

7 Development, Learning, and Plasticity

We have so far considered the basis by which the auditory system can detect, localize, and identify the myriad sounds that we might encounter. But how does our perception of the acoustic environment arise during development? Are we born with these abilities or do they emerge gradually during childhood? It turns out that much of the development of the auditory system takes place before birth, enabling many species, including humans, to respond to sound as soon as they are born. Nonetheless, the different parts of the ear and the central auditory pathways continue to mature for some time after that. This involves a lot of remodeling in the brain, with many neurons failing to survive until adulthood and others undergoing changes in the number and type of connections they form with other neurons. Not surprisingly, these wiring modifications can result in developmental changes in the auditory sensitivity of the neurons. As a consequence, auditory perceptual abilities mature over different timescales, in some cases not reaching the levels typically seen in adults until several years after birth.

A very important factor in the development of any sensory system is that the anatomical and functional organization of the brain regions involved is shaped by experience during so-called “sensitive” or “critical” periods of early postnatal life. These terms are often used interchangeably, but some researchers use them to describe distinct phases of development. A sensitive period would then refer to the phase during which altered experience can change behavior or neuronal response properties, whereas a critical period covers the longer phase during which these changes can be reversed if normal sensory inputs are experienced. We will therefore stick to the term sensitive period. The plasticity seen during this stage of development helps to optimize brain circuits to an individual’s sensory environment. But this also means that abnormal experience—such as a loss of hearing in childhood—can have a profound effect on the manner in which neurons respond to different sounds, and therefore on how we perceive them.

Although sensitive periods of development have been described for many species and for many aspects of auditory function, including the emergence of

linguistic and musical abilities, we must remember that learning is a lifelong process. Indeed, extensive plasticity is seen in the adult brain, too, which plays a vital function in enabling humans and animals to interact effectively with their acoustic environment and provides the basis on which learning can improve perceptual abilities.


7.1 When Does Hearing Start?

The development of the auditory system is a complex, multistage process that begins in early embryonic life. The embryo comprises three layers, which interact to produce the various tissues of the body. One of these layers, the ectoderm, gives rise to both neural tissue and skin. The initial stage in this process involves the formation of the otic placode, a thickening of the ectoderm in the region of the developing hindbrain. As a result of signals provided by the neural tube, from which the brain and spinal cord are derived, and by the mesoderm, the otic placode is induced to invaginate and fold up into a structure called the otocyst, from which the cochlea and otic ganglion cells—the future auditory nerve—are formed. Interestingly, the external ear and the middle ear have different embryological origins from that of the inner ear. As a consequence, congenital abnormalities can occur independently in each of these structures.

The neurons that will become part of the central auditory pathway are produced within the ventricular zone of the embryo's neural tube, from where they migrate to their final destination in the brain. Studies in animals have shown that the first auditory neurons to be generated give rise to the cochlear nucleus, superior olivary complex, and medial geniculate nucleus, with the production of neurons that form the inferior colliculus and auditory cortex beginning slightly later. In humans, all the subcortical auditory structures can be recognized by the eighth fetal week. The cortical plate, the first sign of the future cerebral cortex, also emerges at this time, although the temporal lobe becomes apparent as a distinct structure only in the twenty-seventh week of gestation (Moore & Linthicum, 2009).

To serve their purpose, the newly generated neurons must make specific synaptic connections with other neurons. Consequently, as they are migrating, the neurons start to send out axons that are guided toward their targets by a variety of chemical guidance cues those structures produce. These molecules are detected by receptors on the exploring growth cones that form the tips of the growing axons, while other molecules ensure that axons make contact with the appropriate region of the target neurons. Robust synaptic connections can be established at an early stage—by the fourteenth week of gestation in the case of the innervation of hair cells by the spiral ganglion cells. On the other hand, another seven weeks elapse before axons from the thalamus start to make connections with the cortical plate.

At this stage of development, the axons lack their insulating sheaths of myelin, which are required for the rapid and reliable conduction of action potentials that is so important in the adult auditory system. In humans, myelination of the auditory nerve and the major brainstem pathways begins at the twenty-sixth week of gestation, and it is at around this age that the first responses to sound can be measured. One way of showing this is to measure event-related potentials from the scalp of premature infants born soon after this age. But even within the womb it is possible to demonstrate that the fetus can hear by measuring the unborn baby's movements or changes in heart rate that occur in response to vibroacoustic stimulation applied to the mother's abdomen. Such measurements have confirmed that hearing onset occurs at around the end of the second trimester.

 External sounds will, of course, be muffled by the mother's abdominal wall and masked by noises produced by her internal organs. A video clip showing the likely sounds the fetus will encounter is available on the book's Web site. It is therefore perhaps not immediately clear what types of sound would actually reach the fetus. Attempts to record responses from the inner ear of fetal sheep, however, suggest that low-frequency speech could be audible to human infants (Smith et al., 2003), and there is some evidence that, toward the end of pregnancy, the human fetus not only responds to but can even discriminate between different speech sounds (Shahidullah & Hepper, 1994).

7.2 Hearing Capabilities Improve after Birth

Because of the extensive prenatal development of the auditory system, human infants are born with a quite sophisticated capacity to make sense of their auditory world. They can readily distinguish between different phonemes, and are sensitive to the pitch and rhythm of their mother's voice. Within a few days of birth, babies show a preference for their mother's voice over that of another infant's mother, presumably as a result of their prenatal experience (DeCasper & Fifer, 1980). Perhaps more surprisingly, various aspects of music perception can be demonstrated early in infancy. These include an ability to distinguish different scales and chords and a preference for consonant or pleasant-sounding intervals, such as the perfect fifth, over dissonant intervals (Trehub, 2003), as well as sensitivity to the beat of a rhythmic sound pattern (Winkler et al., 2009b).

Whether these early perceptual abilities are unique to human infants or specifically related to language and music is still an open question. Mark Hauser at Harvard University and others have addressed these questions from an evolutionary perspective by investigating whether animals, and in particular nonhuman primates, can perceive speech and music in a related fashion. In one such study, Kuhl and Miller (1975) showed that adult chinchillas are able to perceive phonemes categorically in a similar

fashion to human infants. But while some marked similarities certainly exist between the abilities of humans and some other species to distinguish speech sounds, pointing to the involvement of common processing mechanisms, few behavioral studies have been carried out in very young animals.

It would be wrong to conclude from this, however, that human infants can hear the world around them in the same way that adults do. Almost all auditory perceptual abilities improve gradually after birth, and the age at which adult performance is reached varies greatly with the task. For example, sounds have to be played at a greater intensity to evoke a response from an infant, and, particularly for low-frequency tones, it can take as long as a decade until children possess the same low detection thresholds seen in adults. The capacity to detect a change in the frequency of two sequentially played tones also continues to improve over several years, although frequency resolution—the detection of a tone of one frequency in the presence of masking energy at other frequencies—seems to mature earlier.

Another aspect of hearing that matures over a protracted period of postnatal development is sound localization. While parents will readily attest to the fact that newborn infants can turn toward their voices, the accuracy of these orienting responses increases with age. Figure 7.1 shows that the minimum audible angle—the smallest detectable change in sound source location—takes about 5 years to reach adult values. As we saw in chapter 5, having two ears also helps in detecting target sounds against a noisy background. The measure of this ability, the binaural masking level difference, takes

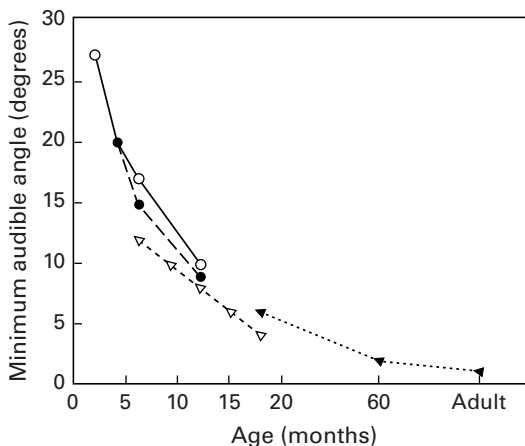


Figure 7.1

Minimum audible angles, a measure of the smallest change in the direction of a sound source that can be reliably discriminated, decrease with age in humans.

Based on Clifton (1992).

at least 5 years and possibly much longer to mature (Hall, Buss, & Grose, 2007). This is also the case for the precedence effect (Litovsky, 1997), indicating that the capacity to perceive sounds in the reverberant environments we encounter in our everyday lives emerges over a particularly long period.

Highly relevant to the perception of speech and music is the development of auditory temporal processing. Estimates of the minimum time period within which different acoustic events can be distinguished have been obtained using a variety of methods. These include the detection of amplitude and frequency modulation, gap detection—the smallest detectable silent interval in a sound—and nonsimultaneous masking paradigms. Although quite wide variations have been found in the age at which adult values are attained with the precise task and type of sound used, it is clear that temporal resolution also takes a long time to reach maturity. For example, “backward masking,” which measures the ability of listeners to detect a tone that is followed immediately by a noise, has been reported to reach adult levels of performance as late as 15 years of age.

To make sense of all this, we need to take several factors into account. First, there is, of course, the developmental status of the auditory system. Although the ear and auditory pathways are sufficiently far advanced in their development to be able to respond to sound well before birth in humans, important and extensive changes continue to take place for several years into postnatal life. Second, nonsensory or cognitive factors will contribute to the performance measured in infants. These factors include attention, motivation, and memory, and they often present particular challenges when trying to assess auditory function in the very young.

We can account for the maturation of certain hearing abilities without having to worry about what might be happening in the brain at the time. This is because changes in auditory performance can be attributed to the postnatal development of the ear itself. For instance, the elevated thresholds and relatively flat audiogram seen in infancy are almost certainly due to the immature conductive properties of the external ear and the middle ear that are found at that age. As these structures grow, the resonant frequencies of the external ear decrease in value and the acoustic power transfer of the middle ear improves. In both cases, it takes several years for adult values to be reached, a timeframe consistent with age-related improvements in hearing sensitivity.

Growth of the external ears and the head also has considerable implications for sound localization. As we saw in chapter 5, the auditory system determines the direction of a sound source from a combination of monaural and binaural spatial cues. The values of those cues will change as the external ears grow and the distance between them increases (figure 7.2). As we shall see later, when we look at the maturation of the neural circuits that process spatial information, age-related differences in the cue values can account for the way in which the spatial receptive fields of auditory neurons

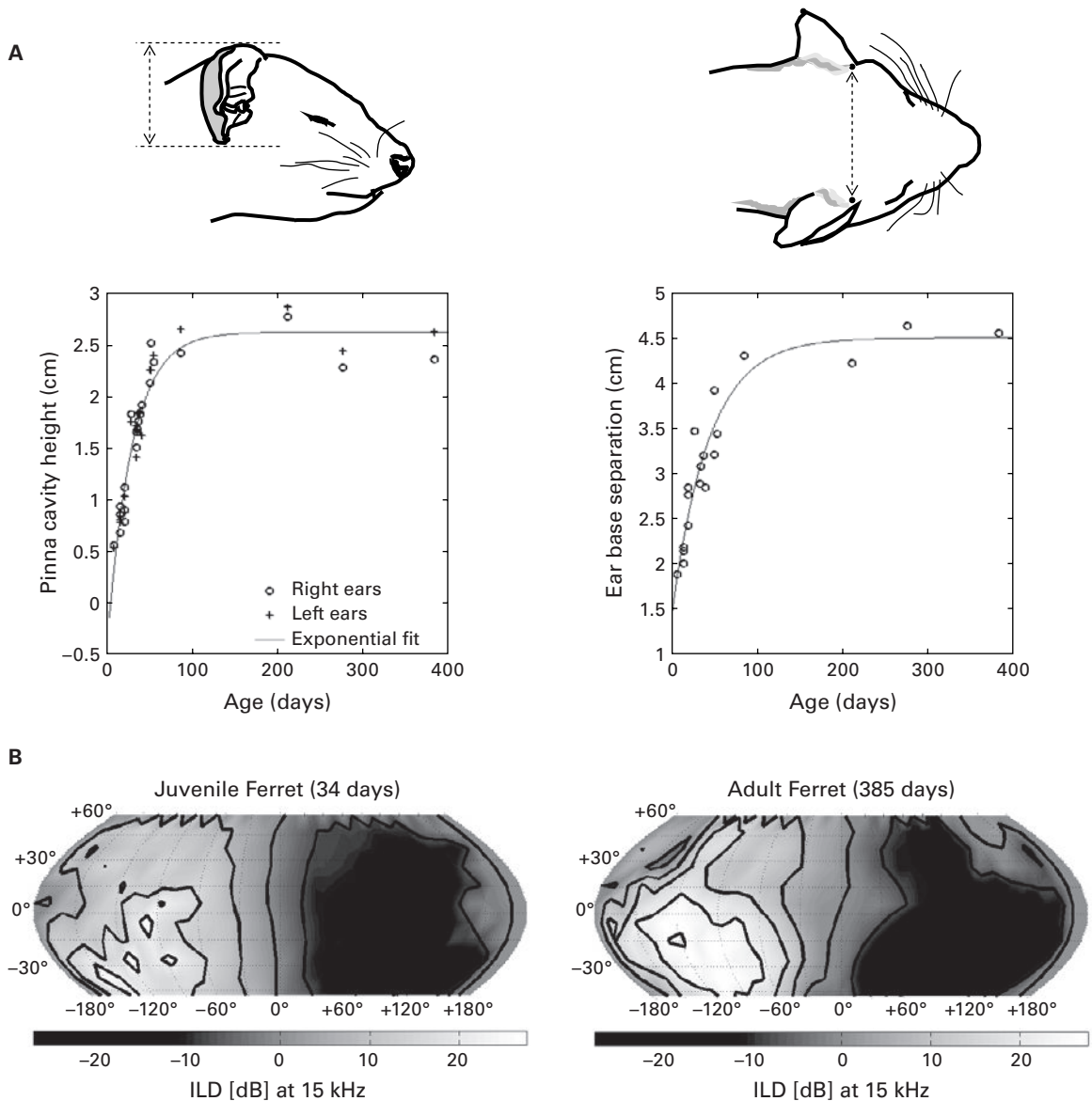


Figure 7.2

Growth of the head and external ears changes the acoustic cue values corresponding to each direction in space. (A) Age-related changes in the height of the external ear and in the distance between the ears of the ferret, a species commonly used for studying auditory development. These dimensions mature by around 4 months of age. (B) Variation in interaural level differences (ILDs) for a 15-kHz tone as a function of azimuth and elevation in a 34-day-old juvenile ferret (left) and in an adult animal at 385 days of age (right). The range of ILDs is larger and their spatial pattern is somewhat different in the older animal.

Based on Schnupp, Booth, and King (2003).

change during development. In turn, it is likely that this will contribute to the gradual emergence of a child's localization abilities.

The range of audible frequencies appears to change in early life as a result of developmental modifications in the tonotopic organization of the cochlea. You should now be very familiar with the notion that the hair cells near the base of the cochlea are most sensitive to high-frequency sounds, whereas those located nearer its apex are tuned to progressively lower frequencies. Although the basal end of the cochlea matures first, studies in mammals and chicks have shown that this region initially responds to lower sound frequencies than it does in adults. This is followed by an increase in the sound frequencies to which each region of the cochlea is most responsive, leading to an upward expansion in the range of audible sound frequencies. Such changes have not been described in humans, but it is possible that they take place before birth.

While the maturation of certain aspects of auditory perception is constrained by the development of the ear, significant changes also take place postnatally in the central auditory system. An increase in myelination of the auditory pathways results in a progressive reduction in the latency of the evoked potentials measured at the scalp in response to sound stimulation. At the level of the human brainstem, these changes are thought to be complete within the first 2 years of life. However, Nina Kraus and colleagues have recently shown that the brainstem responses evoked by speech sounds in 3- to 4-year-old children are delayed and less synchronous than those recorded in older children, whereas this difference across age is not observed with simpler sounds (Johnson et al., 2008). But it is the neural circuits at higher levels of the auditory system that mature most slowly, with sound-evoked cortical potentials taking around 12 years to resemble those seen in adults (Wunderlich & Cone-Wesson, 2006).

7.3 The Importance of Early Experience: Speech and Music

Although it remains difficult to determine how important the acoustic environment of the fetus is for the prenatal development of hearing, there is no doubt that the postnatal maturation of the central auditory pathways is heavily influenced by sensory experience. Because this process is so protracted, there is ample opportunity for the development of our perceptual faculties to be influenced by experience of the sounds we encounter during infancy. As we shall see in the following section, this also means that reduced auditory inputs, which can result, for example, from early hearing loss, and even information provided by the other senses can have a profound impact on the development of the central auditory system.

The importance of experience in shaping the maturing auditory system is illustrated very clearly by the acquisition of language during early childhood. Infants are initially

able to distinguish speech sounds in any language. But as they learn from experience, this languagewide capacity quickly narrows. Indeed, during the first year of life, their ability to perceive phonetic contrasts in their mother tongue improves, while they lose their sensitivity to certain sound distinctions that occur only in foreign languages. You may remember from chapter 4 that this is nicely illustrated by the classic example of adult Japanese speakers, who struggle to distinguish the phonetic units “r” from “l,” even though, at 7 months of age, Japanese infants are as adept at doing so as native English speakers (figure 7.3). In Japanese, these consonants fall within a single perceptual category, so Japanese children “unlearn” the ability to distinguish them. This process of becoming more sensitive to acoustic distinctions at phoneme boundaries of one’s mother tongue, while becoming less sensitive to distinctions away from them, has been found to begin as early as 6 months of age for vowels and by 10 months for consonants (Kuhl & Rivera-Gaxiola, 2008). Perceptual narrowing based on a child’s experience during infancy is not restricted to spoken language. Over the same time period, infants also become more sensitive to the correspondence between speech sounds and the talker’s face in their own language, and less so for non-native language (Pons et al., 2009).

These changes in speech perception during the first year of life are driven, at least in part, by the statistical distribution of speech sounds in the language to which the infant is exposed. Thus, familiarizing infants with artificial speech sounds in which

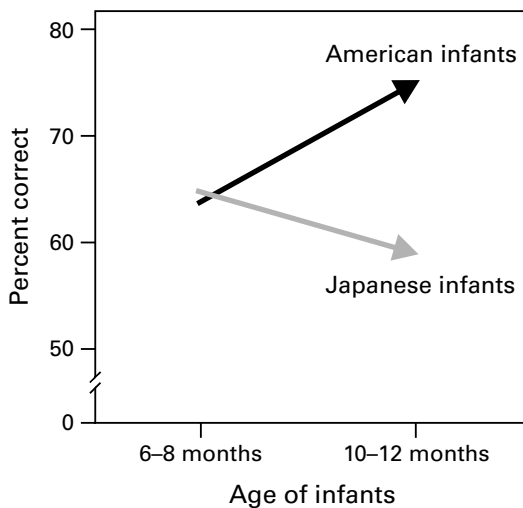


Figure 7.3

The effects of age on speech perception performance in a cross-language study of the perception of American English /r-l/ sounds by American and Japanese infants.

Based on Kuhl et al. (2006).

this distribution has been manipulated experimentally alters their subsequent ability to distinguish some of those sounds (Maye, Werker, & Gerken, 2002). But social interactions also seem to play a role. Kuhl, Tsao, and Liu (2003) showed that 9-month-old American infants readily learn phonemes and words in Mandarin Chinese, but only if they were able to interact with a live Chinese speaker. By contrast, no learning occurred if the same sounds were delivered by television or audiotape.

Not surprisingly, as a child's perceptual abilities become increasingly focused on processing the language(s) experienced during early life, the capacity to learn a new language declines. In addition to the loss in the ability to distinguish phonemes in other languages during the first year of life, other aspects of speech acquisition, including the syntactic and semantic aspects of language, appear to be developmentally regulated (Ruben, 1997). The sensitive period of development during which language can be acquired with little effort lasts for about 7 years. New language learning then becomes more difficult, despite the fact that other cognitive abilities improve with age.

Sensitive periods have also been characterized for other aspects of auditory development. Perhaps the most relevant to language acquisition in humans is vocal learning in songbirds (figure 7.4). Young birds learn their songs by listening to adults during an initial sensitive period of development, the duration of which varies from one species to another and with acoustic experience and the level of hormones such as testosterone. After this purely sensory phase of learning, the birds start to make their own highly variable vocal attempts, producing what is known as "subsong," the equivalent of babbling in babies. They then use auditory feedback during a sensorimotor phase of learning to refine their vocalizations until a stable adult song is crystallized (Brainard & Doupe, 2002). Examples of the different song stages can be found on the



book's Web site.

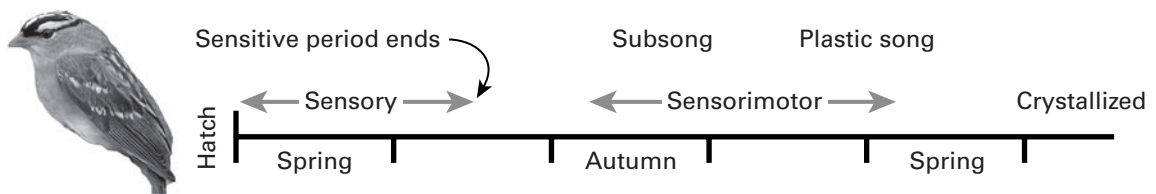


Figure 7.4

Birdsong learning stages. In seasonal species, such as the white-crowned sparrow, the sensory and sensorimotor phases of learning are separated in time. The initial vocalizations ("subsong") produced by young birds are variable and generic across individuals. Subsong gradually evolves into "plastic song," which, although still highly variable, begins to incorporate some recognizable elements of tutor songs. Plastic song is progressively refined until the bird crystallizes its stable adult song. Other songbirds show different time courses of learning.

Adapted from Brainard and Doupe (2002) with permission from Macmillan Publishers Ltd.

Thus, both human speech development and birdsong learning rely on the individual being able to hear the voices of others, as illustrated by Peter Marler's intriguing observation that, like humans, some songbirds possess regional dialects (Marler & Tamura, 1962). The importance of hearing the tutor song during a sensitive period of development has been demonstrated by raising songbirds with unrelated adults of the same species; as they mature, these birds start to imitate the songs produced by the tutor birds. On the other hand, birds raised in acoustic isolation—so that they are prevented from hearing the song of conspecific adults—produce abnormal vocalizations. This is also the case if songbirds are deafened before they have the opportunity to practice their vocalizations, even if they have previously been exposed to tutor songs; this highlights the importance of being able to hear their own voices as they learn to sing. In a similar vein, profound hearing loss has a detrimental effect on speech acquisition in children.

A related area where experience plays a key role is in the development of music perception. We have already pointed out that human infants are born with a remarkably advanced sensitivity to different aspects of music. As with their universal capacity to distinguish phonemes, infants initially respond in a similar way to the music of any culture. Their perceptual abilities change with experience, however, and become increasingly focused on the style of music to which they have been exposed. For example, at 6 months of age, infants are sensitive to rhythmic variations in the music of different cultures, whereas 12-month-olds show a culture-specific bias (Hannon & Trehub, 2005). The perception of rhythm in foreign music can nonetheless be improved at 12 months by brief exposure to an unfamiliar style of music, whereas this is not the case in adults.

Findings such as these again point to the existence of a sensitive period of development during which perceptual abilities can be refined by experience. As with the maturation of speech perception, passive exposure to the sounds of a particular culture probably leads to changes in neural sensitivity to the structure of music. But we also have to consider the role played by musical training. In chapter 3, we introduced the concept of absolute pitch—the ability to identify the pitch of a sound in the absence of a reference pitch. It seems likely that some form of musical training during childhood is a requirement for developing absolute pitch, and the likelihood of having this ability increases if that training starts earlier. This cannot, however, be the only explanation, as not all trained musicians possess absolute pitch. In addition, genetic factors appear to play a role in determining whether or not absolute pitch can be acquired.

There is considerable interest in being able to measure what actually goes on in the brain as auditory perceptual abilities change during development and with experience. A number of noninvasive brain imaging and electrophysiological recording methods are available to do this in humans (details of these methods are described briefly in Kuhl & Rivera-Gaxiola, 2008). Using these approaches, it has been shown that although

language functions are lateralized at birth, the regions of the cerebral cortex involved are less specialized and the responses recorded from them are much slower in infants than they are in adults (Friederici, 2006; Kuhl & Rivera-Gaxiola, 2008). Event-related potentials (ERPs) are particularly suitable for studying time-locked responses to speech in young children. ERP measurements suggest that by 7.5 months of age, the brain is more sensitive to phonetic contrasts in the child's native language than in a non-native language (figure 7.5; Kuhl & Rivera-Gaxiola, 2008). This is in line with behavioral studies of phonetic learning. Intriguingly, the differences seen at this age in the ERP responses to native and non-native contrasts seem to provide an indicator of the rate at which language is subsequently acquired. Neural correlates of word learning can be observed toward the end of the first year of life, whereas violations of syntactic word order result in ERP differences at around 30 months after birth.

Some remarkable examples of brain plasticity have been described in trained musicians. Of course, speech and music both involve production (or playing, in the case of a musical instrument) as much as listening, so it is hardly surprising that motor as

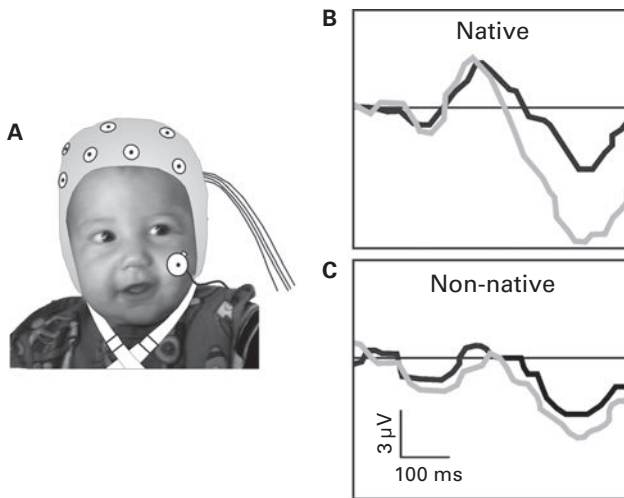


Figure 7.5

Neural correlates of speech perception in infancy. (A) Human infant wearing an ERP electrocap. (B) ERP waveforms recorded at 7.5 months of age from one sensor location in response to a native (English) and non-native (Mandarin Chinese) phonetic contrast. The black waveforms show the response to a standard stimulus, whereas the gray waveforms show the response to the deviant stimulus. The difference in amplitude between the standard and deviant waveforms is larger in the case of the native English contrast, implying better discrimination than for the non-native speech sounds.

Based on Kuhl and Rivera-Gaxiola (2008).

well as auditory regions of the brain can be influenced by musical training and experience. Neuroimaging studies have shown that musical training can produce structural and functional changes in the brain areas that are activated during auditory processing or when playing an instrument, particularly if training begins in early childhood. These changes most commonly take the form of an enlargement of the brain areas in question and enhanced musically related activity in them. One study observed structural brain plasticity in motor and auditory cortical areas of 6-year-old children who received 15 months of keyboard lessons, which was accompanied by improvements in musically relevant skills (Hyde et al., 2009). Because no anatomical differences were found before the lessons started between these children and an age-matched control group, it appears that musical training can have a profound effect on the development of these brain areas. In fact, plasticity is not restricted to the cerebral cortex, as functional differences are also found in the auditory brainstem of trained musicians (Kraus et al., 2009).

Imaging studies have also provided some intriguing insights into the basis of musical disorders. We probably all know someone who is tone deaf or unable to sing in tune. This condition may arise as a result of a reduction in the size of the arcuate fasciculus, a fiber tract that connects the temporal and frontal lobes of the cerebral cortex (Loui, Alsop, & Schlaug, 2009). Consequently, tone deafness, which is found in about 10% of the population, is likely to reflect reduced links between the brain regions involved in the processing of sound, including speech and music, and those responsible for vocal production.

7.4 Maturation of Auditory Circuits in the Brain

To track the changes that take place in the human brain during development and learning, we have to rely on noninvasive measures of brain anatomy and function. As in the mature brain, however, these methods tell us little about what is happening at the level of individual nerve cells and circuits. This requires a different approach, involving the use of more invasive experimental techniques in animals. In this section, we look at some of the cellular changes that take place during development within the central auditory pathway, and examine how they are affected by changes in sensory inputs.

The connections between the spiral ganglion cells and their targets in the cochlea and the brainstem provide the basis for the tonotopic representation of sound frequency within the central auditory system. These connections therefore have to be organized very precisely, and are thought to be guided into place at a very early stage of development by chemical signals released by the target structures (Fekete & Campero, 2007). The action potentials that are subsequently generated by the axons are not responsible just for conveying signals from the cochlea to the brain. They also influ-

ence the maturation of both the synaptic endings of the axons, including the large endbulbs of Held, which, as we saw in chapter 5, are important for transmitting temporal information with high fidelity, and the neurons in the cochlear nucleus (Rubel & Fritzsch, 2002). This is initially achieved through auditory nerve action potentials that are generated spontaneously, in the absence of sound, which are critical for the survival of the cochlear nucleus neurons until the stage at which hearing begins.

The earliest sound-evoked responses are immature in many ways. During the course of postnatal development, improvements are seen in the thresholds of auditory neurons, in their capacity to follow rapidly changing stimuli, and in phase locking, while maximum firing rates increase and response latencies decrease. Some of these response properties mature before others, and the age at which they do so varies at different levels of the auditory pathway (Hartley & King, 2010). Because it is the last structure to mature, a number of studies have focused on the development of the auditory cortex. Changes occur in the frequency selectivity of cortical neurons during infancy, a process that is greatly influenced by the acoustic environment. For example, Zhang, Bao, and Merzenich (2001) showed that exposing young rats to repeated tones of one frequency leads to a distortion of the tonotopic map, with a greater proportion of the auditory cortex now devoted to that frequency than to other values. This does not necessarily mean that the animals now hear better at these frequencies though; they actually end up being less able to discriminate sound frequencies within the enlarged representation, but better at doing so for those frequencies where the tonotopic map is compressed (Han et al., 2007). This capacity for cortical reorganization is restricted to a sensitive period of development, and different sensitive periods have been identified for neuronal sensitivity to different sound features, which coincide with the ages at which those response properties mature (Insanally et al., 2009). Linking studies such as these, in which animals are raised in highly artificial and structured environments, to the development of auditory perception in children is obviously not straightforward. It is clear, however, that the coding of different sounds by cortical neurons is very dependent on experience during infancy, and this is highly likely to influence the emergence of perceptual skills.

While the aforementioned studies emphasize the developmental plasticity of the cortex, subcortical circuits can also undergo substantial refinements under the influence of cochlear activity. These changes can have a considerable impact on the coding properties—particularly those relating to sound source localization—of auditory neurons. Neural sensitivity to ILDs and ITDs has been observed at the youngest ages examined in the lateral superior olive (LSO) (Sanes & Rubel, 1988) and medial superior olive (MSO) (Seidl & Grothe, 2005), respectively. The inhibitory projection from the medial nucleus of the trapezoid body to the LSO, which gives rise to neural sensitivity to ILDs (see chapter 5), undergoes an activity-dependent reorganization during the normal course of development (Kandler, 2004). Many of the initial connections die off and those that remain, rather bizarrely, switch from being excitatory to inhibitory before

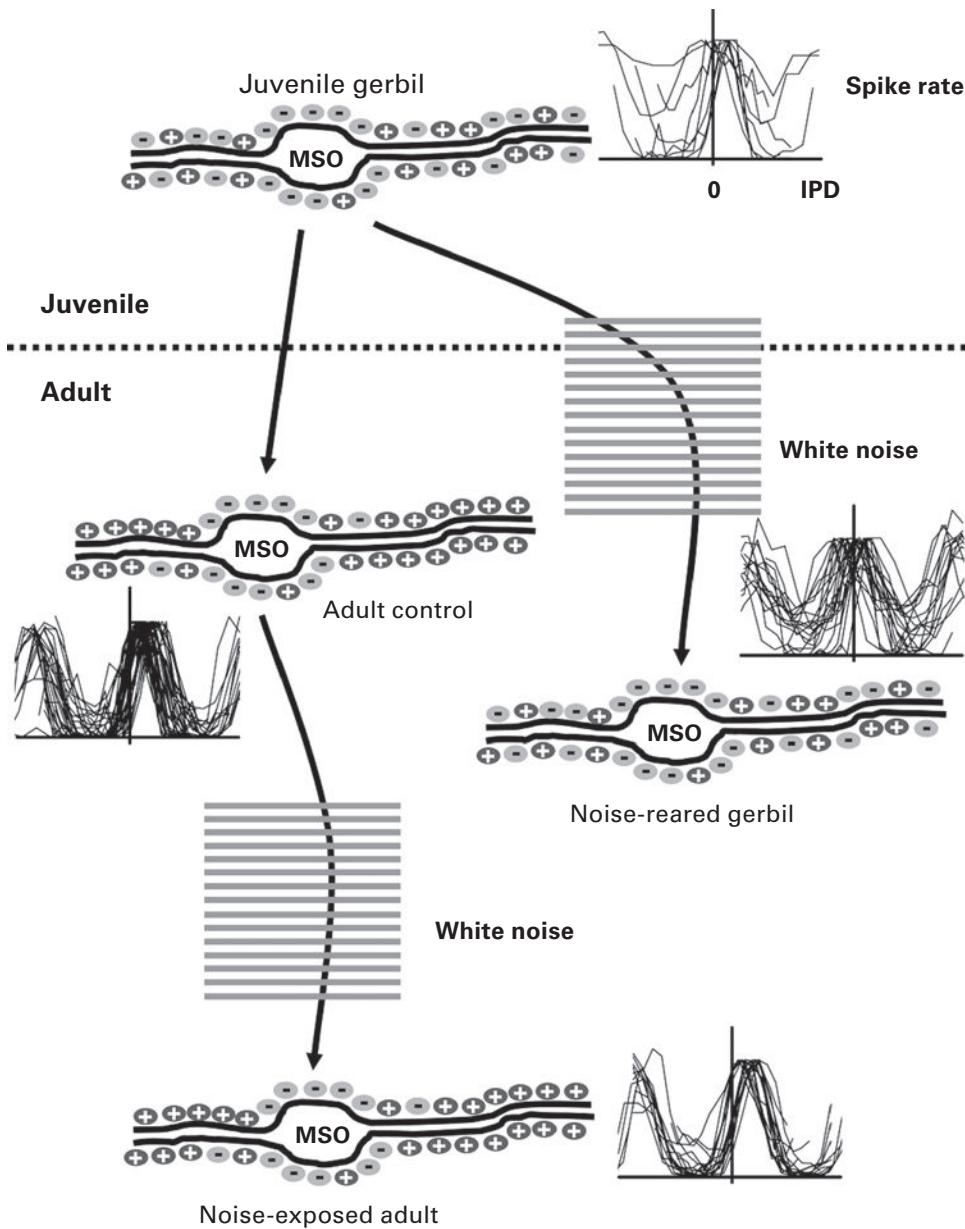


Figure 7.6

Maturation of brainstem circuits for processing interaural time differences. In juvenile gerbils, at around the time of hearing onset, excitatory (indicated by the pluses) and inhibitory inputs (the minuses) are distributed on the dendrites and somata of neurons in the medial superior olive

undergoing further structural remodeling. In chapter 5, we saw that precisely timed inhibitory inputs to the gerbil MSO neurons can adjust their ITD sensitivity, so that the steepest—and therefore most informative—regions of the tuning functions lie across the range of values that can occur naturally given the size of the head. Benedikt Grothe and colleagues (Kapfer et al., 2002; Seidl and Grothe, 2005) showed that in very young gerbils these glycinergic synapses are initially distributed uniformly along each of the two dendrites of the MSO neurons. A little later in development, they disappear, leaving inhibitory inputs only on or close to the soma of the neurons, which is the pattern seen in adult gerbils (figure 7.6). This anatomical rearrangement alters the ITD sensitivity of the neurons, but occurs only if the animals receive appropriate auditory experience. If they are denied access to binaural localization cues, the infant distribution persists and the ITD functions fail to mature properly.

Changes in binaural cue sensitivity would be expected to shape the development of the spatial receptive fields of auditory neurons and the localization behaviors to which they contribute. Recordings from the superior colliculus (Campbell et al., 2008) and auditory cortex (Mrsic-Flogel, Schnupp, & King, 2003) have shown that the spatial tuning of the neurons is indeed much broader in young ferrets than it is in adult animals. But it turns out that this is due primarily to the changes in the localization cue values that take place as the head and ears grow. Thus, presenting infant animals with stimuli through “virtual adult ears” led to an immediate sharpening in the spatial receptive fields. This demonstrates that both peripheral and central auditory factors have to be taken into account when assessing how adult processing abilities are reached.

Nevertheless, it is essential that the neural circuits involved in sound localization are shaped by experience. As we have seen, the values of the auditory localization cues depend on the size and shape of the head and external ears, and consequently will vary from one individual to another. Each of us therefore has to learn to localize with our own ears. That this is indeed the case has been illustrated by getting listeners to localize sounds through someone else’s ears. Once again, this can be achieved using virtual acoustic space stimuli. They fare much better when the stimuli are generated from acoustical measurements made from their own ears—the ones they have grown up with (Wenzel et al., 1993).

(MSO). At this age, neurons prefer interaural phase differences (IPD) around 0. By contrast, in adult gerbils, glycinergic inhibition is restricted to the cell soma and is absent from the dendrites and IPD response curves are shifted away from 0, so that the maximal slope lies within the physiological range. This developmental refinement depends on acoustic experience, as demonstrated by the effects of raising gerbils in omnidirectional white noise to eliminate spatial cues, which preserves the juvenile state. Exposing adults to noise has no effect on either the distribution of glycinergic synapses on the MSO neurons or their IPD functions.

From Seidl and Grothe (2005) with permission from the American Physiological Society.

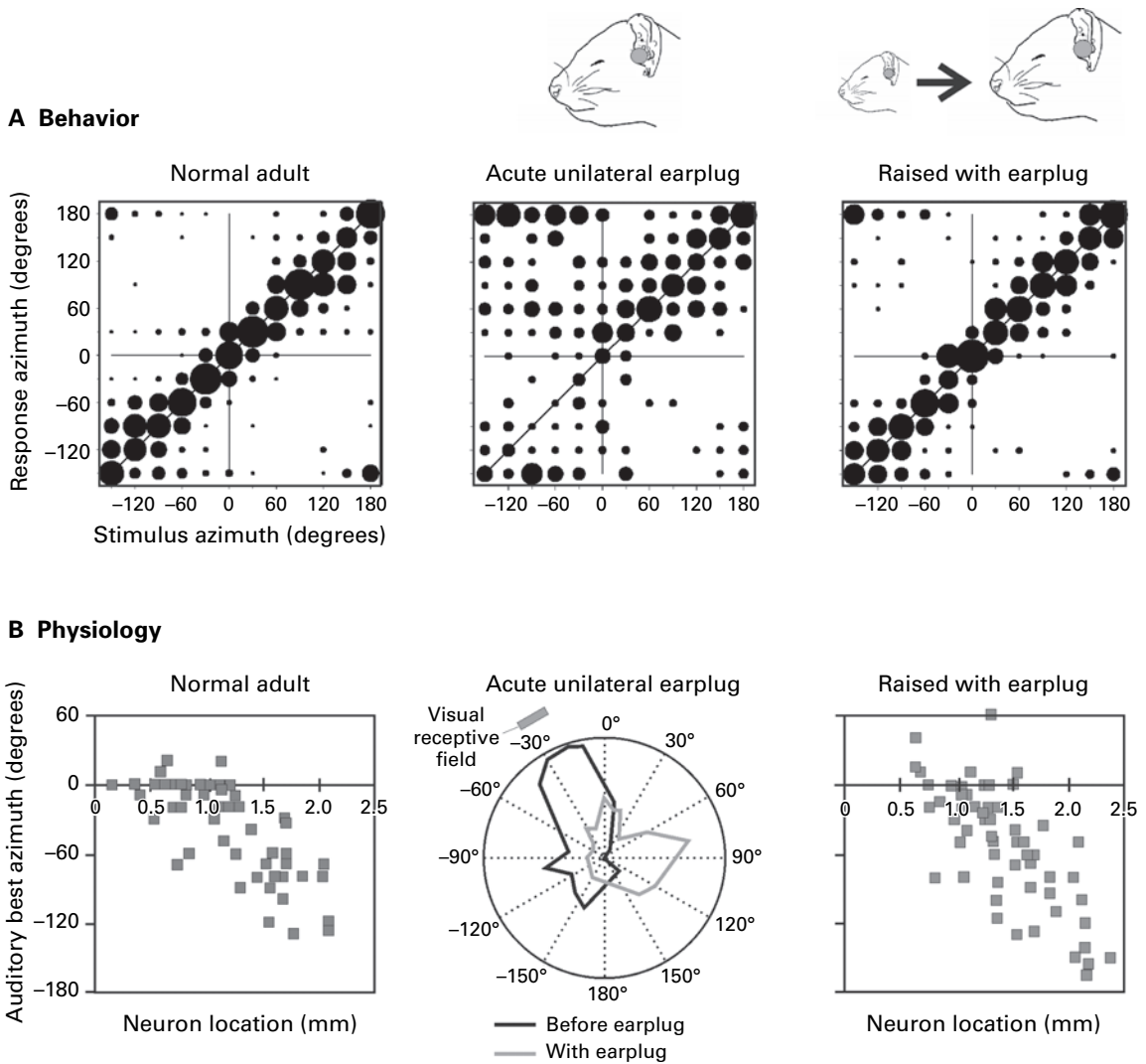


Figure 7.7

Auditory experience shapes the maturation of sound localization behavior and the map of auditory space in the superior colliculus. (A) Stimulus-response plots showing the combined data of three normally reared ferrets (normal adults), another three animals just after inserting an earplug into the left ear (adult unilateral earplug), and three ferrets that had been raised and tested with the left ear occluded with a plug that produced 30- to 40-dB attenuation (raised with earplug). These plots illustrate the distribution of approach-to-target responses (ordinate) as a function of stimulus location (abscissa). The stimuli were bursts of broadband noise. The size of the dots indicates, for a given speaker angle, the proportion of responses made to different response

Plasticity of auditory spatial processing has been demonstrated by manipulating the sensory cues available. For example, inducing a reversible conductive hearing loss by plugging one ear will alter the auditory cue values corresponding to different directions in space. Consequently, both sound localization accuracy and the spatial tuning of auditory neurons will be disrupted. However, if barn owls (Knudsen, Esterly, & Knudsen, 1984) or ferrets (King, Parsons, & Moore, 2000) are raised with a plug inserted in one ear, they learn to localize sounds accurately (figure 7.7A). Corresponding changes are seen in the optic tectum (Knudsen, 1985) and superior colliculus (King et al., 2000), where, despite the abnormal cues, a map of auditory space emerges in register with the visual map (figure 7.7B).

At the end of chapter 5, we discussed the influence that vision can have over judgments of sound source location in humans. A similar effect is also seen during development if visual and auditory cues provide spatially conflicting information. This has been demonstrated most clearly by providing barn owls with spectacles containing prisms that shift the visual world representation relative to the head. A compensatory shift in the accuracy of sound-evoked orienting responses and in the auditory spatial receptive fields of neurons in the optic tectum occurs in response to the altered visual inputs, which is brought about by a rewiring of connections in the midbrain (figure 7.8; Knudsen, 1999). A video clip of barn owl localization behavior during prism learning is available on the book's Web site. This experiment was possible because barn owls have a very limited capacity to move their eyes. In mammals, compensatory eye movements would likely confound the results of using prisms. Nevertheless, other approaches suggest that vision also plays a guiding role in aligning the different sensory representations in the mammalian superior colliculus (King et al., 1988). Studies in barn owls have shown that experience-driven plasticity is most pronounced during development, although the sensitive period for visual refinement of both the auditory space map and auditory localization behavior can be extended under certain conditions (Brainard & Knudsen, 1998).

Finally, we need to consider how complex vocalizations are learned. This has so far been quite difficult to investigate in nonhuman species, but studies of birdsong learning have provided some intriguing insights into the neural processing of complex

locations. Occluding one ear disrupts sound localization accuracy, but adaptive changes take place during development that enable the juvenile plugged ferrets to localize sound almost as accurately as the controls. (B) The map of auditory space in the ferret SC, illustrated by plotting the best azimuth of neurons versus their location within the nucleus. Occluding one ear disrupts this spatial tuning (in the example shown, by shifting the azimuth response profile to a different region of space), but, as with the behavioral data, near-normal spatial tuning is present in ferrets that were raised with one ear occluded. This indicates that adaptive plasticity is also seen in the neural responses.

Based on King, Parsons, and Moore (2000).

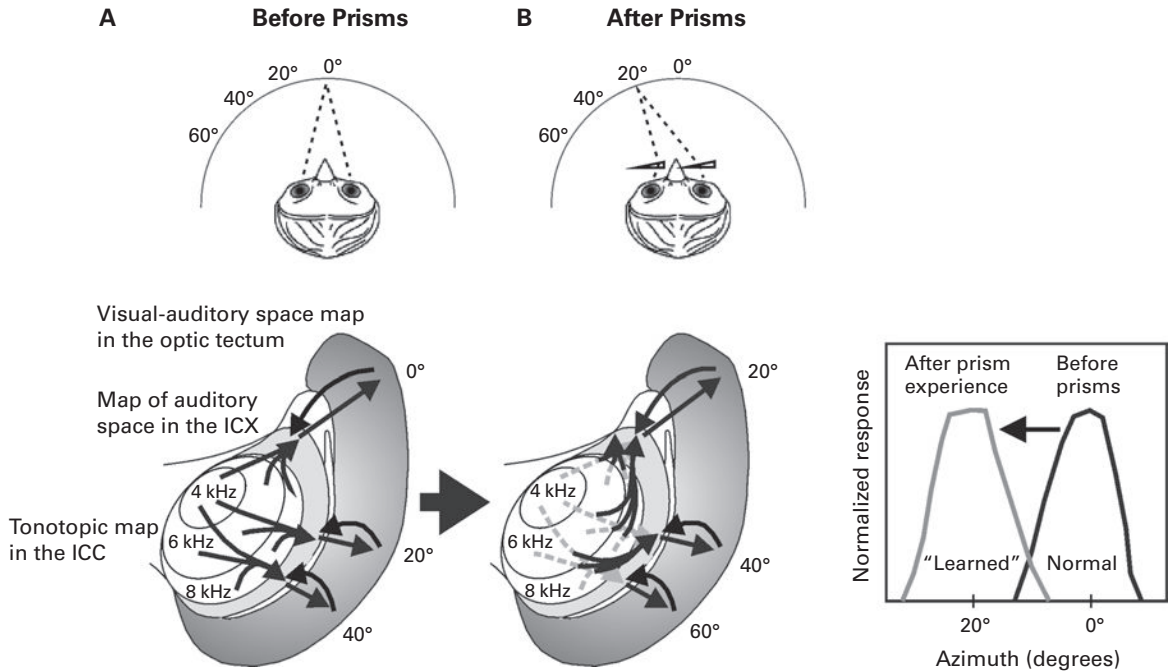


Figure 7.8

Visual experience shapes the map of auditory space in the midbrain of the barn owl. (A) The owl's inferior colliculus (ICX) contains a map of auditory space, which is derived from topographic projections that combine spatial information across different frequency channels in the central nucleus of the inferior colliculus (ICC). The ICX map of auditory space is then conveyed to the optic tectum, where it is superimposed on a map of visual space. (B) The auditory space maps in both the optic tectum and the ICX can be refined by visual experience during development. This has been demonstrated by chronically shifting the visual field in young owls by mounting prisms in front of their eyes. The same visual stimulus now activates a different set of neurons in the optic tectum. The auditory space maps in the ICX and tectum gradually shift by an equivalent amount in prism-reared owls, thereby reestablishing the alignment with the optically displaced visual map in the tectum. This involves growth of novel projections from the ICC to the ICX (black arrows); the original connections remain in place but are suppressed (dashed gray arrows). (C) Illustration for one neuron of the shift in auditory spatial tuning produced by prism rearing.

signals that evolve over time, and there is every reason to suppose that similar principles will apply to the development of sensitivity to species-specific vocalizations in mammals. In section 7.3, we described how vocal learning in songbirds is guided by performance feedback during a sensitive period of development. Several forebrain areas are thought to be involved in the recognition of conspecific song. In juvenile zebra finches, neurons in field L, the avian equivalent of the primary auditory cortex, are less acoustically responsive and less selective for natural calls over statistically equivalent synthetic sounds than they are in adult birds (Amin, Doupe, & Theunissen, 2007). Neuronal selectivity for conspecific songs emerges at the same age at which the birds express a behavioral preference for individual songs (Clayton, 1988), implicating the development of these response properties in the maturation of song recognition. The auditory forebrain areas project to a cluster of structures, collectively known as the “song system,” which have been shown to be involved in vocal learning. Recording studies have shown that certain neurons of the song system prefer the bird’s own song or the tutor’s song over other complex sounds, including songs from other species (Margoliash, 1983), and that these preferences emerge following exposure to the animal’s own vocal attempts (Solis & Doupe, 1999).

7.5 Plasticity in the Adult Brain

We have seen that many different aspects of auditory processing and perception are shaped by experience during sensitive periods of development. While the length of those periods can vary with sound property, brain level, and species, and may be extended by hormonal or other factors, it is generally accepted that the potential for plasticity declines with age. That would seem to make sense, since more stability may be desirable and even necessary in the adult brain to achieve the efficiency and reliability of a mature nervous system. But it turns out that the fully mature auditory system shows considerable adaptive plasticity that can be demonstrated over multiple timescales.

Numerous examples have been described where the history of stimulation can determine the responsiveness or even the tuning properties of auditory neurons. For example, if the same stimulus, say a tone of a particular frequency, is presented repeatedly, neurons normally show a decrease in response strength. However, the response can be restored if a different frequency is presented occasionally (Ulanovsky, Las, & Nelken, 2003). As we discussed in chapter 6, this phenomenon is known as stimulus-specific adaptation, and facilitates the detection of rare events and sudden changes in the acoustic environment. On the other hand, the sensitivity of auditory neurons can be adjusted so that the most frequently occurring stimuli come to be represented more precisely. A nice example of this “adaptive coding” was described by Dean and colleagues (2005), who showed that the relationship between the firing rate of inferior colliculus neurons

and sound level can change to improve the coding of those levels that occur with the highest probability (figure 7.9). One important consequence of this is that a greater range of sound levels can be encoded, even though individual neurons have a relatively limited dynamic range.

These changes occur in passive hearing conditions and are therefore caused solely by adjustments in the statistics of the stimulus input. If a particular tone frequency is given behavioral significance by following it with an aversive stimulus, such as a mild electric shock, the responses of cortical neurons to that frequency can be enhanced (Weinberger, 2004). Responses to identical stimuli can even change over the course of a few minutes in different ways in a task-dependent fashion (Fritz, Elhilali, &

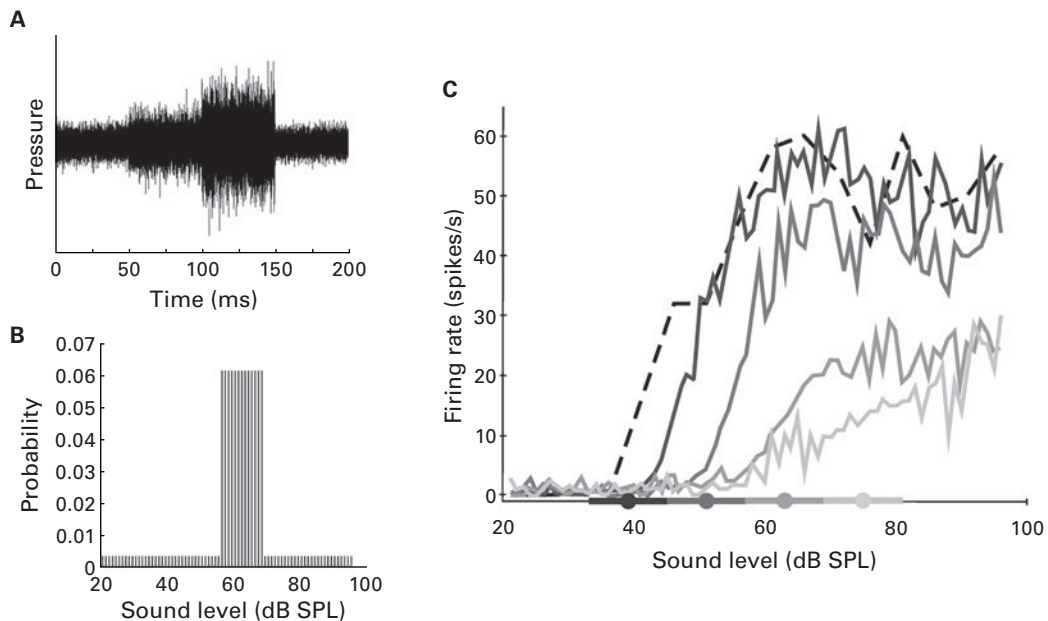


Figure 7.9

Adaptive coding of sound level by neurons in the inferior colliculus. (A) Changes in the sensitivity of these neurons can be induced by presenting broadband stimuli for several seconds in which the sound level varies every 50ms, but with a high-probability region centered on different values. (B) Distribution of sound levels in a stimulus with a high-probability region centered on 63 dB SPL. (C) Rate-level functions for one neuron for four different sound level distributions, as indicated by the filled circles and thick lines on the x axis. Note that the functions shift as the range of levels over which the high-probability region is presented changes, so that maximum sensitivity is maintained over the range of sound levels that are most commonly encountered. Adapted from Dean, Harper, and McAlpine (2005) with permission from Macmillan Publishers Ltd.

Shamma, 2005), implying that this plasticity may reflect differences in the meaning of the sound according to the context in which it is presented.

Over a longer time course, the tonotopic organization of the primary auditory cortex of adult animals can change following peripheral injury. If the hair cells in a particular region of the cochlea are damaged as a result of exposure to a high-intensity sound or some other form of acoustic trauma, the area of the auditory cortex in which the damaged part of the cochlea would normally be represented becomes occupied by an expanded representation of neighboring sound frequencies (Robertson & Irvine, 1989). A similar reorganization of the cortex has been found to accompany improvements in behavioral performance that occur as a result of “perceptual learning.” Recanzone, Schreiner, and Merzenich (1993) trained monkeys on a frequency discrimination task and reported that the area of cortex representing the tones used for training increased in parallel with improvements in discrimination performance. Since then, a number of other changes in cortical response properties have been reported as animals learn to respond to particular sounds. This does not necessarily involve a change in the firing rates or tuning properties of the neurons, as temporal firing patterns can be altered as well (Bao et al., 2004; Schnupp et al., 2006).

There is a key difference between the cortical changes observed following training in adulthood and those resulting from passive exposure to particular sounds during sensitive periods of development, in that the sounds used for training need to be behaviorally relevant to the animals. This was nicely demonstrated by Polley, Steinberg, and Merzenich (2006), who trained rats with the same set of sounds on either a frequency or a level recognition task. An enlarged representation of the target frequencies was found in the cortex of animals that learned the frequency recognition task, whereas the representation of sound level in these animals was unaltered. By contrast, training to respond to a particular sound level increased the proportion of neurons tuned to that level without affecting their tonotopic organization. These findings suggest that attention or other cognitive factors may dictate how auditory cortical coding changes according to the behavioral significance of the stimuli, which is thought to be signaled by the release in the auditory cortex of “neuromodulators” such as acetylcholine. Indeed, simply coupling the release of acetylcholine with the repeated presentation of a sound stimulus in untrained animals is sufficient to induce a massive reorganization of the adult auditory cortex (Kilgard, 2003).

Training can also dramatically improve the auditory perceptual skills of humans, and the extent to which learning generalizes to other stimuli or tasks can provide useful insights into the underlying neural substrates (Wright & Zhang, 2009). As in the animal studies, perceptual learning in humans can be accompanied by enhanced responses in the auditory cortex (Alain et al., 2007; van Wassenhove & Nagarajan, 2007). It is not, however, necessarily the case that perceptual learning directly reflects changes in brain areas that deal with the representation of the sound attribute in

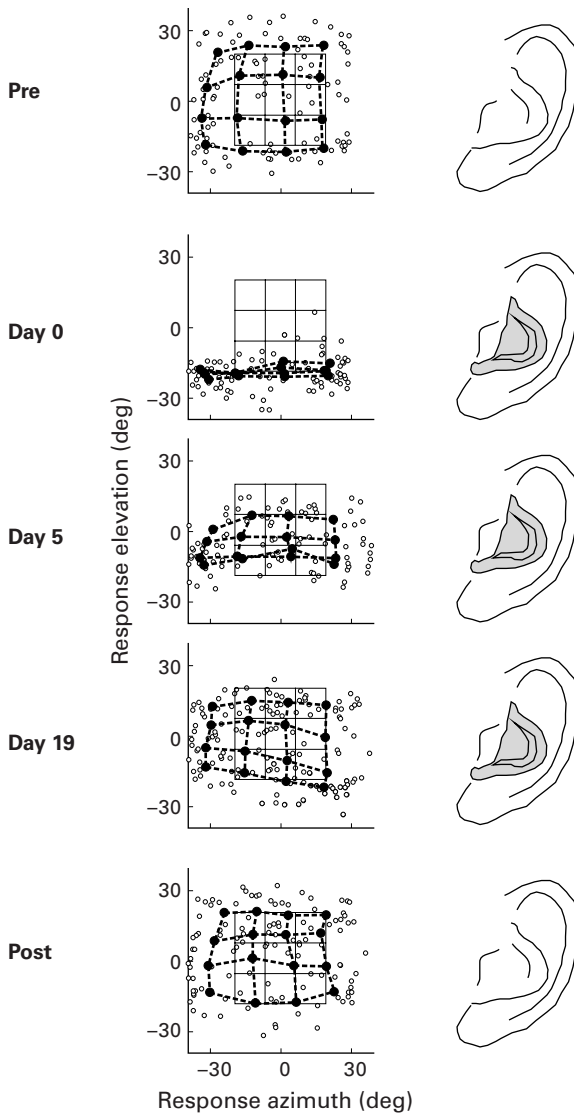


Figure 7.10

Learning to localize sounds with new ears in adult humans. In this study, the accuracy of sound localization was assessed by measuring eye movements made by human listeners toward the location of broadband sound sources. The stimuli were presented at random locations encompassed by the black grid in each of the middle panels. The end points of all the saccadic eye movements made by one subject are indicated by the small circles. The black dots and connecting lines represent the average eye movement vectors for targets located within neighboring sectors of the

question. Thus, a substantial part of the improvement seen in pitch discrimination during perceptual learning tasks is nonspecific—for example, subjects playing a computer game while hearing pure tones (but not explicitly attending to these sounds) improve in pitch discrimination. The same was shown to be true even for subjects who played a computer game without hearing any pure tones (Amitay, Irwin, & Moore, 2006)! Such improvement must be due to general factors governing task performance rather than to specific changes in the properties of neurons in the auditory system.

In addition to improving the performance of subjects with normal hearing, training can promote the capacity of the adapt brain to adjust to altered inputs. This has been most clearly demonstrated in the context of sound localization. In the previous section, we saw that the neural circuits responsible for spatial hearing are shaped by experience during the phase of development when the localization cues are changing in value as a result of head growth. Perhaps surprisingly, the mature brain can also relearn to localize sound in the presence of substantially altered auditory spatial cues. Hofman, Van Riswick, and Van Opstal (1998) showed that adult humans can learn to use altered spectral localization cues. To do this, they inserted a mold into each external ear, effectively changing its shape and therefore the spectral cues corresponding to different sound directions. This led to an immediate disruption in vertical localization, with performance gradually recovering over the next few weeks (figure 7.10).

Because it relies much more on binaural cues, localization in the horizontal plane becomes inaccurate if an earplug is inserted in one ear. Once again, however, the mature auditory system can learn to accommodate the altered cues. This has been shown in both humans (Kumpik, Kacelnik, & King, 2010) and ferrets (Kacelnik et al., 2006), and seems to involve a reweighting away from the abnormal binaural cues so that greater use is made of spectral-shape information. This rapid recovery of sound localization accuracy occurs only if appropriate behavioral training is provided (figure 7.11). It is also critically dependent on the descending pathways from the auditory cortex to the midbrain (Bajo et al., 2010), which can modulate the responses of

stimulus grid. The overlap between the response and target matrices under normal listening conditions (pre) shows that saccadic eye movements are quite accurate in azimuth and elevation. Molds were then fitted to each external ear, which altered the spatial pattern of spectral cues. Measurements made immediately following application of the molds (day 0) showed that elevation judgments were severely disrupted, whereas azimuth localization within this limited region of space were unaffected. The molds were left in place for several weeks, and, during this period, localization performance gradually improved before stabilizing at a level close to that observed before the molds were applied. Interestingly, no aftereffect was observed after the molds were removed (post), as the subjects were able to localize sounds as accurately as they did in the precontrol condition. Adapted from Hofman, Van Riswick, and Van Opstal (1998) with permission from Macmillan Publishers Ltd.

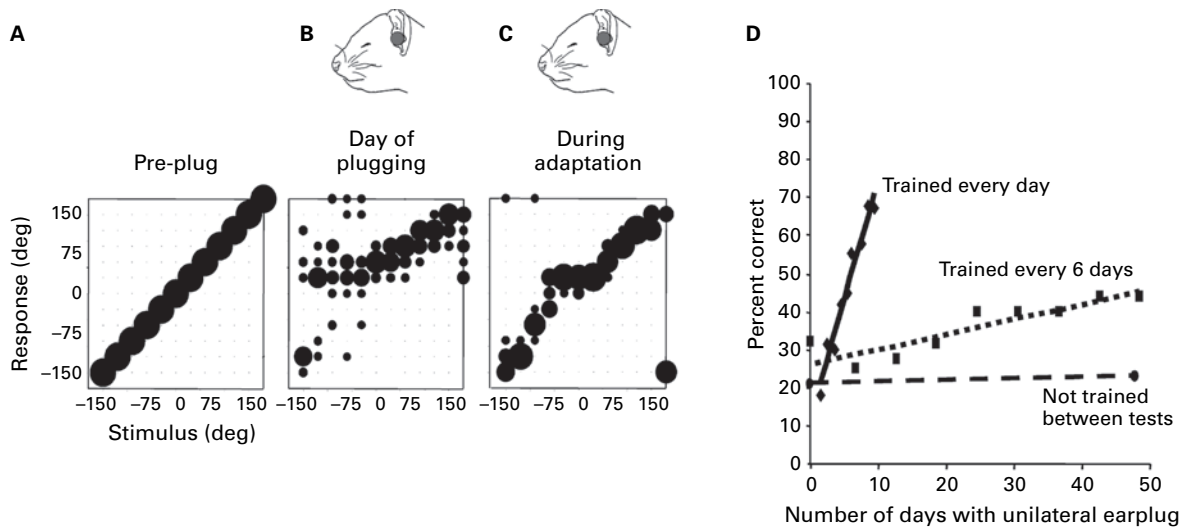


Figure 7.11

Plasticity of spatial hearing in adult ferrets. (A–C) Stimulus-response plots showing the distribution of responses (ordinate) made by a ferret as a function of stimulus location in the horizontal plane (abscissa). The size of the dots indicates, for a given speaker angle, the proportion of responses made to different locations. Correct responses are those that fall on the diagonal, whereas all other responses represent errors of different magnitude. Prior to occlusion of the left ear, the animal achieved 100% correct scores at all stimulus directions (A), but performed poorly, particularly on the side of the earplug, when the left ear was occluded (B). Further testing with the earplug still in place, however, led to a recovery in localization accuracy (C). (D) Mean change in performance (averaged across all speaker locations) over time in three groups of ferrets with unilateral earplugs. No change was found in trained ferrets ($n = 3$) that received an earplug for 7 weeks, but were tested only at the start and end of this period (circles and dashed regression line). These animals therefore received no training between these tests. Two other groups of animals received an equivalent amount of training *while* the left ear was occluded. Although the earplug was in place for less time, a much faster rate of improvement was observed in the animals that received daily training ($n = 3$; diamonds and solid regression line) compared to those that were tested every 6 days ($n = 6$; squares and dotted regression line).

From Kacelnik et al. (2006).

the neurons found there in a variety of ways (Suga & Ma, 2003). This highlights a very important, and often ignored, aspect of auditory processing, namely, that information passes down as well as up the pathway. As a consequence of this, plasticity in subcortical as well as cortical circuits is likely to be involved in the way humans and other species interact with their acoustic environments.

7.6 Summary: The Pros and Cons of Plasticity

We have seen in this chapter that the auditory system possesses a truly remarkable and often underestimated capacity to adapt to the sensory world. This is particularly the case in the developing brain, when newly formed neural circuits are refined by experience during specific and often quite narrow time windows. But the capacity to learn and adapt to the constantly changing demands of the environment is a lifelong process, which requires that processing in certain neural circuits can be modified in response to both short-term and long-term changes in peripheral inputs. The value of this plasticity is clear: Without it, it would not be possible to customize the brain to the acoustical cues that underlie our ability to localize sound or for the processing of native language. But the plasticity of the central auditory system comes at a potential cost, as this means that a loss of hearing, particularly during development, can induce a rewiring of connections and alterations in the activity of neurons, which might give rise to conditions such as tinnitus, in which phantom sounds are experienced in the absence of acoustic stimulation (Eggermont, 2008). At the same time, however, experience-dependent learning provides the auditory system with the capacity to accommodate the changes in input associated with hearing loss and its restoration, a topic that we shall return to in the final chapter.