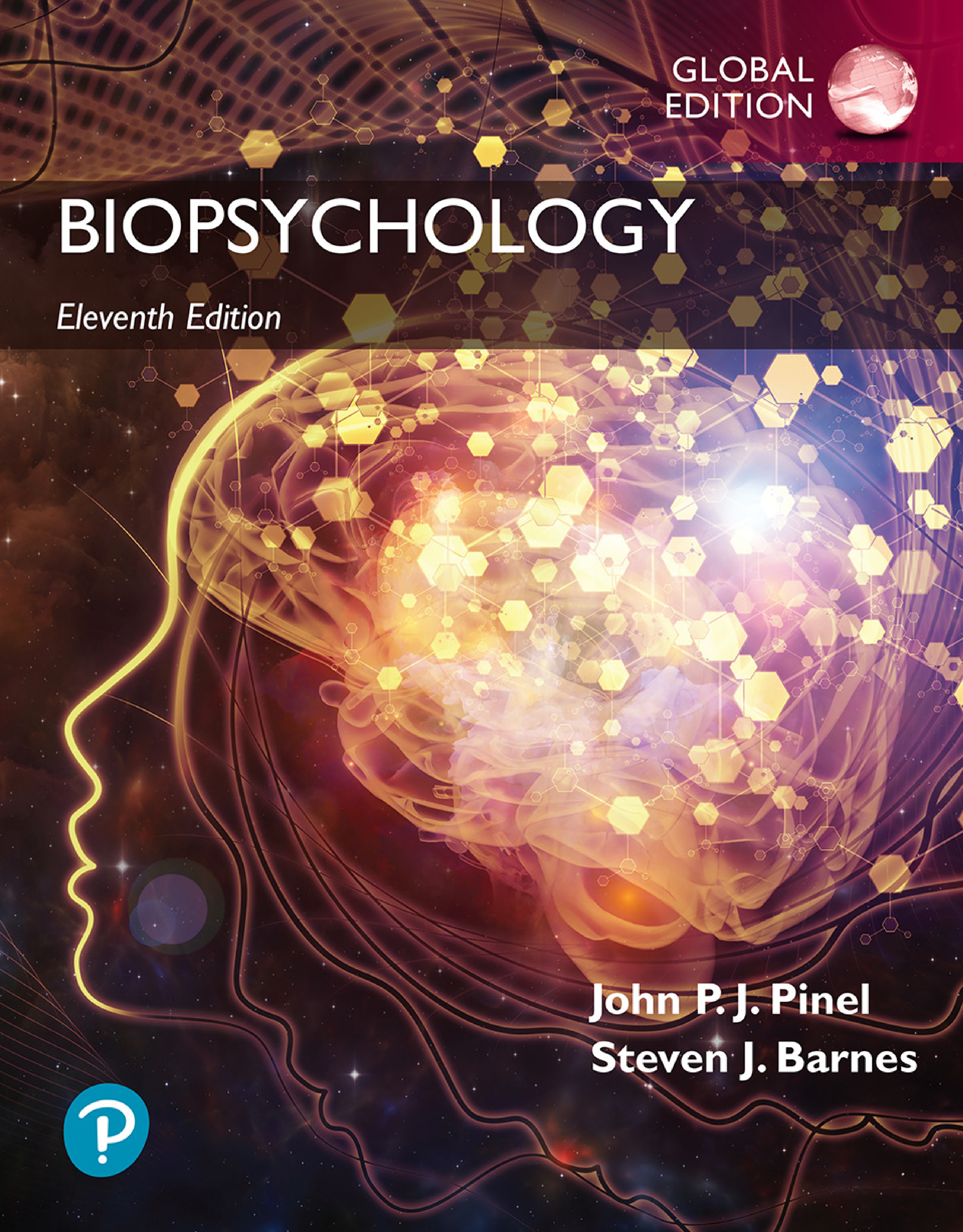

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Case of the Man Who Mistook His Wife for a Hat*

Dr. P. was a highly respected musician and teacher—a charming and intelligent man. He had been referred to the eminent neurologist Oliver Sacks for help with a vision problem. At least, as Dr. P. explained to the neurologist, other people seemed to think that he had a vision problem, and he did admit that he sometimes made odd errors.

Dr. Sacks tested Dr. P.'s vision and found his visual acuity to be excellent—Dr. P. could easily spot a pin on the floor. The first sign of a problem appeared when Dr. P. needed to put his shoe back on following a standard reflex test. Gazing at his foot, he asked Sacks if it was his shoe.

Continuing the examination, Dr. Sacks showed Dr. P. a glove and asked him what it was. Taking the glove and puzzling over it, Dr. P. could only guess that it was a container divided into five compartments for some reason. Even when Sacks asked whether the glove might fit on some part of the body, Dr. P. displayed no signs of recognition.

At that point, Dr. P. seemed to conclude that the examination was over and, from the expression on his face, that he had done rather well. Preparing to leave, he turned and grasped his wife's head and tried to put it on his own. Apparently, he thought it was his hat.

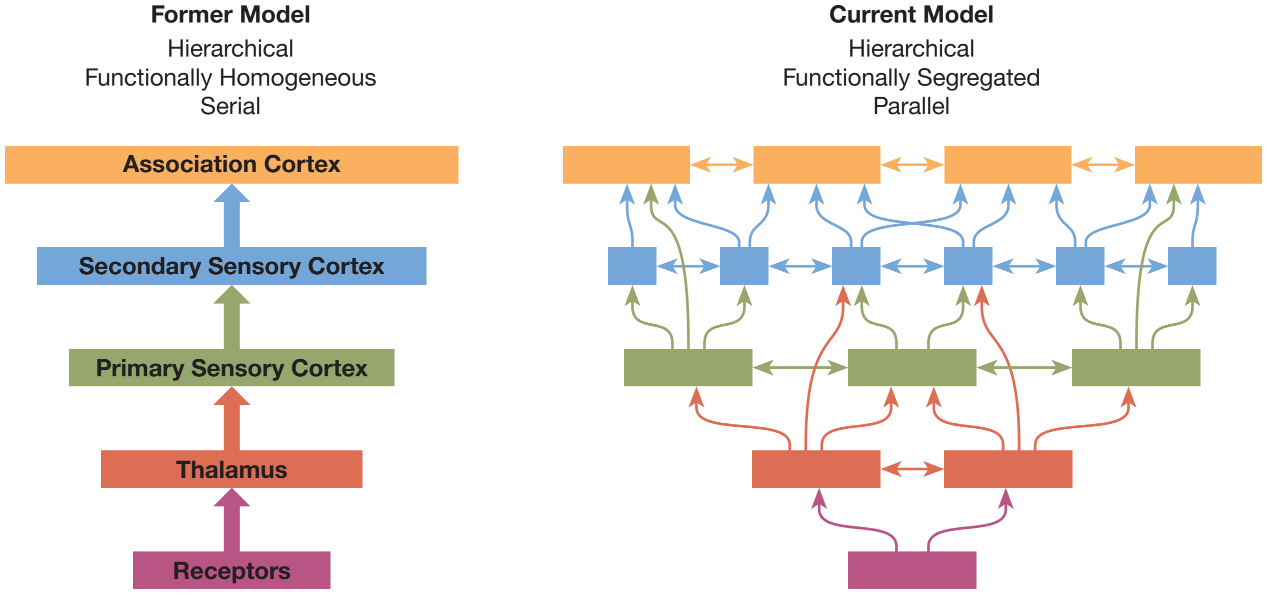
Mrs. P. showed little surprise. That kind of thing happened a lot.

FUNCTIONAL SEGREGATION. It was once assumed that the primary, secondary, and association areas of a sensory system were each *functionally homogeneous*. That is, it was assumed that all areas of cortex at any given level of a sensory hierarchy acted together to perform the same function. However, research has shown that **functional segregation**, rather than functional homogeneity, characterizes the organization of sensory systems. It is now clear that each of the three levels of cerebral cortex—primary, secondary, and association—in each sensory system contains functionally distinct areas that specialize in different kinds of analysis.

PARALLEL PROCESSING. It was once believed that the different levels of a sensory hierarchy were connected in a serial fashion. In a *serial system*, information flows among the components over just one pathway, like a string through a strand of beads. However, we now know that sensory systems are *parallel systems* in which information flows through the components over multiple pathways (see Lleras et al., 2017). Parallel systems feature **parallel processing**—the simultaneous analysis of a signal in different ways by the multiple parallel pathways of a neural network.

SUMMARY MODEL OF SENSORY SYSTEM ORGANIZATION. Figure 7.1 summarizes the information in this module by illustrating how thinking about the organization of sensory systems has changed. In the 1960s, sensory systems were believed to be hierarchical, functionally homogeneous,

Figure 7.1 Two models of sensory system organization: The former model was hierarchical, functionally homogeneous, and serial; the current model, which is more consistent with the evidence, is hierarchical, functionally segregated, and parallel. Not shown in the current model are the many descending pathways—one means by which higher levels of sensory systems can influence sensory input.



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*Based on *The Man Who Mistook His Wife for a Hat and Other Clinical Tales* by Oliver Sacks. Copyright © 1970, 1981, 1983, 1984, 1986 by Oliver Sacks.

and serial. However, subsequent research has established that sensory systems are hierarchical, functionally segregated, and parallel (see Rauschecker, 2015).

Not shown in Figure 7.1 are the many neurons that descend through the sensory hierarchies. Although sensory systems carry information from lower to higher levels of their respective hierarchies, they also conduct information in the opposite direction (from higher to lower levels). These are known as *top-down signals* (see Bressler & Richter, 2015; Marques et al., 2018; Ruff, 2013).

Now that you have an understanding of the general principles of sensory system organization, let's take a look in sequence at the auditory system, the somatosensory system, and the chemical sensory systems (smell and taste).

Figure 7.2 The relation between the physical and perceptual dimensions of sound.

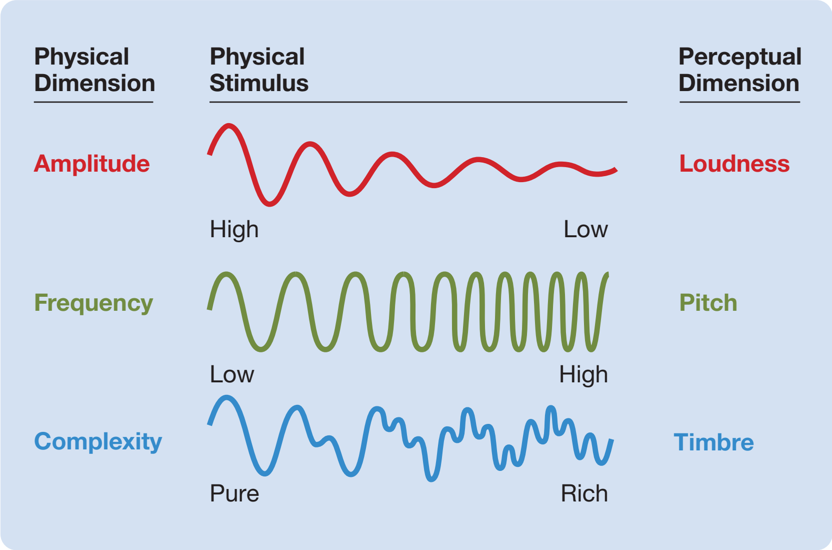
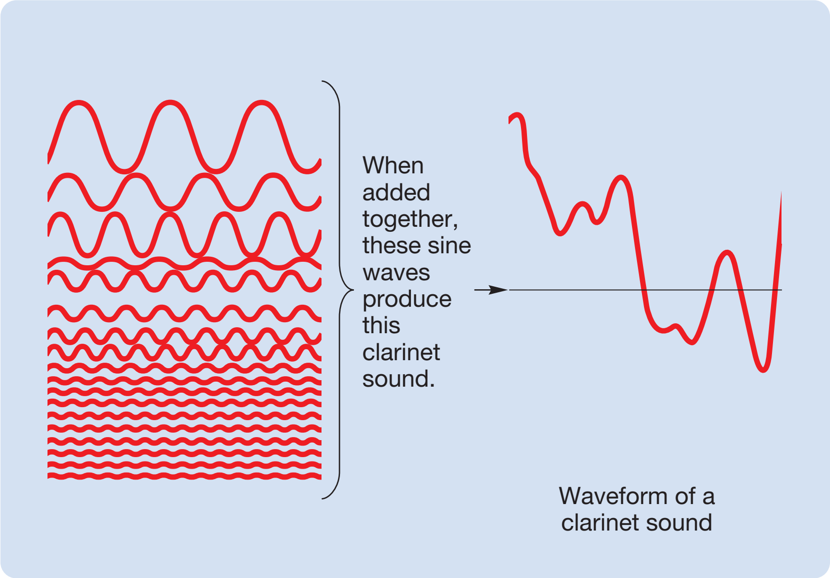


Figure 7.3 The breaking down of a sound—in this case, the sound of a clarinet—into its component sine waves by Fourier analysis. When added together, the component sine waves produce the complex sound wave.



Auditory System

The function of the auditory system is the perception of sound. Sounds are vibrations of air molecules that stimulate the auditory system; humans hear only those molecular vibrations between about 20 and 20,000 *hertz* (cycles per second).

Physical and Perceptual Dimensions of Sound

LO 7.3 **Explain the relationship between the physical and perceptual dimensions of sound.**

Figure 7.2 illustrates how sounds are commonly recorded in the form of waves and the relation between the physical dimensions of sound vibrations and our perceptions of them. The *amplitude*, *frequency*, and *complexity* of the molecular vibrations are most closely linked to perceptions of *loudness*, *pitch*, and *timbre*, respectively.

Pure tones (sine wave vibrations) exist only in laboratories and sound recording studios; in real life, sound is always associated with complex patterns of vibrations. For example, Figure 7.3 illustrates the complex sound wave associated with one note of a clarinet. The figure also illustrates that any complex sound wave can be broken down mathematically into a series of sine waves of various frequencies and amplitudes; these component sine waves produce the original sound when they are added together. **Fourier analysis** is the mathematical procedure for breaking down complex waves into their component sine waves. One theory of audition is that the auditory system performs a Fourier-like analysis of complex sounds in terms of their component sine waves.

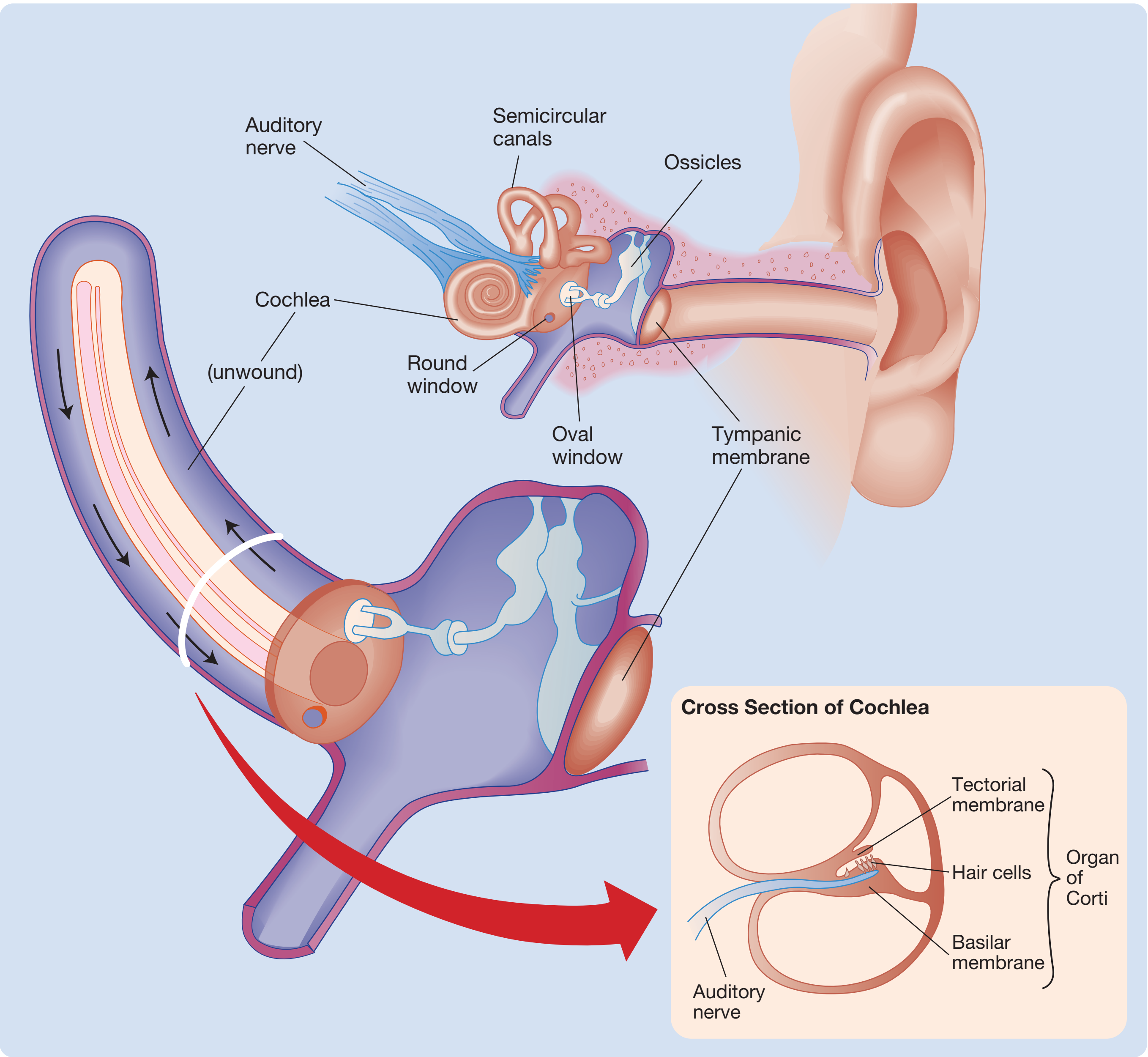
For any pure tone, there is a close relationship between the frequency of the tone and its perceived pitch; however, the relation between the frequencies that make up natural sounds (which are always composed of a mixture of frequencies) and their perceived pitch is complex (see Bidelman & Grall, 2014): The pitch of such sounds is related to their *fundamental frequency*: the frequency that is the highest common *divisor* (a number that divides another number) for the various component frequencies. For example, a sound that is a mixture of 100, 200, and 300 Hz frequencies normally has a pitch related to 100 Hz because 100 Hz is the highest common divisor of the three components. An extremely important characteristic of pitch perception is the fact that the pitch of a complex sound may not be directly related to the frequency of any of the sound's components (see Lau & Werner, 2014). For example, a mixture of pure tones with frequencies of 200, 300, and 400 Hz would be perceived as having the same pitch as a pure tone of 100 Hz—because 100 Hz is the fundamental frequency (i.e., the highest common divisor) of 200, 300, and 400 Hz. This important aspect of pitch perception is referred to as the *missing fundamental* (see Oxenham, 2018).

The Ear

LO 7.4 Describe the components of the human ear, and explain how sound is processed within its various structures.

The ear is illustrated in Figure 7.4. Sound waves travel from the outer ear down the auditory canal and cause the **tympanic membrane** (the eardrum) to vibrate.

Figure 7.4 Anatomy of the ear.



These vibrations are then transferred to the three **ossicles**—the small bones of the middle ear: the *malleus* (the hammer), the *incus* (the anvil), and the *stapes* (the stirrup). The vibrations of the stapes trigger vibrations of the membrane called the **oval window**, which in turn transfers the vibrations to the fluid of the snail-shaped **cochlea** (*kokhlos* means "land snail"). The cochlea is a long, coiled tube with an internal structure running almost to its tip. This internal structure is the auditory receptor organ, the **organ of Corti**.

Each pressure change at the oval window travels along the organ of Corti as a wave. The organ of Corti is composed of several membranes; we will focus on two of them: the basilar membrane and the tectorial membrane. The auditory receptors, the **hair cells**, are mounted in the **basilar membrane**, and the **tectorial membrane** rests on the hair cells. Accordingly, a deflection of the organ of Corti at any point along its length produces a shearing force on the hair cells at the same point. This force stimulates the hair cells, which in turn increase firing in axons of the **auditory nerve** (see Wu et al., 2017)—a branch of the *auditory-vestibular nerve* (one of the 12 cranial nerves). The vibrations of the cochlear fluid are ultimately dissipated by the *round window*, an elastic membrane in the cochlear wall.

The cochlea is remarkably sensitive (see Hudspeth, 2014). Humans can hear differences in pure tones that differ in frequency by only 0.2 percent. The major principle of cochlear coding is that different frequencies produce maximal stimulation of hair cells at different points along the basilar membrane—with higher frequencies producing greater activation closer to the windows and lower frequencies producing greater activation at the tip of the basilar membrane. Thus, the many component frequencies that compose each complex sound activate hair cells at many different points along the basilar membrane, and the many signals created by a single complex sound are carried out of the ear by many different auditory neurons. Like the cochlea, most other structures of the auditory system are arrayed according to frequency. Thus, in the same way that the organization of the visual system is largely **retinotopic**, the organization of the auditory system is largely **tonotopic** (see Schreiner & Polley, 2014).

This brings us to the major unsolved mystery of auditory processing. Imagine yourself in a complex acoustic environment such as a party. The music is playing; people are dancing, eating, and drinking; and numerous conversations are going on around you. Because the component frequencies in each individual sound activate many sites along your basilar membrane, the number of sites simultaneously activated at any one time by the party noises is enormous. But somehow your auditory system manages to sort these individual frequency messages into separate categories and combine them so that you hear each source of complex sounds independently (see Bremen & Middlebrooks, 2013; Christison-Lagay & Cohen, 2014; Christison-Lagay, Gifford, & Cohen, 2015). For example, you hear the speech of the person standing next to you as a separate sequence of sounds, despite the fact that it contains many of the same component frequencies coming from other sources. The mechanism underlying this important ability has yet to be identified, but one theory is that it is due to the synchronous relationship over time of the frequency elements of each sound source (see Oxenham, 2018).

Figure 7.4 also shows the **semicircular canals**—the receptive organs of the **vestibular system**. The vestibular system carries information about the direction and intensity of head movements, which helps us maintain our balance (see Brandt & Dieterich, 2017; Gu, 2018).

From the Ear to the Primary Auditory Cortex

LO 7.5 Describe the major pathways that lead from the ear to the primary auditory cortex.

There is no major auditory pathway to the cortex comparable to the visual system's retina-geniculate-striate pathway. Instead, there is a network of auditory pathways, some of which are illustrated in Figure 7.5. The axons of each *auditory nerve* synapse in the ipsilateral *cochlear nuclei*, from which many projections lead to the **superior olives** on both sides of the brain stem at the same level. The axons of the olivary neurons project via the *lateral lemniscus* to the **inferior colliculi**, where they synapse on neurons that project to the **medial geniculate nuclei** of the thalamus, which in turn project to the *primary auditory cortex*. Notice that signals from each ear are combined at a very low level (in the superior olives) and are transmitted to both ipsilateral and contralateral auditory cortex.

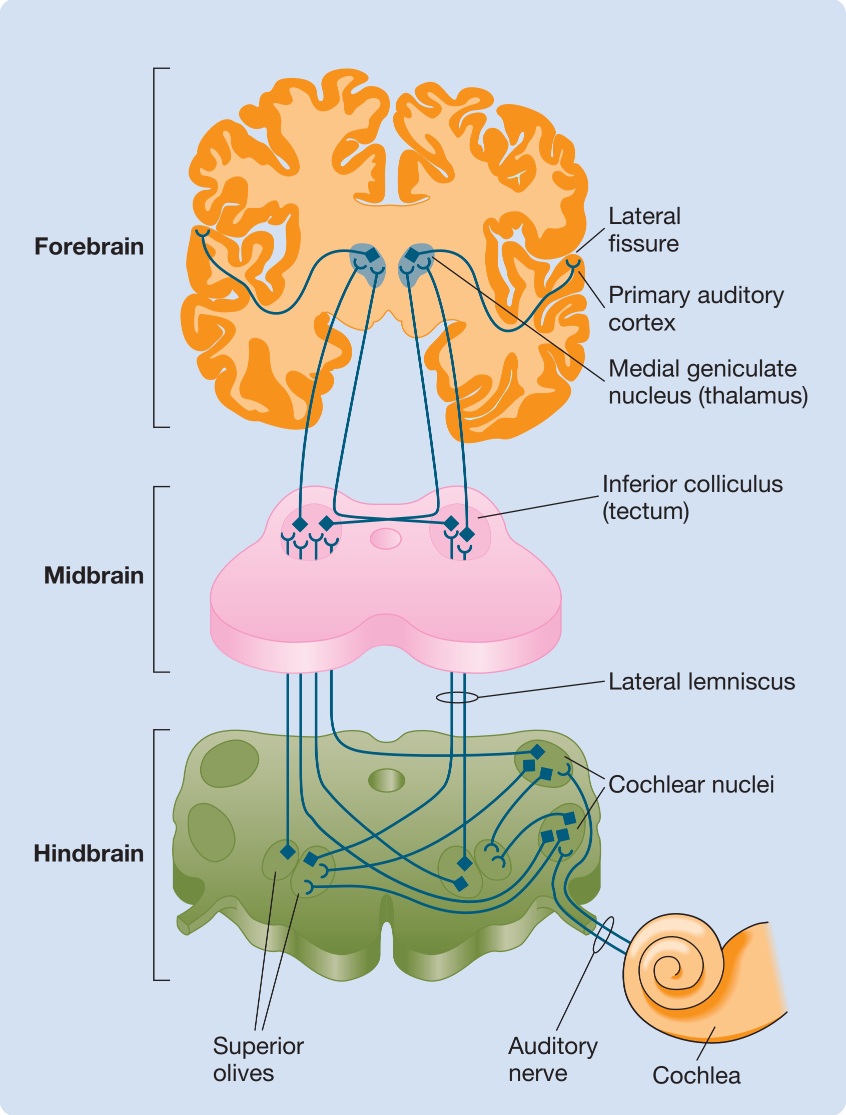
The subcortical pathways of the auditory system are inherently complex, and they have many more synapses than the other senses (see Jasmin, Lima, & Scott, 2019; Wang, 2018). Some researchers believe that the complex subcortical organization of the auditory system is related to the complexity of the analyses that the auditory system has to perform (see Wang, 2018).

Auditory Cortex

LO 7.6 Describe the organization of auditory cortex.

Recent progress in the study of human auditory cortex has resulted from the convergence of functional brain-imaging studies in humans and invasive neural recording studies in monkeys (see Saenz & Langers, 2014). Still, primate auditory cortex is far from being well understood—for example, our understanding of it lags far behind our current understanding of the visual cortex.

Figure 7.5 Some of the pathways of the auditory system that lead from one ear to the cortex.

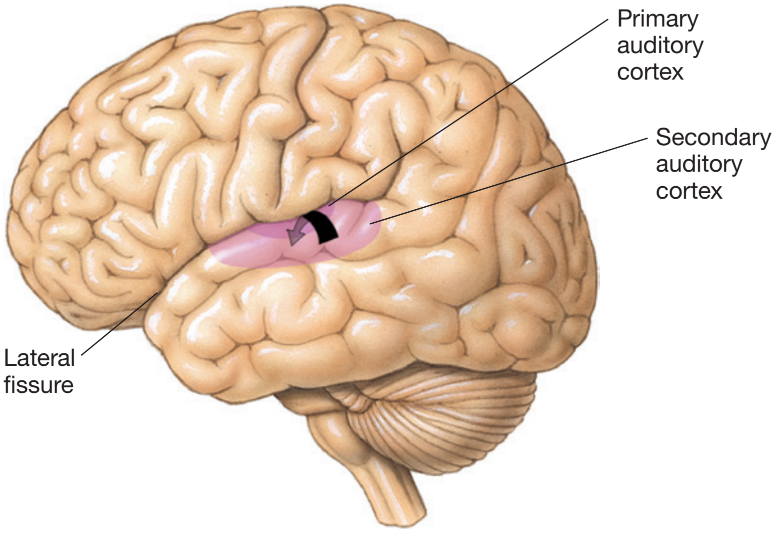


In primates, the primary auditory cortex, which receives the majority of its input from the medial geniculate nucleus, is located in the temporal lobe, hidden from view within the lateral fissure (see Figure 7.6). Primate primary auditory cortex comprises three adjacent areas (see Moerel, De Martino, & Formisano, 2014): Together these three areas are referred to as the *core region*. Surrounding the core region is a band—often called the *belt*—of areas of secondary auditory cortex. Areas of secondary auditory cortex outside the belt are called *parabelt areas* (Jasmin, Lima, & Scott, 2019). In total, there seem to be about 13 separate areas of auditory cortex in primates (see Brewer & Barton, 2016).

ORGANIZATION OF PRIMATE AUDITORY CORTEX. Three important principles of organization of primary auditory cortex have been identified. First, like the primary visual cortex, the primary auditory cortex is organized in functional columns (see Mizrahi, Shalev, & Nelken, 2014): All of the neurons encountered during a vertical microelectrode penetration of primary auditory cortex (i.e., a penetration at right angles to the cortical layers) tend to respond optimally to sounds in the same frequency range. Second, like the cochlea, auditory cortex has a tonotopic organization (see Jasmin, Lima, & Scott, 2019; Schreiner & Polley, 2014): Each area of auditory cortex appears to have a gradient of frequencies from low to high along its length. Third, auditory cortex is also organized according to the temporal components of sound; that is, variations in the amplitude of particular sound frequencies over time. For example, our auditory environments almost never consist of sounds that do not vary in their intensity over time. It seems that auditory cortex is sensitive to such fluctuations. This third organizing principle of auditory cortex is known as **periodotopy** (see Brewer & Barton, 2016).

WHAT SOUNDS SHOULD BE USED TO STUDY AUDITORY CORTEX? Why has research on auditory cortex lagged behind research on visual cortex? There are several reasons, but a major one is a lack of clear understanding of the dimensions along which auditory cortex evaluates

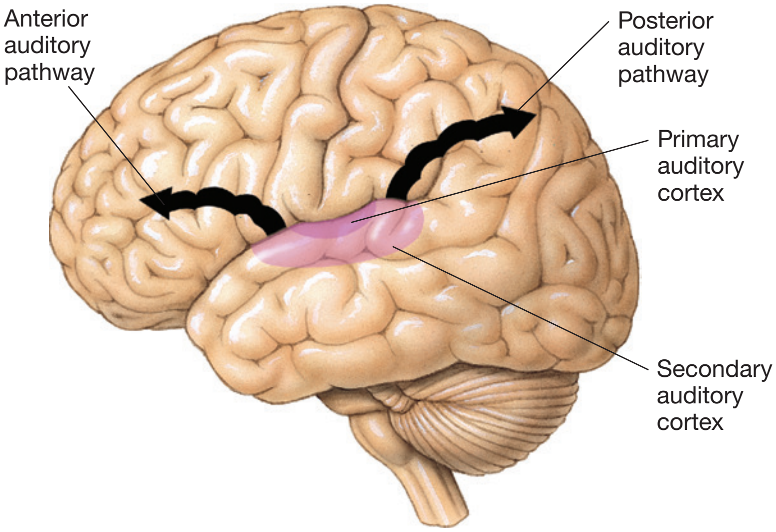
Figure 7.6 General location of the primary auditory cortex and areas of secondary auditory cortex. Most auditory cortex is hidden from view in the lateral fissure.



sound (Sharpee, Atencio, & Schreiner, 2011). You may recall that research on the visual cortex did not start to progress rapidly until it was discovered that most visual neurons respond to contrast. There is clear evidence of a hierarchical organization in auditory cortex—the neural responses of secondary auditory cortex tend to be more complex and varied than those of primary auditory cortex (see Jasmin, Lima, & Scott, 2019).

Many neurons in auditory cortex respond only weakly to simple stimuli such as pure tones, which have been widely employed in electrophysiological studies of auditory cortex. This practice is changing, however, partly in response to the discovery that natural sounds, in general, are better at eliciting responses from neurons in mammalian auditory cortex (see Gervain & Geffen, 2019; Kopp-Scheinpflug, Sinclair, & Linden, 2019).

Figure 7.7 The hypothesized anterior and posterior auditory pathways.



WHAT ANALYSES DOES THE AUDITORY CORTEX PERFORM? We now know that calculations by the auditory cortex produce signals that are not faithful representation of sounds (see Tsunada et al., 2016; Wang, 2018). More specifically, auditory cortex is now known to integrate information about the current perceptions and behaviors of an animal in order to produce auditory signals that are relevant to the animal's current situation (see Kuchibhotla & Bathellier, 2018; Lima, Krishnan, & Scott, 2016; Schneider & Mooney, 2018).

One example of an output signal from auditory cortex that is particularly relevant to an animal's current situation is the creation of representations of *auditory objects*. For example, it is believed that the auditory cortex can take the complex mixture of frequencies produced by a piano and convert it into a sound representation that allows us to say "That's the sound of a piano!" (see Angeloni & Geffen, 2018; Kuchibhotla & Bathellier, 2018; Tsunada et al., 2016).

TWO STREAMS OF AUDITORY CORTEX. Thinking about the general organization of auditory cortex has been inspired by research on visual cortex. Researchers have proposed that, just as there are two main cortical streams of visual analysis (dorsal and ventral), there are two main cortical streams of auditory analysis. Auditory signals are ultimately conducted to two large areas of association cortex: prefrontal cortex and posterior parietal cortex. There is good evidence that the *anterior auditory pathway* is more involved in identifying sounds (what), whereas the *posterior auditory pathway* is more involved in locating sounds (where)—see Jasmin, Lima, & Scott (2019) and van der Heijden et al. (2019). These pathways are illustrated in Figure 7.7.

AUDITORY–VISUAL INTERACTIONS. Sensory systems have traditionally been assumed to interact in association cortex. Indeed, as you have already learned, association cortex is usually defined as areas of cortex where such interactions, or associations, take place. Much of the research on sensory system interactions has focused on interactions between the auditory and visual systems, particularly on those that occur in the posterior parietal cortex (see Brang et al., 2013; Cohen, 2009). In one study of monkeys (Mullette-Gillman, Cohen, & Groh, 2005), some posterior parietal neurons were found to have visual receptive fields, some were found to have auditory receptive fields, and some were found to have both.

Functional brain imaging is widely used to investigate sensory system interactions. One advantage of functional brain imaging is that it does not focus on any one part of the brain; it records activity throughout the brain. Functional brain-imaging studies have confirmed that sensory interactions do occur in association cortex, but more importantly, they have repeatedly found evidence of sensory interactions at the lowest level of the sensory cortex hierarchy, in areas of primary sensory cortex (see Man et al., 2013; Smith & Goodale, 2015). This discovery is changing how we think about the interaction of sensory systems: Sensory system interaction is not merely tagged on after *unimodal* (involving one system) analyses are complete; sensory system interactions seem to be an early and integral part of sensory processing.

WHERE DOES THE PERCEPTION OF PITCH OCCUR? Recent research has answered one fundamental question about auditory cortex: Where does the perception of pitch likely occur? This seemed like a simple question to answer because most areas of auditory cortex have a clear tonotopic organization. However, when experimenters used sound stimuli in which frequency and pitch were