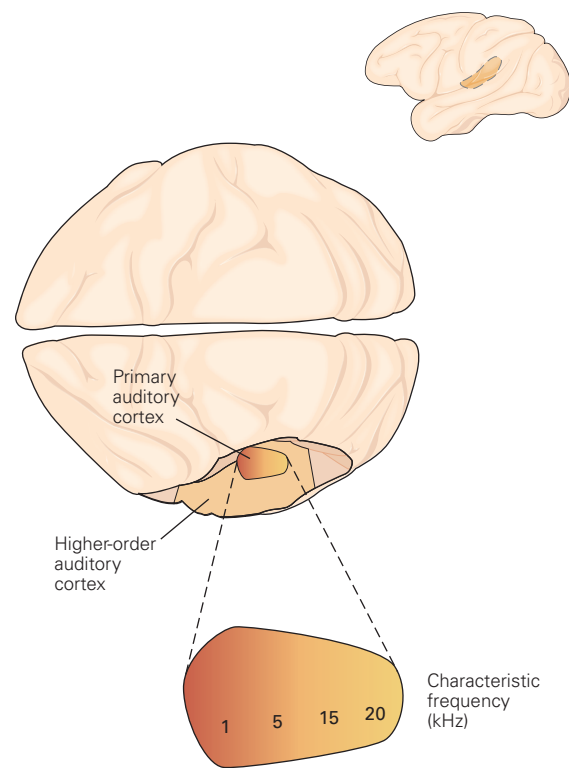


were puzzled by how difficult it was to drive neurons in the auditory cortex of awake cats. Now we know it was because they were probably recording from highly selective neurons and using nonpreferred stimuli. The availability of digital technology since then has made it possible to create and test a large battery of acoustic stimuli in search of the preferred stimulus of a highly selective neuron in auditory cortex. The overall picture elucidated by experimenters is that when a sound is heard, the auditory cortex first responds with transient discharges (encoding the onset of a sound) across a relatively large population of neurons. As the time passes, the activation becomes restricted to a smaller population of neurons that are preferentially driven by the sound (Figure 28-9C), which results in a selective representation of the sound within the neuronal population and over time. Because each neuron has its own preferred stimulus that differs from preferred stimuli of other neurons, neurons in the auditory cortex collectively cover the entire acoustic space with their sustained firing regions. Therefore, any particular sound can evoke sustained firing throughout its duration in a particular population of neurons in the auditory cortex. In other words, the region of auditory cortex activated by acoustic stimulation in whole-brain imaging (eg, functional magnetic resonance imaging [fMRI], positron emission tomography [PET]) comprises neurons that are preferentially driven by the acoustic stimulus.

### The Auditory Cortex Maps Numerous Aspects of Sound

The auditory cortex includes multiple distinct functional areas on the dorsal surface of the temporal lobe. The most prominent projection is from the ventral division of the medial geniculate nucleus to the primary auditory cortex (A1, or Brodmann's area 41). As in the subcortical structures, the neurons in this cytoarchitectonically distinct region are arranged tonotopically. In monkeys, neurons tuned to low frequencies are found at the rostral end of A1, while those responsive to high frequencies are in the caudal region (Figure 28-10). Thus, like the visual and somatosensory cortices, A1 contains a map reflecting the sensory periphery.

Because the cochlea encodes discrete frequencies at different points along the basilar membrane, however, a one-dimensional frequency map from the periphery is spread across the two-dimensional surface of the cortex, with a smooth frequency gradient in one direction and isofrequency contours along the other direction. In many species, subregions of the auditory cortex that represent biologically significant frequencies are larger than others because of extensive



**Figure 28-10** The auditory cortex of primates has multiple primary and secondary areas. The expanded figure of the primary auditory cortex shows its tonotopic organization. The primary areas are surrounded by higher-order areas (see Figure 28-11).

inputs, similar to the large area in the primary visual cortex devoted to inputs from the fovea.

In addition to frequency, other features of auditory stimuli are mapped in the primary auditory cortex, although the overall organization is less clear and precise than for vision. Auditory neurons in A1 are excited either by input from both ears (EE neurons), with the contralateral input usually stronger than the ipsilateral contribution, or by a unilateral input (EI). The EI neurons are inhibited by stimulation of the opposite ear.

Certain neurons in A1 also seem to be organized according to bandwidth, that is, according to their responsiveness to a narrow or broad range of frequencies. Neurons near the center of the isofrequency contours are tuned more narrowly to bandwidth or frequency than those located away from the center. Distinct subregions of A1 form clusters of cells with narrow or broadband tuning within individual isofrequency contours. Within intracortical circuits, neurons receive input primarily from neurons with similar bandwidths and characteristic frequencies.

This modular organization of bandwidth selectivity may allow redundant processing of incoming signals through neuronal filters of varying bandwidths as well as center frequencies, which could be useful for the analysis of spectrally complex sounds such as species-specific vocalizations, including speech.

Several other parameters are represented in A1. These include neuronal response latency, loudness, modulation of loudness, and the rate and direction of frequency modulation. Although it remains to be seen how these various maps intersect, this array of parameters clearly endows each neuron and each location in A1 with the ability to represent many independent variables of sound and thus allows for a great diversity of neuronal selectivity.

As is true for visual and somatosensory areas of the cortex, sensory representation in A1 can change in response to alterations in input pathways. After peripheral hearing loss, tonotopic mapping in A1 can be altered so that neurons that were previously responsive to sounds within the lost range of hearing will begin to respond to adjacent frequencies. The work of Michael Merzenich and others has shown that behavioral training of adult animals can also result in large-scale reorganization of the auditory cortex, so that the most behaviorally relevant frequencies—those specifically associated with attention or reinforcement—come to be overrepresented.

The auditory areas of young animals are particularly plastic. In rodents, the frequency organization of A1 emerges gradually during development from an early, crude frequency map. Raising animals in acoustic environments in which they are exposed to repeated tone pulses of a particular frequency results in a persistent expansion of cortical areas devoted to that frequency, accompanied by a general deterioration and broadening of the tonotopic map. This result not only suggests that the development of A1 is experience-dependent but also raises the possibility that early exposure to abnormal sound environments can create long-term disruptions of high-level sensory processing. A greater understanding of how this happens and whether it is also true for human fetuses and infants may provide insights into the origin and remediation of disorders in which central auditory processing is impaired, such as many forms of dyslexia. Moreover, the ability to induce plasticity in the auditory cortex of adults by engaging attention or reward raises new hopes for brain repair even in adulthood.

The primary auditory area of mammals is surrounded by multiple distinct regions, some of which are tonotopic. Adjacent tonotopic fields have

mirror-image tonotopy: The direction of tonotopy reverses at the boundary between fields. In monkeys, as many as 7 to 10 secondary (belt) areas surround the three or four primary or primary-like (core) areas (see Figure 28–11). The secondary areas receive input from the core areas of the auditory cortex and, in some cases, from thalamic nuclei. Electrophysiological and imaging studies have confirmed that A1 in humans lies on Heschl's gyrus, in the temporal lobe, medial to the Sylvian fissure. In addition, recent fMRI studies have revealed that in humans, just as in monkeys, pure tones activate primarily core areas, whereas the neurons of belt areas prefer complex sounds such as narrowband noise bursts.

### **A Second Sound-Localization Pathway From the Inferior Colliculus Involves the Cerebral Cortex in Gaze Control**

Many neurons in the auditory cortex have broad spatial tuning, but neurons with narrow spatial tuning are also found when studied in awake animals. In monkeys, auditory cortex neurons are tuned to both frontal space and rear space (outside the coverage of vision), as well as the space above and below the horizontal plane. In contrast to the auditory midbrain, however, there is yet no evidence for a spatially organized map of sound in any of the cortical areas sensitive to sound location.

The sound-localization pathways in the cortex originate in the central nucleus of the inferior colliculus and ascend through the auditory thalamus and the primary and secondary cortical areas, eventually reaching the frontal eye fields involved in gaze control. Eye or head movements can be elicited by stimulating the frontal eye fields, which connect directly to brain stem tegmentum premotor nuclei that mediate gaze changes as well as to the superior colliculus. But why should there be this second sound-localization pathway connected to gaze control circuitry when the midbrain pathway from location-sensitive neurons in the inferior colliculus to the superior colliculus to gaze control circuitry directly controls orientation movements of the head, eyes, and ears?

Behavioral experiments shed light on this question. Although lesions of A1 can result in profound sound-localization deficits, no deficiency is seen when the task is simply to indicate the side of the sound source by pushing a lever. The deficit becomes apparent only when the animal must approach the location of a brief sound source; that is, when the task is the more complex one of forming an image of the source, remembering it, and moving toward it.

Experiments in barn owls have produced particularly compelling evidence. The ability of owls to orient to sounds in space is unaffected by inactivation of the avian equivalent of the frontal eye fields. Similarly, when the midbrain sound localization pathway is disrupted by pharmacological inactivation of the superior colliculus, the probability of an accurate head turn is decreased, but animals still respond correctly more than half of the time. In contrast, when both structures are inactivated, animals are completely unable to orient accurately to acoustic stimuli on the contralateral side. Thus, cortical and subcortical sound-localization pathways have parallel access to gaze control centers, perhaps providing some redundancy. Moreover, when only the frontal eye fields are inactivated, birds lose their ability to orient their gaze toward a target that has been extinguished and must be remembered, just as is seen with mammalian A1 lesions. Thus, in both mammals and birds, cortical pathways are required for more complex sound-localization tasks.

This appears to be a general difference between cortical and subcortical pathways. Subcortical circuits are important for rapid and reliable performance of behaviors that are critical to survival. Cortical circuitry allows for working memory, complex recognition tasks, and selection of stimuli and evaluation of their significance, resulting in slower but more differentiated performance. Examples of this also exist in auditory pathways not involved in localization. Conditioned fear responses to simple auditory stimuli are mediated by direct rapid pathways from the auditory thalamus to the amygdala; they can still be elicited after cortical inactivation. However, fear responses that require more complex discrimination of auditory stimuli require pathways through the cortex and are accordingly slower but more specific.

### **Auditory Circuits in the Cerebral Cortex Are Segregated Into Separate Processing Streams**

In the visual system, the output from the primary visual cortex is segregated into separate dorsal and ventral streams concerned respectively with object location in space and object identification. A similar division of labor is thought to exist in the somatosensory cortex, and recent evidence suggests that the auditory cortex also follows this plan.

Anatomical tracing studies of the three most accessible belt areas in monkeys show that the more rostral and ventral areas connect primarily to the more rostral and ventral areas of the temporal lobe, whereas the more caudal area projects to the dorsal and caudal temporal lobe. In addition, these belt areas and their

temporal lobe targets both project to largely different areas of the frontal lobes (Figure 28–11).

The frontal areas receiving anterior auditory projections are generally implicated in nonspatial functions, whereas those that are targets of posterior auditory areas are implicated in spatial processing. Electrophysiological and imaging studies provide support for this. Caudal and parietal areas are more active when a stimulus must be localized or moves, and ventral areas are more active during identification of the same stimulus or analysis of its pitch. Thus anterior-ventral pathways may identify auditory objects by analyzing spectral and temporal characteristics of sounds, whereas the more dorsal-posterior pathways may specialize in sound-source location, detection of sound-source motion, and spatial segregation of sources.

Although the idea that all sensory areas of the cerebral cortex initially segregate object identification and location is attractive, it is likely an oversimplification. It is clear that the medial-belt areas of the auditory cortex project to both dorsal and ventral frontal cortices, and neurons with broad spatial responsiveness are distributed throughout caudal and anterior areas. Nonetheless, although the details may differ between systems, the basic concept holds that sensory systems deconstruct stimuli into features and analyze each type in discrete pathways.

### **The Cerebral Cortex Modulates Sensory Processing in Subcortical Auditory Areas**

An intriguing feature of all mammalian cortical areas, and one shared by the auditory system, is the massive projection from the cortex back to lower areas. There are almost 10 times as many corticofugal fibers entering the sensory thalamus as there are axons projecting from the thalamus to the cortex. Projections from the auditory cortex also innervate the inferior colliculus, olivocochlear neurons, some basal ganglionic structures, and even the dorsal cochlear nucleus.

Insights into possible functions of this feedback have come from the bat's auditory system. Silencing of frequency-specific cortical areas leads to decreased responses in thalamus and inferior colliculus in the corresponding frequency-specific areas, whereas activation of cortical projections increases and sharpens the responses of some neurons. The auditory cortex can therefore actively adjust and improve auditory signal processing in subcortical structures. A variety of evidence suggests that cortical feedback also occurs in other mammals. This challenges the view of ascending



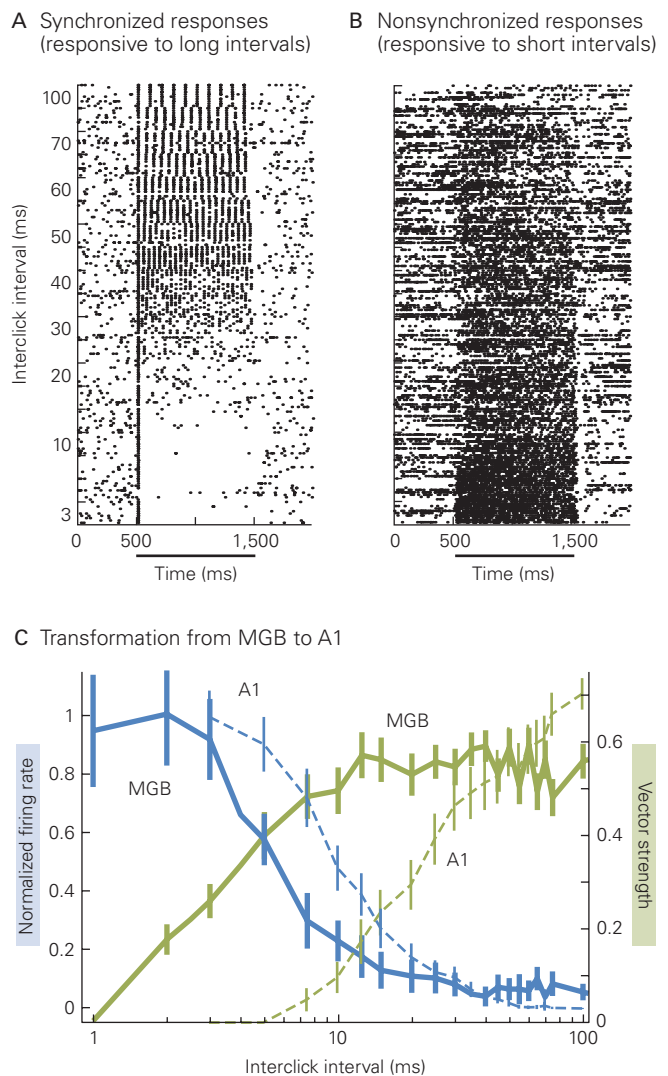


at long interclick intervals, but instead fires increasingly rapidly as the interclick interval becomes shorter (Figure 28–12B). These two populations of A1 neurons, referred to as *synchronized* and *nonsynchronized*, respectively, have complementary response properties. Neurons of the synchronized population *explicitly* represent slowly occurring sound events by synchronized neural firing (a temporal code), whereas neurons of the nonsynchronized population *implicitly* represent rapidly changing sound events by changes in average firing rates (a rate code).

The nonsynchronized neurons have been observed in the auditory cortex of awake primates and rodents. In A1, neural representation changes from a temporal code to a rate code at the interclick interval of about 25 ms, corresponding to a repetition rate of approximately 40 Hz (Figure 28–12A,B). This is near the boundary where our perception of a periodic click train changes from being “discrete” to “continuous.”

The combination of temporal and rate codes to represent the whole range of time-varying sounds is the consequence of a progressive transformation beginning in the auditory nerve, where only a temporal code (phase-locking) is available. The progressive reduction in the upper limit of the phase-locking along the ascending auditory pathway is accompanied by the emergence of firing-rate-based representations. In the medial geniculate body of the thalamus, the intersection between temporal and rate codes is at a shorter interclick interval than in A1 (Figure 28–12C). This indicates that neurons in the medial geniculate body can phase-lock to more rapidly time-varying sounds than A1 neurons, but still utilize a rate code to represent rapidly changing sounds beyond their phase-locking limit.

The prevalence of rate-coding neurons in A1 has important functional implications. It shows that a considerable transition from temporal to rate coding has taken place by the time auditory signals reach the auditory cortex. The importance of the nonsynchronized neural responses is that they represent transformed instead of preserved temporal information. It suggests that cortical processing of sound streams operates on a segment-by-segment basis rather than on a moment-by-moment basis, as found in the auditory nerve. This is necessary for complex integration because higher-level processing tasks require temporal integration over a time window. The reduction in A1 of the upper limit of phase-locking is a prerequisite for multisensory integration in the cerebral cortex. Auditory information is encoded at the periphery at a much faster temporal modulation rate than visual or tactile information, but phase-locking is similar across



**Figure 28–12** Temporal and rate coding of time-varying sounds.

**A.** Stimulus-synchronized responses of a neuron to periodic click trains recorded from A1 of an awake marmoset. The horizontal bar below the x-axis indicates the duration of the stimulus. (Adapted, with permission, from Lu, Liang, and Wang 2001. Copyright © 2001 Springer Nature.)

**B.** Nonsynchronized responses of a neuron to periodic click trains recorded from A1 in an awake marmoset. (Adapted, with permission, from Lu, Liang, and Wang 2001. Copyright © 2001 Springer Nature.)

**C.** Comparison of temporal response properties between primary auditory cortex (A1) and medial geniculate body of the thalamus (MGB). Stimulus-synchronized responses are quantified by vector strength, a measure of the strength of phase-locking. Nonsynchronized responses are quantified by the normalized firing rate (data curves identified as A1 rate and MGB rate). Error bars represent standard error of the mean. (Adapted, with permission, from Bartlett and Wang 2007.)

primary sensory areas of the cortex. The slowing of the phase-locking limit along the ascending auditory pathway and accompanying transition from a temporal code to a rate code are necessary for auditory information to be integrated in the cerebral cortex with information from other sensory modalities that are intrinsically slower.

### Primates Have Specialized Cortical Neurons That Encode Pitch and Harmonics

Pitch perception is crucial for perceiving speech and music and for recognizing auditory objects in a complex acoustic environment. Pitch is the percept that allows harmonically structured periodic sounds to be perceived and ordered on a musical scale. Pitch carries crucial linguistic information in tonal languages such as Chinese and prosodic information in European languages. We use pitch to identify a particular voice from a noisy background in a cocktail party. When listening to an orchestra, we hear the melody of the soloist over the background of accompanying instruments.

An important phenomenon for understanding pitch is the perception of “missing fundamental,” also referred to as the residue pitch. When the harmonics of a fundamental frequency are played together, the pitch is perceived as the fundamental frequency even if the fundamental frequency is missing. For example, the harmonics of the fundamental frequency of 200 Hz are at 400, 600, 800 Hz, and so on. Playing the frequencies 400, 600, and 800 Hz together will generate a pitch perception of 200 Hz, even though a distinct frequency component of 200 Hz is not physically present in the sound. We encounter this phenomenon routinely when we listen to music over speakers that are too small to generate sounds at low frequencies.

Many combinations of frequencies can give rise to a common fundamental frequency or pitch, making it a particularly valuable auditory cue. This is especially useful when pitch conveys behaviorally important information, as in the case of human speech or animal vocalizations. Sounds propagated through the environment can become spectrally degraded, losing high or low frequencies. While such spectral filtering distorts spectral information, the perception of the missing fundamental is robust despite the loss of some harmonic components.

The ability to perceive pitch is not unique to humans; birds, cats, and monkeys can also pick out pitch. Monkeys are capable of spectral pitch discrimination, melody recognition, and octave generalization, each of which requires the perception of pitch. Marmoset monkeys (*Callithrix jacchus*), a highly vocal New

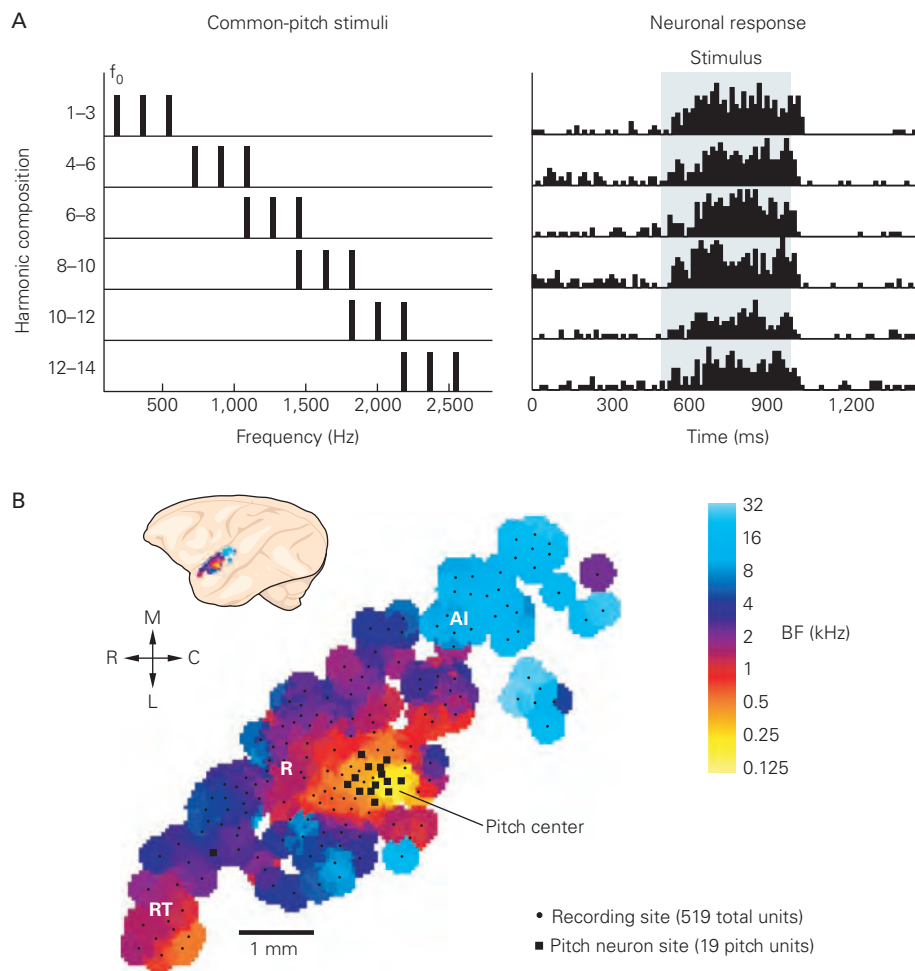
World primate species whose hearing range is similar to that of humans, exhibit human-like pitch perception. Marmosets are able to discriminate a missing fundamental in harmonic sounds with a precision as small as one semitone for the periodicity above 440 Hz.

Given that both humans and some animals experience a pitch that generalizes across a variety of sounds with the same periodicity (including harmonic sounds with a missing fundamental), it is reasonable to expect that some neurons extract pitch from complex sounds. Xiaoqin Wang and his colleagues discovered a decade ago that a small region in the auditory cortex of marmoset monkeys contains “pitch-selective neurons.” These neurons are tuned to pure tones with a best frequency and respond to harmonic complexes with a fundamental frequency near its best frequency even when the harmonics lay outside the neuron’s excitatory-frequency response area (Figure 28–13A).

A pitch-selective neuron responds to pitch-evoking sounds (eg, harmonic sounds, click trains) when the pitch is near the neuron’s preferred best frequency. Pitch-selective neurons increase their firing rates as the behavioral salience of pitch increases and prefer sounds with periodicity over aperiodic sounds. It is important to note that the pitch-selective neurons in marmoset monkeys, which extract and code for pitch embedded in harmonic sounds (a highly nonlinear computation), are distinctly different from neurons in subcortical areas or A1 that merely “reflect” information on pitch in their firing patterns.

The region containing the pitch-selective neurons in marmoset monkeys is confined to the low-frequency border of A1, the rostral auditory cortex (area R), and lateral belt areas (Figure 28–13B). Human imaging studies have identified a restricted region at the lateral end of Heschl’s gyrus anterolateral to A1 that extracts pitch of harmonic complex sounds and is sensitive to changes in pitch salience. The location of this region mirrors the location of the pitch center in marmoset monkeys (Figure 28–13B).

The core regions of auditory cortex in marmosets also contain a class of harmonic template neurons that respond weakly or not at all to pure tones or two-tone combinations but respond strongly to particular combinations of multiple harmonics. The harmonic template neurons show stronger responses to harmonic sounds than inharmonic sounds and selectivity for particular harmonic structures. In contrast to the pitch-selective neurons that are localized within a small cortical region lateral to the low-frequency border between A1 and R and have best frequencies



**Figure 28-13** Pitch is encoded by specialized neurons in primate auditory cortex.

**A.** An example of a pitch-selective neuron recorded from marmoset auditory cortex. *Left:* Frequency spectra of a series of harmonic stimuli that share the same fundamental frequency ( $f_0$ ). *Right:* Peristimulus time histogram of the neuron's response to the stimuli (stimulus duration indicated by the shaded region). (Adapted, with permission, from Bendor and Wang 2005. Copyright © 2005 Springer Nature.)

**B.** Anatomical organization of the marmoset auditory cortex and the location of a pitch center. **Top:** Side view of the marmoset brain. **Bottom:** Tonotopic map of the left auditory cortex characterized in one marmoset. Pitch-selective neurons (**black squares**) are clustered near the low-frequency border between A1 and area R (rostral auditory cortex). Frequency reversals indicate the borders between A1/R and R/RT (rostrotemporal auditory cortex). (BF: best frequency.) (Adapted from Bendor and Wang 2005. Copyright © 2005 Springer Nature.)

less than 1,000 Hz, the harmonic template neurons are distributed across A1 and R and have best frequencies ranging from approximately 1 kHz to approximately 32 kHz, a range that covers the entire hearing range of marmosets.

Whereas in the periphery single auditory nerve fibers encode individual components of harmonic sounds, the properties of the harmonic template neurons reveal harmonically structured receptive fields for extracting harmonic patterns. The change in neural representation of harmonic sounds from auditory

nerve fibers to the auditory cortex reflects a principle of neural coding in sensory systems. Neurons in sensory pathways transform the representation of physical features, such as the frequency of sounds in hearing or luminance of images in vision, into a representation of perceptual features, such as pitch in hearing or curvature in vision. Such features lead to the formation of auditory or visual percepts. The harmonic template neurons in the auditory cortex are key to processing sounds with harmonic structures such as animal vocalizations, human speech, and music.

### Insectivorous Bats Have Cortical Areas Specialized for Behaviorally Relevant Features of Sound

Although it is generally assumed that upstream auditory areas perform increasingly specialized functions related to hearing, much less is known about the functions of serial relays in the auditory system compared to the visual system. In humans, one of the most important aspects of audition is its role in processing language, but we know relatively little about how speech sounds are analyzed by neural circuits. New techniques for imaging the human brain are gradually providing insights into the functional specialization of cortical areas associated with language (Chapter 55).

Evidence for specialized analysis of complex auditory signals in the cerebral cortex comes from studies of insectivorous bats. These animals find their prey almost entirely through *echolocation*, emitting ultrasonic pulses of sound that are reflected by flying insects. Bats analyze the timing and structure of the echoes to help locate and identify the targets, and discrete auditory areas are devoted to processing different aspects of the echoes.

Many bats, such as the mustached bat studied by Nobuo Suga and his collaborators, emit echolocating pulses with two components. An initial *constant-frequency* (CF) component consists of several harmonically related sounds. These harmonics are emitted stably for tens to hundreds of milliseconds, akin to human vowel sounds. The constant-frequency component is followed by a sound that decreases steeply in frequency, the *frequency-modulated* (FM) component, which resembles the rapidly changing frequency of human consonants (Figure 28–14A).

The FM sounds are used to determine the distance to the target. The bat measures the interval between the emitted sound and the returning echo, which corresponds to a particular distance, based on the relatively constant speed of sound. Neurons in the FM-FM area of auditory cortex (Figure 28–14B) respond preferentially to pulse-echo pairs separated by a specific delay. Moreover, these neurons respond better to particular combinations of sounds than to the individual sounds in isolation; such neurons are called *feature detectors* (Figure 28–14C). The FM-FM area contains an array of such detectors, with preferred delays systematically ranging from 0.4 to 18 ms, corresponding to target ranges of 7 to 280 cm (Figure 28–14B). These neurons are organized in columns, each of which is responsive to a particular combination of stimulus frequency and delay. In this way, the bat, like the barn owl in its inferior colliculus, is able to represent an acoustic feature that is not directly represented by sensory receptors.

The CF components of bat calls are used to determine both the speed of the target relative to the bat and the acoustic image of the target. When an echolocating bat is flying toward an insect, the sounds reflected from the insect are Doppler-shifted to a higher frequency at the bat's ear, for the bat is moving toward the returning sound waves from the target, causing a relative speeding up of these waves at its ear. Similarly, a receding insect yields reflections of lowered frequency at the bat's ear. Neurons in the CF-CF area (Figure 28–14B) are sharply tuned to a combination of frequencies close to the emitted frequency or its harmonics. Each neuron responds best to a combination of a pulse of a particular fundamental frequency with an echo corresponding to the first or second harmonic of the pulse, Doppler-shifted to a specific extent. As in the FM-FM area, neurons do not respond to the pulse or echo alone, but rather to the combination of the two CF signals.

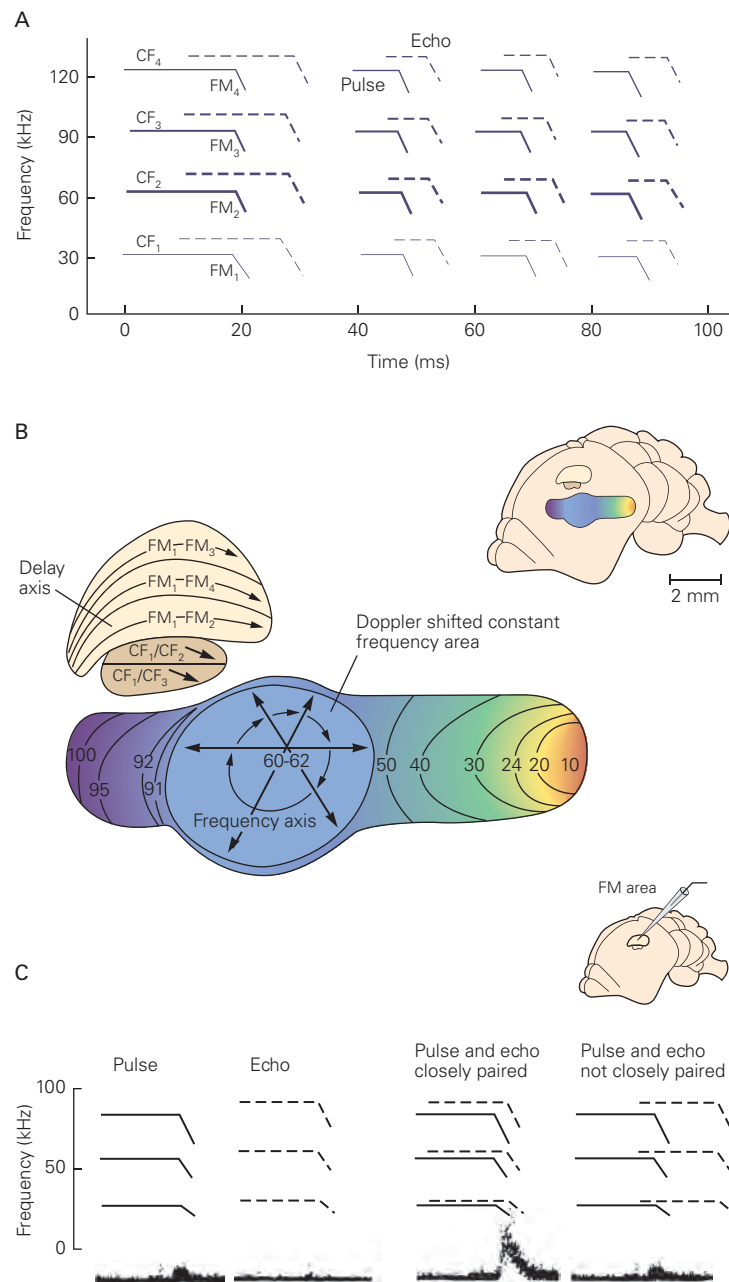
CF-CF neurons are arranged in columns, each encoding a particular combination of frequencies. These columns are arranged regularly along the cortical surface, with the fundamental frequency along one axis and the echo harmonics along a perpendicular axis. This dual-frequency coordinate system creates a map wherein a specific location corresponds to a particular Doppler shift and thus a particular target velocity, ranging systematically from  $-2$  m/s to 9 m/s.

The CF components of returning echoes are also used for detailed frequency analysis of the acoustic image, presumably important in its identification. The Doppler-shifted constant-frequency area (DSCF) of the mustached bat is a dramatic expansion of the primary auditory cortex's representation of frequencies between 60 kHz and 62 kHz, corresponding well to the set of returning echoes from the major CF component of the bat's call (Figure 28–14B). Within the DSCF area, individual neurons are extremely sharply tuned to frequency, so that the tiny changes in frequency created by fluttering moth wings are easily detected.

Transient inactivation of some of these specialized cortical areas while the bat performs a discrimination task strikingly supports the importance of their functional specialization in behavior. Silencing of the DSCF selectively impairs fine frequency discrimination while leaving time perception intact. Conversely, inactivation of the FM-FM area impairs the bat's ability to detect small differences in the time of arrival of two echoes, while leaving frequency perception unchanged.

Investigation of this auditory system was greatly facilitated by knowledge of the stimuli relevant to bats. It remains to be seen whether these cortical areas are functionally or anatomically analogous to particular





**Figure 28-14** The auditory system of the bat has specialized areas for locating sounds.

**A.** A sonogram of an animal's calls (solid lines) and the resultant echoes (dashed lines) illustrates the two components of the call: the protracted, harmonically related constant-frequency (CF) signal and the briefer frequency-modulated (FM) signal. The duration of the calls declines as the animal approaches its target. (Adapted, with permission, from Suga 1984.)

**B.** A view of the cerebral hemisphere of the mustached bat shows three of the functional areas within the auditory cortex. The FM area is where the distance from the target is computed; the CF area is where the velocity of the target is

computed; and the Doppler-shifted CF area is specialized for the identification of small fluttering objects. The expanded cortical representation of Doppler-shifted CF signals near the second harmonic of the call frequency (60–62 kHz) forms the acoustic "fovea." (Adapted, with permission, from Suga 1984.)

**C.** The FM-FM combination-sensitive neuron shown does not respond significantly to either pulses or echoes alone, but responds very strongly to a closely paired pulse-echo. However, the neuron is also sensitive to the time difference between the pulse and echo, as seen in the record on the right, where the neuron fails to respond to a pulse-echo combination that is not closely paired. (Adapted, with permission, from Suga et al. 1983.)