ANATOMY OF THE CENTRAL AUDITORY NERVOUS SYSTEM

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1 INTRODUCTION

The central auditory system is the neural system devoted to processing information about acoustic stimuli. It includes many design features typical of complex neural systems. For example, the auditory system is composed of specialized parts with specific functions, and it uses parallel processing to concurrently process acoustic information. Auditory pathways have a frequency (tonotopic) organization. The ascending auditory pathways (Fig. 1) are the routes auditory information follows as it enters the central nervous system. These ascending pathways emerge from the cochlea in the ear and synapse in the cochlear nucleus, superior olivary complex, inferior colliculus, medial geniculate body, and finally end in the cerebral cortex. The descending auditory pathways (Fig. 2) follow the reverse course and create feedback loops that ultimately influence the function of the cochlea. Together, these ascending and descending systems underlie our ability to perceive sounds. Connections of the auditory system with other neural systems allow the organism to respond to sound and to incorporate acoustical events into learning and memory. Detailed presentations of the anatomy of the auditory system can be found in several recent books.\textsuperscript{1–3} Readers also may want to consult general neuroanatomical and neuroscience texts.\textsuperscript{4–6}

2 DESIGN FEATURES OF THE CENTRAL AUDITORY NERVOUS SYSTEM

2.1 Specialized Parts

The central auditory nervous system, a complex biological system created by evolution, contains many parts (see Fig. 1). The function of each part is determined by the types of neurons present, their structure, their biophysical properties, their inputs, and their outputs. While the parts of the auditory system are evident, the specific functions of each part are not as clear. All parts are auditory by virtue of the connections between the cochlea and the brain made by the eighth cranial nerve. However, some cell types and patterns of connections are unique to only one part of the system, and these give rise to unique computational properties. For example, binaural processing is only possible when information from the two ears is combined in a single neural structure such as the superior olivary complex (Fig. 1, SOC).

2.2 Parallel Processing

Neural systems employ parallel processing on a massive scale. Parallel processing allows many neural events to happen concurrently. Thus, the nervous system is superior to a digital computer that employs only serial processing and executes one instruction at a time. Parallel processing allows more than one aspect of an acoustic stimulus to be processed simultaneously.

Two types of anatomical arrangements subserve parallel processing in the auditory system. Within a pathway,
Fig. 1  Simplified wiring diagram of the ascending auditory pathways. The dominant flow of information from the ventral and dorsal cochlear nucleus (DCN, VCN) and superior olivary complex (SOC) crosses the midline (broad dotted line) to terminate in the inferior colliculus (IC). Pathways that convey monaural information (black) and binaural information (gray) both pass through the lateral lemniscus (LL). From the colliculus, projections ascend to the medial geniculate body (MGB) and auditory cortex (CORTEX).

Fig. 2  Simplified wiring diagram of the descending auditory pathways. Descending pathways pass from the cortex (CORTEX) to the medial geniculate body (MGB) or inferior colliculus (IC). Descending pathways to the cochlea utilize the lateral (LAT) and medial (MED) periolivary nuclei of the superior olivary complex. The olivocochlear bundle terminates on the outer hair cells (OHC) and radial fibers (RAD) in the cochlea. The retrocochlear nucleus projections from MED and LAT terminate in the cochlear nucleus (CN).
there are hundreds or thousands of neurons of the same cell type. They have the same properties, the same inputs, and project to the same target but may differ in one variable such as frequency specificity. The inputs and outputs of these neurons are in parallel. Parallel pathways originate in different parts of the system and may function relatively independently. For example, the pathways that carry information from only one ear, the monaural pathways, may function in parallel to pathways that processes information about both ears, the binaural pathways.

2.3 Tonotopic Organization

The central auditory system has a precise frequency organization, for example, tonotopic organization, that is imparted by the connections with the cochlea. Frequency of the acoustic stimulus is encoded along the length of the cochlea (see Chapter 107), and this cochleotopic organization is transmitted to the brain. Thus, the frequency of the stimulus is translated to a spatial, tonotopic map in the brain. The tonotopic organization is maintained throughout the auditory pathways by focused, point-to-point connections that link the map at one level to the map at the next level.

3 ASCENDING AUDITORY PATHWAYS

The ascending auditory pathways begin with the eighth cranial nerve (vestibulo-cochlear) that connects the ear to the brain. Acoustic stimuli excite the hair cells of the cochlear partition, which activate the spiral ganglion and the eighth nerve. The peripheral portion of the nerve innervates the cochlea, and the central portion projects into the brain where it synapses in the cochlear nucleus of the medulla (Fig. 1, DCN, VCN, see also Chapter 109). Excitation of the nerve leads to excitation of the neurons in the cochlear nucleus. The cochlear nucleus sends projections centrally to the superior olivary complex in the medulla (Fig. 1, SOC) and the inferior colliculus in the midbrain (Fig. 1, IC). The superior olivary complex is the first site where information from both ears is combined, and it also projects to the inferior colliculus. From the inferior colliculus, the auditory pathway ascends to the medial geniculate body in the thalamus (Fig. 1, MGB) and the auditory cortex in the telencephalon (Fig. 1, CORTEX).

3.1 Cochlear Nucleus

The cochlear nucleus is the first processing center in the auditory pathway and is composed of dorsal and ventral nuclei (Fig. 1, DCN, VCN). The nerve branches into an ascending branch that terminates exclusively in the anteroventral cochlear nucleus (Fig. 3, AVCN) while the descending branch terminates in the posteroverentral cochlear nucleus (Fig. 3, PVCN) and then continues into the dorsal cochlear nucleus (Fig. 3, DCN). The projections of the eighth nerve are tonotopically organized. The fibers from the basal, high-frequency part of the cochlea terminate in the dorso-caudal part of the anteroventral, posteroverental, and dorsal cochlear nuclei. The fibers from the apical, low-frequency part of the cochlea terminate in the rostro-ventral part of the same nuclei.

Unique cell types define each part of the cochlear nucleus, process information about acoustic stimuli, and project to different parts of the auditory system. In the anteroventral cochlear nucleus, the principal cell types are the bushy (Fig. 3, B, G) and stellate cells (Fig. 3, S). Bushy cells have very round cell bodies and usually only one proximal dendrite that forms a distinctive bushlike dendritic tree. There are two varieties of bushy cells, the spherical (Fig. 3, B) and the globular (Fig. 3, G). The spherical bushy cells receive a unique type of synaptic ending from the vestibulo-cochlear nerve, the endbulb of Held. Only one or two endbulbs terminate on each bushy cell, but these are sufficient in size to surround the cell body and provide massive excitation in response to stimulation of the nerve. The spherical bushy cells project to the superior olivary complex. The globular bushy cells are located more posteriorly in the anteroventral cochlear nucleus, receive synaptic inputs from more numerous and smaller axonal endings from the nerve, and also project to the superior olivary complex. Stellate cells (Fig. 3, S) are the second major cell type in the anteroventral cochlear nucleus. Unlike bushy cells, the stellate cells receive numerous small inputs from the eighth nerve primarily on their dendrites. Many stellate cells project to the inferior colliculus of the midbrain and may not synapse in the superior olive. Some stellate cells have axons that remain within the cochlear nucleus.

In the posteroverentral cochlear nucleus, the octopus cell (Fig. 3, O), is usually the only cell type found in the most caudal part of that nucleus. This cell, which resembles its namesake in appearance, receives inputs from large numbers of eighth nerve fibers as they course through the nucleus. The octopus cells project primarily to the periolivary nuclei that surround the main nuclei of the superior olive and participate in feedback loops. They may also participate in ascending pathways through projections to the nuclei of the lateral lemniscus. Other cell types (not shown) are found in the rostral posteroverentral cochlear nucleus and are similar to the bushy and stellate cells of the anteroventral cochlear nucleus.

In the dorsal cochlear nucleus, the principal cell type is the fusiform cell (Fig. 3, F). This cell has a vertically oriented dendritic tree that receives many inputs from the eighth nerve. The main target of the fusiform cell is the
inferior colliculus. Most of the other cells (not shown) in the dorsal cochlear nucleus are smaller internuclear neurons except the giant cells whose axons project either to the midbrain or to the opposite cochlear nucleus.

3.2 Superior Olivary Complex

The superior olivary complex (Fig. 1, SOC, and Fig. 4) is the primary site of binaural interactions in the auditory system. As shown in Fig. 1, it receives inputs from the cochlear nucleus on the same and opposite side of the brain. The two principal nuclei of the olive are the medial superior olive (Fig. 4, MSO) and the lateral superior olive (Fig. 4, LSO). These nuclei project to the inferior colliculus (Fig. 5). Surrounding the principal nuclei are the periolivary nuclei. Some periolivary cells participate in ascending projections (see Section 2.2) while others are part of feedback loops (Fig. 2 and Section 4).

The medial superior olive (Fig. 4, MSO) is designed to encode interaural time differences. This nucleus has a three-dimensional structure that represents frequency in the dorsoventral direction and time in the rostrocaudal direction. Dorsal cells in the medial superior olive respond to low frequency (Fig. 4, L). Ventral cells respond to higher frequencies (Fig. 4, H). However, the highest frequencies are under represented compared to other auditory nuclei. The rostrocaudal dimension of the medial superior olive may encode interaural time differences (see Chapters 111 and 117). Each row of neurons receives excitatory inputs from the ventral cochlear nucleus bilaterally, for example, from both sides. These axons (Fig. 4, B) are from the spherical bushy cells and run along the rostrocaudal axis of the row. Specific locations along the horizontal azimuth (translated to interaural time differences) appear to be represented in different parts of the medial superior olive. Neurons in the rostral part of the nucleus respond to stimuli in front of the animal where there is zero interaural time difference (Fig. 4, 0 ITD). Neurons in the caudal part respond best to larger time differences usually to stimuli from the contralateral side (Fig. 4, CONTRA ITD). In addition to the inputs from the cochlear nucleus, the medial superior olive also receives inputs from the medial nucleus of the trapezoid body (Fig. 4, MNTB). These may provide inhibitory inputs to the medial superior olive and decrease the responses to unfavorable interaural time differences.

The anatomy of the lateral superior olive may be specialized to encode interaural intensity (level) differences by means of an interesting inhibitory mechanism. This nucleus contains neurons arranged in an S-shaped layer with a complete tonotopic map. Low frequencies are lat-
Fig. 4  Principal nuclei of the superior olivary complex. Medial superior olive (MSO) has bilateral inputs from axons of spherical bushy cells (B). Lateral superior olive (LSO) has similar inputs from the ipsilateral side, but contralateral inputs from axons of globular bushy cells (G) arise via a synapse in the medial nucleus of the trapezoid body (MNTB). Frequency organization (H, high frequency; L, low frequency) is present in MSO and LSO. Interaural time delay (ITD) in MSO ranges from zero ITD (0 ITD) to increasingly larger ITDs for stimuli on the contralateral side (CONTRA ITD). Directional arrows: C, caudal; D, dorsal; L, lateral; M, medial; R, rostral; V, ventral.

4. H). It lacks the long rostrocaudal dimension of the medial olive. The lateral superior olive has two primary inputs. Sounds in one ear excite the cochlear nucleus and the lateral superior olive on the same side of the brain via axons from spherical bushy cells (Fig. 4, B). However, stimuli to the opposite ear produce inhibition in the lateral superior olive via a two-neuron circuit. Globular bushy cells from the opposite cochlear nucleus synapse in the medial nucleus of the trapezoid body with specialized axonal endings, the calyx of Held. This is the largest synaptic ending in the brain, and it activates the neurons in the medial nucleus of the trapezoid body that, in turn, project to and inhibit the neurons in the lateral superior olive. The combination of bilateral inhibitory and excitatory inputs creates a mechanism sensitive to small interaural intensity differences.

3.3 Nuclei of Lateral Lemniscus

The lateral lemniscus (Fig. 1, LL) contains the fibers from the cochlear nucleus and superior olivary complex that travel to the inferior colliculus. These fibers surround and penetrate through the nuclei of the lateral lemniscus. The ventral nucleus of the lateral lemniscus (Fig. 5, VLL) receives inputs primarily from the opposite cochlear nucleus and projects to the inferior colliculus on the same side. Neurons in the ventral lateral lemniscus may respond only to acoustic stimuli in the opposite ear. In contrast, the dorsal nucleus of the lateral lemniscus (Fig. 5, DLL) may participate in binaural functions. The dorsal nucleus receives most of the same inputs as the inferior colliculus (see below). Major inputs arise in the superior olive and the cochlear nuclei. The output of the dorsal nucleus is a bilateral projection to the inferior colliculus. While the ventral and dorsal nuclei of the lateral lemniscus are distinguished in their responses to monaural and binaural stimuli, both may provide inhibitory inputs to the inferior colliculus. Ascending inhibitory inputs to the inferior colliculus could modify the bandwidth or the temporal responses of neurons in the inferior colliculus.

3.4 Inferior Colliculus

The inferior colliculus integrates the ascending auditory pathways. It contains three major parts: a central nucleus (Figs. 5 and 6, IC-CEN), a cortex (Figs. 5 and 6, DC), and a paracentral collection of nuclei (Figs. 5 and 6, PARA). The central nucleus of the inferior colliculus contains layers of neurons arranged to make a single tonotopic map. Inputs from both monaural and binaural pathways terminate on this map, but the inputs do not converge completely. Thus, many functional properties found in the lower system are preserved by the projections to the colliculus. For example, tonotopically organized inputs from the lateral and medial superior olive (Fig. 5, MSO, LSO) and the dorsal nucleus of the lateral lemniscus (Fig. 5, DLL) may transmit different binaural properties. The projections from the dorsal and ventral cochlear nucleus (Fig. 5, DCN, VCN) convey monaural information. Some inputs, for example, the ventral nucleus of the lateral lemniscus, seem to have a poor
Fig. 5 Wiring diagram of parallel pathways to the inferior colliculus. Inferior colliculus contains central nucleus (IC-CEN), paracentral nuclei (PARA), and cortex (DC, dorsal cortex). Binaural pathways from superior olivary complex (LSO, MSO) are in black. Monaural pathways from cochlear nucleus (DCN, VCN) are in light gray. Inhibitory pathways from the nuclei of the lateral lemniscus (DLL, VLL) are in dark gray.

Tonotopic organization but still terminate within the central nucleus.

Outside the central nucleus, the remaining inferior colliculus is less strictly concerned with the ascending auditory pathway and involves convergence with descending and other sensory information. The dorsal cortex of the inferior colliculus contains layers that are parallel to the surface of the inferior colliculus. The dorsal cortex (Fig. 5, DC) receives both ascending inputs and descending projections from the cerebral cortex. Its tonotopic organization is similar to that of the central nucleus and is primarily related to the organization of the ascending afferent fibers. Paracentral nuclei of the inferior colliculus receive minimal inputs from the ascend-

Fig. 6 Wiring diagram of the parallel pathways in the forebrain auditory system. Primary auditory cortex (CORTEX, AI) receives inputs from the central nucleus of the inferior colliculus (IC, IC-CEN) via a synapse in the ventral division (V) of the medial geniculate body (MGB). Multiple secondary cortical areas collectively illustrated as AII receive inputs from dorsal division (D) of the MGB whose inputs are from the dorsal cortex (DC) of the inferior colliculus and from the superior colliculus (SC) and reticular formation (RF). The medial division (M) of the MGB projects to all auditory cortical areas especially insular-temporal cortex (IT), and it receives inputs from all caudal structures including the paracentral nuclei (PARA) of the IC.
ing auditory pathways but do receive inputs from the spinal cord, somatosensory system, and reticular formation. There is little evidence for tonotopic organization within the paracentral nuclei.

3.5 Medial Geniculate Body

The **medial geniculate body** (Fig. 1, MGB) controls the flow of auditory information to the cerebral cortex. The geniculate contains ventral, dorsal, and medial divisions. The ventral division of the medial geniculate body (Fig. 6, V) contains layers that are tonotopically organized and functions as the primary relay of auditory information to cortex. Its main input is from the central nucleus of the inferior colliculus. The dorsal division of the medial geniculate body (Fig. 6, D) is more complex in anatomy and function. It contains several subdivisions and lacks a clear-cut tonotopic organization. Inputs are from outside the mainstream auditory system, for example, the dorsal cortex of the inferior colliculus, the superior colliculus (Fig. 6, SC), and the reticular formation (Fig. 6, RF) of the midbrain. The medial division of the medial geniculate body (Fig. 6, M) contains large cells and is often called the magnocellular nucleus. It receives converging inputs from auditory and nonauditory sources including spinal cord. The medial geniculate also may play a role in forming memories and emotional content through its projections to the amygdala in the limbic system.

3.6 Auditory Cortex

The ascending auditory pathways terminate in the **auditory cortex** (Figs. 1 and 6, CORTEX). In most mammals, including humans, the auditory cortex is recognized as having a primary cortex that is surrounded by secondary cortical regions. In humans, the **primary auditory cortex** is found in the temporal lobe in the first transverse gyrus of Heschl. The primary cortex (Fig. 6, A1) contains a complete tonotopic map and receives most of its inputs from the ventral division of the medial geniculate body. A number of **secondary auditory cortical areas** exist, for example, AII, insular, temporal (Fig. 6, AII, IT). Some areas like AII have well-developed tonotopic maps, others do not. The secondary areas usually receive inputs from both the dorsal division of the medial geniculate body and the primary cortex. One of the most elaborate auditory cortices is seen in the mustache bat. Specific cortical areas in the bat encode the constant-frequency and frequency-modulated components of the sounds emitted by the bat and the echoes of these sounds (see Chapter 113). In most mammals, there appear to be fewer cortical areas, and the specific functions of individual areas are less well defined. The primary connections of the auditory cortex are to the other parts of the cerebral cortex and telencephalon. These connections provide information about the acoustic environment to neural systems concerned with higher cognitive functions.

4 FEEDBACK LOOPS

The descending auditory pathways function to modify information traveling in the ascending pathways. They are separate from circuits that send information about sound to the motor systems or to other neural systems. There are two separate sets of descending inputs. One originates in the auditory cortex. The other system originates in the superior olive.

4.1 Descending Pathways from Cortex

Auditory cortex (Fig. 2) sends descending projections to the thalamus and midbrain. **Corticothalamic projections** terminate in the medial geniculate body (Fig. 2, MGB). In addition, **corticocollicular projections** synapse in the inferior colliculus (Fig. 2, IC), superior colliculus, and adjacent brainstem. Interestingly, the main component of the ascending pathways in the midbrain, the central nucleus of the inferior colliculus, receives the least descending input from the auditory cortex and the least feedback from cortex. Most of the descending inputs from telencephalon terminate in the dorsal cortex of the inferior colliculus or in the dorsomedial paracentral nucleus.

4.2 Olivocochlear System

Projections from the periolivary nuclei (Fig. 2) in the superior olive terminate in the cochlea and modify the response of the hair cells. The olivocochlear system is composed of medial and lateral parts that bear differing relationships to the hair cells of the cochlea. The lateral periolivary system (Fig. 2, LAT) projects primarily to the ipsilateral radial fibers (Fig. 2, RAD) that are the most processes of the spiral ganglion beneath the inner hair cells in the cochlea. Depending on the species, the cells of origin for the lateral olivocochlear system are either within the lateral superior olive or in the adjacent dorsolateral periolivary nucleus. The **medial olivocochlear system** (Fig. 2, MED) terminates primarily on the outer hair cells (Fig. 2, OHC). Slightly more than half of the medial system terminates in the contralateral cochlea, and the remainder projects to the ipsilateral cochlea. Cells of origin for the medial system are in the medial periolivary nuclei including the medial nucleus of the trapezoid body, the ventral nucleus of the trapezoid body, and the dorsomedial periolivary nucleus.

Many of the same periolivary nuclei that contribute to the olivocochlear systems also send projections to the cochlear nucleus. These **retrocochlear nucleus projec-**
tions originate in the ventral periolivary nuclei (the ventral and lateral nuclei of the trapezoid body). The lateral group projects primarily to the ipsilateral cochlear nucleus, while the more medially placed ventral nucleus projects to the contralateral cochlear nucleus. Although the periolivary nuclei contain neurons that project to the cochlea, cochlear nucleus, and inferior colliculus, separate neurons apparently project to each site.

Both the periolivary nuclei and the cochlear nucleus receive descending inputs from the inferior colliculus (Fig. 2, IC). Most projections from the inferior colliculus to the superior olive terminate in the medial periolivary region (primarily the ventral nucleus of the trapezoid body). These projections arise principally in the central nucleus of the inferior colliculus. The central nucleus also projects directly to the cochlear nucleus where most of the descending fibers terminate in the dorsal cochlear nucleus. Neither the colliculo-olivary and colliculo-cochlear nucleus projections appear to be a direct continuation of the descending pathways from the auditory cortex.

REFERENCES


