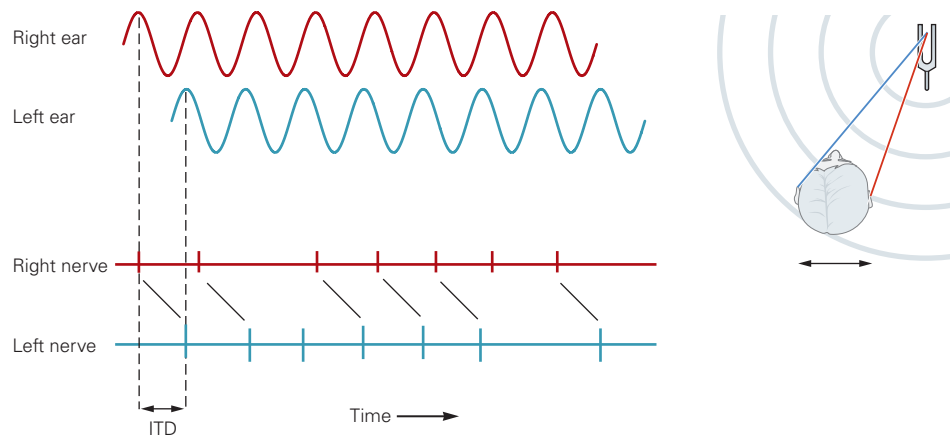
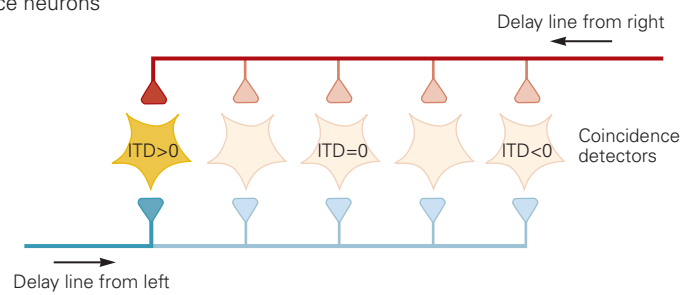


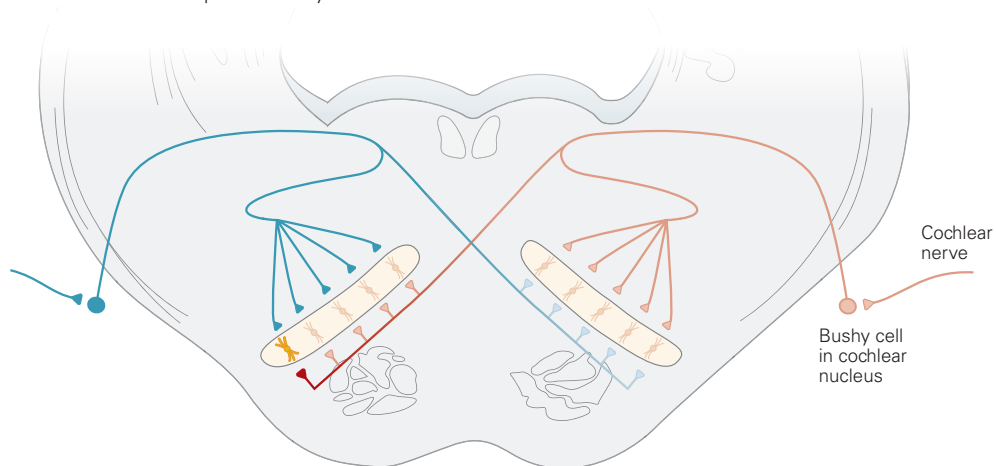
A Phase-locked firing in bushy cells



B Mapping of ITD onto array of neuronal coincidence neurons



C Bilateral medial superior olivary nuclei



intensity at the near ear to be greater than that at the far ear. In humans, interaural intensities can differ in sounds that have frequencies greater than about 2 kHz. Interaural intensity differences produced by such *head shadowing* are detected by a neuronal circuit that includes the medial nucleus of the trapezoid body and the lateral superior olive.

Although the lateral superior olive does not form a map of the location of sounds in the horizontal plane, it performs the first of several integrative steps that use interaural intensity differences to localize sounds. Neurons in this nucleus balance ipsilateral excitation with contralateral inhibition. Excitation comes from small spherical bushy cells and stellate cells in the ipsilateral ventral cochlear nucleus. Inhibition comes from a disynaptic pathway that includes globular bushy cells in the contralateral ventral cochlear nucleus and principal neurons of the ipsilateral medial nucleus of the trapezoid body (Figure 28–6A). Sounds that arise ipsilaterally generate relatively strong excitation and

relatively weak inhibition, whereas those that arise contralaterally generate stronger inhibition than excitation. Neurons in the lateral superior olive are activated more strongly by sounds from the ipsilateral than from the contralateral hemifield. The firing of lateral superior olivary neurons is a function of the location of the sound source and thus carries information about where sounds arise in the horizontal plane (Figure 28–6B).

In order to balance excitation and inhibition stimulated by one sound, the ipsilateral excitation and contralateral inhibition must arrive at neurons in the lateral superior olive at the same time. Thus, excitation that arises monosynaptically from the ipsilateral ventral cochlear nucleus must arrive at the same time as inhibition that arises disynaptically from the contralateral ventral cochlear nucleus. The inhibition comes from the medial nucleus of the trapezoid body whose inputs through large axons of globular bushy cells and large calyces of Held produce synaptic responses

Figure 28–5 (Opposite) Interaural differences in the arrival of a sound help localize sound in the horizontal plane.

A. When a sound such as a pure tone arises from the right, the right ear detects the sound earlier than the left ear. The difference in the time of arrival at the two ears is the interaural time delay (ITD). Cochlear nerve fibers and their bushy cell targets fire in phase with pressure changes. Although individual bushy cells may fail to fire at some cycles, a set of cells will encode the timing of a low-frequency sound and its frequency with every cycle. Comparison of the onset of action potentials in the bushy cells at the two sides reveals the ITDs (**slanted black lines**).

B. Interaural time differences can be measured by an array of neurons whose inputs from the two ears are delay lines as proposed by Lloyd Jeffress (1948). Action potentials propagate to reach the nearest terminals before they reach the farthest ones; thus, in the delay line from the right, terminals will generate synaptic potentials sequentially from right to left, and in the delay line from the left, terminals will generate synaptic potentials sequentially from left to right. Suppose that such postsynaptic neurons are coincidence detectors, firing only when they receive excitatory postsynaptic potentials (EPSPs) simultaneously from the right and left. Sounds that arise at the midline reach the right and left ears simultaneously with no interaural time disparity (ITD = 0). The neuron in the middle of the array that receives input from equally long axons from the two sides will thus receive simultaneous EPSPs from the two sides. When sounds come from the right, signals from the right ear arrive at the central nervous system earlier than those from the left ear (ITD > 0). Sound from the right generates synchronous EPSPs in the (**yellow**) neuron because the earlier arrival of sound from the right (**red**) is compensated by a longer conduction delay relative to that from the left (**blue**). Likewise, when sound arises from the left, the ITD < 0 and conduction delays

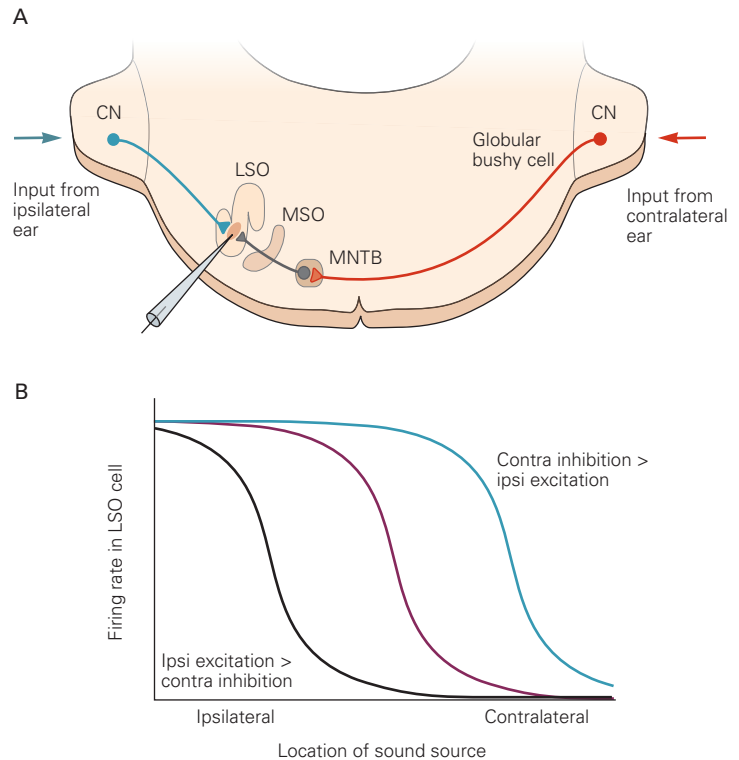
from the left (**blue**) compensate for the early arrival at the left. Such a neuronal circuit produces a map of interaural time disparities in the coincidence detectors; as sounds move from the right to left, they activate coincidence detectors sequentially from left to right. Such an arrangement of delay lines has been found in the nucleus laminaris of the barn owl, the homolog of the mammalian medial superior olivary nucleus.

C. Mammals use delay lines only in the nucleus contralateral to a sound source to form a map of interaural time differences. The bifuited neurons of the medial superior olivary nucleus form a sheet that is contacted on its lateral face by bushy cells from the ipsilateral cochlear nucleus and on the medial face by bushy cells from the contralateral cochlear nucleus. (Although it is depicted here schematically in a coronal section of the brain stem, the encoding of interaural disparities is in a sheet of neurons that also has a rostrocaudal dimension.) On the ipsilateral side, the branches of the bushy cell axon are of equal length and thus initiate synaptic currents in their targets in the medial superior olive simultaneously. On the contralateral side, the branches deliver synaptic currents sequentially first to the regions closest to the midline, and then to progressively more lateral regions. Neurons of the medial superior olive detect synchronous excitation from the two ears only when sounds arise from the contralateral half of space. When sounds arise from the right side, their early arrival at the right ear is compensated by progressively longer conduction delays to activate neurons more and more toward the lateral end of the left medial superior olive (the **yellow cell** is activated by a sound from the far right, as in part **B**). When sounds arise from the front and there is no interaural time difference, neurons in the anterior end of the medial superior olive are activated synchronously from both sides. Each medial superior olive forms a map of where sounds arise in the contralateral hemifield. (Adapted, with permission, from Yin 2002.)

Figure 28–6 Interaural differences in the intensity of a sound also help localize sound in the horizontal plane.

A. Principal cells of the lateral superior olivary nucleus (LSO) receive excitatory input from the ipsilateral cochlear nucleus (CN) and inhibitory input from the contralateral cochlear nucleus. A coronal section through the brain stem of a cat illustrates the anatomical connections. Small spherical bushy cells and stellate cells in the ipsilateral ventral cochlear nucleus provide direct excitation. Globular bushy cells in the contralateral ventral cochlear nucleus project across the midline and excite neurons in the medial nucleus of the trapezoid body (MNTB) via large terminals, the calyces of Held. Cells of the medial nucleus of the trapezoid body inhibit neurons in the lateral superior olive as well as in the medial superior olive (MSO). For neurons of the lateral superior olive to compare intensities of the same sound, the timing of the ipsilateral excitatory input must be matched with the timing of the contralateral inhibitory input. To this end, globular bushy cells have particularly large axons that terminate in a calyx of Held in the medial nucleus of the trapezoid body where synaptic transmission is strong and thus the synaptic delay is short and invariant in its timing.

B. The firing of neurons in the lateral superior olive reflects a balance of ipsilateral excitation and contralateral inhibition. When sounds arise from the ipsilateral side, excitation is relatively stronger and inhibition is relatively weaker than when sounds arise from the contralateral side. The transition between the dominance of excitation and inhibition reflects the location of the sound source.



with short and consistently timed delays. The axons of small spherical bushy cells and stellate cells that carry ipsilateral excitation conduct more slowly than those of globular bushy cells.

The terminals of the globular bushy cells, the calyces of Held, engulf the cell bodies of trapezoid-body neurons so dramatically that they caught the attention of early anatomists and modern biophysicists. A single somatic terminal releases neurotransmitter at numerous release sites and generates large synaptic currents. The reliability of pre- and postsynaptic recordings at this synapse makes the site ideal for detailed studies of the mechanisms of synaptic transmission (Chapter 15).

The Superior Olivary Complex Provides Feedback to the Cochlea

Although sensory systems are largely afferent, bringing sensory information to the brain, recent studies have led to an appreciation of the importance of efferent signaling at many levels of the auditory system.

Olivocochlear neurons form a feedback loop from the superior olivary complex to hair cells in the cochlea. Their cell bodies lie around the major dense clusters of cell bodies in the olivary nuclei. In mammals, two groups of olivocochlear neurons have been functionally distinguished. The medial olivocochlear neurons' axons terminate on the outer hair cells bilaterally; the lateral olivocochlear neuron axons terminate ipsilaterally on the afferent fibers associated with inner hair cells.

Most medial olivocochlear neurons, with cell bodies that lie ventral and medial within the olivary complex, send their axons to the contralateral cochlea (Figure 28–7), but many also project to the ipsilateral cochlea. These cholinergic neurons act on hair cells through a special class of nicotinic acetylcholine receptor-channels formed from $\alpha 9$ and $\alpha 10$ subunits. The influx of Ca^{2+} through these channels leads to the opening of K^{+} channels that hyperpolarize outer hair cells. These neurons thus mediate tuned negative feedback and are binaural, being driven predominantly but not exclusively by stellate cells of the contralateral

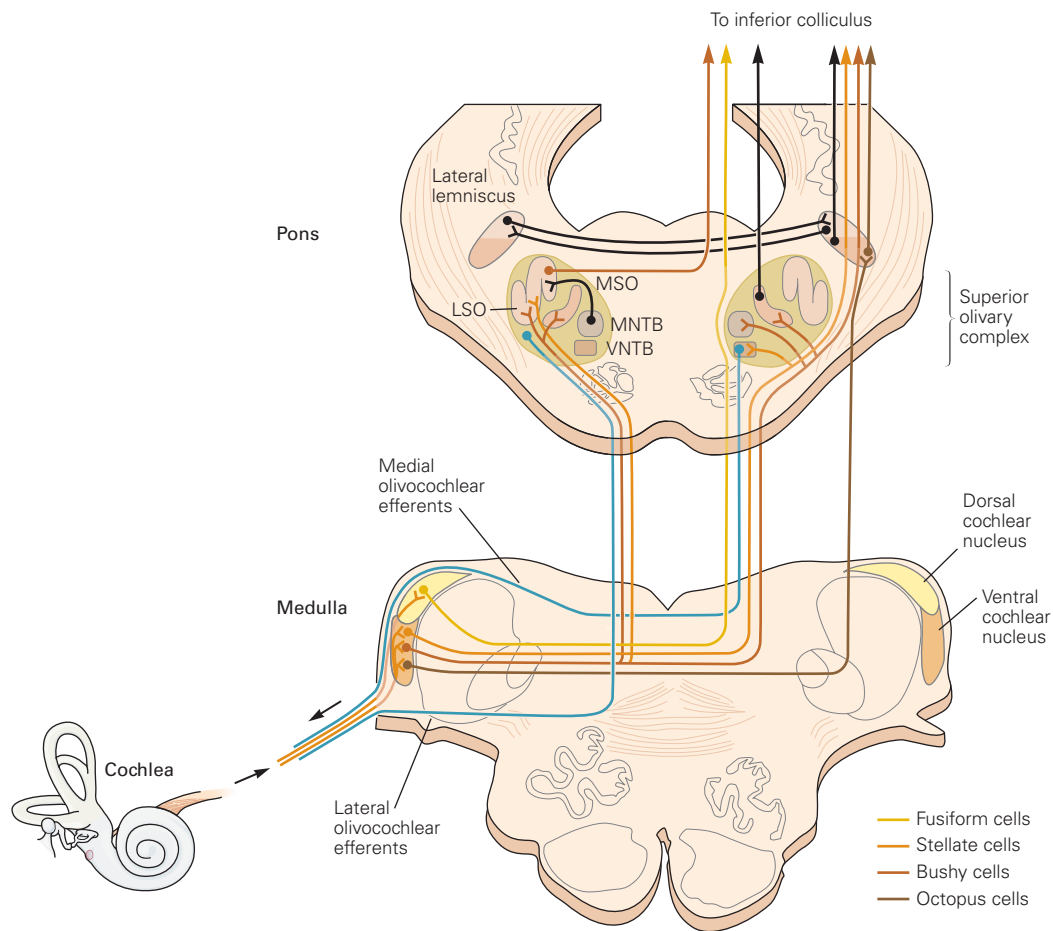


Figure 28–7 Major components of the ascending and descending auditory pathways. The auditory pathway is bilaterally symmetrical; the major connections among the nuclei that form the early auditory pathway are shown. The ascending pathway begins in the cochlea and progresses through several parallel pathways through the cochlear nuclei: the cochlear nuclei, the superior olivary nuclei, and the ventral and dorsal nuclei of the lateral lemniscus. These signals converge in the inferior colliculus, which projects to the medial geniculate

body of the thalamus and thence to the cerebral cortex (see Figure 28–2). Some of the connections are through excitatory pathways (colored lines) and others through inhibitory pathways (black lines). These same nuclei are also interconnected through descending pathways (blue lines) and bilaterally through commissural projections. (LSO, lateral superior olivary nucleus; MNTB, medial nucleus of the trapezoid body; MSO, medial superior olive; VNTB, ventral nucleus of the trapezoid body).

ventral cochlear nucleus. Activity in these efferent fibers reduces the sensitivity of the cochlea and protects it from damage by loud sounds. Collateral branches of medial olivocochlear neurons terminate on stellate cells in the cochlear nucleus, acting on conventional nicotinic and muscarinic acetylcholine receptors, forming an excitatory feedback loop.

Lateral olivocochlear neurons, with cell bodies that lie in and around the lateral superior olive, send their axons exclusively to the ipsilateral cochlea, where they terminate on the afferent fibers from inner hair cells. Charles Liberman and his colleagues demonstrated

that these efferents balance the excitability of cochlear nerve fibers at the two ears.

Ventral and Dorsal Nuclei of the Lateral Lemniscus Shape Responses in the Inferior Colliculus With Inhibition

Fibers from the cochlear and superior olivary nuclei run in a band, or lemniscus, along the lateral edge of the brain as they ascend from the brainstem to the inferior colliculus. Along this band of fibers are groups of neurons that form the dorsal and ventral nuclei of the

lateral lemniscus. Neurons in the ventral nuclei of the lateral lemniscus receive input from all major groups of principal cells of the ventral cochlear nuclei and respond predominantly to monaural input, driven by the contralateral ear, while neurons in the dorsal nucleus receive input from the lateral and medial superior olivary nuclei and respond to inputs from both ears. Neurons in both subdivisions are inhibitory and project to the inferior colliculus. Their roles are intriguing but not fully understood.

Since understanding the meaning of sounds is not greatly compromised by the loss of one ear, it would make sense that the largely monaural functions of the ventral nuclei of the lateral lemniscus involve the processing of the meaning of sounds. Furthermore, mammals vary in the information they extract from their acoustic environments, which may account for differences between species in the structure and function of the ventral nuclei of the lateral lemniscus.

A border that is more distinct in some mammalian species than in others separates the ventral and intermediate nuclei and the subdivisions of the ventral nucleus of the lateral lemniscus. Neurons differ in their shapes, biophysical properties, and pattern of convergence of cochlear nuclear inputs. One group of glycinergic neurons is innervated by large calyceal terminals from octopus cells. These could generate inhibitory temporal reference signals in the inferior colliculus. Some broadly tuned neurons fire almost exclusively at the onset of tones with sharply timed action potentials but convey periodicity in complex sounds, raising the question of whether these neurons might have a role in encoding pitch in music and speech. Others respond by firing as long as a tone is present; these neurons track the fluctuations in intensity or the envelopes of sounds, a feature that is useful for understanding the meaning of sounds including speech. Tuning curves of the neurons are variable, with many being broad or W-shaped.

Neurons in the dorsal nucleus are predominantly binaural, receiving input from the ipsilateral medial superior olive and from the lateral superior olive, primarily from the contralateral side. These neurons are GABAergic, targeting the inferior colliculi on both sides and also targeting the contralateral dorsal nucleus of the lateral lemniscus. Excitation in neurons of the dorsal nucleus is amplified by NMDA-type glutamate receptors so that the inhibition they generate in their targets outlasts sound stimuli for tens of milliseconds and thus has been termed persistent inhibition. To localize sounds accurately, animals must ignore the reflections of sounds from surrounding surfaces that arrive after the initial direct wave front. Psychophysical

experiments have shown that mammals suppress all but the first-arriving sound, a phenomenon termed the *precedence effect*. It has been proposed that persistent inhibition in the inferior colliculus from the dorsal nucleus of the lateral lemniscus serves to suppress spurious localization cues such as echoes and thus that it contributes to the precedence effect.

Afferent Auditory Pathways Converge in the Inferior Colliculus

The inferior colliculus occupies a central position in the auditory pathway of all vertebrate animals because all auditory pathways ascending through the brain stem converge there (Figure 28–7). The most important sources of excitation are stellate cells from the contralateral ventral cochlear nucleus, fusiform cells from the contralateral dorsal cochlear nucleus, principal cells of the ipsilateral medial superior olive and of the contralateral lateral superior olive, principal cells of ipsilateral and contralateral dorsal nuclei of the lateral lemniscus, commissural connections from the contralateral inferior colliculus, and pyramidal cells in layer V of the auditory cortex. Important sources of inhibition include the nuclei of the lateral lemniscus, the ipsilateral lateral superior olive, the superior paraolivary nucleus, and the contralateral inferior colliculus.

The inferior colliculus of mammals is subdivided into the central nucleus, dorsal cortex, and external cortex. The central nucleus is tonotopically organized. Low frequencies are represented dorsolaterally and high frequencies ventromedially in laminae that have similar best frequencies. Fine mapping has shown that the tonotopic organization is discontinuous; the separation between best frequencies corresponds to psychophysically measured critical bands of approximately one-third octave. Although the central nucleus is organized tonotopically, the spectral range of inputs to these neurons is broader than at earlier stages in the auditory pathway. Inhibition can be broad and narrows the responses of excitatory neurons. Furthermore, tuning can be modulated by descending inputs from the cortex.

Many neurons in the central nucleus carry information about the location of sound sources. The majority of these cells are sensitive to interaural time and intensity differences, essential cues for localizing sounds in the horizontal plane. Neurons are also sensitive to spectral cues that localize sounds in the vertical plane. Physiological correlates of the precedence effect have been measured in the inferior colliculus, where inhibition suppresses simulated reflections of sounds.

The inferior colliculus is not only a convergence point but also a branch point for ascending or outflow pathways. Neurons of the central nucleus project to the external cortex of the inferior colliculus and also to the thalamus and the nucleus of the brachium of the inferior colliculus, both of which then project to the superior colliculus (or the optic tectum in birds).

Sound Location Information From the Inferior Colliculus Creates a Spatial Map of Sound in the Superior Colliculus

The inferior colliculus is not only a convergence point but also a branch point for ascending or outflow pathways. Central nucleus neurons project to the thalamus and also to the external cortex of the inferior colliculus and the nucleus of the brachium of the inferior colliculus, both of which then project to the superior colliculus (or the optic tectum in birds).

The superior colliculus is critical for reflexive orienting movements of the head and eyes to acoustic and visual cues in space. By the time the binaural sound cues and the monaural spectral cues that underlie mammalian sound localization reach the superior colliculus, they have been merged to create a spatial map of sound in which neurons are unambiguously tuned to specific sound directions. This convergence is critical since binaural differences in level and timing alone cannot unambiguously code for a single position in space. The spectral cues that provide information about vertical location must be taken into account, as different locations in the vertical plane can give rise to identical interaural differences in time or intensity. Such unambiguous spatial mapping occurs both in birds and in some mammals (Figure 28–8). In ferrets and guinea pigs, it occurs in the external cortex and the nucleus of the brachium of the inferior colliculus.

Within the superior colliculus, the auditory map is aligned with maps of visual space and the body surface. Unlike the visual and somatosensory spatial maps, the auditory spatial map does not reflect the peripheral receptor surface; instead, it is computed from a combination of cues that identify the specific position of a sound source in space.

Auditory, visual, and somatosensory neurons in the superior colliculus all converge on output pathways in the same structure that controls orienting movements of the eyes, head, and external ears. The motor circuits of the superior colliculus are mapped with respect to motor targets in space and are aligned with the sensory maps. Such sensory-motor correspondence facilitates the sensory guiding of movements.

The Inferior Colliculus Transmits Auditory Information to the Cerebral Cortex

Auditory information ascends from the inferior colliculus to the medial geniculate body of the thalamus and from there to the auditory cortex. The pathways from the inferior colliculus include a lemniscal or core pathway and extralemniscal or belt pathways. Descending projections from the auditory cortex to the medial geniculate body are prominent both anatomically and functionally.

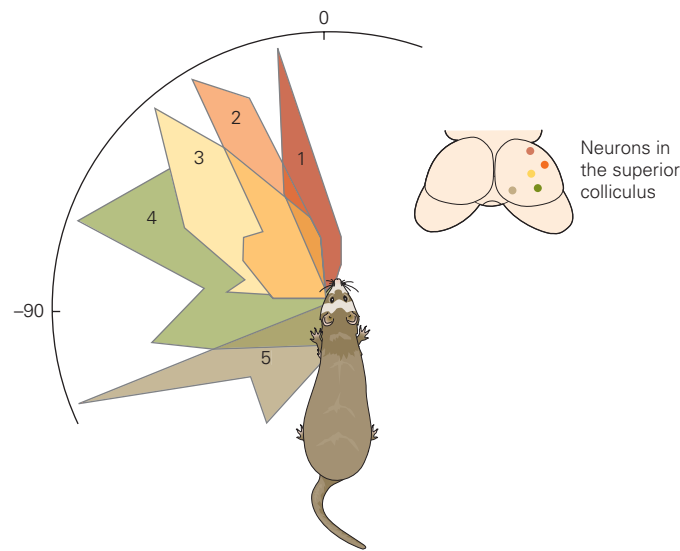
Stimulus Selectivity Progressively Increases Along the Ascending Pathway

A marked feature of auditory neurons at structures along the ascending pathway is their progressively increased stimulus selectivity. An auditory nerve fiber is primarily selective to one stimulus dimension, the frequency of a pure tone. The stimulus selectivity of neurons in the central auditory system may be multidimensional, such as frequency, spectral bandwidth, sound intensity, modulation frequency, and spatial location. In this multidimensional acoustic space, neurons become more selective at successive auditory areas along the ascending pathway.

Many neurons in the auditory cortex (especially those in upper cortical layers) are highly selective to acoustic stimuli, such that the preferred (nearly optimal) stimulus of a neuron occupies only a small region of its receptive field in the multidimensional acoustic space. The region of the preferred stimulus becomes increasingly smaller at structures along the path to the auditory cortex (Figure 28–9A). Pure tones and broadband noises are two extreme cases of a wide range of acoustic stimuli that could preferentially drive auditory cortex neurons. The majority of neurons in the auditory cortex are preferentially driven by stimuli with greater spectral and temporal complexity than pure tones and broadband noises.

The increased stimulus selectivity is also accompanied by changes in a neuron's firing pattern. When neurons are driven by their preferred stimuli, they respond not only with higher firing rates but also with sustained firing throughout the stimulus duration (Figure 28–9B). The receptive field of a cortical neuron contains a "sustained firing region" (corresponding to preferred stimuli) within a larger "onset firing region" (corresponding to nonpreferred stimuli). This explains why it is common for experimenters to observe onset (phasic) responses in auditory cortex when a continuous sound is played.

A Directional tuning of neurons in the ferret



B Directional tuning of a neuron in the barn owl

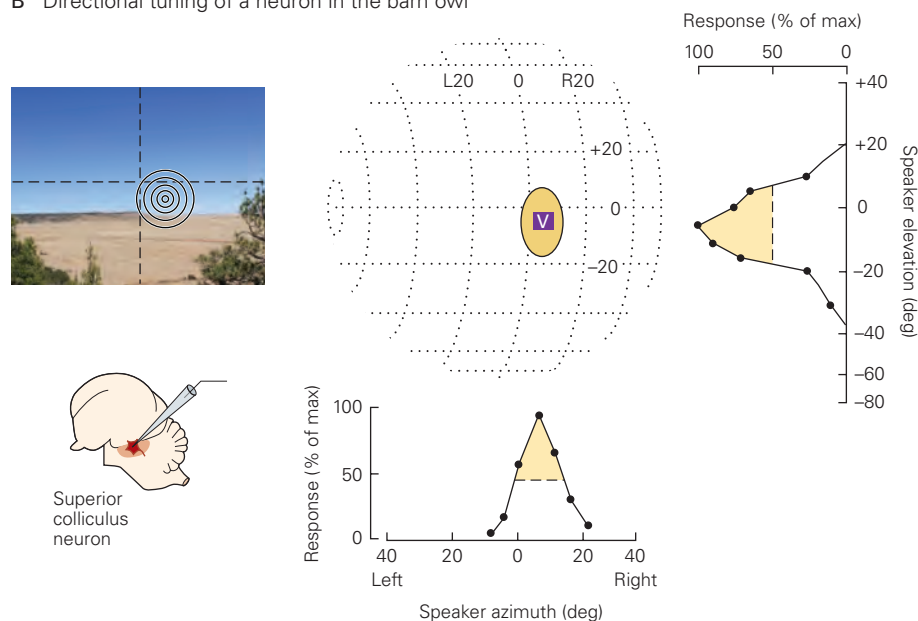


Figure 28–8 A spatial map of sound is formed in the superior colliculus.

A. Neurons in the ferret's superior colliculus are directionally tuned to sound in the horizontal plane. The illustration shows the firing rate profiles of collicular neurons 1 through 5 as a function of where the sounds are located, plotted in polar coordinates centered on the head. The drawing on the right shows the location of the recorded neurons in the colliculus. Note that neuron 1 responds best to sounds in front of the animal, whereas neurons that are located progressively more caudally in the colliculus gradually shift their responses to sounds that originate farther contralaterally. (Adapted, with permission, from King 1999.)

B. The normalized responses of a neuron in the superior colliculus of a barn owl to noise bursts presented at various

locations along the horizon are plotted below (*bottom right*). The **yellow areas** in these tuning curves indicate where responses exceed 50% of the maximum. The sensitivity of the neuron to a particular location along the horizon or a particular elevation (*top right*) creates a discrete best auditory area in space for this neuron (*top middle*), shown as the colored ellipse on a plot of spatial locations with respect to a point straight in front of the owl. The neuron also responds to visual cues from the same area (the box labeled **V**). The photo illustrates the neuron's best area in space with respect to the position of the head (the intersection of the vertical and horizontal dotted lines indicates where the owl's head is pointing). The recording site for this neuron is also shown. (Adapted, with permission, from Cohen and Knudsen 1999. Copyright © 1999 Elsevier Science.)

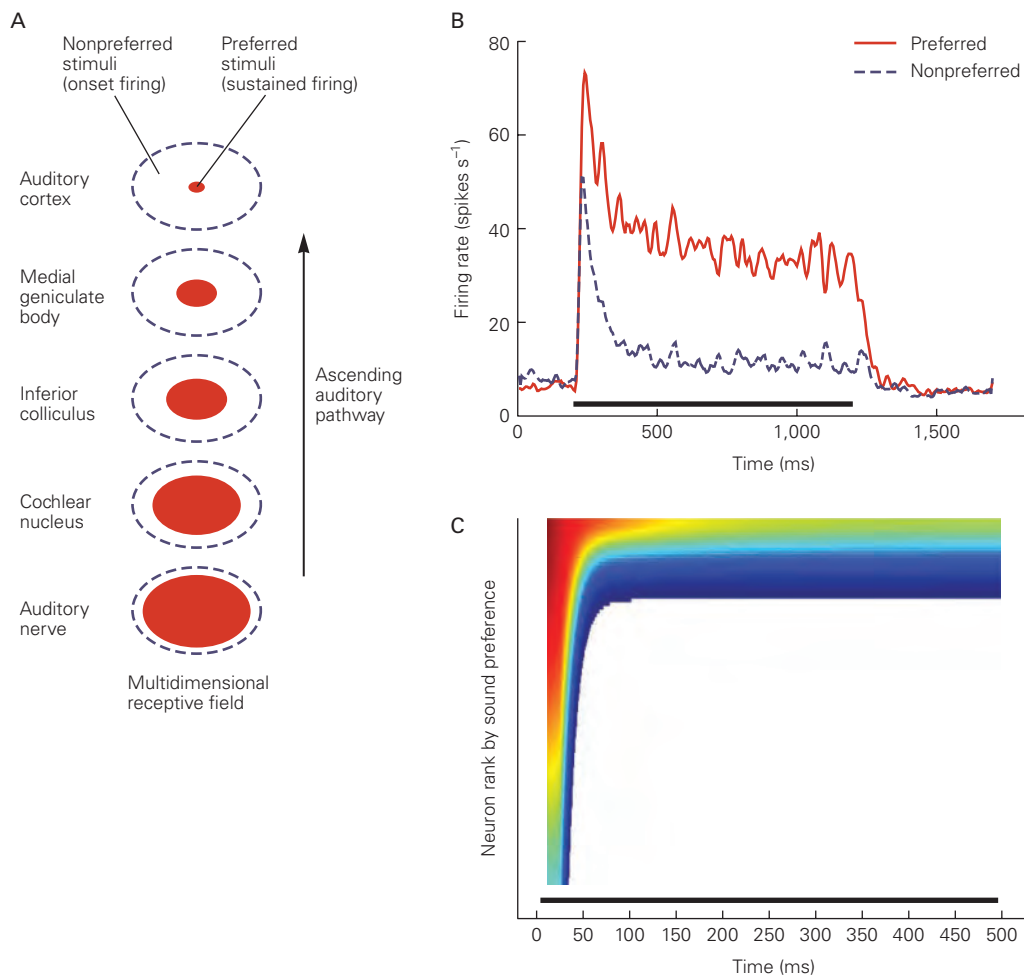


Figure 28-9 Stimulus selectivity increases along the ascending auditory pathway.

A. Stimulus selectivity and the relationship between sustained and onset firings along the ascending auditory pathway. Each open ellipse represents the multidimensional receptive field (RF) of a neuron illustrated on a two-dimensional plane. The filled ellipse represents the “sustained firing region” (corresponding to preferred stimuli) of a neuron’s RF. The rest of the area within the RF is the “onset firing region” (corresponding to nonpreferred stimuli). A neuron exhibits sustained or onset firing depending on which region of the RF is stimulated. The neuron does not fire if stimuli fall outside the RF. (Adapted, with permission, from Wang 2018.)

B. Population-averaged firing rate in response to each neuron’s preferred and nonpreferred stimuli from primary auditory cortex

(A1). Extracellular recordings were made in awake marmoset monkeys. **Thick bar** = stimulus duration. (Adapted, with permission, from Wang et al. 2005. Copyright © 2005 Springer Nature.)

C. Distribution of activity among A1 neurons in response to a sound burst. On the y-axis, all A1 neurons are ranked according to their preference for a particular stimulus. The **blue-to-red color gradient** represents increasing firing rate. The neuron with the highest firing rate is located at the top end of the y-axis. **Black bar** = stimulus duration. Most neurons show a brief phasic response to the onset of the sound, but only those particularly tuned to the sound maintain their response until the end of the sound. (Adapted, with permission, from Middlebrooks 2005. Copyright © 2005 Springer Nature.)

The discovery of how sustained firing is evoked in the auditory cortex is important because it provides a direct link between neural firing and the perception of a continuous acoustic event. Such sustained firing by auditory cortex neurons has been observed only in awake animals. In contrast, an auditory nerve fiber

typically shows sustained firing in response to a wide range of acoustic signals as long as the spectral energy of the stimulus falls within the neuron’s receptive field, under either anesthetized or awake conditions. When David Hubel and his colleagues ventured into the auditory cortex more than half a century ago, they

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

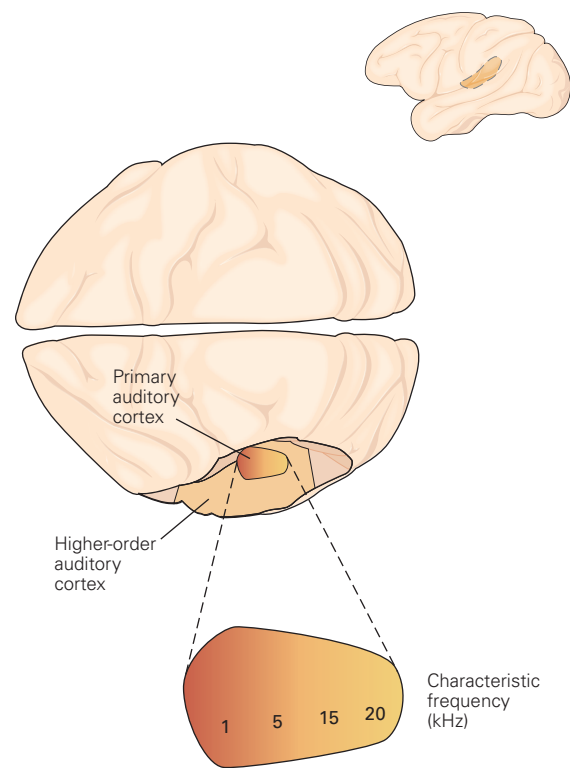


Figure 28-10 The auditory cortex of primates has multiple primary and secondary areas. The expanded figure of the primary auditory cortex shows its tonotopic organization. The primary areas are surrounded by higher-order areas (see Figure 28-11).

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.