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Abstract

Audition is the process by which organisms use sound to derive information about the world. This chapter aims to provide a bird's-eye view of contemporary audition research, spanning systems and cognitive neuroscience as well as cognitive science. The author provides brief overviews of classic areas of research as well as some central themes and advances from the past ten years. The chapter covers the sound transduction of the cochlea, subcortical and cortical anatomical and functional organization of the auditory system, amplitude modulation and its measurement, adaptive coding and plasticity, the perception of sound sources (with a focus on the classic research areas of location, loudness, and pitch), and auditory scene analysis (including sound segregation, streaming, filling in, and reverberation perception). The chapter concludes with a discussion of where hearing research seems to be headed at present.

Key Words: sound transduction, auditory system anatomy, modulation, adaptation, plasticity, pitch perception, auditory scene analysis, sound segregation, streaming, reverberation

Introduction

From the cry of a baby to the rumble of a thunderclap, many events in the world produce sound. Sound is created when matter in the world vibrates, and takes the form of pressure waves that propagate through the air, containing clues about the environment around us. Audition is the process by which organisms utilize these clues to derive information about the world.

Audition is a crucial sense for most organisms. Humans, in particular, use sound to infer a vast number of important things—what someone said, their emotional state when they said it, and the whereabouts and nature of objects we cannot see, to name but a few. When hearing is impaired (via congenital conditions, noise exposure, or aging), the consequences can be devastating, such that a large industry is devoted to the design of prosthetic hearing devices.

As listeners we are largely unaware of the computations underlying our auditory system's success, but they represent an impressive feat of engineering. The computational challenges of everyday audition are reflected in the gap between biological and machine hearing systems—machine systems for interpreting sound currently fall far short of human abilities. Understanding the basis of our success in perceiving sound will hopefully help us to replicate it in machine systems and to restore it in biological auditory systems when their function becomes impaired.

The goal of this chapter is to provide a bird's-eye view of contemporary hearing research. I provide brief overviews of classic areas of research as well as some central themes and advances from the past ten years. The first section describes the sensory transduction of the cochlea. The second section outlines subcortical and cortical functional organization.

The third section discusses modulation and its measurement by subcortical and cortical regions of the auditory system, a key research focus of the past few decades. The fourth section describes adaptive coding and plasticity, encompassing the relationship between sensory coding and the environment as well as its adaptation to task demands. The fifth section discusses the perception of sound sources, focusing on location, loudness, and pitch. The sixth section presents an overview of auditory scene analysis. I conclude with a discussion of where hearing research is headed at present. Because other chapters in this handbook are devoted to auditory attention, music, and speech, I will largely avoid these topics.

The Problem

Just by listening, we can routinely apprehend many aspects of the world around us: the size of a room in which we are talking, whether it is windy or raining outside, the speed of someone approaching from behind, or whether the surface someone is walking on is gravel or marble. These abilities are nontrivial because the properties of the world that are of interest to a listener are generally not explicit in the acoustic input—they cannot be easily recognized or discriminated using the sound waveform itself. The brain must process the sound entering the ear to generate representations in which the properties of interest are more evident. One of the main objectives of hearing science is to understand the nature of these transformations and their instantiation in the brain.

Like other senses, audition is further complicated by a second challenge—that of scene analysis. Although listeners are generally interested in the properties of individual objects or events, the ears are rarely presented with the sounds from isolated sources. Instead, the sound signal that reaches the ear is typically a mixture of sounds from different sources. Such situations occur frequently in natural auditory environments, for example, in social settings, where a single speaker of interest may be talking among many others, and in music. From the mixture it receives as input, the brain must derive representations of the individual sound sources of interest, as are needed to understand someone's speech, recognize a melody, or otherwise guide behavior. Known as the “cocktail party problem” (Cherry, 1953), or “auditory scene analysis” (Bregman, 1990), this problem has analogues in other sensory modalities, but the auditory version presents some uniquely challenging features.

Sound Measurement—The Peripheral Auditory System

The transformation of the raw acoustic input into representations that are useful for behavior is apparently instantiated over many brain areas and stages of neural processing, spanning the cochlea, midbrain, thalamus, and cortex (Figure 8.1). The early stages of this cascade are particularly intricate in the auditory system relative to other sensory systems, with many processing stations occurring before the cortex. The sensory organ of the cochlea is itself a complex multicomponent system, whose investigation remains a considerable challenge—the mechanical nature of the cochlea renders it much more difficult to probe (e.g., with electrodes) than the retina or olfactory epithelium, for instance. Peripheral coding of sound is also unusual relative to that of other senses in its degree of clinical relevance. Unlike vision, for which the most common forms of dysfunction are optical in nature, and can be fixed with glasses, hearing impairment typically involves altered peripheral neural processing, and its treatment has benefited from a detailed understanding of the processes that are altered. Much of hearing research has accordingly been devoted to understanding the nature of the measurements made by the auditory periphery, and they provide a natural starting point for any discussion of how we hear.

Frequency Selectivity and the Cochlea

Hearing begins with the ear, where the sound pressure waveform carried by the air is transduced into action potentials that are sent to the brain via the auditory nerve. Action potentials are a binary code, but what is conveyed to the brain is far from simply a binarized version of the incoming waveform. The transduction process is marked by several distinctive signal transformations, the most obvious of which is produced by frequency tuning.

The coarse details of sound transduction are well understood (Figure 8.2). Sound induces vibrations of the eardrum, which are transmitted via the bones of the middle ear to the cochlea, the sensory organ of the auditory system. The cochlea is a coiled, fluid-filled tube, containing several membranes that extend along its length and vibrate in response to sound. Transduction of this mechanical vibration into an electrical signal occurs in the organ of Corti, a mass of cells attached to the basilar membrane. The organ of Corti in particular contains what are known as hair cells, named for the stereocilia that protrude from them. The *inner hair cells* are

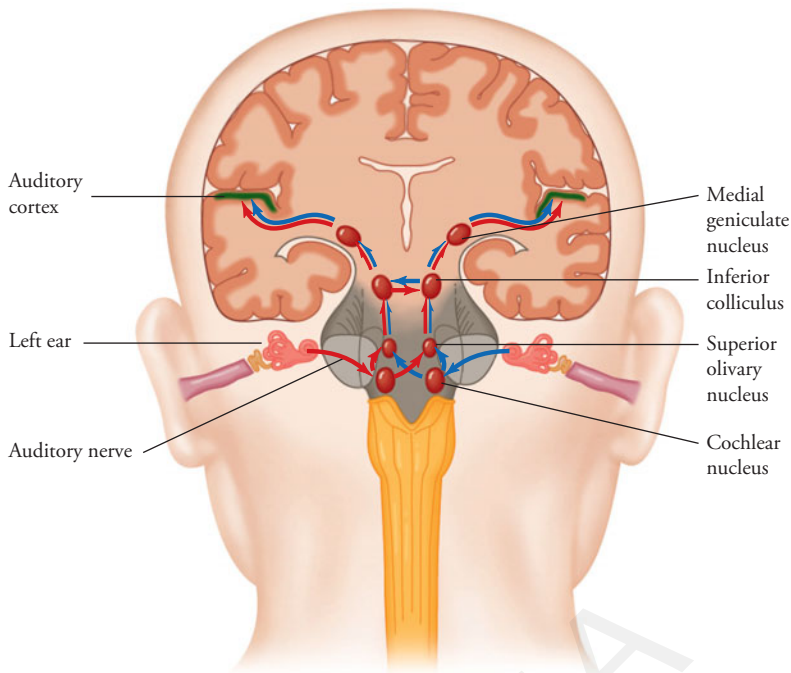


Figure 8.1 The auditory system. Sound is transduced by the cochlea, processed by an interconnected set of subcortical areas, and then fed into the core regions of auditory cortex.

responsible for sound transduction. When the section of membrane on which they lie vibrates, the resulting deformation of the hair cell body opens mechanically gated ion channels, inducing a voltage change within the cell. Neurotransmitter release is triggered by the change in membrane potential, generating action potentials in the auditory nerve fiber that the hair cell synapses with. This electrical signal is carried by the auditory nerve fiber to the brain.

The frequency tuning of the transduction process occurs because different parts of the basilar membrane vibrate in response to different frequencies. This is partly due to mechanical resonances—the thickness and stiffness of the membrane vary along its length, producing a different resonant frequency at each point. However, the mechanical resonances are actively enhanced via a feedback process, believed to be mediated largely by a second set of cells, called the *outer hair cells*. The outer hair cells abut the inner hair cells on the organ of Corti and serve to alter the basilar membrane vibration rather than transduce it. They expand and contract in response to sound through mechanisms that are only partially understood (Ashmore, 2008; Dallos, 2008; Hudspeth, 2008). Their motion alters the passive mechanics of the basilar membrane, amplifying

the response to low-intensity sounds and tightening the frequency tuning of the resonance. The upshot is that high frequencies produce vibrations at the basal end of the cochlea (close to the eardrum), whereas low frequencies produce vibrations at the apical end (far from the eardrum), with frequencies in between stimulating intermediate regions. The auditory nerve fibers that synapse onto individual inner hair cells are thus frequency tuned—they fire action potentials in response to a local range of frequencies, collectively providing the rest of the auditory system with a frequency decomposition of the incoming waveform. As a result of this behavior, the cochlea is often described functionally as a set of bandpass filters—filters that each pass frequencies within a particular range, and eliminate those outside of it.

The frequency decomposition of the cochlea is conceptually similar to the Fourier transform, but differs in the way that the frequency spectrum is decomposed. Whereas the Fourier transform uses linearly spaced frequency bins, each separated by the same number of hertz, the tuning bandwidth of auditory nerve fibers increases with their preferred frequency. This characteristic can be observed in Figure 8.3A, in which the frequency response of a set of auditory nerve fibers is

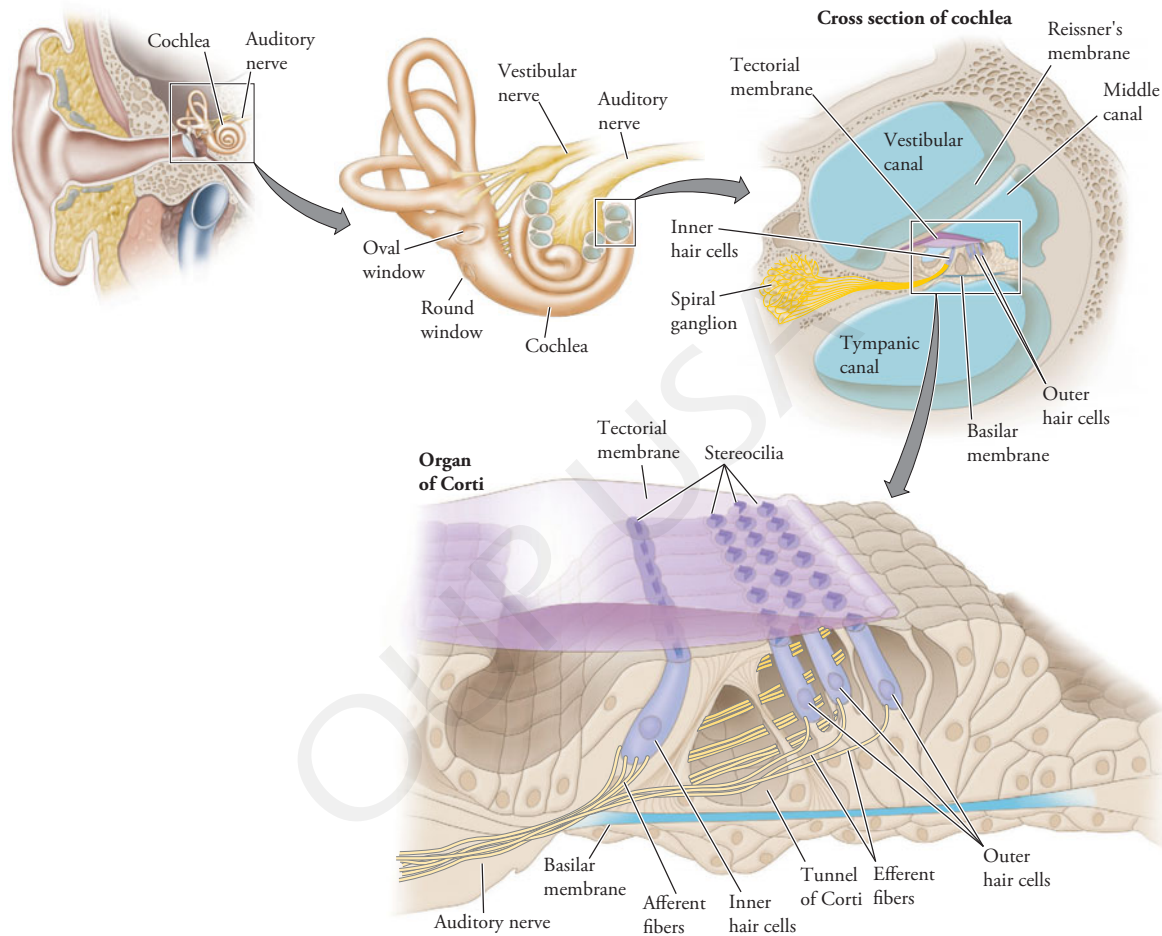


Figure 8.2 Structure of the peripheral auditory system. **Top right**, Diagram of ear. The eardrum transmits sound to the cochlea via the middle ear bones (ossicles). **Top middle**, Inner ear. The semicircular canals abut the cochlea. Sound enters the cochlea via the oval window and causes vibrations along the basilar membrane, which runs through the middle of the cochlea. **Top left**, Cross section of cochlea. The organ of Corti, containing the hair cells that transduce sound into electrical potentials, sits on top of the basilar membrane. **Bottom**, Schematic of section of organ of Corti. The shearing that occurs between the basilar and tectorial membranes when they vibrate (in response to sound) causes the hair cell stereocilia to deform. The deformation causes a change in the membrane potential of the inner hair cells, transmitted to the brain via afferent auditory nerve fibers. The outer hair cells, which are three times more numerous than the inner hair cells, serve as a feedback system to alter the basilar membrane motion, tightening its tuning and amplifying the response to low amplitude sounds.

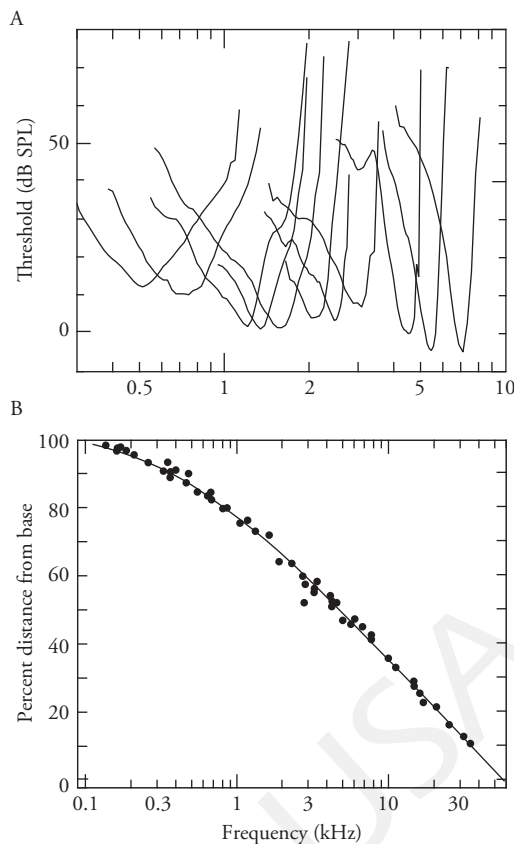


Figure 8.3 Frequency selectivity. **A**, Threshold tuning curves of auditory nerve fibers from a cat ear, plotting the level that was necessary to evoke a criterion increase in firing rate for a given frequency (Miller, Schilling, et al., 1997). **B**, The tonotopy of the cochlea. The position along the basilar membrane at which auditory nerve fibers synapse with a hair cell (determined by dye injections) is plotted vs. their best frequency (Lieberman, 1982).

Both parts of this figure are courtesy of Eric Young, 2010., who replotted data from the original sources.

plotted on a logarithmic frequency scale. Although the lowest frequency fibers are broader on a log scale than the high-frequency fibers, in absolute terms their bandwidths are much lower—several hundred hertz instead of several thousand. The distribution of best frequency along the cochlea follows a roughly logarithmic function, apparent in Figure 8.3B, which plots the best frequency of a large set of nerve fibers against the distance along the cochlea of the hair cell that they synapse with. These features of frequency selectivity are present in most biological auditory systems. It is partly for this reason that a log scale is commonly used for frequency.

Cochlear frequency selectivity has a host of perceptual consequences—our ability to detect a particular frequency is limited largely by the signal-to-noise ratio of the cochlear filter centered on the frequency, for instance. There are many treatments of frequency selectivity and perception (Moore,

2003); it is perhaps the most studied aspect of hearing.

Although the frequency tuning of the cochlea is uncontroversial, the teleological question of *why* the cochlear transduction process is frequency-tuned remains less settled. How does frequency tuning aid the brain's task of recovering useful information about the world from its acoustic input? Over the past two decades, a growing number of researchers have endeavored to explain properties of sensory systems as optimal for the task of encoding natural sensory stimuli, initially focusing on coding questions in vision, and using notions of efficiency as the optimality criterion (Field, 1987; Olshausen & Field, 1996). Lewicki and colleagues have applied similar concepts to hearing, using algorithms that derive efficient and sparse representations of sounds (Lewicki, 2002; Smith & Lewicki, 2006), properties believed to be desirable of early sensory representations. They report that for speech, or for

combinations of environmental sounds and animal vocalizations, efficient representations for sound look much like the representation produced by auditory nerve fiber responses—sounds are represented with filters whose tuning is localized in frequency. Interestingly, the resulting representations share the dependence of bandwidth on frequency found in biological hearing—bandwidths increase with frequency as they do in the ear. Moreover, representations derived in the same way for “unnatural” sets of sounds, such as samples of white noise, do not exhibit frequency tuning, indicating that the result is at least somewhat specific to the sorts of sounds commonly encountered in the world. These results suggest that frequency tuning provides an efficient means to encode the sounds that were likely of importance when the auditory system evolved, possibly explaining its ubiquitous presence in auditory systems. It remains to be seen whether this framework can explain potential variation in frequency tuning bandwidths across species (humans have recently been claimed to possess narrower tuning than other species (Joris, Bergevin, et al., 2011; Shera, Guinan, et al., 2002), or the broadening of frequency tuning with increasing sound intensity (Rhode, 1978), but it provides one means by which to understand the origins of peripheral auditory processing.

Amplitude Compression

A second salient transformation that occurs in the cochlea is that of amplitude compression, whereby the mechanical response of the cochlea to a soft sound (and thus the neural response as well) is larger than would be expected given the response to a loud sound. The response elicited by a sound is thus not proportional to the sound’s amplitude (as it would be if the response were linear), but rather to a compressive nonlinear function of amplitude. The dynamic range of the response to sound is thus “compressed” relative to the dynamic range of the acoustic input. Whereas the range of audible sounds covers five orders of magnitude, or 100 dB, the range of cochlear response covers only one or two orders of magnitude (Ruggero, Rich, et al., 1997).

Compression appears to serve to map the range of amplitudes that the listener needs to hear (i.e., those commonly encountered in the environment), onto the physical operating range of the cochlea. Without compression, it would have to be the case that either sounds low in level would be inaudible, or sounds high in level would be indiscriminable (for they would fall outside the range that could

elicit a response change). Compression permits very soft sounds to produce a physical response that is (just barely) detectable, while maintaining some discriminability of higher levels.

The compressive nonlinearity is often approximated as a power function with an exponent of 0.3 or so. It is not obvious why the compressive nonlinearity should take the particular form that it does. Many different functions could in principle serve to compress the output response range. It remains to be seen whether compression can be explained in terms of optimizing the encoding of the input, as has been proposed for frequency tuning (but see Escabi, Miller, et al., 2003). Most machine hearing applications also utilize amplitude compression before analyzing sound, however, and it is widely agreed to be useful to amplify low amplitudes relative to large when processing sound.

Amplitude compression was first noticed in measurements of the physical vibrations of the basilar membrane (Rhode, 1971; Ruggero, 1992) but is also apparent in auditory nerve fiber responses (Yates, 1990) and is believed to account for a number of perceptual phenomena (Moore & Oxenham, 1998). The effects of compression are related to “cochlear amplification,” in that compression results from response enhancement that is limited to low-intensity sounds. Compression is achieved in part via the outer hair cells, whose motility modifies the motion of the basilar membrane in response to sound (Ruggero & Rich, 1991). Outer hair cell function is frequently altered in hearing impairment, one consequence of which is a loss of compression, something that hearing aids attempt to mimic.

Neural Coding in the Auditory Nerve

Although frequency tuning and amplitude compression are at this point uncontroversial and relatively well understood, several other empirical questions about peripheral auditory coding remain unresolved. One important issue involves the means by which the auditory nerve encodes frequency information. As a result of the frequency tuning of the auditory nerve, the spike rate of a nerve fiber contains information about frequency (a large firing rate indicates that the sound input contains frequencies near the center of the range of the fiber’s tuning). Collectively, the firing rates of all nerve fibers could thus be used to estimate the instantaneous spectrum of a sound. However, spike timings also carry frequency information. At least for low frequencies, the spikes that are fired in response to sound do not occur randomly,

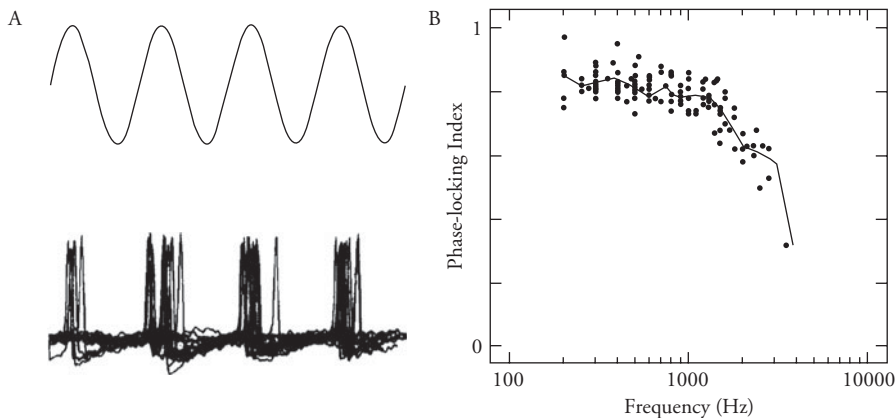


Figure 8.4 Phase locking. **A**, A 200-Hz pure tone stimulus waveform aligned in time with several overlaid traces of an auditory nerve fiber's response to the tone. Note that the spikes are not uniformly distributed in time, but rather occur at particular phases of the sinusoidal input. **B**, A measure of phase locking for each of a set of nerve fibers in response to different frequencies. Phase locking decreases at high frequencies.

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but rather tend to occur at the peak displacements of the basilar membrane vibration. Because the motion of a particular section of the membrane mirrors the bandpass-filtered sound waveform, the spikes occur at the waveform peaks (Rose, Brugge, et al., 1967). If the input is a single frequency, spikes thus occur at a fixed phase of the frequency cycle (Figure 8.4A). This behavior is known as *phase locking* and produces spikes at regular intervals corresponding to the period of the frequency. The spike timings thus carry information that could potentially augment or supercede that conveyed by the rate of firing.

Phase locking degrades in accuracy as frequency is increased (Figure 8.4B) due to limitations in the temporal fidelity of the hair cell membrane potential (Palmer & Russell, 1986) and is believed to be largely absent for frequencies above 4 kHz in most mammals, although there is some variability across species (Johnson, 1980; Palmer & Russell, 1986). The appeal of phase locking as a code for sound frequency is partly due to features of rate-based frequency selectivity that are unappealing from an engineering standpoint. Although frequency tuning in the auditory system (as measured by auditory nerve spike rates or psychophysical masking experiments) is narrow at low stimulus levels, it broadens considerably as the level is raised (Glasberg & Moore, 1990; Rhode, 1978). Phase locking, by comparison, is robust to sound level—even though a nerve fiber responds to a broad range of frequencies when the level is high, the time intervals between spikes continue to convey frequency-specific information, as the peaks in the bandpass-filtered waveform tend to

occur at integer multiples of the periods of the component frequencies.

Our ability to discriminate frequency is impressive, with thresholds on the order of 1 percent (Moore, 1973), and there has been long-standing interest in whether this ability in part depends on fine-grained spike timing information (Heinz, Colburn, et al., 2001). Although phase locking remains uncharacterized in humans because of the unavailability of human auditory nerve recordings, it is presumed to occur in much the same way as in nonhuman auditory systems. Moreover, several psychophysical phenomena are consistent with a role for phase locking in human hearing. For instance, frequency discrimination becomes much poorer for frequencies above 4 kHz (Moore, 1973), roughly the point at which phase locking declines in nonhuman animals. The fundamental frequency of the highest note on a piano is also approximately 4 kHz; this is also the point above which melodic intervals between pure tones (tones containing a single frequency) are much less evident (Attneave & Olson, 1971; Demany & Semal, 1990). These findings provide some circumstantial evidence that phase locking is important for deriving precise estimates of frequency, but definitive evidence remains elusive. It remains possible that the perceptual degradations at high frequencies reflect a lack of experience with such frequencies, or their relative unimportance for typical behavioral judgments, rather than a physiological limitation.

The upper limit of phase locking is also known to decrease markedly at each successive stage of the auditory system (Wallace, Anderson, et al., 2007).

By primary auditory cortex, the upper cutoff is in the neighborhood of a few hundred hertz. It would thus seem that the phase locking that occurs robustly in the auditory nerve would need to be rapidly transformed into a spike rate code if it were to benefit processing throughout the auditory system. Adding to the puzzle is the fact that frequency tuning is not thought to be dramatically narrower at higher stages in the auditory system. Such tightening might be expected if the frequency information provided by phase-locked spikes was transformed to yield improved rate-based frequency tuning at subsequent stages (but see Bitterman, Mukamel, et al., 2008).

II. Organization of the Auditory System

Subcortical Pathways

The auditory nerve feeds into a cascade of interconnected subcortical regions that lead up to the auditory cortex, as shown in Figure 8.1. The subcortical auditory pathways have complex anatomy, only some of which is depicted in Figure 8.1. In contrast to the subcortical pathways of the visual system, which are often argued to largely preserve the representation generated in the retina, the subcortical auditory areas exhibit a panoply of interesting response properties not found in the auditory nerve, many of which remain active topics of investigation. Several subcortical regions will be referred to in the sections that follow in the context of other types of acoustic measurements or perceptual functions.

Feedback to the Cochlea

Like other sensory systems, the auditory system can be thought of as a processing cascade, extending from the sensory receptors to cortical areas believed to mediate auditory-based decisions. This “feedforward” view of processing underlies much auditory research. As in other systems, however, feedback from later stages to earlier ones is ubiquitous and substantial, and in the auditory system is perhaps even more pronounced than elsewhere in the brain. Unlike the visual system, for instance, the auditory pathways contain feedback extending all the way back to the sensory receptors. The function of much of this feedback remains poorly understood, but one particular set of projections—the cochlear efferent system—has been the subject of much discussion.

Efferent connections to the cochlea originate primarily from the superior olivary nucleus, an area of the midbrain a few synapses removed from the cochlea (see Figure 8.1, although the efferent pathways are not shown). The superior olive is divided into two subregions, medial and lateral, and to first

order, these give rise to two efferent projections: one from the medial superior olive to the outer hair cells, called the *medial olivocochlear* (MOC) *efferents*, and one from the lateral superior olive to the inner hair cells, called the *lateral olivocochlear* (LOC) *efferents* (Elgoyhen & Fuchs, 2010). The MOC efferents have been relatively well studied. Their activation (e.g., by electrical stimulation) is known to reduce the basilar membrane response to low-intensity sounds, and causes the frequency tuning of the response to broaden. This is probably because the MOC efferents inhibit the outer hair cells, which are crucial to amplifying the response to low-intensity sounds and to sharpening frequency tuning.

The MOC efferents may serve a protective function by reducing the response to loud sounds (Rajan, 2000), but their most commonly proposed function is to enhance the response to transient sounds in noise (Guinan, 2006). When the MOC fibers are severed, for instance, performance on tasks involving discrimination of tones in noise is reduced (May & McQuone, 1995). Noise-related MOC effects are proposed to derive from its influence on adaptation, which when induced by background noise, reduces the detectability of transient foreground sounds by decreasing the dynamic range of the auditory nerve’s response. Because MOC activation reduces the response to ongoing sound, adaptation induced by continuous background noise is reduced, thus enhancing the response to transient tones that are too brief to trigger the MOC feedback themselves (Kawase, Delgutte, et al., 1993; Winslow & Sachs, 1987). Another interesting but controversial proposal is that the MOC efferents play a role in auditory attention. One study, for instance, found that patients whose vestibular nerve (containing the MOC fibers) had been severed were better at detecting unexpected tones after the surgery, suggesting that selective attention had been altered so as to prevent the focusing of resources on expected frequencies (Scharf, Magnan, et al., 1997). See Guinan, 2006, for a recent review of these and other ideas about MOC efferent function.

Less is known about the LOC efferents. One recent study found that destroying the LOC efferents to one ear in mice caused binaural responses to become “unbalanced” (Darrow, Maison, et al., 2006)—when sounds were presented binaurally at equal levels, responses from the two ears that were equal under normal conditions were generally not equal following the surgical procedure. The suggestion was that the LOC efferents serve to regulate binaural responses so that interaural intensity

differences, crucial to sound localization (see below), can be accurately registered.

Tonotopy

Although many of the functional properties of subcortical and cortical neurons are distinct from what is found in auditory nerve responses, frequency tuning persists. Every subcortical region contains frequency-tuned neurons, and neurons tend to be spatially organized to some extent according to their best frequency, forming “tonotopic” maps. This organization is also evident in the cortex. Many cortical neurons have a preferred frequency, although they are often less responsive to pure tones (relative to sounds with more complex spectra) and often have broader tuning than neurons in peripheral stages (Moshitch, Las, et al., 2006). Cortical frequency maps were one of the first reported findings in single-unit neurophysiology studies of the auditory cortex in animals, and have since been found using functional magnetic resonance imaging (fMRI) in humans (Formisano, Kim, et al., 2003; Humphries, Liebenthal, et al., 2010; Talavage, Sereno, et al., 2004) as well as monkeys (Petkov, Kayser, et al., 2006). Figure 8.5 shows

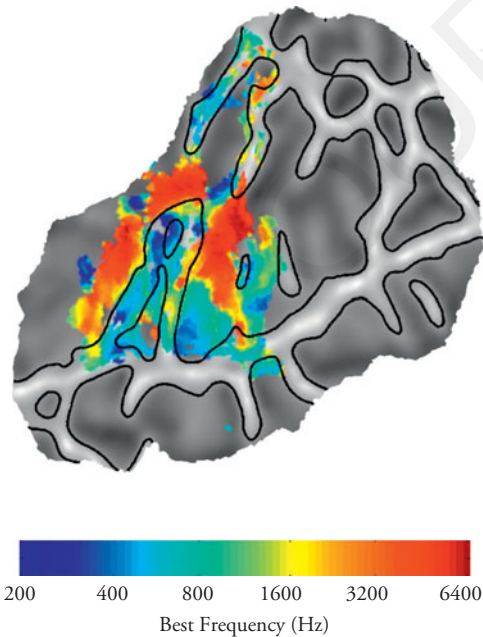


Figure 8.5 Tonotopy. Best frequency of voxels in the human auditory cortex, measured with fMRI, plotted on the flattened cortical surface (Humphries, Liebenthal, et al., 2010). Note that the best frequency varies quasi-smoothly over the cortical surface and is suggestive of two maps that are approximately mirror images of each other.

an example of a tonotopic map obtained in a human listener with fMRI. Although never formally quantified, it seems that tonotopy is less robust than the retinotopy found in the visual system (evident, e.g., in recent optical imaging studies; Bandyopadhyay, Shamma, et al., 2010; Rothschild, Nelken, et al., 2010).

Although the presence of some degree of tonotopy in the cortex is beyond question, its functional importance remains unclear. Frequency selectivity is not the end goal of the auditory system, and it does not obviously bear much relevance to behavior, so it is unclear why tonotopy would be a dominant principle of organization throughout the auditory system. It may be that other principles of organization are in fact more prominent but have yet to be discovered. At present, however, tonotopy remains a staple of textbooks and review chapters such as this.

Functional Organization

Largely on grounds of anatomy and connectivity, mammalian auditory cortex is standardly divided into three sets of regions, shown in Figure 8.6: a core region receiving direct input from the thalamus, a “belt” region surrounding it, and a “parabelt” region beyond that (Kaas & Hackett, 2000; Sweet, Dorph-Petersen, et al., 2005). Within these areas, tonotopy is often used to delineate distinct fields (a field is typically considered to contain a single tonotopic map). The core region is divided in this way into areas A1, R (for rostral), and RT (for rostrotemporal) in primates, with A1 and R receiving direct input from the medial geniculate nucleus of the thalamus. There are also multiple belt areas (Petkov, Kayser, et al., 2006), each receiving input from the core areas. Functional imaging reveals many additional areas that respond to sound in the awake primate, including parts of parietal and frontal cortex (Poremba, Saunders, et al., 2003). There are some indications that the three core regions have different properties (Bendor & Wang, 2008), and that stimulus selectivity increases in complexity from the core to surrounding areas (Kikuchi, Horwitz, et al., 2010; Rauschecker & Tian, 2004; Tian & Rauschecker, 2004), suggestive of a hierarchy of processing. However, at present, there is not a single widely accepted framework for auditory cortical organization. Several principles of organization have been proposed with varying degrees of empirical support; here, we review a few of them.

Some of the proposed organizational principles clearly derive inspiration from the visual system. For

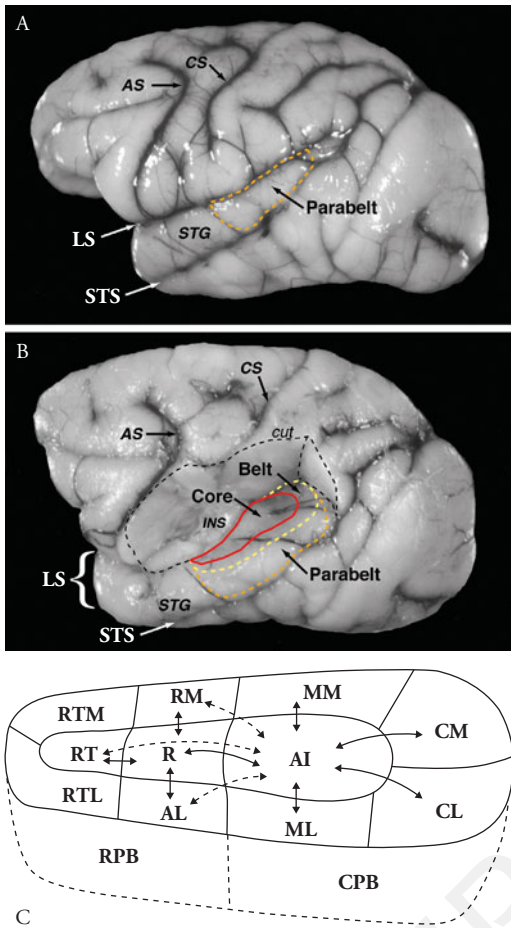


Figure 8.6 Anatomy of auditory cortex. **A**, Lateral view of macaques cortex. The approximate location of the parabelt region is indicated with *dashed orange lines*. **B**, View of the brain from (A) after removal of the overlying parietal cortex. Approximate locations of the core (*solid red line*), belt (*dashed yellow line*), and parabelt (*dashed orange line*) regions are shown. AS, arcuate sulcus; CS, central sulcus; INS, insula; LS, lateral sulcus; STG, superior temporal gyrus; STS, superior temporal sulcus. **C**, Connectivity between core and belt regions. *Solid lines with arrows* denote dense connections; *dashed lines with arrows* denote less dense connections. RT, R, and A1 compose the core; all three subregions receive input from the thalamus. The areas surrounding the core make up the belt, and the two regions outlined with *dashed lines* make up the parabelt. The core has few direct connections with the parabelt or more distant cortical areas. AL, anterolateral; CL, caudolateral; CM, caudomedial; CPB, caudal parabelt; ML, middle lateral; MM, middle medial; RM, rostromedial; RPB, rostral parabelt; RT, rostromedial; RTM, medial rostromedial; RTL, lateral rostromedial.

All parts reprinted from original source: Kaas & Hackett, 2000.

instance, selectivity for vocalizations and selectivity for spatial location have been found to be partially segregated, each being most pronounced in a different part of the lateral belt (Tian, Reser, et al., 2001;

Woods, Lopez, et al., 2006). These regions have thus been proposed to constitute the beginning of ventral “what” and dorsal “where” pathways analogous to those in the visual system, perhaps culminating in the same parts of the prefrontal cortex as the analogous visual pathways (Cohen, Russ, et al., 2009; Romanski, Tian, et al., 1999). Functional imaging results in humans have also been viewed as supportive of this framework (Alain, Arnott, et al., 2001; Warren, Zielinski, et al., 2002). Additional evidence for a “what/where” dissociation comes from a recent study in which sound localization and temporal pattern discrimination in cats were selectively impaired by reversibly deactivating different regions of nonprimary auditory cortex (Lomber & Malhotra, 2008). However, other studies have found less evidence for segregation of tuning properties in early auditory cortex (Bizley, Walker, et al., 2009). Moreover, the properties of the “what” stream remain relatively undefined (Recanzone, 2008); at this point, it has been defined mainly by reduced selectivity to spatial location.

There have been further attempts to extend the characterization of a ventral auditory pathway by testing for specialization for the analysis of particular categories of sounds, analogous to what has been found in the visual system (Kanwisher, 2010). The most widely proposed specialization is for vocalizations. Using functional imaging, regions of the anterior temporal lobe have been identified in both humans (Belin, Zatorre, et al., 2000) and macaques (Petkov, Kayser, et al., 2008) that appear to be somewhat selectively responsive to vocalizations and that could be homologous across species. Evidence for regions selective for other categories is less clear at present (Leaver & Rauschecker, 2010), although see the section below on pitch perception for a discussion of a cortical region putatively involved in pitch processing.

Another proposal is that the left and right auditory cortices are specialized for different aspects of signal processing, with the left optimized for temporal resolution and the right for frequency resolution (Zatorre, Belin, et al., 2002). This idea is motivated by the uncertainty principle of time–frequency analysis, whereby resolution cannot simultaneously be optimized for both time and frequency. The evidence for hemispheric differences comes mainly from functional imaging studies that manipulate spectral and temporal stimulus characteristics (Samson, Zeffiro, et al., 2011; Zatorre & Belin, 2001) and neuropsychology studies that find pitch perception deficits associated with right temporal lesions (Johnsrude, Penhune, et al., 2000; Zatorre,

1985). A related alternative idea is that the two hemispheres are specialized to analyze distinct timescales, with the left hemisphere more responsive to short-scale temporal variation (e.g. tens of milliseconds) and the right hemisphere more responsive to long-scale variation (e.g. hundreds of milliseconds) (Boemio, Fromm, et al., 2005; Poeppel, 2003).

III. Sound Measurement—Modulation *Amplitude Modulation and the Envelope*

The cochlea decomposes the acoustic input into frequency channels, but much of the important information in sound is conveyed by the way that the output of these frequency channels is modulated in amplitude. Consider Figure 8.7A, which displays in blue the output of one such frequency channel for a short segment of a speech signal. The blue waveform oscillates at a rapid rate, but its amplitude waxes and wanes at a much lower rate (evident in the close-up view of Figure 8.7B). This waxing and waning is known as *amplitude modulation* and is a

common feature of many modes of sound production (e.g., vocal articulation). The amplitude is captured by what is known as the *envelope* of a signal, shown in red for the signal of Figures 8.7A and B. Often, the envelopes of each cochlear channel are stacked vertically and displayed as an image called a *spectrogram*, providing a depiction of how the sound energy in each frequency channel varies over time (Figure 8.7C). Figure 8.7D shows the spectra of the signal and envelope shown in Figures 8.7A and B. The signal spectrum is bandpass (because it is the output of a bandpass filter), with energy at frequencies in the audible range. The envelope spectrum, in contrast, is low-pass, with most of the power below 10 Hz, corresponding to the slow rate at which the envelope changes. The frequencies that compose the envelope are typically termed *modulation frequencies*, distinct from the *acoustic frequencies* that compose the signal that the envelope is derived from.

The information carried by a cochlear channel can thus be viewed as the product of “fine structure”—a

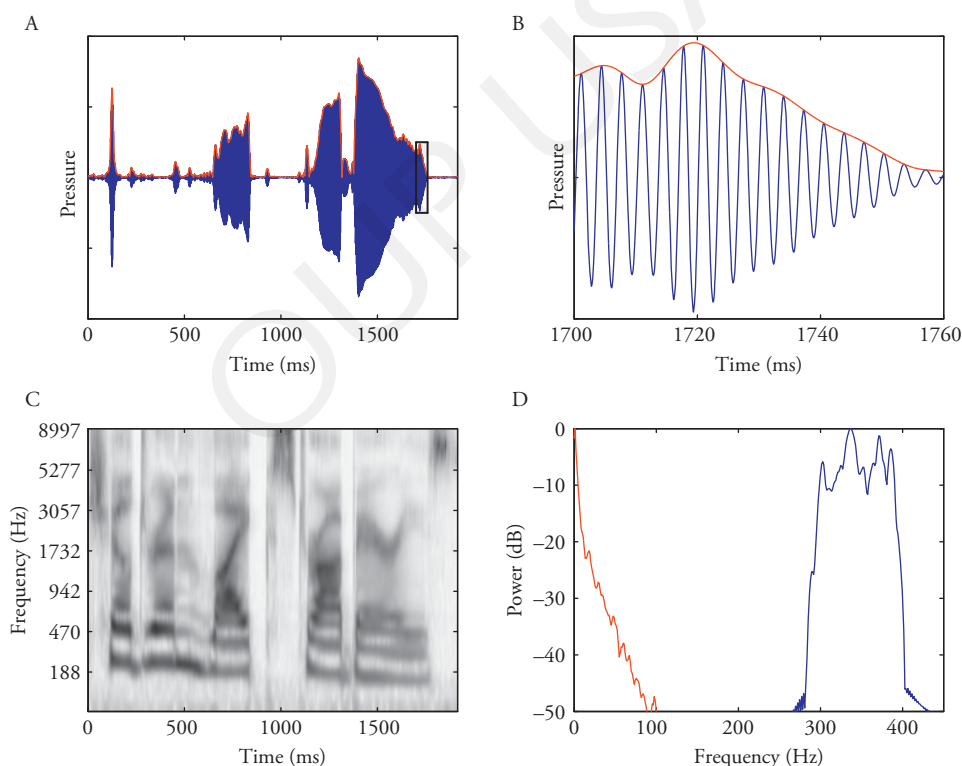


Figure 8.7 Amplitude modulation. **A**, The output of a bandpass filter (centered at 340 Hz) for a recording of speech, plotted in *blue*, with its envelope plotted in *red*. **B**, Close-up of part of **A** (corresponding to the *black rectangle* in **A**). Note that the filtered sound signal (like the unfiltered signal) fluctuates around zero at a high rate, whereas the envelope is positive-valued and fluctuates more slowly. **C**, Spectrogram of the same speech signal. Spectrogram is formed from the envelopes (one of which is plotted in **A**) of a set of filters mimicking the frequency tuning of the cochlea. The spectrogram is produced by plotting each envelope horizontally in grayscale. **D**, Power spectra of the filtered speech signal in **A** and its envelope. Note that the envelope contains power only at low frequencies (modulation frequencies), whereas the filtered signal has power at a restricted range of high frequencies (acoustic frequencies).

waveform that varies rapidly, at a rate close to the center frequency of the channel—and an amplitude envelope that varies more slowly (Rosen, 1992). The envelope and fine structure have a clear relation to common signal processing formulations in which the output of a bandpass filter is viewed as a single sinusoid varying in amplitude and frequency—the envelope describes the amplitude variation, and the fine structure describes the frequency variation. The envelope of a frequency channel is also straightforward to extract from the auditory nerve—it can be obtained by low-pass filtering a spike train (because the amplitude changes reflected in the envelope are relatively slow). Despite the fact that envelope and fine structure are not completely independent (Ghitza, 2001), there has been much interest in the past decade in distinguishing their roles in different aspects of hearing (Smith, Delgutte, et al., 2002) and its impairment (Lorenzi, Gilbert, et al., 2006).

Perhaps surprisingly, the temporal information contained in amplitude envelopes can be sufficient for speech comprehension even when spectral information is severely limited. In a classic paper, Shannon and colleagues isolated the information contained in the amplitude envelopes of speech signals with a stimulus known as *noise-vocoded speech* (Shannon, Zeng, et al., 1995). Noise-vocoded speech is generated by filtering a speech signal and a noise signal into frequency bands, multiplying the frequency bands of the noise by the envelopes of the speech, and then summing the modified noise bands to synthesize a new sound signal. By using a small number of broad frequency bands, spectral information can be greatly reduced, leaving amplitude variation over time (albeit smeared across a broader than normal range of frequencies) as the primary signal cue. Examples are shown in Figure 8.8 for two, four, and eight bands. Shannon and colleagues found that the resulting stimulus was intelligible even when just a few bands were used (i.e., with much broader frequency tuning than is present in the cochlea), indicating that the temporal modulation of the envelopes contains much information about speech content.

Modulation Tuning

Motivated by its perceptual importance, amplitude modulation has been proposed to be analyzed by dedicated banks of filters operating on the envelopes of cochlear filter outputs rather than the sound waveform itself (Dau, Kollmeier, et al., 1997). Early evidence for such a notion came from masking

and adaptation experiments, which found that the detection of a modulated signal was impaired by a masker or adapting stimulus modulated at a similar frequency (Bacon & Grantham, 1989; Houtgast, 1989; Tansley & Suffield, 1983). There is now considerable evidence from neurophysiology that single neurons in the midbrain, thalamus, and cortex exhibit some degree of tuning to modulation frequency (Depireux, Simon, et al., 2001; Joris, Schreiner, et al., 2004; Miller, Escabi, et al., 2001; Rodriguez, Chen, et al., 2010; Schreiner & Urbas, 1986, 1988; Woolley, Fremouw, et al., 2005), loosely consistent with the idea of a modulation filter bank (Figure 8.9A). Because such filters are typically conceived to operate on the envelope of a particular cochlear channel, they are tuned both in acoustic frequency (courtesy of the cochlea) and modulation frequency.

Neurophysiological studies in nonhuman animals (Schreiner & Urbas, 1986, 1988) and neuroimaging results in humans (Boemio, Fromm, et al., 2005; Giraud, Lorenzi, et al., 2000; Schonwiesner & Zatorre, 2009) have generally found that the auditory cortex responds preferentially to low modulation frequencies (in the range of 4–8 Hz), whereas subcortical structures prefer higher rates (up to 100–200 Hz), with preferred modulation frequency generally decreasing up the auditory pathway. Based on this, it is intriguing to speculate that successive stages of the auditory system might process structure at progressively longer (slower) timescales, analogous to the progressive increase in receptive field size that occurs in the visual system from V1 to inferotemporal cortex (Lerner, Honey, et al., 2011). Within the cortex, however, no hierarchy is clearly evident as of yet, at least in the response to simple patterns of modulation (Boemio, Fromm, et al., 2005; Giraud, Lorenzi, et al., 2000). Moreover, there is considerable variation within each stage of the pathway in the preferred modulation frequency of individual neurons (Miller, Escabi, et al., 2001; Rodriguez, Chen, et al., 2010). There are several reports of topographic organization for modulation frequency in the inferior colliculus, in which a gradient of preferred modulation frequency is observed orthogonal to the tonotopic gradient of preferred acoustic frequency (Baumann, Griffiths, et al., 2011; Langner, Sams, et al., 1997). Whether there is topographic organization in the cortex remains unclear (Nelken, Bizley, et al., 2008).

Modulation tuning in single neurons is often studied by measuring spectrotemporal receptive fields (STRFs) (Depireux, Simon, et al., 2001),

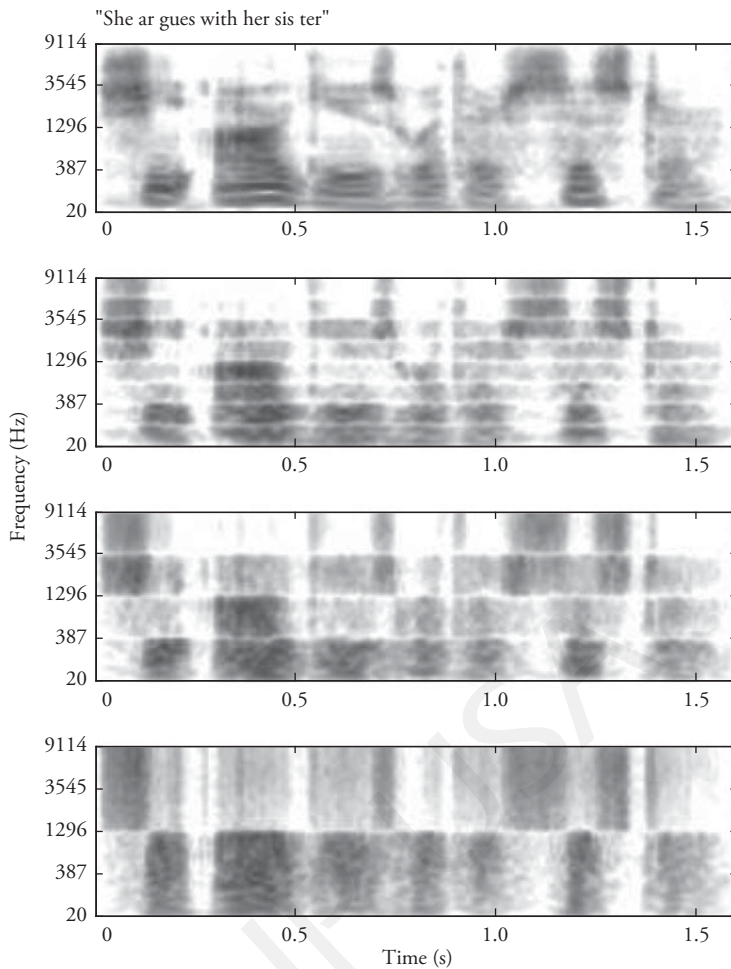


Figure 8.8 Noise-vocoded speech. **A**, Spectrogram of a speech utterance, generated as in Figure 8.7C. **B–D**, Spectrograms of noise-vocoded versions of the utterance from **A**, generated with eight (**B**), four, (**C**), or two (**D**) channels. To generate the noise-vocoded speech, the amplitude envelope of the original speech signal was first measured in each of the frequency bands in **B**, **C**, and **D**. A white noise signal was then filtered into these same bands, and the noise bands were multiplied by the corresponding speech envelopes. These modulated noise bands were then summed to generate a new sound signal. It is visually apparent that the sounds in parts **B** to **D** are spectrally coarser versions of the original utterance. Good speech intelligibility is usually obtained with only four channels, indicating that patterns of amplitude modulation can support speech recognition in the absence of fine spectral detail.

conventionally estimated using techniques such as spike-triggered averaging. To compute an STRF, neuronal responses to a long, stochastically varying stimulus are recorded, after which the stimulus spectrogram segments preceding each spike are averaged to yield the STRF—the stimulus, described in terms of acoustic frequency content over time, that on average preceded a spike. In Figure 8.9B, for instance, the STRF consists of a decrease in power followed by an increase in power in the range of 10 kHz; the neuron would thus be likely to respond well to a rapidly modulated 10 kHz tone, and less so to a tone whose amplitude was constant. This STRF can be viewed as a filter that passes modulations in

a certain range of rates, that is, modulation frequencies. Note, however, that it is also tuned in acoustic frequency (the dimension on the y -axis), responding only to modulations of fairly high acoustic frequencies.

The STRF approximates a neuron's output as a linear function of the cochlear input—the result of convolving the spectrogram of the acoustic input with the STRF. However, it is clear that linear models are inadequate to explain neuronal responses (Christianson, Sahani, et al., 2008; Machens, Wehr, et al., 2004; Rotman, Bar Yosef, et al., 2001; Theunissen, Sen, et al., 2000). Understanding the nonlinear contributions is an important direction

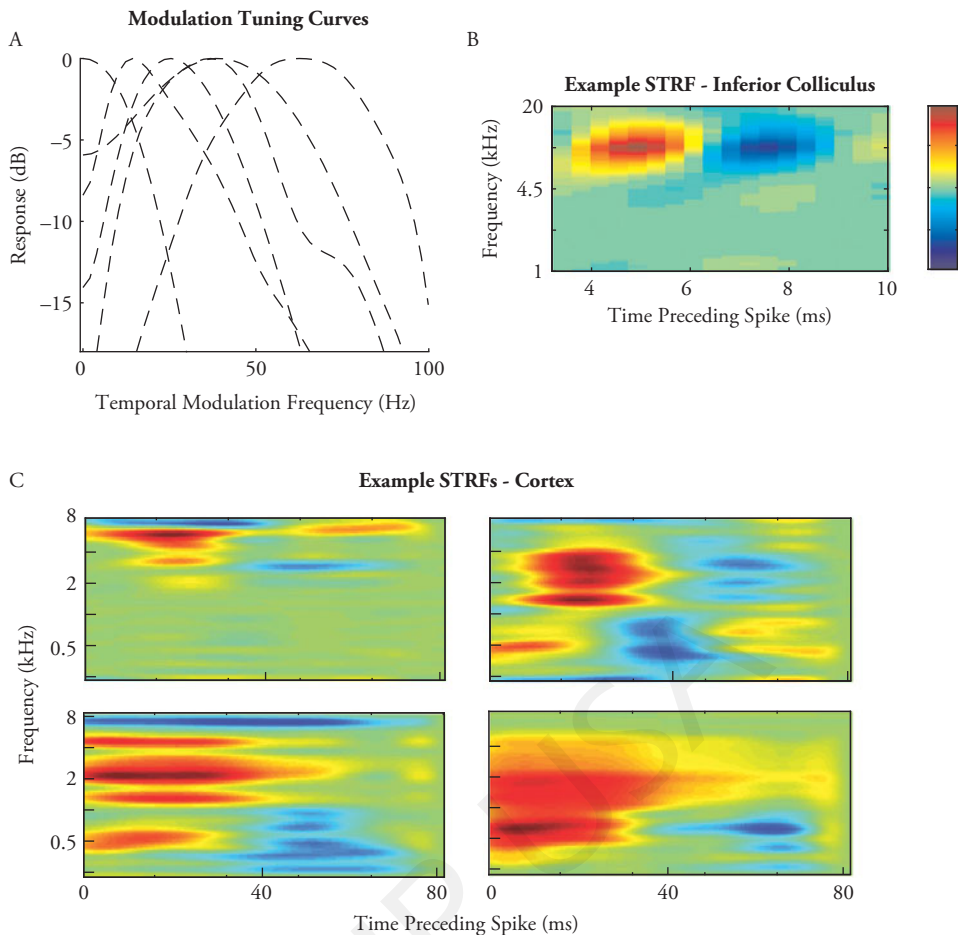


Figure 8.9 Modulation tuning. **A**, Example of temporal modulation tuning curves for neurons in the medial geniculate nucleus of the thalamus (Miller, Escabi, et al., 2002). **B**, Example of the spectrotemporal receptive field (STRF) from a thalamic neuron (Miller, Escabi, et al., 2002). Note that the modulation in the STRF is predominantly along the temporal dimension, and that this neuron would thus be sensitive primarily to temporal modulation. **C**, Example of STRFs from cortical neurons (Mesgarani, David, et al., 2008). Note that the STRFs feature spectral modulation in addition to temporal modulation, and as such are selective for more complex acoustic features. Cortical neurons typically have longer latencies than subcortical neurons, but this is not evident in the STRFs, probably because of nonlinearities in the cortical neurons that produce small artifacts in the STRFs (Stephen David, personal communication).

Figure parts are taken from the original sources.

of future research (Ahrens, Linden, et al., 2008; David, Mesgarani, et al., 2009), as neuronal nonlinearities likely play critical computational roles, but at present much analysis is restricted to linear receptive field estimates. There are established methods for computing STRFs, and they exhibit many interesting properties even though they are clearly not the whole story.

Modulation tuning functions (e.g., those shown in Figure 8.9A) can be obtained via the Fourier transform of the STRF. Temporal modulation tuning is commonly observed, as previously discussed, but some tuning is normally also present for spectral modulation—variation in power that

occurs along the frequency axis. Spectral modulation is often evident as well in spectrograms of speech (e.g., Figure 8.7C) and animal vocalizations. Modulation results both from individual frequency components and from formants—the broad spectral peaks that are present for vowel sounds due to vocal tract resonances. Tuning to spectral modulation is generally less pronounced than to amplitude modulation, especially subcortically (Miller, Escabi, et al., 2001), but is an important feature of cortical responses (Barbour & Wang, 2003; Mesgarani, David, et al., 2008). Examples of cortical STRFs with spectral modulation sensitivity are shown in Figure 8.9C.

IV. Adaptive Coding and Plasticity

Because the auditory system evolved to enable behavior in natural auditory environments, it is likely to be adapted for the representation of naturally occurring sounds. Natural sounds thus in principle should provide hearing researchers with clues about the structure and function of the auditory system (Attias & Schreiner, 1997). In recent years there has been increasing interest in the use of natural sounds as experimental stimuli and in computational analyses of the relation between auditory representation and the environment. Most of the insights gained thus far from this approach are “postdictive”—they offer explanations of previously observed phenomena rather than revealing previously unforeseen mechanisms. For instance, we described earlier the attempts to explain cochlear frequency selectivity as optimal for encoding natural sounds (Lewicki, 2002; Smith & Lewicki, 2006).

The efficient coding hypothesis has also been proposed to apply to modulation tuning in the inferior colliculus. Modulation tuning bandwidth tends to increase with preferred modulation frequency (Rodriguez, Chen, et al., 2010), as would be predicted if the low-pass modulation spectra of most natural sounds (Attias & Schreiner, 1997; McDermott, Wroblewski, et al., 2011; Singh & Theunissen, 2003) were to be divided into channels conveying equal power. Inferior colliculus neurons have also been found to convey more information about sounds whose amplitude distribution follows that of natural sounds rather than that of white noise (Escabi, Miller, et al., 2003). Along the same lines, studies of STRFs in the bird auditory system indicate that neurons are tuned to the properties of bird song and other natural sounds, maximizing discriminability of behaviorally important sounds (Hsu, Woolley, et al., 2004; Woolley, Fremouw, et al., 2005). Similar arguments have been made about the coding of binaural cues to sound localization (Harper & McAlpine, 2004).

Other strands of research have explored whether the auditory system might further adapt to the environment by changing its coding properties in response to changing environmental statistics, so as to optimally represent the current environment. Following on research showing that the visual system adapts to local contrast statistics (Fairhall, Lewen, et al., 2001), numerous groups have reported evidence for neural adaptation in the auditory system—responses to a fixed stimulus that vary depending on the immediate history of stimulation (Ulanovsky, Las, et al., 2003; Kvale &

Schreiner, 2004). In some cases, it can be shown that this adaptation increases information transmission. For instance, the “tuning” of neurons in the inferior colliculus to sound intensity (i.e., the function relating intensity to firing rate) depends on the mean and variance of the local intensity distribution (Dean, Harper, et al., 2005). Qualitatively, the rate–intensity curves shift so that the point of maximum slope (around which neural discrimination of intensity is best) is closer to the most commonly occurring intensity. Quantitatively, this behavior results in increased information transmission about stimulus level.

Some researchers have recently taken things a step further, showing that auditory responses are dependent not just on the stimulus history but also on the task a listener is performing. Fritz and colleagues found that the STRFs measured for neurons in the primary auditory cortex of awake ferrets change depending on whether the animals are performing a task (Fritz, Shamma, et al., 2003), and that the nature of the change depends on the task (Fritz, Elhilali, et al., 2005). For instance, STRF changes serve to accentuate the frequency of a tone being detected, or to enhance discrimination of a target tone from a reference. These changes are mirrored in sound-evoked responses in the prefrontal cortex (Fritz, David, et al., 2010), which may drive the changes that occur in auditory cortex during behavior. In some cases the STRF changes persist long after the animals are finished performing the task, and as such may play a role in sensory memory and perceptual learning.

Perhaps surprisingly, long-term plasticity appears to occur as early as the brainstem, where recent evidence in humans suggests considerable experience-dependent variation across individuals. The data in question derive from an evoked electrical potential known as the *auditory brainstem response* (ABR) (Skoe & Kraus, 2010). The ABR is recorded at the scalp but is believed to originate in the brainstem. It often mirrors properties of the stimulus, such that its power spectrum, for instance, often resembles that of the acoustic input. The extent to which the ABR preserves the stimulus can thus be interpreted as a measure of processing integrity. Interestingly, the ABR more accurately tracks stimulus frequency for musician listeners than nonmusicians (Wong, Skoe, et al., 2007). This could in principle reflect innate differences in auditory ability that predispose listeners to become musicians or not, but it could also reflect the substantial differences in auditory experience between the two groups. Consistent

with the latter notion, 10 hours of training on a pitch discrimination task is sufficient to improve the fidelity of the ABR response to frequency, providing clear evidence of experience-dependent plasticity (Carcagno & Plack, 2011). Aspects of the ABR are also altered in listeners with reading problems (Banai, Hornickel, et al., 2009). This line of research suggests that potentially important individual differences are present at early stages of the auditory system, and that these differences are in part the result of plasticity.

V. Sound Source Perception

Ultimately, we wish to understand not only what acoustic measurements are made by the auditory system, as were characterized in the previous sections, but also how these measurements give rise to perception—what we hear when we listen to sound. Following Helmholtz, we might suppose that the purpose of audition is to infer something about the events in the world that produce sound. We can often identify sound sources with a verbal label, for instance, and realize that we heard a finger snap, a flock of birds, or construction noise. Even if we cannot determine the object that caused the sound, we may nonetheless know something about what happened: that something fell onto a hard floor, or into water (Gaver, 1993). Despite the richness of these aspects of auditory recognition, remarkably little is known about them at present (speech recognition stands alone as an exception), mainly because they are rarely studied (but see Gygi, Kidd, et al., 2004; Lutfi, 2008; McDermott & Simoncelli, 2011).

Perhaps because they are more easily controlled and manipulated, researchers have been more inclined to instead study the perception of isolated properties of sounds or their sources. Much research has concentrated in particular on three well-known properties of sound: spatial location, pitch, and loudness. This focus is in some sense unfortunate because auditory perception is much richer than the hegemony of these three attributes in hearing science would indicate. However, their study has nonetheless given rise to fruitful lines of research that have yielded many useful insights about hearing more generally.

Localization

Localization is less precise in hearing than in vision but is nonetheless of great value, because sound enables us to localize objects that we may not be able to see. Human observers can judge the location of a source to within a few degrees if conditions

are optimal. The processes by which this occurs are among the best understood in hearing.

Spatial location is not made explicit on the cochlea, which provides a map of frequency rather than of space, and instead must be derived from three primary sources of information. Two of these are binaural, resulting from differences in the acoustic input to the two ears. Due to the difference in path length from the source to the ears, and to the acoustic shadowing effect of the head, sounds to one side of the vertical meridian reach the two ears at different times and with different intensities. These interaural time and level differences vary with direction and thus provide a cue to a sound source's location. Binaural cues are primarily useful for deriving the location of a sound in the horizontal plane, because changes in elevation do not change interaural time or intensity differences much. To localize sounds in the vertical dimension, or to distinguish sounds coming from in front of the head from those from in back, listeners rely on a third source of information: the filtering of sounds by the body and ears. This filtering is direction specific, such that a spectral analysis can reveal peaks and valleys in the frequency spectrum that are signatures of location in the vertical dimension (Figure 8.10; discussed further below).

Interaural time differences (ITDs) are typically a fraction of a millisecond, and just-noticeable ITDs (which determine spatial acuity) can be as low as 10 microseconds (Klump & Eady, 1956). This is striking given that neural refractory periods (which determine the minimal interspike interval for a single neuron) are on the order of a millisecond, which one might think would put a limit on the temporal resolution of neural representations. Typical interaural level differences (ILDs) can be as large as 20 dB, with a just-noticeable difference of about 1 dB. ILDs result from the acoustic shadow cast by the head. To first order, ILDs are more pronounced for high frequencies because low frequencies are less affected by the acoustic shadow (because their wavelengths are comparable to the dimensions of the head). ITDs, in contrast, support localization most effectively at low frequencies, when the time difference between individual cycles of sinusoidal sound components can be detected via phase-locked spikes from the two ears (phase locking, as we discussed earlier, degrades at high frequencies). That said, ITDs between the envelopes of high-frequency sounds can also produce percepts of localization. The classic “duplex” view that localization is determined by either ILDs or ITDs, depending

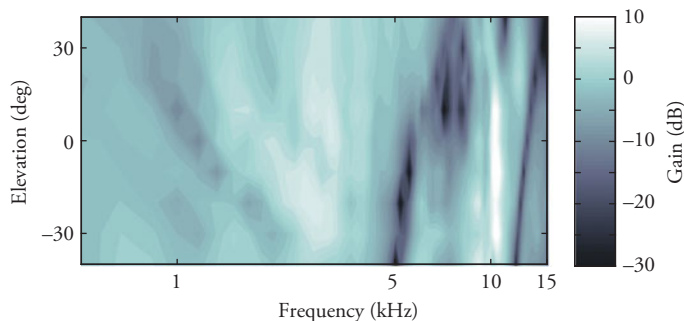


Figure 8.10 Head-related transfer function (HRTF). Example HRTF for the left ear of one human listener. The gray level represents the amount by which a frequency originating at a particular elevation is attenuated or amplified by the torso, head, and ear of the listener. Sounds are filtered differently depending on their elevation, and the spectrum that is registered by the cochlea thus provides a localization cue. Note that most of the variation in elevation-dependent filtering occurs at high frequencies (above 4 kHz).

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on the frequency (Rayleigh, 1907), is thus not fully appropriate for realistic natural sounds, which in general produce perceptible ITDs across the spectrum. See Middlebrooks and Green (1991), for a review of much of the classic behavioral work on sound localization.

The binaural cues to sound location are extracted in the superior olive, a subcortical region where inputs from the two ears are combined. In most animals there appears to be an elegant segregation of function, with ITDs being extracted in the medial superior olive (MSO) and ILDs being extracted in the lateral superior olive (LSO). In both cases, accurate coding of interaural differences is made possible by neural signaling with unusually high temporal precision. This precision is needed to encode both sub-millisecond ITDs and ILDs of brief transient events, for which the inputs from the ears must be aligned in time. Brain structures subsequent to the superior olive largely inherit its ILD and ITD sensitivity. See Yin and Kuwada, 2010, for a recent review of the physiology of binaural localization.

Binaural cues are of little use in distinguishing sounds at different locations on the vertical dimension (relative to the head), or in distinguishing front from back, because interaural time and level differences are largely unaffected by changes across these locations. Instead, listeners rely on spectral cues provided by the filtering of a sound by the torso, head, and ears of a listener. The filtering results from the reflection and absorption of sound by the surfaces of a listener's body, with sound from different directions producing different patterns of reflection and thus different patterns of filtering. The effect of these interactions on the sound that reaches the

ear drum can be described by a linear filter known as the *head-related transfer function* (HRTF). The overall effect is that of amplifying some frequencies while attenuating others. A broadband sound entering the ear will thus be endowed with peaks and valleys in its frequency spectrum (see Figure 8.10).

Compelling sound localization can be perceived when these peaks and valleys are artificially induced. The effect of the filtering is obviously confounded with the spectrum of the unfiltered sound source, and the brain must make some assumptions about the source spectrum. When these assumptions are violated, as with narrowband sounds whose spectral energy occurs at a peak in the HRTF of a listener, sounds are mislocalized (Middlebrooks, 1992). For broadband sounds, however, HRTF filtering produces signatures that are sufficiently distinct as to support localization in the vertical dimension to within 5 degrees or so in some cases, although some locations are more accurately perceived than others (Makous & Middlebrooks, 1990; Wightman & Kistler, 1989).

The bulk of the filtering occurs in the outer ear (the pinna), the folds of which produce distinctive pattern of reflections. Because pinna shapes vary across listeners, the HRTF is listener specific as well as location specific, with spectral peaks and valleys that are in different places for different listeners. Listeners appear to learn the HRTFs for their set of ears. When ears are artificially modified with plastic molds that change their shape, localization initially suffers considerably, but over a period of weeks, listeners regain the ability to localize with the modified ears (Hofman, Van Riswick, et al., 1998). Listeners thus learn at least some of the details of their particular HRTF through experience, although sounds

can be localized even when the peaks and valleys of the pinna filtering are somewhat blurred (Kulkarni & Colburn, 1998). Moreover, compelling spatialization is often evident even if a generic HRTF is used.

The physiology of HRTF-related cues for localization is not as developed as it is for binaural cues, but there is evidence that midbrain regions may again be important. Many inferior colliculus neurons, for instance, show tuning to sound elevation (Delgutte, Joris, et al., 1999). The selectivity for elevation presumably derives from tuning to particular spectral patterns (peaks and valleys in the spectrum) that are diagnostic of particular locations (May, Anderson, et al., 2008).

Although the key cues for sound localization are extracted subcortically, lesion studies reveal that the cortex is essential for localizing sound. Ablating auditory cortex typically produces large deficits in localization (Heffner & Heffner, 1990), with unilateral lesions producing deficits specific to locations contralateral to the side of the lesion (Jenkins & Masterton, 1982). Consistent with these findings, tuning to sound location is widespread in auditory cortical neurons, with the preferred location generally positioned in the contralateral hemifield (Middlebrooks, 2000). Topographic representations of space have not been found to be evident within individual auditory cortical areas, although one recent report argues that such topography may be evident across multiple areas (Higgins, Storace, et al., 2010).

Pitch

Although the word pitch is often used colloquially to refer to the perception of sound frequency, in hearing research it has a more specific meaning—pitch is the perceptual correlate of periodicity. Vocalizations, instrument sounds, and some machine sounds are all often produced by periodic physical processes. Our vocal cords open and close at regular intervals, producing a series of clicks separated by regular temporal intervals. Instruments produce sounds via strings that oscillate at a fixed rate, or via tubes in which the air vibrates at particular resonant frequencies, to give two examples. Machines frequently feature rotating parts, which often produce sounds at every rotation. In all these cases, the resulting sounds are periodic—the sound pressure waveform consists of a single shape that repeats at a fixed rate (Figure 8.11A). Perceptually, such sounds are heard as having a pitch that can vary from low to high, proportional to the frequency at which the

waveform repeats (the fundamental frequency, i.e., the F0). The periodicity is distinct from whether a sound's frequencies fall in high or low regions of the spectrum, although in practice periodicity and the spectral center of mass are sometimes correlated.

Pitch is important because periodicity is important—the period is often related to properties of the source that are useful to know, such as its size, or tension. Pitch is also used for communicative purposes, varying in speech prosody, for instance, to convey meaning or emotion. Pitch is a centerpiece of music, forming the basis of melody, harmony, and tonality. Listeners also use pitch to track sound sources of interest in auditory scenes.

Many physically different sounds—all those with a particular period—have the same pitch. Historically, pitch has been a focal point of hearing research because it is an important perceptual property with a nontrivial relationship to the acoustic input, whose mechanistic characterization has been resistant to unambiguous solution. Debates on pitch and related phenomena date back at least to Helmholtz, and continue to occupy many researchers today (Plack, Oxenham, et al., 2005).

One central debate concerns whether pitch is derived from an analysis of frequency or time. Periodic waveforms produce spectra whose frequencies are harmonically related—they form a harmonic series, being integer multiples of the fundamental frequency, whose period is the period of the waveform (Figure 8.11B). Although the fundamental frequency determines the pitch, the fundamental need not be physically present in the spectrum for a sound to have pitch—sounds missing the fundamental frequency but containing other harmonics of the fundamental are still perceived to have the pitch of the fundamental, an effect known as the *missing fundamental illusion*. What matters for pitch perception is whether the frequencies that are present are harmonically related. Pitch could thus conceivably be detected with harmonic templates applied to an estimate of a sound's spectrum obtained from the cochlea (Goldstein, 1973; Shamma & Klein, 2000; Terhardt, 1974; Wightman, 1973). Alternatively, periodicity could be assessed in the time domain, for instance via the autocorrelation function (Cariani & Delgutte, 1996; de Cheveigne & Kawahara, 2002; Meddis & Hewitt, 1991). The autocorrelation measures the correlation of a signal with a delayed copy of itself. For a periodic signal that repeats with some period, the autocorrelation exhibits peaks at multiples of the period (Figure 8.11C).

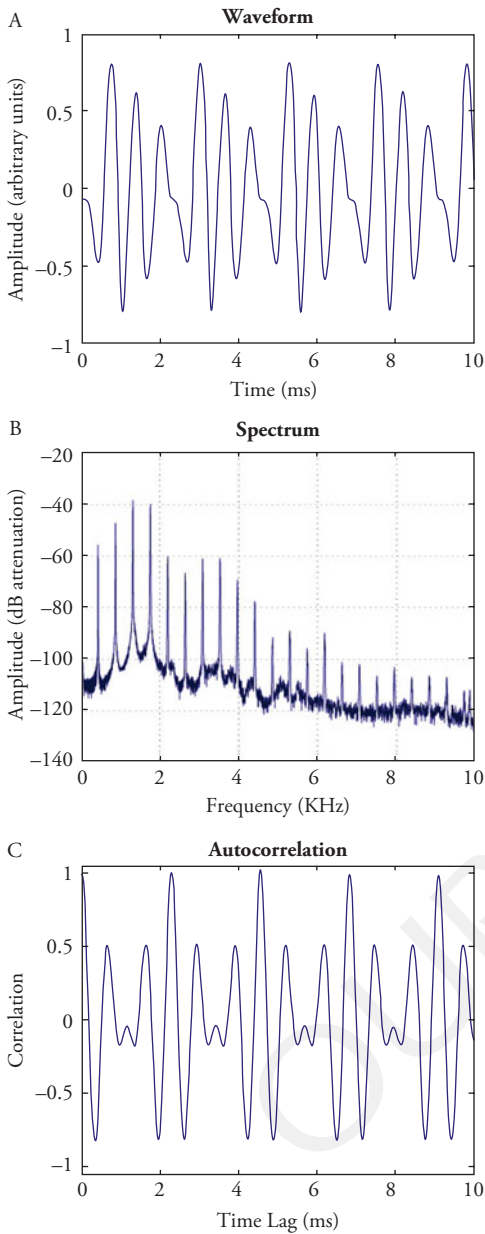


Figure 8.11 Periodicity and pitch. Waveform, spectrum, and autocorrelation function for a note played on an oboe. The note shown is the A above middle C, with a fundamental frequency (F_0) of 440 Hz. **A**, Excerpt of waveform. Note that the waveform repeats every 2.27 ms (the period). **B**, Spectrum. Note the peaks at integer multiples of the F_0 , characteristic of a periodic sound. In this case, the F_0 is physically present, but the second, third, and fourth harmonics actually have higher amplitude. **C**, Autocorrelation. The correlation coefficient is always 1 at a lag of 0 ms, but because the waveform is periodic, correlations close to 1 are also found at integer multiples of the period (2.27, 4.55, 6.82, and 9.09 ms in this example).

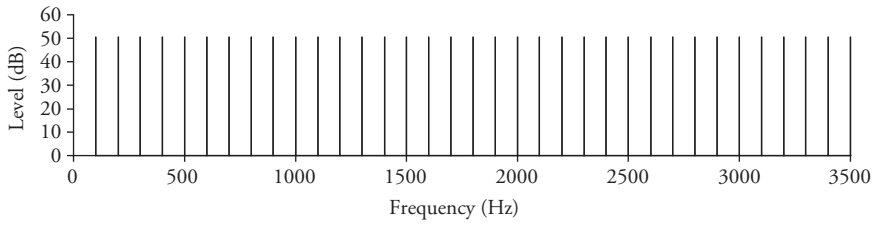
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Such analyses are in principle functionally equivalent because the power spectrum is related to the autocorrelation via the Fourier transform, and detecting periodicity in one domain versus the other might simply seem a question of implementation. In the context of the auditory system, however, the two concepts diverge, due to information being limited by distinct factors in the two domains. Time-domain models are typically assumed to utilize fine-grained spike timing (i.e., phase locking), with concomitant temporal resolution limits. In contrast, frequency-based models (often known as *place models*, in reference to the frequency-place mapping that occurs on the basilar membrane) rely on the pattern of excitation along the cochlea, which is limited in resolution by the frequency tuning of the cochlea (Cedolin & Delgutte, 2005). Cochlear frequency selectivity is present in time-domain models of pitch as well, but its role is typically not to estimate the spectrum but simply to restrict an autocorrelation analysis to a narrow frequency band (Bernstein & Oxenham, 2005), which might help improve its robustness in the presence of multiple sound sources. Reviews of the current debates and their historical origins are available elsewhere (de Cheveigne, 2004; Plack & Oxenham, 2005), and we will not discuss them exhaustively here. Suffice it to say that despite being a centerpiece of hearing research for decades, the mechanisms underlying pitch perception remain under debate.

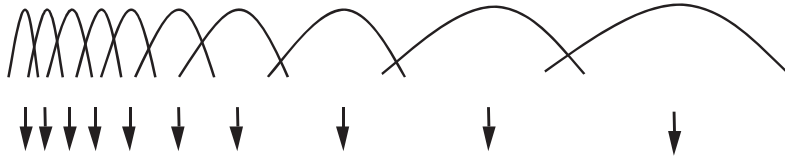
Research on pitch has provided many important insights about hearing even though a conclusive account of pitch remains elusive. One contribution of pitch research has been to reveal the importance of the resolvability of individual frequency components by the cochlea, a principle that has importance in other aspects of hearing as well. Because the frequency resolution of the cochlea is approximately constant on a logarithmic scale, whereas the components of a harmonic tone are equally spaced on a linear scale (separated by a fixed number of hertz, equal to the fundamental frequency of the tone; Figure 8.12A), multiple high-numbered harmonics fall within a single cochlear filter (Figure 8.12B). Because of the nature of the log scale, this is true regardless of whether the fundamental is low or high. As a result, the excitation pattern induced by a tone on the cochlea (of a human with normal hearing) is believed to contain resolvable peaks for only the first ten or so harmonics (Figure 8.12C).

There is now abundant evidence that resolvability places strong constraints on pitch perception. For instance, the perception of pitch is determined

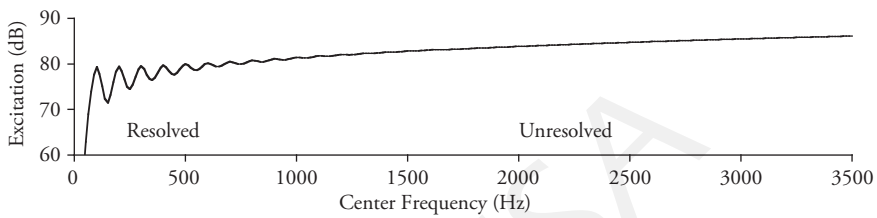
A Input Spectrum



B Auditory Filterbank



C Excitation Pattern



D Basilar Membrane Vibration

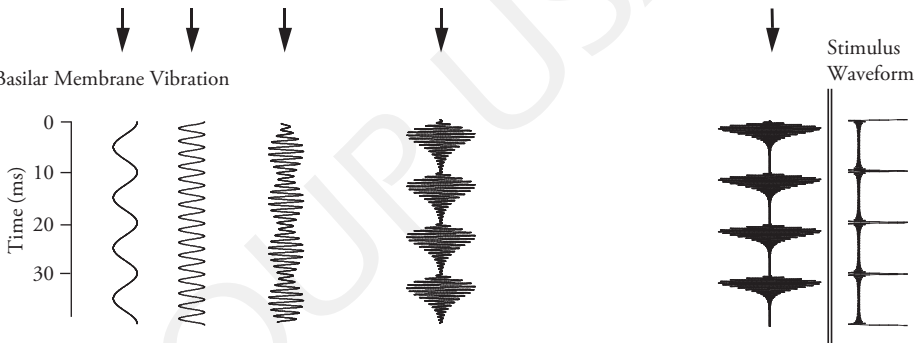


Figure 8.12 Resolvability. **A**, Spectrum of a harmonic complex tone composed of thirty-five harmonics of equal amplitude. The fundamental frequency is 100 Hz—the frequency of the lowest component in the spectrum and the amount by which adjacent harmonics are separated. **B**, Frequency responses of auditory filters, each of which represents a particular point on the cochlea. Note that because a linear frequency scale is used, the filters increase in bandwidth with center frequency, such that many harmonics fall within the passband of the high frequency filters. **C**, The resulting pattern of excitation along the cochlea in response to the tone in **A**. The excitation is the amplitude of vibration of the basilar membrane as a function of characteristic frequency (the frequency to which a particular point on the cochlea responds best, i.e., the center frequency of the auditory filter representing the response properties of the cochlea at that point). Note that the first ten or so harmonics produce resolvable peaks in the pattern of excitation, but that higher numbered harmonics do not. The latter are thus said to be “unresolved.” **D**, The pattern of vibration that would be observed on the basilar membrane at several points along its length. When harmonics are resolved, the vibration is dominated by the harmonic close to the characteristic frequency, and is thus sinusoidal. When harmonics are unresolved, the vibration pattern is more complex, reflecting the multiple harmonics that stimulate the cochlea at those points.

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predominantly by low-numbered harmonics (harmonics one to ten or so in the harmonic series), presumably owing to the peripheral resolvability of these harmonics. Moreover, the ability to discriminate pitch is much poorer for tones synthesized with only high-numbered harmonics than for tones containing only low-numbered harmonics, an effect not

accounted for simply by the frequency range in which the harmonics occur (Houtsma & Smurzynski, 1990; Shackleton & Carlyon, 1994). This might be taken as evidence that the spatial pattern of excitation, rather than the periodicity that could be derived from the autocorrelation, underlies pitch perception, but variants of autocorrelation-based models have also been

proposed to account for the effect of resolvability (Bernstein & Oxenham, 2005). Resolvability has since been demonstrated to constrain sound segregation as well as pitch (Micheyl & Oxenham, 2010); see below.

Just as computational theories of pitch remain a matter of debate, so do its neural correlates. One might expect that neurons at some stage of the auditory system would be tuned to stimulus periodicity, and there is one recent report of this in marmosets (Bendor & Wang, 2005). However, comparable results have yet to be reported in other species (Fishman, Reser, et al., 1998), and some have argued that pitch is encoded by ensembles of neurons with broad tuning rather than single neurons selective for particular fundamental frequencies (Bizley, Walker, et al., 2010). In general, pitch-related responses can be difficult to disentangle from artifactual responses to distortions introduced by the nonlinearities of the cochlea (de Cheveigne, 2010; McAlpine, 2004).

Given the widespread presence of frequency tuning in the auditory system, and the importance of harmonic frequency relations in pitch, sound segregation (Darwin, 1997), and music (McDermott, Lehr, et al., 2010), it is natural to think there might be neurons with multi-peaked tuning curves selective for harmonic frequencies. There are a few isolated reports of such tuning (Kadia & Wang, 2003; Sutter & Schreiner, 1991), but the tuning peaks do not always correspond to harmonic frequencies, and whether they relate to pitch is unclear. At least given how researchers have looked for it thus far, tuning for harmonicity is not as evident in the auditory system as might be expected.

If pitch is analyzed in a particular part of the brain, one might expect the region to respond more to stimuli with pitch than to those lacking it, other things being equal. Such response properties have in fact been reported in regions of auditory cortex identified with functional imaging in humans (Hall, Barrett, et al. 2005; Patterson, Uppenkamp, et al., 2002; Penagos, Melcher, et al., 2004; Schonwiesner & Zatorre, 2008). The regions are typically reported to lie outside primary auditory cortex, and could conceivably be homologous to the region claimed to contain pitch-tuned neurons in marmosets (Bendor & Wang, 2006), although again there is some controversy over whether pitch per se is implicated (Hall & Plack, 2009). See Winter, 2005, and Walker, Bizley, et al., 2010, for recent reviews of the brain basis of pitch.

In many contexts (e.g., the perception of music or speech intonation), it is the changes in pitch over

time that matter rather than the absolute value of the F0. For instance, pitch increases or decreases are what capture the identity of a melody or the intention of a speaker. Less is known about how this *relative* pitch information is represented in the brain, but the right temporal lobe has been argued to be important, in part on the basis of brain-damaged patients with apparently selective deficits in relative pitch (Johnsrude, Penhune, et al., 2000). See McDermott and Oxenham, 2008, for a review of the perceptual and neural basis of relative pitch.

Loudness

Loudness is the perhaps the most immediate perceptual property of sound, and has been actively studied for more than 150 years. To first order, loudness is the perceptual correlate of sound intensity. In real-world listening scenarios, loudness exhibits additional influences that suggest it serves to estimate the intensity of a sound source, as opposed to the intensity of the sound entering the ear (which changes with distance and the listening environment). However, loudness models that capture exclusively peripheral processing nonetheless have considerable predictive power.

For a sound with a fixed spectral profile, such as a pure tone or a broadband noise, the relationship between loudness and intensity can be approximated via the classic Stevens power law (Stevens, 1955). However, the relation between loudness and intensity is not as simple as one might imagine. For instance, loudness increases with increasing bandwidth—a sound whose frequencies lie in a broad range will seem louder than a sound whose frequencies lie in a narrow range, even when their physical intensities are equal.

Standard models of loudness thus posit something somewhat more complex than a simple power law of intensity: that loudness is linearly related to the total amount of neural activity elicited by a stimulus at the level of the auditory nerve (ANSI, 2007; Moore & Glasberg, 1996). The effect of bandwidth on loudness is explained via the compression that occurs in the cochlea: loudness is determined by the neural activity summed across nerve fibers, the spikes of which are generated after the output of a particular cochlear location is nonlinearly compressed. Because compression boosts low responses relative to high responses, the sum of several responses to low amplitudes (produced by the several frequency channels stimulated by a broadband sound) is greater than a single response to a high amplitude (produced by a single frequency

channel responding to a narrowband sound of equal intensity). Loudness also increases with duration for durations up to half a second or so (Buus, Florentine, et al., 1997), suggesting that it is computed from neural activity integrated over some short window.

The ability to predict perceived loudness is important in many practical situations, and is a central issue in the fitting of hearing aids. Cochlear compression is typically reduced in hearing-impaired listeners, and amplification runs the risk of making sounds uncomfortably loud unless compression is introduced artificially. There has thus been long-standing interest in quantitative models of loudness.

Loudness is also influenced in interesting ways by the apparent distance of a sound source. Because intensity attenuates with distance from a sound source, the intensity of a sound at the ear is determined conjointly by the intensity and distance of the source. At least in some contexts, the auditory system appears to use loudness as a perceptual estimate of a source's intensity (i.e., the intensity at the point of origin), such that sounds that appear more distant seem louder than those that appear closer but have the same overall intensity. Visual cues to distance have some influence on perceived loudness (Mershon, Desaulniers, et al., 1981), but the cue provided by the amount of reverberation also seems to be important. The more distant a source, the weaker the direct sound from the source to the listener, relative to the reverberant sound that reaches the listener after reflection off of surfaces in the environment (see Figure 8.14). This ratio of direct to reverberant sound appears to be used both to judge distance and to calibrate loudness perception (Zahorik & Wightman, 2001), although how the listener estimates this ratio from the sound signal remains unclear at present. Loudness thus appears to function somewhat like size or brightness perception in vision, in which perception is not based exclusively on retinal size or light intensity (Adelson, 2000).

VI. Auditory Scene Analysis

Thus far we have discussed how the auditory system represents single sounds in isolation, as might be produced by a note played on an instrument, or a word uttered by someone talking. The simplicity of such isolated sounds renders them convenient objects of study, yet in many auditory environments, isolated sounds are not the norm. It is often the case that many things make sound at the same time, causing the ear to receive a mixture of multiple

sources as its input. Consider Figure 8.13, which displays spectrograms of a single “target” speaker along with that of the mixture that results from adding to it the utterances of one, three, and seven additional speakers, as might occur in a social setting. The brain's task in this case is to take such a mixture as input and recover enough of the content of a target sound source to allow speech comprehension or otherwise support behavior. This is a nontrivial task. In the example of Figure 8.13, for instance, it is apparent that the structure of the target utterance is progressively obscured as more speakers are added to the mixture. Machine systems for recognizing speech suffer dramatically under such conditions, performing well in quiet, but much worse in the presence of multiple speakers (Lippmann, 1997). The presence of competing sounds greatly complicates the computational extraction of just about any sound source property, from pitch (de Cheveigne, 2006) to location. Human listeners, however, parse auditory scenes with a remarkable degree of success. In the example of Figure 8.13, the target remains largely audible to most listeners even in the mixture of eight speakers. This is the classic “cocktail party problem” (Bee & Micheyl, 2008; Bregman, 1990; Bronkhorst, 2000; Carlyon, 2004; Cherry, 1953; Darwin, 1997; McDermott, 2009).

Historically, the “cocktail party problem” has referred to two conceptually distinct problems that in practice are closely related. The first, known as *sound segregation*, is the problem of deriving representations of individual sound sources from a mixture of sounds. The second is the task of directing attention to one source among many, as when listening to a particular speaker at a party. These tasks are related because the ability to segregate sounds is probably dependent on attention (Carlyon, Cusack, et al., 2001; Shinn-Cunningham, 2008), although the extent and nature of this dependence remains an active area of study (Macken, Tremblay, et al., 2003). Here, we will focus on the first problem, of sound segregation, which is usually studied under conditions in which listeners pay full attention to a target sound. Al Bregman, a Canadian psychologist, is typically credited with drawing interest to this problem and pioneering its study (Bregman, 1990).

Sound Segregation and Acoustic Grouping Cues

Sound segregation is a classic example of an ill-posed problem in perception. Many different sets of sounds are physically consistent with the mixture

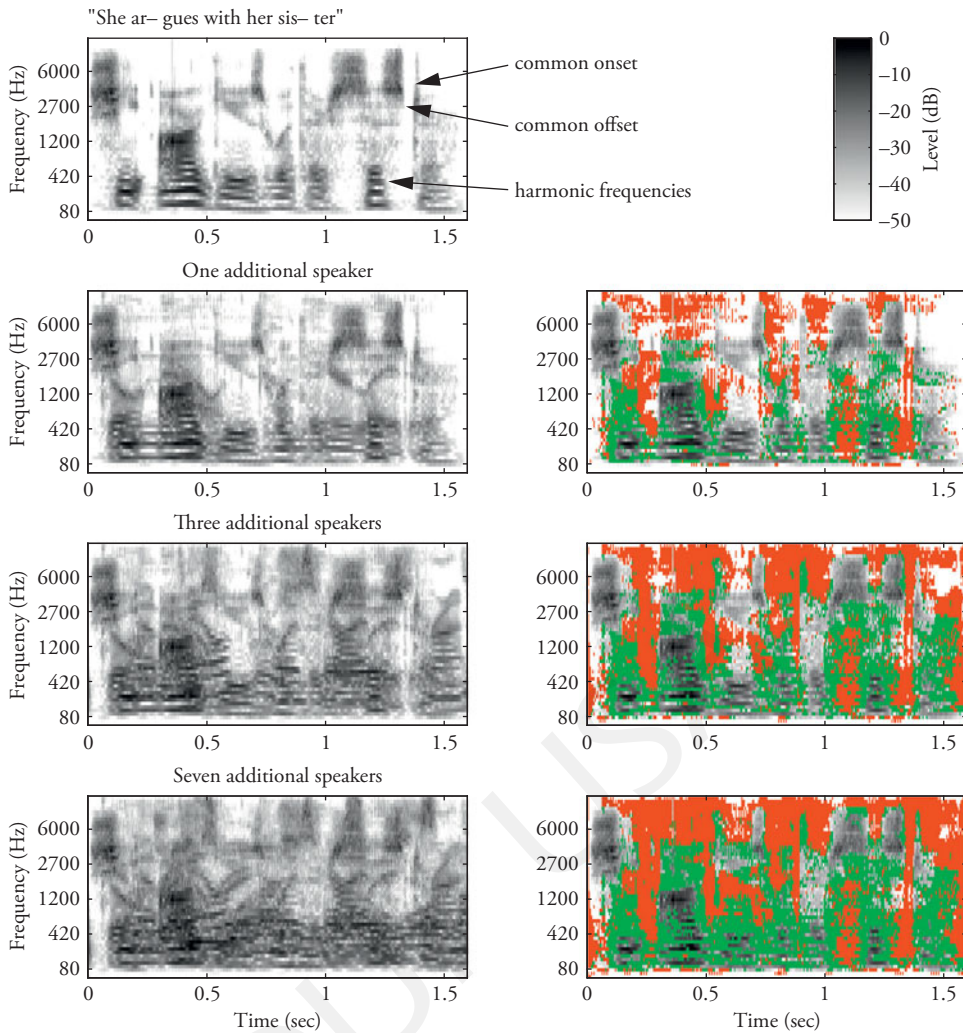


Figure 8.13 The cocktail party problem. Spectrograms of a single “target” utterance (*top row*), and the same utterance mixed with one, three, and seven additional speech signals from different speakers. The mixtures approximate the signal that would enter the ear if the additional speakers were talking as loud as the target speaker, but were standing twice as far away from the listener (to simulate cocktail party conditions). The grayscale denotes attenuation from the maximum energy level across all of the signals (in dB), such that gray levels can be compared across spectrograms. Spectrograms in the right column are identical to those on the left except for the superimposed color masks. Pixels labeled *green* are those where the original target speech signal is more than -50 dB but the mixture level is at least 5 dB higher, and thus masks the target speech. Pixels labeled *red* are those where the target had less than -50 dB and the mixture had more than -50 dB energy. Spectrograms were computed from a filter bank with bandwidths and frequency spacing similar to those in the ear. Each pixel is the rms amplitude of the signal within a frequency band and time window.

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that enters the ear (in that their sum is equal to the mixture), only one of which actually occurred in the world. The auditory system must infer the set of sounds that actually occurred. As in other ill-posed problems, this inference is only possible with the aid of assumptions that constrain the solution. In this case, the assumptions concern the nature of sounds in the world, and are presumably learned from experience with natural sounds (or perhaps hard-wired into the auditory system via evolution).

Grouping cues (i.e., sound properties that dictate whether sound elements are heard as part of the same sound) are examples of these assumptions. For instance, natural sounds that have pitch, such as vocalizations, contain frequencies that are harmonically related, evident as banded structures in lower half of the spectrogram of the target speaker in Figure 8.13. Harmonically related frequencies are unlikely to occur from the chance alignment of multiple different sounds, and thus when they

are present in a mixture, they are likely to be due to the same sound and are generally heard as such (de Cheveigne, McAdams, et al., 1995; Roberts & Brunstrom, 1998). Moreover, a component that is mistuned (in a tone containing otherwise harmonic frequencies) segregates from the rest of the tone (Moore, Glasberg, et al., 1986). Understanding sound segregation requires understanding the acoustic regularities, such as harmonicity, that characterize natural sound sources and that are used by the auditory system.

Perhaps the most important generic acoustic grouping cue is common onset: frequency components that begin and end at the same time are likely to belong to the same sound. Onset differences, when manipulated experimentally, cause frequency components to perceptually segregate from each other (Cutting, 1975; Darwin, 1981). Interestingly, a component that has an earlier or later onset than the rest of a set of harmonics has reduced influence over the perceived pitch of the entire tone (Darwin & Ciocca, 1992), suggesting that pitch computations operate on frequency components that are deemed likely to belong together, rather than on the raw acoustic input.

Onset may be viewed as a special case of *comodulation*—amplitude modulation that is common to different spectral regions. In some cases relatively slow comodulation promotes grouping of different spectral components (Hall, Haggard, et al., 1984), although abrupt onsets seem to be most effective. Common offset also promotes grouping but is less effective than common onset (Darwin, 1984), perhaps because abrupt offsets are less common in natural sounds (Cusack & Carlyon, 2004).

Not every intuitively plausible grouping cue produces a robust effect when assessed psychophysically. For instance, frequency modulation (FM) that is shared (“coherent”) across multiple frequency components, as in voiced speech, has been proposed to promote their grouping (Bregman, 1990; McAdams, 1989). However, listeners are poor at discriminating coherent from incoherent FM if the component tones are not harmonically related, indicating that sensitivity to FM coherence may simply be mediated by the deviations from harmonicity that occur when harmonic tones are incoherently modulated (Carlyon, 1991).

One might also think that the task of segregating sounds would be greatly aided by the tendency of distinct sound sources in the world to originate from distinct locations. In practice, spatial cues are indeed of some benefit, for instance, in hearing a

target sentence from one direction amid distracting utterances from other directions (Bronkhorst, 2000; Hawley, Litovsky, et al., 2004; Ihlefeld & Shinn-Cunningham, 2008; Kidd, Arbogast, et al., 2005). However, spatial cues are surprisingly ineffective at segregating one frequency component from a group of others (Culling & Summerfield, 1995), especially when pitted against other grouping cues such as onset or harmonicity (Darwin & Hukin, 1997). The benefit of listening to a target with a distinct location (Bronkhorst, 2000; Hawley, Litovsky, et al., 2004; Ihlefeld & Shinn-Cunningham, 2008; Kidd, Arbogast, et al., 2005) may thus be due to the ease with which the target can be attentively tracked over time amid competing sound sources, rather than to a facilitation of auditory grouping per se (Darwin & Hukin, 1999). Moreover, humans are usually able to segregate monaural mixtures of sounds without difficulty, demonstrating that spatial separation is often not necessary for high performance. For instance, much popular music of the twentieth century was released in mono, and yet listeners have no trouble distinguishing many different instruments and voices in any given recording. Spatial cues thus contribute to sound segregation, but their presence or absence does not seem to fundamentally alter the problem.

The weak effect of spatial cues on segregation may reflect their fallibility in complex auditory scenes. Binaural cues can be contaminated when sounds are combined or degraded by reverberation (Brown & Palomaki, 2006) and can even be deceptive, as when caused by echoes (whose direction is generally different from the original sound source). It is possible that the efficacy of different grouping cues in general reflects their reliability in natural conditions. Evaluating this hypothesis will require statistical analysis of natural auditory scenes, an important direction for future research.

Sequential Grouping

Because the spectrogram approximates the input that the cochlea provides to the rest of the auditory system, it is common to view the problem of sound segregation as one of deciding how to group the various parts of the spectrogram (Bregman, 1990). However, the brain does not receive an entire spectrogram at once. Rather, the auditory input arrives gradually over time. Many researchers thus distinguish between the problem of simultaneous grouping (determining how the spectral content of a short segment of the auditory input should be segregated) and sequential grouping (determining how the

groups from each segment should be linked over time, e.g., to form a speech utterance or a melody) (Bregman, 1990).

Although most of the classic grouping cues (e.g., onset/comodulation, harmonicity, ITD) are quantities that could be measured over short timescales, the boundary between what is simultaneous and what is sequential is unclear for most real-world signals, and it may be more appropriate to view grouping as being influenced by processes operating at multiple timescales rather than two cleanly divided stages of processing. There are, however, contexts in which the bifurcation into simultaneous and sequential grouping stages is natural, as when the auditory input consists of discrete sound elements that do not overlap in time. In such situations interesting differences are sometimes evident between the grouping of simultaneous and sequential elements. For instance, spatial cues, which are relatively weak as a simultaneous cue, have a stronger influence on sequential grouping of tones (Darwin & Hukin, 1997).

Another clear case of sequential processing can be found in the effects of sound repetition. Sounds that occur repeatedly in the acoustic input are detected by the auditory system as repeating, and are inferred to be a single source. Perhaps surprisingly, this is true even when the repeating source is embedded in mixtures with other sounds, and is never presented in isolation (McDermott, Wroblewski, et al., 2011). In such cases the acoustic input itself does not repeat, but the source repetition induces correlations in the input that the auditory system detects and uses to extract the repeating sound. The informativeness of repetition presumably results from the fact that mixtures of multiple sounds tend not to occur repeatedly, such that when a structure does repeat, it is likely to be a single source.

Effects of repetition are also evident in classic results on “informational masking”—masking-like effects on the detectability of a target tone, so-called because they cannot be explained in terms of conventional “energetic masking,” (in which the response to the target is swamped by a masker that falls within the same peripheral channel). Demonstrations of informational masking typically present a target tone along with other tones that lie outside a “protected region” of the spectrum, such that they are unlikely to stimulate the same filters as the target tone. These “masking” tones nonetheless often elevate the detection threshold for the target, sometimes quite dramatically (Durlach, Mason, et al., 2003; Lutfi, 1992; Neff, 1995; Watson,

1987). The effect is presumably due to impairments in the ability to segregate the target tone from the masker tones, and can be reduced when the target is repeatedly presented (Kidd, Mason et al., 1994; Kidd, Mason et al., 2003).

Streaming

One type of sequential segregation effect has particularly captured the imagination of the hearing community and merits special mention. When two pure tones of different frequency are repeatedly presented in alternation, one of two perceptual states is commonly reported by listeners: one in which the two repeated tones are heard as a single “stream” whose pitch varies over time, and one in which two distinct streams are heard, one with the high tones and one with the low tones (Bregman & Campbell, 1971). If the frequency separation between the two tones is small, and if the rate of alternation is slow, one stream is generally heard. When the frequency separation is larger or the rate is faster, two streams tend to be heard, in which case “streaming” is said to occur (van Noorden, 1975).

An interesting hallmark of this phenomenon is that when two streams are perceived, judgments of the temporal order of elements in different streams are impaired (Bregman & Campbell, 1971; Micheyl & Oxenham, 2010). This latter finding provides compelling evidence for a substantive change in the representation underlying the two percepts. Subsequent research has demonstrated that separation along most dimensions of sound can elicit streaming (Moore & Gockel, 2002). The streaming effects in these simple stimuli may be viewed as a variant of grouping by similarity—elements are grouped together when they are similar along some dimension, and segregated when they are sufficiently different, presumably because this similarity reflects the likelihood of having been produced by the same source.

Filling in

Although it is common to view sound segregation as the problem of grouping the spectrogram-like output of the cochlea across frequency and time, this cannot be the whole story, in part because large swaths of a sound’s time–frequency representation are often physically obscured (masked) by other sources and are thus not physically available to be grouped. Masking is evident in the green pixels of Figure 8.13, which represent points where the target source has substantial energy, but where the mixture exceeds it in level. If these points are simply assigned

to the target, or omitted from its representation, the target's level at those points will be misconstrued, and the sound potentially misidentified. To recover an accurate estimate of the target source, it is necessary to infer not just the grouping of the energy in the spectrogram but also the structure of the target source in the places where it is masked.

There is in fact considerable evidence that the auditory system does just this, from experiments investigating the perception of partially masked sounds. For instance, tones that are interrupted by noise bursts are “filled in” by the auditory system, such that they are heard as continuous in conditions in which physical continuity is plausible given the stimulus (Warren, Obusek, et al., 1972). Known as the “continuity effect”, it occurs only when the interrupting noise bursts are sufficiently intense in the appropriate part of the spectrum to have masked the tone should it have been present continuously. Continuity is also heard for frequency glides (Ciocca & Bregman, 1987; Kluender & Jenison, 1992) as well as oscillating frequency-modulated tones (Carlyon, Micheyl, et al., 2004). The perception of continuity across intermittent maskers was actually first reported for speech signals interrupted by noise bursts (Warren, 1970). For speech, the effect is often termed *phonemic restoration*, and likely indicates that knowledge of speech acoustics (and perhaps of other types of sounds as well) influences the inference of the masked portion of sounds. Similar effects occur in the spectral domain—regions of the spectrum are perceptually filled in when evidence indicates they are likely to have been masked, e.g. by a continuous noise source (McDermott & Oxenham, 2008). Filling-in effects in hearing are conceptually similar to completion under and over occluding surfaces in vision, although the ecological constraints provided by masking (involving the relative intensity of two sounds) are distinct from those provided by occlusion (involving the relative depth of two surfaces). Neurophysiological evidence indicates that the representation of tones in primary auditory cortex reflects the perceived continuity, responding as though the tone were continuously present despite being interrupted by noise (Petkov, O'Connor, et al., 2007; Riecke, van Opstal, et al., 2007).

Brain Basis of Sound Segregation

Recent years have seen great interest in how sound segregation is instantiated in the brain. One proposal that has attracted interest is that sounds are heard as segregated when they are represented in

non-overlapping neural populations at some stage of the auditory system. This idea derives largely from studies of the pure-tone streaming phenomena described earlier, with the hope that it will extend to more realistic sounds.

The notion is that conditions that cause two tones to be represented in distinct neural populations are also those that cause sequences of two tones to be heard as separate streams (Bee & Klump, 2004; Fishman, Arezzo, et al., 2004; Micheyl, Tian, et al., 2005; Pressnitzer, Sayles, et al., 2008). Because of tonotopy, different frequencies are processed in neural populations whose degree of overlap decreases as the frequencies become more separated. Moreover, tones that are more closely spaced in time are more likely to reduce each other's response (via what is termed *suppression*), which also reduces overlap between the tone representations—a tone on the outskirts of a neuron's receptive field might be sufficiently suppressed as to not produce a response at all. These two factors, frequency separation and suppression, predict the two key effects in pure-tone streaming: that streaming should increase when tones are more separated in frequency or are presented more quickly (van Noorden, 1975).

Experiments over the past decade in multiple animal species indicate that pure-tone sequences indeed produce non-overlapping neural responses under conditions in which streaming is perceived by human listeners (Bee & Klump, 2004; Fishman, Arezzo, et al., 2004; Micheyl, Tian, et al., 2005; Pressnitzer, Sayles, et al., 2008). Some of these experiments take advantage of another notable property of streaming—its strong dependence on time. Specifically, the probability that listeners report two streams increases with time from the beginning of the sequence, an effect termed *buildup* (Bregman, 1978). Buildup has been linked to neurophysiology via neural adaptation. Because neural responses decrease with stimulus repetition, over time it becomes less likely that two stimuli with distinct properties will both exceed the spiking threshold for the same neuron, such that the neural responses to two tones become increasingly segregated on a timescale consistent with that of perceptual buildup (Micheyl, Tian, et al., 2005; Pressnitzer, Sayles, et al., 2008). For a comprehensive review of these and related studies, see Snyder and Alain, 2007, and Fishman and Steinschneider, 2010.

A curious feature of these studies is that they suggest that streaming is an accidental side effect of what would appear to be general features of the auditory system—tonotopy, suppression, and

adaptation. Given that sequential grouping seems likely to be of great adaptive significance (because it affects our ability to recognize sounds), it would seem important for an auditory system to behave close to optimally, that is, for the perception of one or two streams to be related to the likelihood of one or two streams in the world. It is thus striking that the phenomenon is proposed to result from apparently incidental features of processing. Consistent with this viewpoint, a recent study showed that synchronous high- and low-frequency tones produce neural responses that are just as segregated as those for the classic streaming configuration of alternating high and low tones, even though perceptual segregation does not occur when the tones are synchronous (Elhilali, Ma, et al., 2009). This finding indicates that non-overlapping neural responses are not sufficient for perceptual segregation, and that the relative timing of neural responses may be more important. The significance of neural overlap thus remains unclear, and the brain basis of streaming will undoubtedly continue to be debated in the years to come.

Separating Sound Sources from the Environment

Thus far we have mainly discussed how the auditory system segregates the signals from multiple sound sources, but listeners face a second important scene analysis problem. The sound that reaches the ear from a source is almost always altered to some extent by the surrounding environment, and these environmental influences must be separated from those of the source if the source content is to be estimated correctly. Typically the sound produced by a source reflects off multiple surfaces on its way to the ears, such that the ears receive some sound directly from the source, but also many reflected versions (Figure 8.14). These reflected versions (echoes) are delayed because their path to the ear is lengthened, but generally they also have altered frequency spectra because reflective surfaces absorb some frequencies more than others. Because each reflection can be well described with a linear filter applied to the source signal, the signal reaching the ear, which is the sum of the direct sound along with all the reflections, can be described simply as the result of applying a single composite linear filter to the source (Gardner, 1998). Significant filtering of this sort occurs in almost every natural listening situation, such that sound produced in anechoic conditions (in which all surfaces are minimally reflective) sounds noticeably strange and unnatural.

Listeners are often interested in the properties of sound sources, and one might think of the environmental effects as a nuisance that should simply be discounted. However, environmental filtering imbues the acoustic input with useful information—for instance, about the size of a room where sound is produced and the distance of the source from the listener. It is thus more appropriate to think of separating source and environment, at least to some extent, rather than simply recovering the source. Reverberation is commonly used in music production, for instance, to create a sense of space or to give a different feel to particular instruments or voices.

The loudness constancy phenomena discussed earlier are one example of the brain inferring the properties of the sound source as separate from that of the environment, but there are many others. One of the most interesting involves the treatment of echoes in sound localization. The echoes that are common in most natural environments pose a problem for localization because they generally come from directions other than that of the source (Figure 8.14B). The auditory system appears to solve this problem by perceptually fusing similar impulsive sounds that occur within a brief interval of each other (on the order of 10 ms or so), and using the sound that occurs first to determine the perceived location. This *precedence effect*, so called because of the dominance of the sound that occurs first, was described and named by Hans Wallach (Wallach, Newman, et al., 1949), one of the great gestalt psychologists, and has since been the subject of a large and interesting literature. For instance, the maximal delay at which echoes are perceptually suppressed increases as two pairs of sounds are repeatedly presented (Freyman, Clifton, et al., 1991), presumably because the repetition provides evidence that the second sound is indeed an echo of the first, rather than being due to a distinct source (in which case it would not occur at a consistent delay following the first sound). Moreover, reversing the order of presentation can cause an abrupt breakdown of the effect, such that two sounds are heard rather than one, each with a different location. See Litovsky, Colburn, et al., 1999, for a review.

Reverberation poses a problem for sound recognition in addition to localization because different environments alter the sound from a source in different ways. Large amounts of reverberation (with prominent echoes at very long delays), as are present in some large auditoriums, can in fact greatly reduce the intelligibility of speech. Moderate amounts of

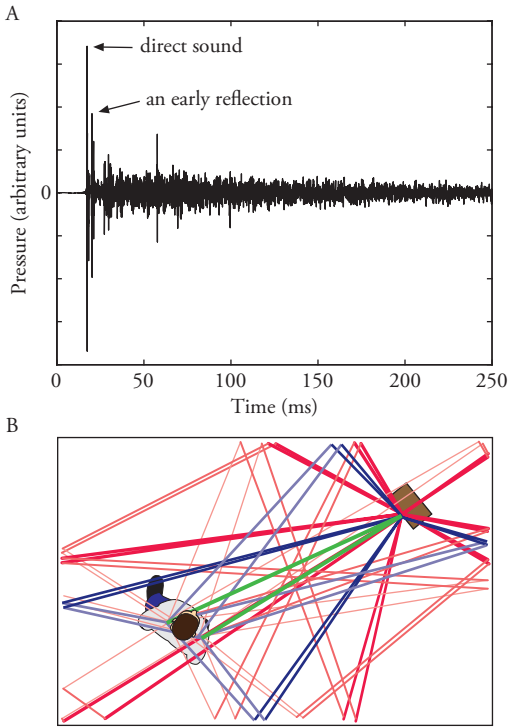


Figure 8.14 Reverberation. **A**, Impulse response for a classroom. This is the sound waveform recorded in this room in response to a click (impulse) produced at a particular location in the room. The *top arrow* indicates the impulse that reaches the microphone directly from the source (that thus arrives first). The *lower arrow* indicates one of the subsequent reflections, i.e., echoes. After the early reflections, a gradually decaying reverberation tail is evident (cut off at 250 ms for clarity). The sound signal resulting from an arbitrary source could be produced by convolving the sound from the source with this impulse response. **B**, Schematic diagram of the sound reflections that contribute to the signal that reaches a listener’s ears in a typical room. The *brown box* in the upper right corner depicts the speaker producing sound. The *green lines* depict the path taken by the direct sound to the listener’s ears. *Blue and red lines* depict sound reaching the ears after one and two reflections, respectively. Sound reaching the ear after more than two reflections is not shown.

Part **B** is reprinted with permission from Culling & Akeroyd, 2010.

reverberation, however, as are present most of the time, typically have minimal effect on our ability to recognize speech and other sounds. Recent work indicates that part of our robustness to reverberation derives from a process that adapts to the history of echo stimulation. In reverberant conditions, the intelligibility of a speech utterance has been found to be higher when preceded by another utterance than when not, an effect that does not occur in anechoic conditions (Brandewie & Zahorik, 2010). Such results, like those of the precedence effect, are consistent with the idea that listeners construct a model of the environment’s contribution to the

acoustic input and use it to partially discount the environment when judging properties of a source. Analogous effects have been found with nonspeech sounds. When listeners hear instrument sounds preceded by speech or music that has been passed through a filter that “colors” the spectrum, the instrument sound is identified differently, as though listeners internalize the filter, assume it to be an environmental effect, and discount it to some extent when identifying the sound (Stilp, Alexander, et al., 2010).

VII. Current and Future Directions

Hearing science is one of the oldest areas of psychology and neuroscience, with a strong research tradition dating back over 100 years, yet there remain many important open questions. Although research on each of the senses need not be expected to proceed according to a single fixed trajectory, the contrast between hearing and vision nonetheless provides useful reminders of what remains poorly understood in audition. The classic methods of psychophysics were initially developed largely within hearing research, and were then borrowed by vision scientists to explore sensory encoding processes in vision. But while vision science quickly embraced perceptual and cognitive questions, hearing science remained more focused on the periphery. This can be explained in part by the challenge of understanding the cochlea, the considerable complexity of the early auditory system, and the clinical importance of peripheral audition. However, the focus on the periphery has left many central aspects of audition underexplored, and recent trends in hearing research reflect a shift toward the study of these neglected mid- and high-level questions.

One important set of questions concerns the interface of audition with the rest of cognition, via attention and memory. Attention research ironically also flourished in hearing early on (with Cherry’s [1953] classic dichotic listening studies), but then largely moved to the visual domain. Recent years have seen renewed interest (see chapter 11 in this volume), but there remain many open questions. Much is still unclear about what is represented about sound in the absence of attention, about how and what auditory attention selects, and about the role of attention in perceptual organization.

Another promising research area involves working memory. Auditory short-term memory may have some striking differences with its visual counterpart (Demany, Trost, et al., 2008) and appears closely linked to auditory scene analysis (Conway, Cowan,

et al., 2001). Studies of these topics in audition also hold promise for informing us more generally about the structure of cognition—the similarities and differences with respect to visual cognition will reveal much about whether attention and memory mechanisms are domain general (perhaps exploiting central resources) or specific to particular sensory systems.

Interactions between audition and the other senses are also attracting increased interest. Information from other sensory systems likely plays a crucial role in hearing given that sound on its own often provides ambiguous information. The sounds produced by rain and applause, for instance, can in some cases be quite similar, such that multisensory integration (using visual, somatosensory, or olfactory input) may help to correctly recognize the sound source. Cross-modal interactions in localization (Alais & Burr, 2004) are similarly powerful. Understanding cross-modal effects within the auditory system (Bizley, Nodal, et al., 2007; Ghazanfar, 2009; Kayser, Petkov, et al., 2008) and their role in behavior will be a significant direction of research going forward.

In addition to the uncharted territory in perception and cognition, there remain important open questions about peripheral processing. Some of these unresolved issues, such as the mechanisms of outer hair cell function, have great importance for understanding hearing impairment. Others may dovetail with higher level function. For instance, the role of efferent connections to the cochlea is still uncertain, with some hypothesizing a role in attention or segregation (Guinan, 2006). The role of phase locking in frequency encoding and pitch perception is another basic issue that remains controversial and that has widespread relevance to mid-level audition.

As audition continues to evolve as a field, I believe useful guidance will come from a computational analysis of the inference problems the auditory system must solve (Marr, 1982). This necessitates thinking about the behavioral demands of real-world listening situations, as well as the constraints imposed by the way that information about the world is encoded in a sound signal. Many of these issues are becoming newly accessible with recent advances in computational power and signal processing techniques.

For instance, one of the most important tasks a listener must perform with sound is surely that of recognition—determining what it was in the world that caused a sound, be it a particular type of object, or of a type of event, such as something falling on

the floor (Gaver, 1993; Lutfi, 2008). Recognition is computationally challenging because the same type of occurrence in the world typically produces a different sound waveform each time it occurs. A recognition system must generalize across the variation that occurs within categories, but not the variation that occurs across categories (DiCarlo & Cox, 2007). Realizing this computational problem allows us to ask how the auditory system solves it. One place where these issues have been explored to some extent is speech perception (Holt & Lotto, 2010). The ideas explored there—about how listeners achieve invariance across different speakers and infer the state of the vocal apparatus along with the accompanying intentions of the speaker—could perhaps be extended to audition more generally (Rosenblum, 2004).

The inference problems of audition can also be better appreciated by examining real-world sound signals, and formal analysis of these signals seems likely to yield valuable clues. As discussed in previous sections, statistical analysis of natural sounds has been a staple of recent computational auditory neuroscience (Harper & McAlpine, 2004; Rodriguez, Chen, et al., 2010; Smith & Lewicki, 2006), where natural sound statistics have been used to explain the mechanisms observed in the peripheral auditory system. However, sound analysis seems likely to provide insight into mid- and high-level auditory problems as well. For instance, the acoustic grouping cues used in sound segregation are almost surely rooted to some extent in natural sound statistics, and examining such statistics could reveal unexpected cues. Similarly, because sound recognition must generalize across the variability that occurs within sounds produced by a particular type of source, examining this variability in natural sounds may provide clues to how the auditory system achieves the appropriate invariance in this domain.

The study of real-world auditory competence will also necessitate measuring auditory abilities and physiological responses with more realistic sound signals. The tones and noises that have been the staple of classical psychoacoustics and auditory physiology have many uses, but also have little in common with many everyday sounds. One challenge of working with realistic signals is that actual recordings of real-world sounds are often uncontrolled, and typically introduce confounds associated with their familiarity. Methods of synthesizing novel sounds with naturalistic properties (Cavaco & Lewicki, 2007; McDermott, Wroblewski et al.,

2011; McDermott & Simoncelli, 2011) are thus likely to be useful experimental tools. Simulations of realistic auditory environments are also increasingly within reach, with methods for generating three-dimensional auditory scenes (Wightman & Kistler, 1989; Zahorik, 2009) being used in studies of sound localization and speech perception in realistic conditions.

We must also consider more realistic auditory behaviors. Hearing does not normally occur while we are seated in a quiet room, listening over headphones, and paying full attention to the acoustic stimulus, but rather in the context of everyday activities in which sound is a means to some other goal. The need to respect this complexity while maintaining sufficient control over experimental conditions presents a challenge, but not one that is insurmountable. For instance, neurophysiology experiments involving naturalistic behavior are becoming more common, with preparations being developed that will permit recordings from freely moving animals engaged in vocalization (Eliades & Wang, 2008) or locomotion—ultimately, perhaps a real-world cocktail party.

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