are relevant only for complex sounds because the relative amplitudes and phases across a range of frequencies must be interpreted in order to use this cue. These cues are particularly significant for stimuli that vary in position along the vertical meridian (the plane that bisects the head along the saggital plane) for which there are essentially no ITD or ILD cues because of the head's symmetry.

ENCODING OF PURE TONES ALONG THE AUDITORY PATHWAY

The acoustic stimulus employed in most physiological experiments has been the pure tone. Many basic response properties can be characterized with pure tones, and responses of neurons at different levels along the pathways can be compared. However, because the auditory periphery and subsequent neural processing mechanisms are highly nonlinear, responses to pure tones do not typically provide accurate predictions for responses to more complex stimuli. Therefore, responses to several different complex stimuli are discussed separately.

Responses of auditory neurons can be described in terms of discharge rate or in terms of temporal response patterns. In general, both aspects of the responses are involved in the encoding of both frequency and level. Discharge rate, usually measured as the average rate over the stimulus duration, plays a role in encoding both frequency and level, but only at relatively low levels; at middle to high levels, the discharge rate saturates for the majority (but not all) of auditory neurons. Discharge timing, which reflects the synchronization of discharge times to the temporal fluctuations of the stimulus, can provide information at very low sound levels (below the rate threshold for low frequencies) and also varies with sound level over a wide dynamic range because of the nonlinearity of the inner ear. The following sections describe

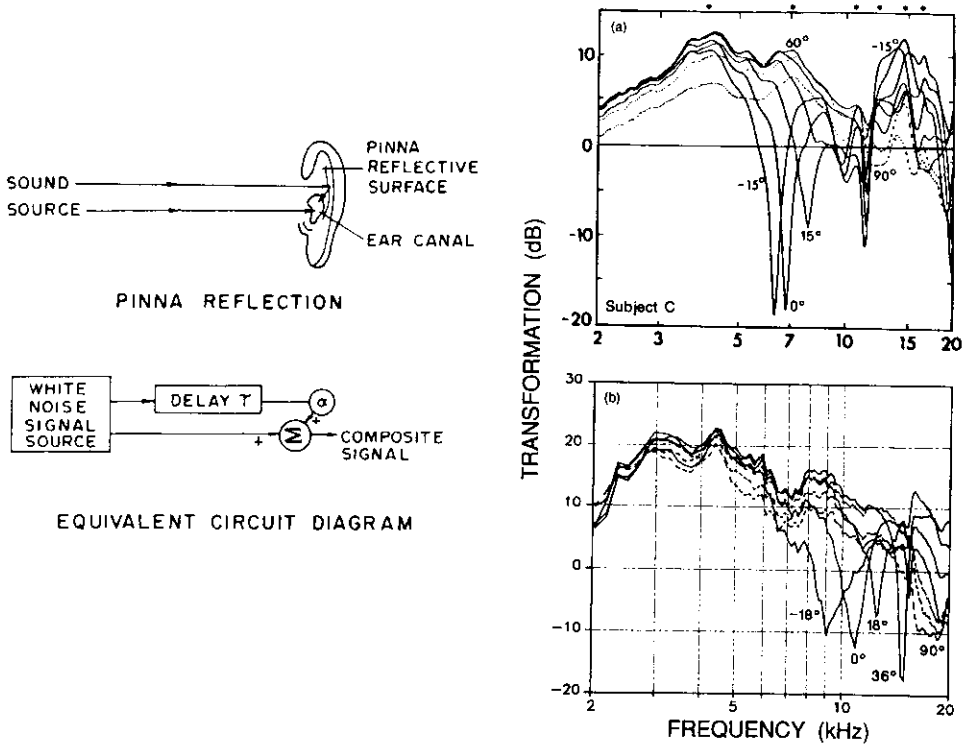

Figure 9.18 Drawing of the pinna schematically showing the interaction between an incident waveform and a slightly delayed version of the waveform that is reflected off the pinna (left).
NOTE: Summing a waveform with a delayed replica results in deep spectral notches, such as those seen in the head-related transfer functions (HRTFs; right). The amount of delay depends on the angle of incidence, due to the asymmetry of the pinna, and thus the spectral notches change systematically with angle of incidence. The HRTFs represent the sound pressure measured using a probe tube placed near the tympanic membrane, referenced to the free-field sound in the absence of the head.
SOURCE: Left: from Wright, Hebrank, & Wilson (1974). Reprinted with permission. Right: from Musicant, Chan, & Hind (1990). Reprinted with permission. Top panel: originally from Shaw (1982). Reprinted with permission.

aspects of both rate and temporal coding, as well as their interactions, for several different stimuli.

Frequency Tuning

One of the most basic properties of the responses of auditory neurons is frequency tuning. At every level of the auditory pathway there are neurons that are sharply tuned in frequency; the frequency to which a neuron is most sensitive will be referred to as its characteristic frequency (CF). The frequency tuning of a neuron can be described by a frequency-threshold tuning curve, which shows the sound level that just elicits a measurable excitatory response, plotted as a function of frequency (Figure 9.19; Kiang, 1984; Kiang & Moxon, 1978). The general nature of tuning curves is similar across species; relatively sharp, V-shaped tuning curves are seen in the periphery and in at least some cells at all levels, including the auditory cortex. More complex tuning, in some cases

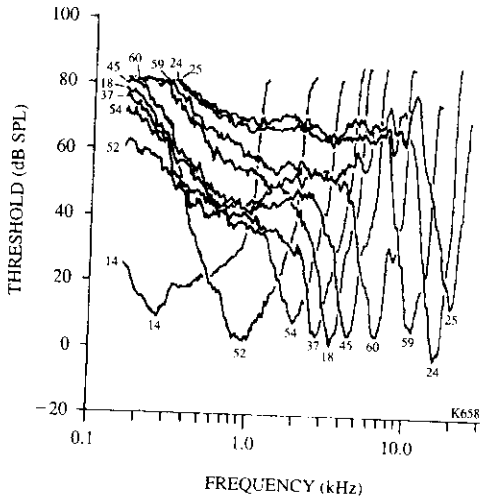

Figure 9.19 Tuning curves for AN fibers in the cat (data redrawn from Kiang, 1984).
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reflecting interactions between excitatory and inhibitory inputs, is often observed at higher levels in the pathway. The sharpness of tuning and the range of frequencies over which the population of peripheral fibers is tuned varies from species to species (Manley, 1990).

In addition to being tuned in frequency, most auditory nuclei have a tonotopic spatial arrangement. The frequency maps vary in specifics (e.g., orientation and orderliness of maps) from place to place, but they are generally maintained at all levels of the pathway, from the AN to the cortex (Irvine, 1992). An additional complexity of frequency tuning is that the best frequency shifts with sound level; in cats, the best frequency shifts downward with increased level for CFs greater than approximately 1500 Hz, upward for CFs less than approximately 750 Hz, and stays constant for CFs between 750 and 1500 Hz (Carney, McDuffy, & Shekhter, 1999). These shifts in frequency tuning are caused by the interaction between the nonlinear cochlear amplifier (related to the active process in the inner ear; discussed earlier) and frequency glides in the impulse responses of the basilar membrane, hair cells, and AN fibers (e.g., Zhang & Zwislocki, 1996; Carney et al., 1999; de Boer & Nuttall, 1997; Recio, Narayan, & Ruggero, 1997; reviewed in Carney, 1999).

If the response rates of auditory neurons were linearly related to the energy in the neurons' receptive fields (as defined by their tuning curves), the frequency tuning and tonotopy would be sufficient to provide a substrate for encoding the frequency and sound level of pure tones. Also, such a scheme could encode the spectra of complex sounds in the form of average discharge rate versus place or location within the tonotopic map (indeed, only knowledge of the neuron's frequency tuning is required, not strict tonotopy). However, discharge rates are typically related to sound level in a nonlinear manner at all levels of the pathway, and it is necessary to look in more depth at other neural response properties to determine how even simple stimulus attributes, such as sound level and frequency, are encoded. In general, changes in both average discharge rate and temporal response properties, combined across populations of neurons, are required to explain encoding of sounds. Different response features and different neurons convey information, depending on the frequency, level, and complexity of the stimulus.

Response to Tones of Auditory-Nerve Fibers

The discharge rate (average rate over the time course of the stimulus, in spikes/s) of an AN fiber to a tone at its CF is characterized by (a) Poisson-distributed spontaneous activity at very low sound levels; (b) a range of levels at which discharge times become phase-locked, or aligned in time, with temporal features of the stimulus for low stimulus frequencies; (c) a threshold at which the rate is just increased (typically by a criterion of 20 spikes/s, measured over a 50-ms time

window; Liberman, 1978); (d) a dynamic range of levels over which the response rate increases as tone level increases; and (e) a maximal, or saturated, rate that remains relatively constant at higher levels. (For detailed reviews of AN response properties, see Javel, 1986; Ruggero, 1992a.)

In mammals, AN fibers vary in their spontaneous rates (SRs), which are correlated to their tone thresholds (Liberman, 1978): The majority (61%) have high-SRs (>18 spikes/s) and low thresholds; medium-SR fibers (23%, 1–18 spikes/s) have higher thresholds; and low-SR fibers (16%, <1 spike/s) have the highest thresholds. The form of rate-level functions varies across these groups (Figure 9.20). High-SR fibers have steep rate-level functions because of their low thresholds,

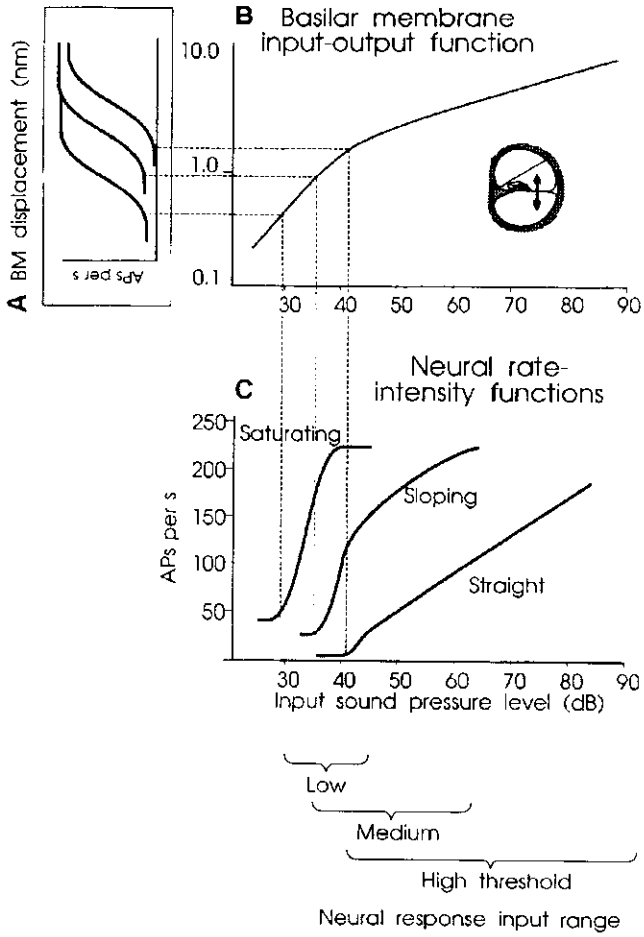

Figure 9.20 Illustration of rate vs. level functions for AN fibers with different spontaneous rates, and the dependence of the rate-level functions on the basilar-membrane (BM) input-output function.
NOTE: The BM output is enhanced at low levels, due to the cochlear amplifier. The gain of the cochlear amplifier is reduced at moderate to high levels by saturation of the active process, reflected in the slope of the BM input-output function (discussed in the text).
SOURCE: Reprinted from *Trends in Neurosciences, 15,* G. K. Yates, B. M. Johnstone, R. B. Patuzzi, & D. Robertson, "Mechanical preprocessing in the mammalian cochlea," pp. 57–61. Copyright © 1992, with permission from Elsevier Science.

which are in the low-SPL range where the cochlear amplifier is at maximal gain (discussed earlier). Medium- and low-SR fibers have higher thresholds, and their rate-level functions are less steep because of the reduction in gain of the cochlear amplifier as sound level increases (Figure 9.20; Sachs & Abbas, 1974; Sokolowski, Sachs, & Goldstein, 1989; Yates et al., 1992). Thus, the range of levels over which discharge rate varies with sound level, or the dynamic range, varies significantly across the three SR groups.

Obviously, the discharge rate's ability to encode sound level is constrained by these dynamic ranges. To explain quantitatively level coding over a wide range of levels requires combinations across frequencies (Siebert, 1968) or across groups of fibers with different SRs (Colburn, 1981; Delgutte, 1987; Viemeister, 1988; Winter & Palmer, 1991; reviewed by Delgutte, 1996). However, it is important to note that the presence of the straight rate-level functions for the low-SR fibers depends on a large amount of cochlear amplification, which is only present at the high-frequency end of the cochlea. Straight rate-level functions are not observed at CFs below 1500 Hz in guinea pig (Winter & Palmer, 1991) and are not observed in cats at any CF (e.g., Sachs & Abbas, 1974; Winslow & Sachs, 1988). Thus, encoding of level by low-CF fibers cannot depend on wide-dynamic range fibers and must be explained either by spread of excitation across the population (which only applies to pure tones) or by temporal response properties (Carney, 1994; Colburn, Carney, & Heinz, 2001; Heinz, Colburn, & Carney, 2001b).

Two different temporal cues are available in the responses of AN fibers: synchrony and phase. Synchrony, or phase locking to the fine structure of the stimulus waveform (Figure 9.21A), is detectable at levels of approximately 20 dB below the rate threshold (for high-SR fibers) and persists up to the highest levels tested (Johnson, 1980). As shown in Figure 9.21A, synchronized discharges typically do not occur on every cycle of the stimulus; when they do occur, however, they are aligned in time with a particular phase of the stimulus (phase-locked). The strength of synchrony of the response times to the stimulus waveform increases to a maximum over a relatively narrow range of levels, peaks at about 20 dB above rate threshold, and then drops slightly at higher levels (Johnson, 1980). Thus, changes in synchrony with sound level may contribute to encoding of sound level at very low levels, but not at medium to high sound levels (Colburn, 1981; Colburn et al., 2001). In addition, the ability of AN fibers to synchronize to the fine structure of tones is limited to low frequencies (Figures 9.21B–D; Johnson, 1980; Koppl, 1997). This limitation is imposed by the low-pass filtering associated with the membranes of IHCs, as well as by other neural processes (Weiss & Rose, 1988). Although high-CF fibers do not synchronize well to tones at their CF (Figure 9.21C), high-CF fibers do synchronize extremely well to low-frequency tones presented at high levels (Joris, Smith, & Yin, 1994) and to the envelopes of complex high-frequency sounds (discussed later).

The synchronized activity of AN fibers provides the substrate for another temporal cue. The phase of the synchronized discharges also conveys information about tone level. Because the gain of the cochlear amplifier changes with sound level, the bandwidth and phase properties of the tuning in the auditory periphery also change with level (e.g., Cheatham & Dallos, 1998; Geisler & Rhode, 1982; Ruggero et al., 1997). The phase of the responses in the cochlea determines the timing of synchronized responses of AN fibers. Thus, the responses of AN fibers to tones near CF have phases that systematically change as sound level is varied (Figure 9.22; D. J.

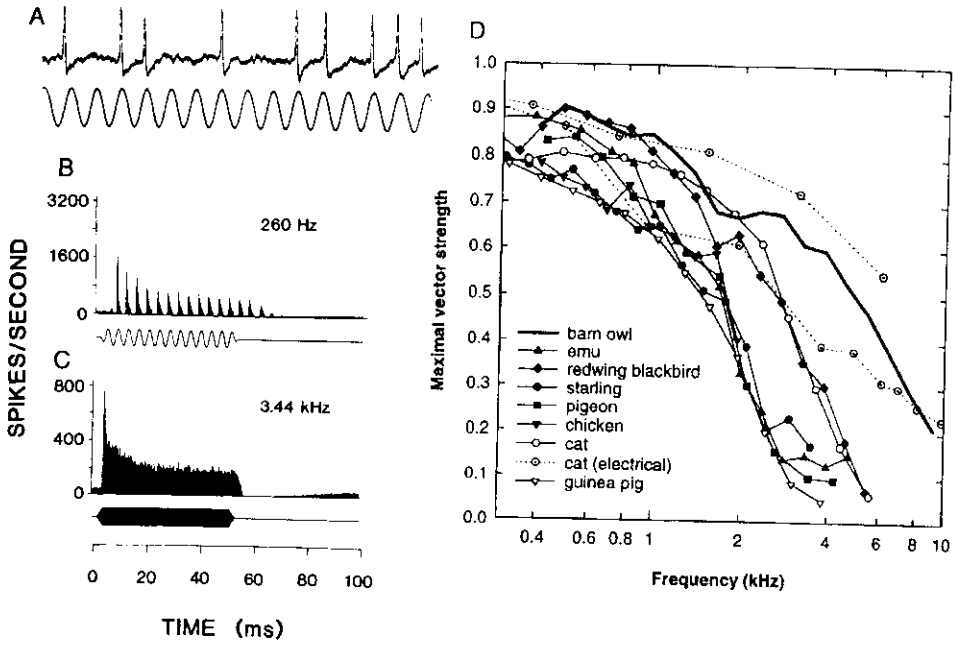

Figure 9.21 Phase-locking of AN responses.

NOTE: A) Example of an auditory nerve fiber's discharges that are phase-locked to the stimulus waveform. The fiber does not discharge on every cycle of the stimulus; when it does discharge, however, it is synchronized, or phase-locked, to a particular phase of the stimulus. B–C) Poststimulus time histograms for two AN fibers responding to tones at CF. Discharge times for 3,000 tone bursts were superimposed to form these histograms. The low-CF fiber responds in synchrony with the temporal features of the sinusoidal stimulus (shown just below the response). The higher-CF fiber's response is not clearly phase-locked to the high-frequency stimulus (shown just below response); at 3.44 kHz, the strength of synchrony is relatively weak (see D). D) Synchronization coefficient of AN responses to tones at CF as a function of frequency for several species. Each measurement was made at the level that yielded the maximum synchronization coefficient for that fiber. Strength of phase locking is typically measured using the synchronization coefficient (equivalent to vector strength), where a value of 0 represents no phase locking and 1 represents perfect phase locking; this measure is the ratio between the energy in the PST histogram at the tone frequency (determined with a Fourier transform) and the overall average rate.

SOURCE: A) Evans (1975). Copyright © 1986 by Springer-Verlag. Reprinted with permission. B–C) From Irvine (1986); redrawn from Kiang (1984). Copyright © 1986 by Springer-Verlag. Reprinted with permission. D) From Koppl (1997). Copyright © 1997 by the Society for Neuroscience. Reprinted with permission.

Anderson, Rose, Hind, & Brugge, 1971), providing a cue for encoding sound level at low frequencies (Carney, 1994; Colburn et al., 2001; Heinz et al., 2001b). This cue can be decoded by a neural coincidence-detection mechanism; no absolute phase reference is required because the relative timing, or degree of coincidence, of discharges on neurons tuned to different CFs systematically varies with sound level (Carney, 1994; Heinz et al., 2001b). It is interesting to note that the nonlinear phase cue, which is associated with the OHC-driven active process in the mammalian cochlea (e.g., Ruggero et al., 1997; discussed earlier), is present also in AN responses of the starling (Gleich & Narins, 1988). The active process in birds is hypothesized to involve active movements of stereocilia, as opposed to

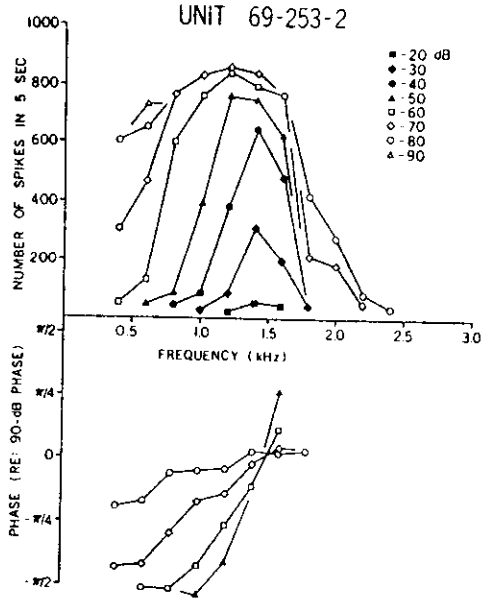

Figure 9.22 The phase of phase-locked responses of low-frequency fibers varies systematically with sound level.

NOTE: Response area for a 1400-Hz CF AN fiber in cats is shown. The upper panel shows average discharge rate as a function of tone frequency at several sound levels. The lower panel shows the phases of the phase-locked responses, referenced to the phase of the response to the 90 dB SPL tone at each frequency.

SOURCE: From Anderson, Rose, Hind, & Brugge (1971). Reprinted by permission of McGraw-Hill.

length changes of the hair cells (see Fettiplace & Fuchs, 1999). Thus, the presence of the level-dependent phase cues may be present across diverse species as a result of different active mechanisms.

Figure 9.22 demonstrates that a combination of rate and temporal encoding strategies can encode level across a wide range of levels, even when processing is restricted to fibers tuned to a limited range of frequencies near the tone (which is important when considering complex stimuli, or masked stimuli; discussed later). For this neuron, discharge rate changes with sound level at frequencies near CF from threshold (about 20 dB SPL) up to about 60 dB SPL, and then saturates. However, the phase of the phase-locked discharges of fibers tuned just below or above the frequency of the tone continues to change up to at least 90 dB. By combining the information available in rate and temporal response properties, sound level can be encoded over the wide range of levels required to explain psychophysical performance (e.g., Heinz et al., 2001a).

These three cues—level-dependent rate, synchrony, and phase—can be combined to encode information over a wide range of stimulus parameters, with different aspects of the responses providing information in different situations, depending on the frequency and sound level of the stimulus (Heinz et al., 2001a). The previous discussion pertains to encoding of pure tones presented in a quiet background; the effects on these different encoding schemes of background noise or other stimulus components, such as in complex sounds, are a topic for future investigation. Also, other factors may play a role in the contribution of average rate to level coding in certain situations. For example, the dynamic range of the onset response of AN fibers is much wider than that of the sustained response (Smith, 1988). Furthermore, the activity of olivocochlear efferents (stimulated electrically or acoustically) may act to shift dynamically the rate-level and phase-level functions of AN fibers, effectively enlarging their dynamic ranges (discussed later; May & Sachs, 1992; Winslow & Sachs, 1988).

Responses to Tones in the Cochlear Nuclear Complex

Responses of neurons at the first level of processing in the brainstem have received a great deal of study. These neurons are of interest because they represent the first level of processing or decoding the information that is

initially encoded in the patterns of discharge of populations of AN fibers. Thus, a better understanding of the response properties of cells in the CN may shed more light on how information is encoded in the AN. In addition, the responses of the various cell types in the brainstem are inherently interesting from a biophysical standpoint; these cells receive essentially the same excitatory inputs—convergent AN fibers—but respond in many different ways. Differences in responses from cell to cell, and from cell type to cell type, presumably depend on the number and synaptic strengths of the inputs, the location of the inputs on the cell, the cell morphology, and the properties of the cell membrane. All of these characteristics vary across the cells of the cochlear nucleus (reviewed by Cant, 1992). Pfeiffer (1966) classified responses in the CN based on the onset responses and the temporal patterning of the sustained responses seen in these peri-stimulus time histograms (PSTs; Figure 9.23). Subsequent classification schemes incorporated information on the inter-spike interval statistics (e.g., Blackburn & Sachs, 1989; Young, Robert, & Shofner, 1988) and on response maps (discharge rate vs. frequency and sound level) that include both excitatory and inhibitory response features (Figure 9.24; Shofner & Young, 1985).

In the mammalian cochlear nucleus, the AVCN contains two major cell types: bushy cells, which are associated with primary-like (i.e., AN-like) PSTs in response to tones at CF (Rhode, Oertel, & Smith, 1983; Rouiller & Ryugo 1984; Smith & Rhode, 1987), and stellate cells, which are associated with chopper (i.e., regularly firing) response PSTs (Figure 9.23; Rhode et al., 1983; Smith & Rhode, 1989). The PVCN contains stellate cells that are associated with onset-chopper responses (Smith & Rhode, 1989) and octopus cells that are associated with onset responses (Rhode et al., 1983). The DCN has several cell types associated with different response properties that are often described in terms of response maps and rate-level functions in response to noise and tones (Figure 9.24), in addition to their PSTs to tones (Figure 9.23).

The mammalian AVCN and PVCN project to the major binaural nuclei in the brainstem and midbrain. The temporal encoding of low-frequency tonal stimuli is apparently enhanced in the AVCN, where bushy cells have synchronization coefficients that are higher than those of AN fibers in response to low-frequency tones (Joris, Carney, Smith, & Yin, 1994). In birds and reptiles, AN fibers project to two brainstem regions, the NM and the NA. Cells in the NM have response properties similar to bushy cells in mammalian AVCN, while those in NA are similar to the stellate cells in mammalian AVCN (Carr & Konishi, 1990; Hausler et al., 1999; Sullivan, 1985; Warchol & Dallos, 1990). Bushy and stellate cells are often described in terms of parallel paths, with the bushy cells conveying temporal information to higher levels and stellate cells conveying information about sound level in terms of average rate (e.g., Shofner & Dye, 1989; Takahashi, Moiseff, & Konishi, 1984). However, most stellate cells have relatively limited dynamic ranges (Carney & Burock, 1997; May & Sachs, 1992), and while they do not phase-lock well to tonal stimuli at CF, stellate cells do phase-lock well to the envelopes of complex sounds (Frisina, Smith, & Chamberlain, 1990; Rhode & Greenberg, 1994). Furthermore, both bushy cells and stellate cells are sensitive to manipulations of the phase spectrum of complex sounds, suggesting that they are sensitive to the relative timing of convergent AN inputs (Carney, 1990). Thus, it is not clear whether the segregation of the pathways is very strict in terms of temporal or average-rate information.

Responses to tones of cells in the DCN, especially the type IV and V neurons, are

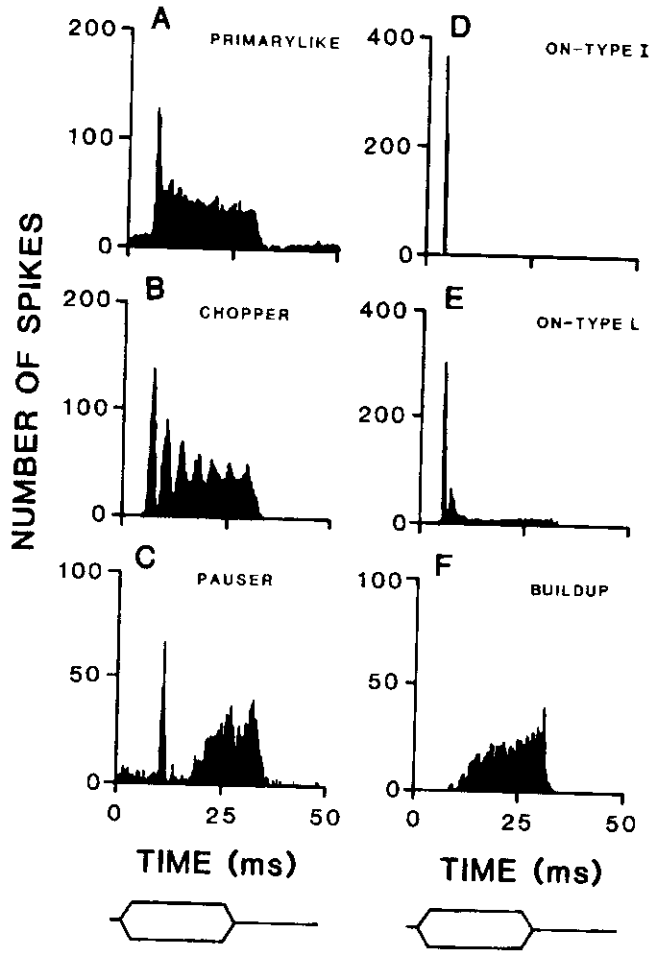

Figure 9.23 Examples of six different PST histogram types in response to brief tone pulses at CF for cells in the cochlear nucleus.

NOTE: The categories proposed by Pfeiffer (1966) are illustrated. Primary-like PSTs are associated with spherical and some globular bushy cells in the AVCN; different varieties of chopper PSTs are associated with the stellate cells in AVCN and multipolar cells in PVCN; Onset-I (pure onset response) PSTs are associated with octopus cells in the PVCN; Onset-L (onset with low-sustained rate) PSTs are associated with globular bushy cells; Pauser and Buildup PSTs are associated with cells in the DCN (reviewed by Young, 1984, 1998; Rhode & Greenberg, 1992).

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highly nonmonotonic as a function of level and usually are not factored into models for encoding of the level and frequency of single tones. Rather, the DCN's more complex response properties have been proposed to reflect a role in the decoding of spectral notches that are associated with the pinna cues for sound localization of stimuli in the vertical plane (discussed later). The neural circuitry of the DCN has been a topic of several physiological and anatomical studies exploring the interactions of the different cell types (reviewed by Young, 1984, 1998).

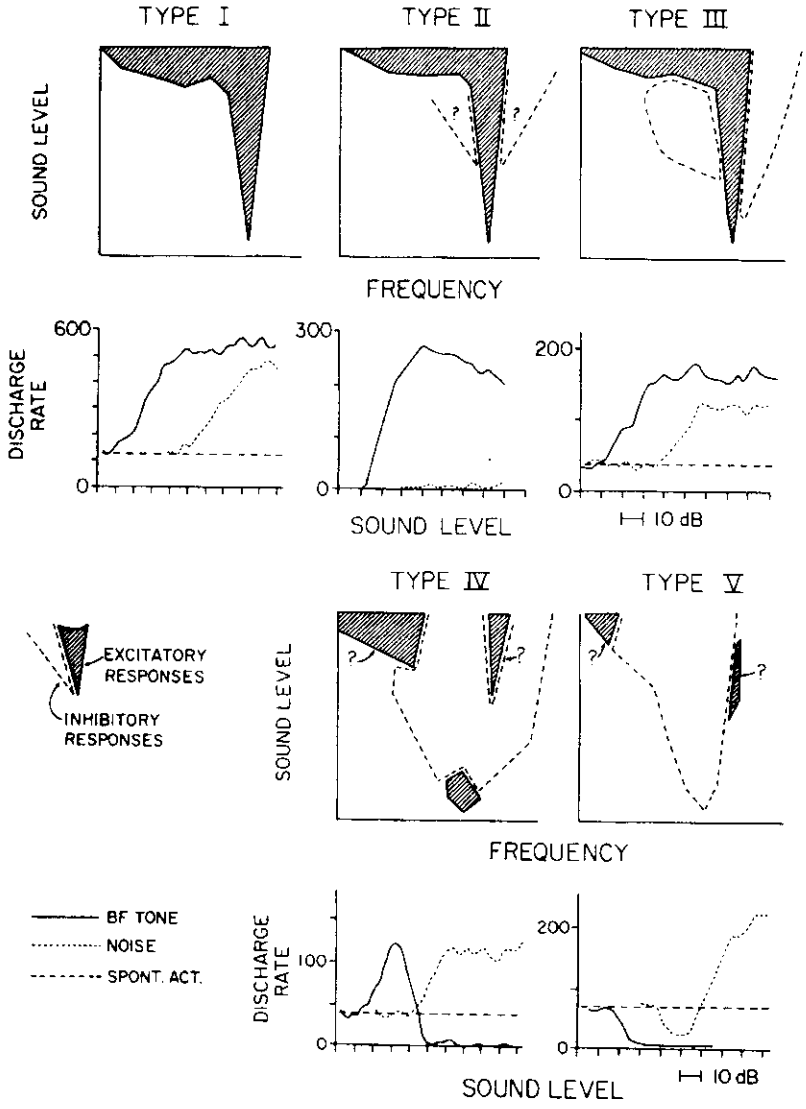

Figure 9.24 Examples of the categories of cells in the cochlear nucleus based on response maps.
NOTE: These response maps (RMs; Shofner & Young, 1985) show the excitatory and inhibitory responses of a neuron to tones across a wide range of frequencies and sound levels. Below each RM are rate-level functions in response to tones at CF and wideband noise. Cells in the AVCN tend to have type I RMs; type III RMs are found in VCN and DCN; and types II, IV, and V are found primarily in DCN (Young, 1984; Rhode & Greenberg, 1992).
SOURCE: From Young (1984). Reprinted with permission.

Responses to Tones in the Superior Olivary Complex and Lateral Lemniscus

Cells in the binaural region of the brainstem have been studied primarily from the viewpoint of sound localization (discussed below). This section presents the basic response properties of these cells to tonal stimuli.

Of all the auditory brainstem nuclei, the thin sheet of cells that makes up the MSO has been the most difficult to study, partly

because the large extracellular fields due to the synchronous activity of these cells makes them difficult to isolate for single-unit recording (Guinan, Norris, & Guinan, 1972; Yin & Chan, 1990). The MSO of the mammal is dominated by cells that are tuned to low frequencies, excited by stimuli to each ear, and often facilitated by stimuli presented to both ears with appropriate binaural parameters. MSO cells have frequency tuning curves in response to stimuli delivered to either ear that are comparable in shape to AN fibers, but with slightly broader tuning, suggesting some convergence across CFs (Yin & Chan, 1990). Rate-level functions for most MSO cells are monotonic and saturating, with dynamic ranges of 20 dB to 30 dB; a few cells have nonmonotonic rate-level functions (Yin & Chan, 1990). The temporal response properties of low-frequency MSO neurons are highly synchronized to tonal stimuli, typically exceeding the highest synchronization coefficients seen in the AN, and comparable to those in bushy cells of the AVCN (Joris et al., 1994; Yin & Chan, 1990). MSO cells are highly sensitive to the relative timing of stimuli to the two ears (Goldberg & Brown, 1969; Yin & Chan, 1990).

Cells in the LSO are typically excited by stimuli to the ipsilateral ear and have frequency tuning that is comparable to that in the AN (Tsuchitani, 1977). The tonotopic map in the LSO is dominated by high-frequency CFs, which do not exhibit significant phase-locking to tones at CF (although, like AN fibers, they phase-lock to the envelopes of complex sounds; discussed later). In response to tones presented to the ipsilateral ear, LSO cells have chopper response patterns that differ in the details of their chopping patterns as well as in their interspike-interval statistics (Tsuchitani & Johnson, 1985). These cells are inhibited by sounds to the contralateral ear, and are thus sensitive to interaural level differences and presumed to play a role in the localization of high-frequency sounds (reviewed by Irvine, 1986, 1992). The inhibitory inputs to the LSO are provided by the principal cells of the ipsilateral MNTB, which receives its input in the form of the large calyces of Held from the globular bushy cells of the contralateral cochlear nucleus (e.g., Smith, Joris, Carney, & Yin, 1991; Stotler, 1953). Because of the secure synapses associated with the calyceal terminals, responses of MNTB are very similar to those of globular bushy cells in the CN (Smith, Joris, & Yin, 1998).

The nuclei of the lateral lemniscus have been the focus of relatively few studies. As it has become increasingly clear that the responses of the IC are significantly more complex than are those of the MSO and LSO, however, the motivation to understand these nuclei that provide strong inputs to the IC has grown. Most of the neurons in the VNLL and DNLL are sharply tuned; a minority has broad or unusual tuning-curve shapes (Guinan et al., 1972). The DNLL has a clear tonotopic arrangement, whereas that of the VNLL and the neighboring INLL is less consistent (Aitkin, Anderson, & Brugge, 1970). Cells in the DNLL have binaural responses due to the inputs from the SOC (e.g., Brugge, Anderson, & Aitkin, 1970; Markovitz & Pollak, 1994; reviewed by Kelly, 1997). Cells in the VNLL are primarily monaural and excited by the contralateral ear, reflecting the dominant input from the contralateral CN. The function of these nuclei is somewhat unclear because all the inputs to the nuclei of the LL provide inputs also to the IC, which is the major target of the NLL outputs (Irvine, 1986). Additional connections between the two DNLLs, and the projections of these nuclei to both ICs, provide a potential for explaining some of the more complex binaural response properties seen for the cells in the IC as compared to the cells in the SOC. For example, to explain responses to some complex stimuli in the IC (discussed later), one requires

convergence of excitatory and inhibitory inputs tuned to different binaural configurations. Binaural processing within the DNLL and its inhibitory projections to both ICs have also been proposed to enhance the laterality of the representation of contralateral space and to enhance the sensitivity of IC neurons to small changes in interaural level and time (Kelly, 1997).

Responses to Tones in the Midbrain: Inferior and Superior Colliculi

In most species the midbrain auditory region is relatively large and is accessible for physiological studies, especially as compared to the lower binaural nuclei in the SOC. For these reasons, it is one of the most studied levels of the auditory pathway. The cells in the IC are typically sensitive to particular combinations of binaural stimuli, reflecting the binaural processing at lower levels of the brainstem, as well as further processing within the IC itself. For example, both EE and EI responses to tones have been described for IC neurons in cats, reflecting the response properties of the MSO and LSO neurons that project to the IC. However, more complex stimulus paradigms (discussed later) make it clear that not all properties of IC neurons can be explained simply by processing at the level of the MSO and LSO.

The shapes of frequency tuning curves of neurons in the ICC are more diverse than at lower levels, probably because of the high degree of convergence at this level. Although there is clearly a tonotopic organization of the nucleus (e.g., Merzenich & Reid, 1974; reviewed by Irvine, 1992), the details of the map are unclear, as are the relationships to other proposed maps, such as those of sharpness of tuning (Schreiner & Langner, 1988), threshold (Stiebler, 1986), or tuning for amplitude-modulated stimuli (Schreiner & Langner, 1988).

Responses of IC neurons to tones also reflect the diversity of inputs to the IC. In contrast to neurons at the levels of the MSO and below, phase-locking to low-frequency stimuli in the ICC is rare and is also seldom observed for frequencies above 600 Hz (Kuwada, Yin, Syka, Buunen, & Wickesberg, 1984). Rate-level functions of ICC neurons vary over a continuum from monotonic to highly nonmonotonic (Figure 9.25; Irvine and Gago, 1990). From these rate-level functions one could hypothesize that level is encoded in terms of the average rates of the monotonic cells, or in terms of a place code based on the nonmonotonic cells (or a combination of both; Irvine, 1992). Neither of these models has been quantitatively tested. In addition to the diversity of rate-level functions, the temporal response patterns in the IC vary significantly; many cells have onset responses followed by long pauses (50-ms pauses are not uncommon) before sustained activity begins, if it is present at all (D. R. Moore & Irvine, 1980; Irvine, 1986). Recent studies of the ICC have also explored the influence of inputs from the contralateral DCN by using response maps to characterize IC responses (e.g., Ramachandran, Davis, & May, 1999). Cells in the ICx are reported to have more complex and typically broader frequency tuning characteristics than ICC has (e.g., Aitkin, Webster, Veale, & Crosby, 1975). A spatial map has been reported in the ICx of the barn owl (e.g., Knudsen & Knudsen, 1983), and most studies of the ICx focus on its role in spatial hearing.

One of the major projections of the central nucleus of the IC is to the deep layers of the superior colliculus (SC). Auditory, visual, and somatosensory inputs converge in this region (e.g., M. A. Meredith & Stein, 1983; Knudsen, 1987), along with inputs from proprioceptive, vestibular, and other systems that are involved in the generation of motor commands. The organization of the deep SC is

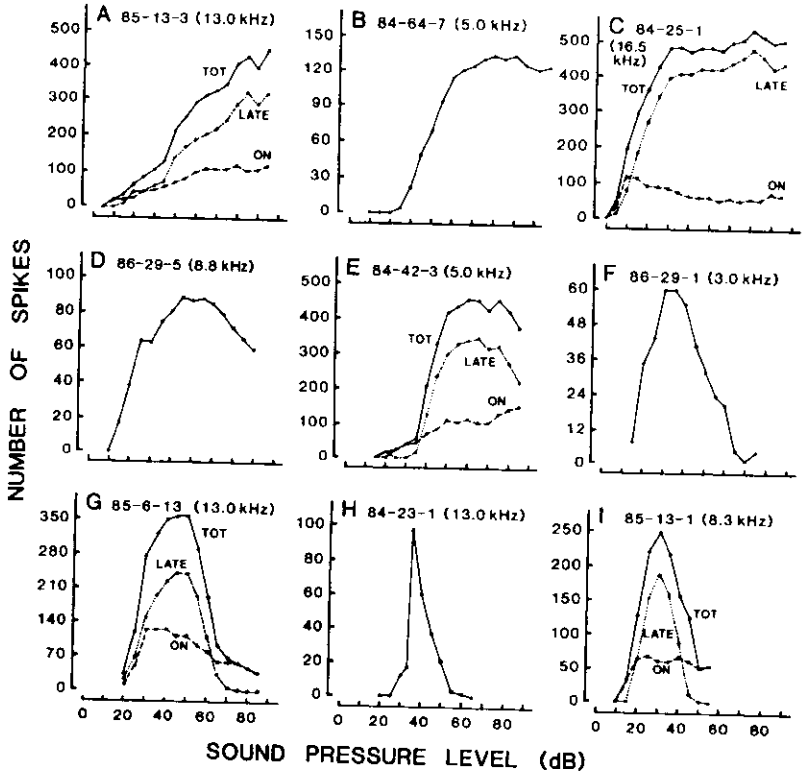

Figure 9.25 Examples showing the diversity of rate-level functions for cells in the ICC in response to tones at CF.

NOTE: The number at the top of each panel (e.g., 85-13-3) is an identifier for each neuron; the number in parentheses refers to the CF of the cell. Responses are averaged over 30 presentations; in some cases, the onset and sustained (late) responses are shown in addition to the total response.

SOURCE: From Irvine & Gago (1990). Reprinted with permission.

described as a motor map; responses of cells depend on the difference between the current and desired locations of the eyes, head, and body (reviewed by Sparks, 1999).

Reponses to tonal stimuli in the SC (which have been recorded primarily in anesthetized animals, in which eye movements were neither elicited nor behaviorally controlled) show a wide diversity of frequency tuning, including very sharp, very broad, and complex multipeaked threshold-tuning curves (Hirsch, Chan, & Yin, 1985; Wise & Irvine, 1983). The SC is dominated by cells tuned to high CFs (Carlile & Pettigrew, 1987; Hirsch et al., 1985; Wise & Irvine, 1983). The SC does not have a simple tonotopic map, but several groups have reported evidence for spatial maps (King & Palmer, 1983; Middlebrooks & Knudsen, 1987). Carlile & Pettigrew (1987) have argued that the complex tonotopy makes sense if it is interpreted in terms of the spectral cues provided by the pinna, which thus may provide the basis for a spatial map in the SC.

The roles of sensory maps for the different represented modalities in the SC, their interactions, and ultimate transformation into motor commands are a fascinating topic. For example, the fact that the eyes move relative to the head (and thus relative to the ears) and that the head moves relative to the rest of the body (and thus relative to the somatosensory system), necessitates the use of proprioceptive

or sensory inputs in order to interpret the dynamic spatial relationships between the different modalities. In the barn owl, which has very limited eye movements, it has been reported that the visual map in the superficial layers of optic tectum and the auditory map of space in deep layers are aligned with each other (Knudsen, 1987). The responses of auditory neurons in the SC are influenced by the position of the eyes (in the monkey, Jay & Sparks, 1984) and the pinnae (in the cat, Middlebrooks & Knudsen, 1987). Recent studies of gaze control (i.e., control of combined eye and head movements) suggest that neural activity in the SC is most consistent with gaze, as opposed to eye, head, or body movements in isolation (Freedman & Sparks, 1997). Furthermore, studies of the SC motor maps conducted on animals with fixed heads have yielded distorted maps (reviewed by Sparks, 1999). The role of the dynamic sensory maps in deep SC and their interaction with a gaze control system are topics for further study.

Responses to Tones in the Thalamus

The other target of cells in the IC is the MGB in the thalamus. The three major regions of the thalamus have basic physiological response properties that mirror the general nature of their anatomical inputs and outputs (reviewed by Clarey, Barone, & Imig, 1992). The ventral division, which receives its input primarily from ICC and projects strongly to auditory cortex, is characterized by an orderly tonotopic map (Aitkin & Webster, 1972; Calford & Webster, 1981; Imig & Morel, 1985b). The dorsal division, which has a more diverse set of inputs and projections, is less strongly tonotopic; most cells in this region have broad and complex (multipeaked) frequency-threshold tuning curves (Calford & Webster, 1981). The medial division, which is most diverse in terms of its cell types, inputs, and projections, has an irregular tonotopic arrangement (Imig & Morel, 1985a; Roullier, Rodrigues-Dagaeff, Simm, de Ribaupierre, Villa, & de Ribaupierre, 1989).

The rate-level functions of the majority of cells in the MGB are nonmonotonic (Aitkin & Dunlop, 1968; Galambos, Rose, Bromiley, & Hughes, 1952; Rouiller, de Ribaupierre, Morel, & de Ribaupierre, 1983). There seems to be a general organization of responses throughout the MGB along the anterior-posterior axis: The anterior regions have a higher percentage of monotonic cells that are more responsive to broad-band stimuli such as noise and clicks, whereas the posterior regions have a higher percentage of nonmonotonic cells that are more responsive to tones and respond poorly to broadband stimuli (Rodrigues-Dagaeff et al., 1989; Rouiller et al., 1983). The anterior and posterior regions also have different projection patterns to the auditory cortex (Morel & Imig, 1987; Rodrigues-Dagaeff et al., 1989).

Responses to Tones in the Auditory Cortex

The tonotopic arrangement of auditory cortex was described earlier because it plays an essential part in the parceling of the different regions of auditory cortex. Responses of cortical neurons to pure tones are sharply tuned in frequency in several of the cortical regions that have orderly tonotopic maps: primary auditory cortex (AI), the anterior field (A or AAF), the posterior field (P), the ventral cortical field (V), and the ventral posterior part of e_p (VP; Figure 9.15; e.g., Reale & Imig, 1980; Winer, 1992). A topographic representation of tone level along iso-frequency strips was reported in AI (Heil, Rajan, & Irvine, 1994). Tone level is also reflected in the synchronization of neural responses in AI and between AI and AAF (Eggermont, 2000). The representation of temporal features of acoustic stimuli in auditory cortex has been recently reviewed

(Schreiner, Mendelson, Raggio, Brosch, & Krueger, 1997).

Regions of auditory cortex other than AI, AAF, V, and VP are notoriously difficult to stimulate with pure tones, and recent studies have turned to the use of more complex stimuli, including vocalizations (e.g., Wang, 1998; discussed later). The difficulty in studying cortex was surmounted most notably by Suga and his colleagues, who have conducted a number of studies of the bat auditory cortex (reviewed in Suga, 1989). Their studies take advantage of the fact that bats echolocate their prey using relatively simple and thoroughly studied vocalizations; thus the processing of cues associated with the task of echolation can be studied using a stimulus that is known to be behaviorally important to the animal.

Physiology of the Descending Pathways

The physiology of the descending pathways that terminate in the central nervous system has only recently become a focus of study. A general framework describing three parallel corticofugal systems was proposed by Huffman and Henson (1990). A series of recent studies have demonstrated a variety of effects of the corticofugal pathways on the response properties of neurons at lower levels in the mustache bat (e.g., Chowdhury & Suga, 2000; Yan & Suga, 1996; Zhang, Suga, & Yan, 1997).

A large number of studies have focused on the olivocochlear system. The influence of the descending auditory pathway has generally been studied by stimulating these neurons and monitoring the effect on AN and basilar membrane responses, rather than by recording from the efferent neurons themselves. In general, stimulation of the crossed olivocochlear bundle (COCB; accessible at the floor of the fourth ventricle) results in a reduction of AN responsiveness. In quiet, stimulation of the COCB elevates thresholds and shifts the RL functions to higher levels (Gifford & Guinan, 1983; Guinan & Gifford, 1988; Wiederhold, 1970; reviewed by Wiederhold, 1986). In the presence of noise, stimulation of the COCB also restores the dynamic range of AN fibers to nearly that observed in quiet and thus may play a role in maintaining information about sound level in the presence of background sounds (Winslow & Sachs, 1987, 1988). Based on the effect of COCB stimulation on basilar-membrane responses to different tones near CF, a likely mechanism for the reduced response is a reduction of the cochlear amplification associated with OHC motility (e.g., Dolan, Guo, & Nuttall, 1997; Murugasu & Russell, 1996). However, more complex features of the effects of COCB stimulation on responses to frequencies away from CF and at high SPLs suggest that additional mechanisms may be necessary to explain the effects (Guinan & Stankovic, 1996; Russell & Murugasu, 1997; Stankovic & Guinan, 1999, 2000).

RESPONSES TO COMPLEX ACOUSTIC STIMULI

Most studies of the auditory system, at all levels of the pathway, have been conducted with pure-tone stimuli. The motivation for this approach is guided by the general strategy of trying to understand the responses of a system to the simplest possible stimulus, after which complex stimuli can be understood. (Using Fourier analysis, complex sounds can be represented as straightforward combinations of simple stimuli). Of course, this strategy works only for linear systems, for which responses to combinations of simple stimuli are just combinations of responses to the simple stimuli. Since the late 1960s and early 1970s, it has become increasingly clear that the auditory system is nonlinear. Indeed, because of the fragile nature of the active process in the

inner ear, the healthy auditory system is much more nonlinear than the impaired system is.

To understand how the nonlinear auditory system processes complex sounds, they must be studied (essentially) one at a time, which opens the door to an infinite parameter space. Psychophysical studies provide insight as to which complex stimuli may be interesting to pursue in physiological studies; for example, it is interesting to consider stimuli, such as masking stimuli, that illustrate significant differences between the healthy and the impaired ear. In contrast, tones in quiet produce relatively little deficit, other than raised thresholds, in impaired listeners. Because the healthy ear has an exquisite ability to pull signals out of noisy backgrounds—an ability that is lost after impairment (e.g., B. C. J. Moore, 1995)—masking stimuli are effective in demonstrating differences between healthy and impaired ears.

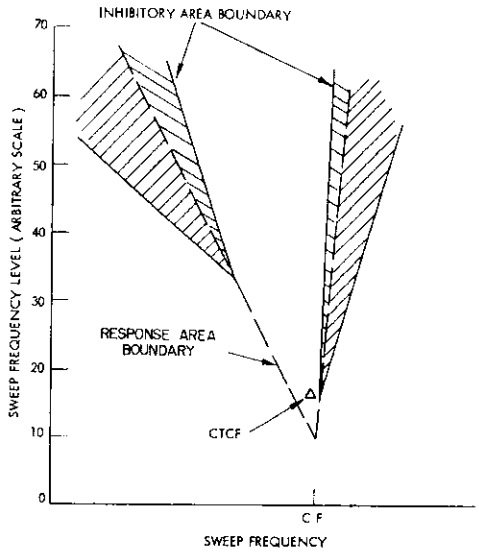

Figure 9.26 Idealized two-tone suppression tuning curve for an AN fiber.
SOURCE: From Sachs & Kiang (1968). Reprinted with permission.

Responses to Combinations of Tones

The simplest and most studied masking stimulus is a second tone; tone-on-tone masking provided one of the earliest and most classic illustrations of auditory nonlinearity: two-tone suppression (Arthur, Pfeiffer, & Suga, 1971; Sachs & Kiang, 1968). The basic illustration of two-tone suppression is the suppression tuning curve (Figure 9.26; note that the term *two-tone suppression* is now used in favor of *two-tone inhibition*). After finding the excitatory threshold tuning curve with a single pure tone, a continuous tone is presented at CF (CTCF) at a fixed level above threshold (indicated by the triangle); then a second tone is varied in frequency and sound level to map the boundary at which it just suppresses the response to the tone at CF. If the frequency and level of the second tone lie within the hatched area (Figure 9.26), this tone is able to suppress the response to the tone at CF. The details of two-tone suppression (e.g., not only its threshold but also the slope at which suppression grows above threshold) vary depending on the CF as well as on the frequency of the supressor relative to CF (Delgutte, 1990). Recent studies of mechanical responses of the basilar membrane have demonstrated that the features of two-tone suppression reported for the AN are present in the mechanics of the inner ear (Cooper, 1996; Nuttall & Dolan, 1993; Ruggero et al., 1992). Furthermore, when the active process is experimentally manipulated (e.g., by applying reversible ototoxic drugs), two-tone suppression is eliminated and recovers with the same time course as does the cochlear amplifier (Ruggero & Rich, 1991). Thus, the effect of the suppressor can be thought of as turning down the gain of the cochlear amplifier (just as a moderate- to high-level tone at CF results in a reduction in amplifier gain). The suppression tuning curve provides information concerning the stimulus frequency range that can affect the gain of the amplifier at a given place (CF).

Responses of AN fibers to harmonic complexes also reveal complex nonlinear interactions (Horst, Javel, & Farley, 1985), which are presumably caused by the interactions of the individual tones and their combined effect on the gain of the cochlear amplifier. Changes in the gain result in a change not only in the magnitude of the response (which is often masked by neural saturation) but also in the phase of responses (discussed earlier). The temporal patterns of responses to complex stimuli are influenced by the relative phases of the responses to the different components of the sounds.

Responses of neurons at higher levels of the auditory pathway to two-tone complexes are more challenging to interpret because they are affected by two-tone suppression at the level of the auditory nerve, as well as by inhibitory interactions at higher levels (e.g., see the response maps in Figure 9.24; Rhode and Greenberg, 1992; Young, 1984, 1998). Two-tone stimuli have been used to investigate the nonlinear response properties of cells in the cochlear nucleus (Nelken, Kim, & Young, 1997; Shofner, Sheft, & Guzman, 1996; Spirou, Davis, Nelken, & Young, 1999).

Responses to Noise and Tones Masked by Noise

Responses of AN fibers to wideband and band-limited noise have been pursued as another approach to the study of the nonlinear response properties of the auditory periphery (Ruggero, 1973; Schalk & Sachs, 1980). Rate-level functions of AN fibers in response to noise typically have a shallower slope than do tone responses. This effect can be understood in terms of the reduction in cochlear amplification by the frequency components in the noise stimulus within the two-tone suppression regions (see Figure 9.26).

Noise responses have been used also as a tool for characterizing peripheral tuning using reverse-correlation techniques (e.g., de Boer & de Jongh, 1978). The reverse-correlation technique provides a transfer-function description (at a given sound level) that can be used to predict responses to other stimuli (Carney & Yin, 1988). Noise has been used also as a tool for testing the cross-correlation model for binaural processing at the level of the MSO (Yin & Chan, 1990) and ICC (Yin, Chan, & Carney, 1987).

The encoding of tones in the presence of wideband noise is a classic problem that has been pursued in many psychophysical studies. Physiologically, responses of AN fibers to tones in the presence of noise have rate-level functions that are shifted to higher levels and have compressed dynamic ranges (Costalupes, Young, & Gibson, 1984; Sinex & Geisler, 1980; Winslow & Sachs, 1988; Young & Barta, 1986). These responses can be interpreted in terms of a wideband suppressive effect elicited by the noise (Sinex & Geisler, 1980) that reduces the gain of the cochlear amplifier. Young and Barta (1986) performed a statistical analysis of discharge rates of AN fibers in comparison with behavioral thresholds and found that performance could be explained by the rates of a few fibers. Miller, Barta, and Sachs (1987) reported that the temporal response properties of AN fibers tuned near the tone frequency provided reliable information for detection of a tone in noise. Neurons with rate-level functions that shift to high sound levels in the presence of noise are also observed at higher levels of the pathway (e.g., auditory cortex; Phillips, 1990). Several binaural physiological studies have investigated responses to tones in the presence of noise, which is relevant to psychophysical studies of binaural detection (e.g., Palmer, Jiang, & McAlpine, 1999).

Responses to Amplitude-Modulated Stimuli

Another class of complex stimuli that has received a significant amount of study, in both

physiology and psychophysics, is amplitude-modulated (AM) sounds. These stimuli typically consist of a tone or noise as a carrier, which is modulated in amplitude by a low-frequency sinusoid. This stimulus is useful because it can be described with relatively few parameters, which can be systematically manipulated. AM stimuli can provide a useful probe into the neural processes involved in analyzing complex stimuli, including naturally occurring sounds with amplitude fluctuations, such as vocalizations.

Detailed studies of neural responses to AM stimuli have been conducted in the AN (e.g., Cooper, Robertson, & Yates, 1993; Joris & Yin, 1992; Palmer, 1982), cochlear nucleus (Frisina et al., 1990; Rhode & Greenberg, 1994), SOC (Joris, 1996; Joris & Yin, 1995, 1998; Kuwada & Batra, 1999), IC (Batra, Kuwada, & Stanford, 1993; Langner & Schreiner, 1988; Rees & Møller, 1983), and auditory cortex (Eggermont, 1999; Schreiner & Urbas, 1988). These studies report modulation transfer functions (MTFs), which describe the magnitude of the response that is synchronized to the envelope of the stimulus as a function of frequency. At the level of the AN, neurons have low-pass MTFs, suggesting that the neurons follow the dynamics of the stimulus envelope for low frequencies and are limited in their ability to follow faster fluctuations (similar to their limited ability to follow the fine structure in the phase-locked responses to pure tones; Joris & Yin, 1992). At higher levels in the auditory pathway, many neurons have band-pass MTFs, suggesting that they are tuned to a specific range of modulation frequencies (e.g., Frisina et al., 1990; Langner & Schreiner, 1988). One interesting feature of neural responses to AM stimuli is their level-dependence, especially in the periphery; envelopes are well represented in the modulated discharge rates of AN fibers near threshold, but the responses saturate at higher levels (Joris & Yin, 1992). The representation of AM across a wide range of SPLs at higher levels in the pathway suggests that (a) information is encoded in AN responses at high SPLs, potentially in the details of the temporal response properties (e.g., nonlinear phase cues), and (b) that neural processing extracts this information into the form of the modulated rates seen at higher levels in the pathway.

Responses to Speech Sounds and Other Vocalizations

Communication sounds represent one of the most interesting classes of acoustic stimuli, but one of the most difficult to study (see Chap. 12, this volume). The use of communication sounds in species that have a limited repertoire of calls can provide an advantage; the specificity of the acoustic cues allows the investigator to zero in on important questions and look for specific processing mechanisms (e.g., bat echolocation, birdsong, frog mating calls). The study of human speech presents a challenge because of the huge diversity of stimuli. The complex acoustical properties of speech are made even more difficult to study by the fact that utterances that are perceived as being the same can have very different acoustical properties (the same problem is faced in automatic speech recognition.) The basic response properties of AN fibers to a wide range of speech sounds have been characterized (reviewed by Delgutte, 1982; May, Le Prell, Hienz, & Sachs, 1997; Sachs, 1984). Nonlinear cochlear amplification influences AN responses to speech sounds by enhancing the representations of spectral peaks, or formants, in the average discharge rate (e.g., Sachs, 1984) and in the temporal response properties, due to capture of synchrony (e.g., Wong, Miller, Calhoun, Sachs, & Young, 1998). The representation of simple speech sounds in terms of discharge rate is enhanced for some cell groups in the AVCN (e.g., May et al., 1997).

An ongoing series of studies of responses to vocalizations (Wang, 1998; Wang, Merzenich, Beitel, & Schreiner, 1995) has focused on the auditory cortex of the marmoset, which has a relatively large, but countable, set of communication sounds (Figure 9.27). These studies have quantitatively characterized the acoustic properties of the animal's vocalizations, and have then systematically studied the responses of neurons to actual vocalizations, as well as to prototypes and sounds that contain only certain temporal or spectral properties of the sounds. One of the most promising outcomes of this approach has been the discovery that mammalian cortical cells are much more responsive than was previously thought, as long as a suitably diverse (and appropriate) arsenal of stimuli are employed.

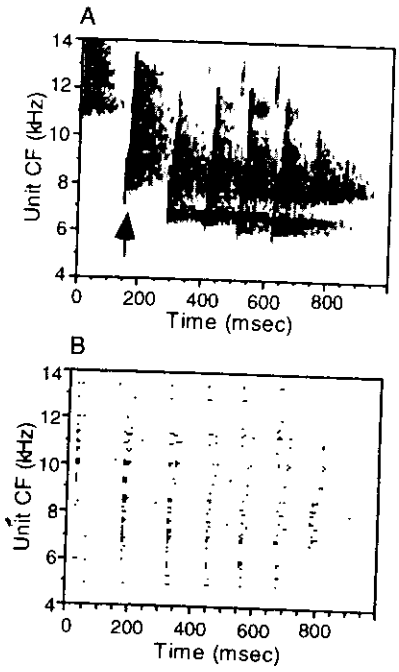

Figure 9.27 Auditory cortex response to a vocalization.

NOTE: A) Spectrogram of a marmoset twitter call. B) Population response from 100 auditory cortex (AI) cells, plotted in 2 ms bins along the time axis. Both temporal and spectral features of the call are represented in the population response.

SOURCE: Reproduced with permission from Wang (1998). Copyright © 1998 by Whurr Publishers Ltd.

PHYSIOLOGY OF SPATIAL HEARING

Unlike vision and touch, for which spatial locations of stimuli are mapped directly onto the receptor arrays, the auditory system must compute the location of stimuli. The information provided for this task consists of the signals from the two ears, which are mapped onto the receptor array in terms of frequency, which is not (in general) correlated to spatial location. By comparing the sounds to the two ears, or by analyzing the profile of the spectrum at either (or both) ears, spatial location can be deduced for simple stimuli in simple acoustical environments. This section begins with a summary of the current knowledge of binaural physiology related to these simple cues and then briefly mentions some of the challenges that are faced as part of the problem of localization in realistic, reverberant environments.

The three primary stimulus features that provide information for localization are interaural time differences (ITDs), interaural level differences (ILDs), and spectral cues (discussed earlier). ITDs are the predominant cue for source azimuth at low frequencies, and the psychoacoustics and physiology of ITD sensitivity have been the subject of a great deal of study. Human listeners are sensitive to changes in ITD on the order of tens of microseconds (reviewed by Durlach & Colburn, 1978). In 1948, Jeffress proposed a neural model for ITD sensitivity that was based on neural delays and coincidence detection of signals from the two ears (Figure 9.28). This model has provided hypotheses for a large number of physiological, anatomical, and behavioral experiments over the last

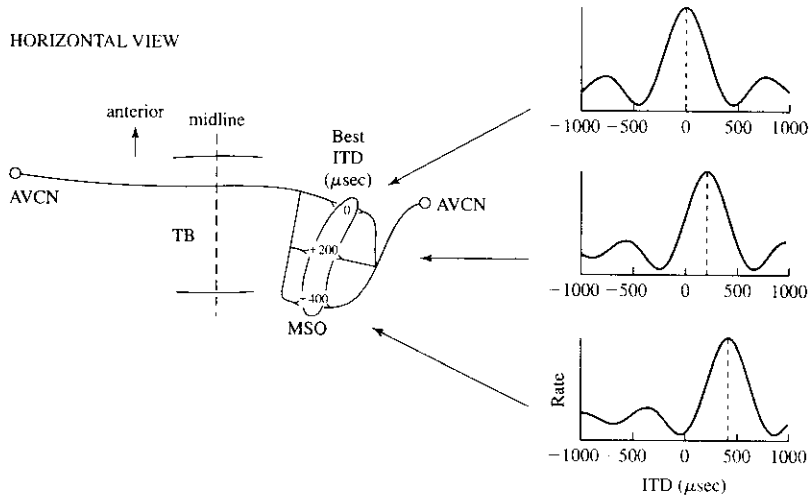

Figure 9.28 Illustration of the anatomical features and basic physiological responses associated with the Jeffress (1948) model.

NOTE: Monaural channels feed into a binaural processor consisting of a bank of cross-correlators that each tap the signal at a different ITD. The contralateral signals arrive with different neural delays, due to the delay line configuration of the axon. There is no apparent delay line on the ipsilateral side, unlike the configuration in Jeffress's original model (Overholt, Rubel, & Hyson, 1992; Smith et al., 1993; Beckius et al., 1999). Cells respond maximally to stimuli with interaural delays (ITDs) that are exactly offset by the neural delays. ITD is mapped out along the length of the MSO in cats (Yin & Chan, 1990) and chicks (Overholt et al., 1992). In owls the ITDs are reported to be mapped across the width of the MSO (Carr & Konishi, 1990).

SOURCE: Figure provided by P. X. Joris, after Joris et al. (1998). Reprinted with permission.

50 years, most of which provide general support for the mechanism of binaural coincidence detection (or, more generally, cross-correlation) in the MSO (e.g., Beckius et al., 1999; Carr & Konishi, 1990; Goldberg & Brown, 1969; Overholt et al., 1992; Smith et al., 1993; Yin & Chan, 1990; reviewed by Kuwada & Yin, 1997; Joris, Smith, & Yin, 1998).

MSO cells are classically described as EE, receiving excitatory inputs from bushy cells in the AVCN of both sides. Their exquisite sensitivity to interaural times (on the order of tens of μ-s, times much smaller than the duration of the input action potentials) can be explained by the nonlinear membrane properties of these cells (Smith, 1995). A slow, low-threshold K+ channel (similar to that described in AVCN bushy cells; Manis & Marx, 1991), which is partially open at rest, is further activated by an excitatory input. In response to a subthreshold input, the activation of the slow, low-threshold K+ channel results in a drop in the membrane resistance, which lasts for a relatively long time due to the long time-constant of the channel. A subsequent input is thus not able to depolarize the cell. The only event that can result in depolarizing the cell to threshold is the coincident arrival of excitatory inputs that act together before the low-threshold K+ channel has a chance to drop the membrane resistance (reviewed by Trussell, 1999).

Recent studies of ITD sensitivity, both in the MSO and at the level of the IC, have begun to explore the role of inhibitory inputs to these

cells (Grothe & Park, 1998). Physiologically based models for sound localization based on ITD have also gone beyond the original Jeffress model to incorporate inhibitory inputs at the level of the MSO (Brughera, Stutman, Carney, & Colburn, 1996), as well as higher-order binaural processing involving the DNLL and IC (Cai, Carney, & Colburn, 1998a, 1998b). Finally, although sensitivity to ITDs is primarily associated with low-frequency processing, subjects are also sensitive to ITDs of the envelopes of complex high-frequency sounds (e.g., Henning, 1974). Physiological studies of ITD sensitivity in the high-frequency regions of the LSO demonstrate that these cells are sensitive to ITDs. This sensitivity is related to their sensitivity to dynamic ILDs, which are created by the envelope ITDs (Joris & Yin, 1995).

ILDs are a major cue for localization of high-frequency sounds (discussed earlier). The LSO, which is biased toward high frequencies, has long been associated with establishing the sensitivity to ILDs by comparison of the excitatory input from the ipsilateral AVCN and inhibitory input (via the MNTB) from the contralateral AVCN (reviewed by Irvine 1986, 1992). For this mechanism to apply over a wide range of sound levels, these cells must depend strongly on the rate information that is initially provided by nonsaturating AN fibers (discussed earlier).

Responses of neurons in the IC and MGB to ITDs and ILDs reflect, in general, the first-order binaural process that occurs in the brainstem, with some sharpening of the representation occurring at higher levels (e.g., Ivarsson, de Ribaupierre, & de Ribaupierre, 1988; Stanford, Kuwada, & Batra, 1992). However, there are cases for which it is clear that further binaural processing, in particular convergence across cells tuned to different ITDs, must occur above the level of the SOC (Kuwada, Stanford, & Batra, 1987; McAlpine, Jiang, & Palmer, 1998).

A separate pathway has been indicated for the processing of spectral cues. The response properties of type IV cells in the DCN (see Figure 9.24) led to the hypothesis that the responses of these cells represent the spectral notches associated with monaural spectral cues (e.g., Young, Spirou, Rice, & Voigt, 1992). These cells are inhibited by spectral notches near CF (Imig, Bibikov, Poirier, & Samson, 2000; Joris, 1998; Nelken & Young, 1994; Spirou & Young, 1991). Behavioral studies involving lesions of the dorsal acoustic stria (the output pathway of the DCN) show little deficit in discrimination of sounds on the vertical meridian, for which spectral cues are most important (Sutherland, Glendenning, & Masterton, 1998). However, this lesion does affect an animal's ability to orient toward sounds in this plane (Sutherland, Masterton, & Glendenning, 1998), suggesting that other pathways may be able to analyze the spectral cues but that the DCN is involved in the orientation response.

Physiological studies of spatial hearing at higher levels of the pathway have explored interactions between the different components of these three spatial cues. Although the cues can be independently manipulated using stimuli delivered over headphones, the three cues covary for free-field stimuli. Using recordings of spectral cues in the ear canal of the cat (e.g., Musicant, Chang, & Hind, 1990), and by manipulating the ITDs, ILDs, and spectral profiles, the relative contributions of these cues to the responses of IC neurons have been investigated (e.g., Delgutte, Joris, Litovsky, & Yin, 1999). The spatial tuning of MGB and cortical neurons has also been studied with wideband free-field stimuli that include combinations of localization cues (e.g., Brugge et al., 1994; Imig, Poirier, Irons, & Samson, 1997; Samson, Clarey, Barone, & Imig, 1993). A recent study involving a combination of neuroanatomical and physiological techniques described separate (but

interacting) pathways for "what" and "where" processing in the auditory cortex (Romanski et al., 1999); these pathways were compared to similar dual-stream organization of the visual and somatosensory cortical pathways. The temporal response patterns of cortical neurons to free-field sounds may also contribute to encoding of spatial position in terms of discharge rate, particularly in cells with "panoramic" responses to stimuli from all directions (Middlebrooks, Clock, Xu, & Green, 1994).

The spatial cues of ITDs and ILDs and spectral cues provide straightforward information about azimuth and elevation of a sound source in a simple, anechoic (echo-free) environment. However, in a realistic environment that contains multiple sound sources and reverberations, these cues are highly distorted. However, the most realistic percepts of space are achieved by simulating reverberant sound fields. The auditory system must do much more than simply compute time and level differences, or detect spectral peaks and notches, in order to localize stimuli in reverberant environments. Suppression of echoes (which is one aspect of the precedence effect; e.g. Blauert, 1997; Litovsky, Colburn, Yost, & Guzman, 1999) by mechanisms such as long-duration inhibition is believed to play an important role in processing complex acoustical environments (e.g., Fitzpatrick, Kuwada, Kim, Parham, & Batra, 1999; Litovsky & Yin, 1998a, 1998b).

FUTURE CHALLENGES

This review has focused on several areas that either are new or have received increasing attention in the years since the last edition of this handbook was published. It is interesting to consider the areas that might be the focus of a future review of this nature. Three areas come to mind:

First, the relationships between physiological response properties and psychophysics and behavior have been based on a combination of lesion studies and comparison of the physiological responses and psychophysical performance. For the most part, the latter have been limited to simple stimuli and simple psychophysical tasks, partly because of the daunting problem of recording or simulating neural population responses to complex sounds. Furthermore, the most interesting difficulties for the impaired auditory system are with complex stimuli, especially in situations in which noise maskers are present. New computational tools for simulating neural responses and for quantifying information in population responses should allow great progress on this front in the next few years.

A related challenge is in developing a better understanding of the active process in the cochlea and how it is involved in encoding complex stimuli. Improved techniques for measuring and imaging the motion of the basilar membrane should allow tests for different hypotheses concerning the electromechanical mechanisms involved in the cochlear amplifier. These tests will allow a clearer picture of the influence of the active process on responses of AN fibers and thus of its impact on encoding complex sounds. Again, it is for complex sounds that the benefits of the cochlear amplifier seem to be most important, as it is these stimuli that present the greatest difficulties for hard-of-hearing listeners in whom the active process is damaged.

Finally, the role of the descending auditory pathways will be an important area for progress in the next few years. The use of awake and behaving animals provides an experimental approach to probing this system, which appears to be as complex as the ascending pathways. The influence of the descending pathways on information processing

at all levels of the auditory pathway and their interaction with the active process in the cochlea are important areas for future study.

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