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Abstract and Keywords

The development of auditory perception is examined in relation to (1) identity and location of objects (auditory scene analysis) and (2) musical structure and meaning. Behavioral and brain research converges to indicate that some capacity to process the frequency, pitch, intensity, timbre, location, and timing of sounds is present very early in development, although there is a protracted experience-driven period of plasticity, with adult levels of maturity typically not reached until well in to childhood. Young infants are also able to process aspects of musical structure. At the same time, enculturation to the specific melodic, harmonic, and rhythmic structure of the musical system of a person's culture depends on the considerable exposure to that musical system experienced by all members of the culture, and intensive musical training affects the speed and degree of that enculturation.

Keywords: auditory perception, music, pitch, rhythm, auditory scene analysis, sound localization, temporal resolution, melody, harmony, meter

Key Concepts:

1. Auditory information informs us about (1) objects and their locations (auditory scene analysis), (2) musical structure and meaning and (3) linguistic structure and meaning.
2. Development of the auditory system is influenced by the particular experiences of each individual.
3. Auditory development for music and language proceeds according to processes of *perceptual narrowing*: Young infants are initially capable of a wide range of discriminations, which subsequently become refined through experience with a particular musical system or language. Specifically, perception improves for discriminations that matter in the particular musical system or language, and become worse for discriminations that do not matter.

4. Although very young infants are already able to process differences in sound frequency, pitch, timbre, intensity, and location, these abilities continue to improve well into the childhood years. Furthermore, EEG measures indicate that mature processing in auditory cortex is not achieved until the late teenage years.
5. Very young infants are sensitive to sensory consonance, octave equivalence, and relative pitch (or transpositional invariance) as well as to different rhythmic (metrical) structures. They also process unequal-interval better than equal-interval musical scales.
6. Through exposure to a particular musical system, infants acquire sensitivity to its scale structure (key membership), harmonic structure, and rhythmic (metrical) structure.
(p. 311) **7**. Formal musical training in infancy and childhood has profound effects on brain development that go beyond those effects that are seen with mere exposure to music.

Introduction

The auditory system is fundamental to human communication through speech and music, and good auditory processing is critical for many aspects of human development. The human auditory system extracts three basic types of information from sound: (1) identity and location of objects, (2) musical structure and meaning, and (3) linguistic structure and meaning. Although object perception is based on contributions from all of the senses, the vast majority of research on this topic focuses on vision. In this chapter we examine the important contribution of the auditory sense to object perception and how it develops. In contrast to object processing, the communicative functions of speech and music are based primarily in the auditory modality, although other senses contribute as well. The development of speech perception is reviewed by Werker and Gervain (in this handbook), so here we focus on the development of basic auditory processes that enable object perception and on the development of musical communication.

It is not possible in one chapter to detail all aspects of auditory development. We will give an overview of what is known about the developmental time course for processing various basic sound features, sounding objects, and musical structure in the context of general developmental principles. Development involves neuroplasticity, or structural and functional changes in the brain that enable the emergence of new processing capabilities and behaviors (see the chapter by Maurer & Lewis in this handbook). Many factors contribute to these changes. Neurons proliferate and migrate to their end locations under genetic guidance (see Markant & Thomas in this handbook). Genes also guide waves of myelination, synaptic proliferation, and pruning. The presence and amount of different neurotransmitters vary across age (Murphy, Beston, Boley, & Jones, 2005). Through these changes, neural processing becomes faster and more efficient, and internal noise is decreased. While genetic programs may constrain the general processes and times over which these changes occur, the details are largely determined by experiential factors. Synaptic connections receiving concurrent input are strengthened, whereas nonuseful connections are eliminated. Thus, the specific auditory input an infant receives has a large influence on how the neurons connect and function, which in the end determines what language the child understands and the musical features to which he or she is sensitive.

One basic principle of auditory development is that of perceptual narrowing. The neuronal connections in auditory cortex are initially somewhat random, making the infant inefficient at sound processing. With experience, the infant develops representations for important sounds in the environment and develops more efficient neural networks for processing and distinguishing details of these sounds, and in the process the brain becomes specialized for these sounds. Thus, with increasing age, learning a new language or a new musical system can become more difficult. However, substantial plasticity is maintained at certain levels of processing, such that specific training in adults can lead to changes seen at the cortical level in terms of altered responses as assessed by functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and magnetoencephalography (MEG). Nonetheless, experience appears to have a greater influence on plasticity at certain developmental stages, termed sensitive periods, although for most basic sound features, we know rather little about sensitive periods.

The cochlea in the inner ear is structurally and functionally adultlike by birth and the auditory system is functioning from around the sixth prenatal month (Werner, 2007). Yet, as outlined below, the auditory system does not reach maturity until well into the teenage years. Thus, from birth, the major changes in auditory abilities stem from changes in neural processing. Furthermore, development of the auditory system cannot be completely understood in isolation. Auditory input converges with other sensory input (e.g., somatosensory) as early as cochlear nucleus (e.g., Shore, Koehler, Oldakowski, Hughes, & Syed, 2008), so the maturation of auditory processing is dependent on the maturation of other sensory systems as well. Furthermore, the auditory system is not simply a feed-forward system where information is processed linearly from one stage to the next. Rather, there are at least as many efferent as afferent connections. Indeed, characteristics of the basilar membrane itself can be changed through feedback from the brainstem (e.g., see Musiek, Weihing, & Oxholm, 2007). In addition, processes such as identifying objects by the sounds they make and recognizing musical melodies involve memory and attention, so the auditory system cannot function without reciprocal connections between auditory cortex and many other cortical (p. 312) areas. Consequently, trajectories of improvement in auditory abilities cannot be understood without reference to these interactions.

Finally, as with all aspects of developmental research, studying auditory development presents a number of methodological challenges. Challenges for behavioral research include the fact that preverbal infants cannot be given explicit instructions, that children of different ages may interpret verbal instructions differently, that the behavioral repertoire of responses that can be measured changes with age, and that improvements in other capacities such as attention and memory will influence performance on various tasks. Physiological measures also have challenges. The no-movement requirements of fMRI and MEG make them difficult to use with young children, and the morphology (what components are present) of EEG recordings changes with age, making comparisons across age difficult. Nonetheless, we have learned a tremendous amount about auditory development over the past few decades. In the following sections, some important findings from this research effort are summarized. Where possible, methodological limitations are discussed, the mechanisms of change are considered, and the extent to which specific experience affects outcome is evaluated.

Development of Basic Auditory Perception

Isolated sounds are generally described as having four main perceptual features: *loudness*, which is related to sound intensity; *pitch*, which is related to sound frequency; *duration*, which is related to sound length; and *timbre*, which describes sound quality and is related to several sound features, most notably the speed of sound onset and the distribution of energy across frequency. Sounds are also perceived as coming from particular *locations* in space. In addition to these basic sound features, important information is contained in patterns of sound, both in terms of sound sequences, such as melodies or sentences, and simultaneous sounds, as in a musical chord. One of the main tasks of the auditory system is to identify over time *what* objects are present and *where* they are located. Indeed, in the real world, sounds rarely occur in isolation, so the method of identifying the features of a sound (loudness, pitch, duration, timbre, location) necessarily involves a process whereby the auditory system must separate incoming complex sound signals into parts that each represent a sounding object in the environment. The process is called *auditory scene analysis*. Research on auditory development has tended to focus on the processing of individual features. In the following sections, we summarize the main findings of this research and then consider the development of auditory scene analysis.

A number of methods have been used to study auditory abilities in infants and young children who cannot understand verbal instructions (see Saffran, Werker, & Werner, 2006; Werner, 2007). Most methods fall into one of two broad categories, behavioral and EEG. In behavioral methods, a motor response of some kind is measured from infants. For example, in the conditioned head turn method, one auditory stimulus or category of stimulus is presented continuously from a speaker to the infant's side, and the infant is rewarded with dancing toys for turning his or her head to occasional changes in the stimulus or stimulus category. Infants can also be familiarized with a particular auditory stimulus and then the precision of their encoding of that stimulus tested in a head turn preference task. In this task, trials of the familiarized auditory stimulus and the stimulus to be discriminated are presented. In each case, the stimulus continues to sound while the infant looks at a light and/or toy and is turned off when the infant looks away. Longer listening times to one or other of the stimuli indicate discrimination. Infants younger than about 5 months of age do not have good motor control of head movements, but head turns can be replaced with eye movement responses. With young infants, nonnutritive sucking can be used: increases or decreases in sucking rate can be paired with one of two auditory stimuli. Finally, observer-based procedures are sometimes used, in which a trained experimenter judges, on the basis of infant movement responses, whether or not a sound was presented on a particular trial.

In EEG methods, electrical potentials generated by the depolarization of neurons in the brain are measured across time at the surface of the head as sounds are presented (e.g., Luck, 2005). The EEG can be analyzed in the frequency domain by examining, for example, the relative power in different frequency bands such as delta (0–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (>30 Hz) bands. Alternatively, event-related potentials (ERPs), representing the brain's response to a presented sound event, can be derived from EEG recordings. To create an electrical field large enough to measure, a group of neurons whose axons point in the same direction must fire synchronously. Even so, on individual trials, there is sufficient "noise" from brain activity unrelated to the processing of the sound that the ERP is difficult to see. Therefore, (p. 313) typically many trials are presented and the EEG measured on each trial is averaged over these trials. Because brain activity unrelated to the processing of the sound is not time-locked to the onset of the sound, it will tend to average to zero as the number of trials in the average is increased, and the resulting ERP will largely show the brain's processing of the sound. Components of the ERP track the stages of processing of a sound through the auditory system, with early components representing subcortical nuclei, later components representing primary and secondary auditory cortex, and still later components representing attentional and decision-making stages. One very useful component for infant research is the mismatch negativity (MMN), which is seen in response to occasional changes in an ongoing sequence of sounds (e.g., Näätänen, Paavilainen, Rinne, & Alho, 2007; Picton, Alain, Otten, Ritter, & Achim, 2000; Trainor & Zatorre, 2009). For example, if a tone of one pitch is repeated over and over, occasional replacement of that tone with a tone of a different pitch will generate an MMN response if the two pitches are discriminable.

Each method used with young children has strengths and weaknesses, so the gold standard should be to use a variety of methods. When they converge on a common answer to a question, we can be most confident that the results accurately reflect infants' abilities.

Thresholds for Hearing and Intensity Discrimination

Perhaps the most basic question in auditory development is that of absolute thresholds: how intense a sound needs to be in order to be detected. The general answer to this question is that fully adult levels are probably not achieved until about 10 years of age, although there are large improvements in absolute thresholds during infancy. However, the question is complicated by both methodological and interpretational issues, and thresholds depend on the frequency of the sound. The fetus will move to externally presented sound by 28 weeks gestation, but the accurate measurement of absolute thresholds is extremely difficult *in utero* (see Lecanuet, 1996). After birth, observing spontaneous responses to sound presentations, Weir (1976, 1979) concluded that in comparison to adults, neonatal thresholds are up to 70 dB higher than those of adults between 250 and 2,000 Hz. Studies using an observer-based procedure, in which a trained experimenter determines on the basis of observing an infant whether or not a sound was presented on a given trial, have found infant/adult differences at 1 to 2 months of about 45 dB at 500 Hz and about 35 dB at 4,000 Hz (Trehub, Schneider, Thorpe, & Judge, 1991; Werner & Gillenwater, 1990). It is not clear whether this represents a large improvement over the first couple of months in sensitivity or whether it is a result of different methods of measurement. By 3 months, infant thresholds improve further, particularly at higher frequencies (by 20 dB at 4,000 Hz and 10 dB at 500 Hz; Olsho, Koch, Carter, Halpin, & Spetner, 1988). The trend for earlier maturation of absolute thresholds for high than for low frequencies continues in childhood, with adult levels achieved by age 5 at 4,000 and 10,000 Hz, but not until age 10 at 1,000 Hz (Trehub, Schneider, Morrengiello, & Thorpe, 1988).

Of more importance for determining *what* an object is, *where* it is located, and whether it is getting closer to you is the ability to *discriminate* sounds of different intensity. Although there are few studies, 7- to 9-month-olds appear to be considerably worse than adults, with thresholds of 6 dB for detecting intensity differences between 1,000-Hz tones compared to adult thresholds of 2 dB (Sinnott & Aslin, 1985), and thresholds of 9 dB for detecting differences in broadband noises compared to adult thresholds of 3 dB (Werner, 2007). By 4 years of age, intensity discrimination appears to be quite good, although improvements are seen until 10 to 12 years of age for both discrimination of sounds with different intensities (Maxon & Hochberg, 1982) and masked thresholds or the ability to detect a change in the intensity of a continuous sound (Schneider, Trehub, Morrongiello, & Thorpe, 1989).

There are likely several factors that contribute to the developmental trajectories for absolute and difference thresholds (Saffran et al., 2006; Werner, 2007). While the inner ear, containing the cochlea where vibrations are translated into neural firings, is essentially adultlike at birth (see Werner, 2007, for a review), the smaller ear canal of the infant is better at conducting high frequencies compared to the adult ear. It has also been documented that there are large improvements (about 20 dB) in the efficiency with which the middle ear conducts sound into the inner ear between birth and adulthood (Keefe, Bulen, Arehart, & Burns, 1993; Keefe & Levi, 1996; Okabe, Tanaka, Hamada, Miura, & Funai, 1988). This improvement in efficiency is largest during infancy and largest for high frequencies. It likely makes a large contribution to absolute threshold improvements with age, and to the earlier maturation of absolute thresholds for high (p. 314) than for low frequencies. Indeed, this has been confirmed with studies measuring auditory brainstem responses (ABR) using electrophysiological recordings (Sininger & Abdala, 1996; Sininger, Abdala, & Cone-Wesson, 1997) and studies using otoacoustic emissions (OAE) that measure inner ear function (Werner & Holmer, 2002).

Middle ear efficiency cannot account for age-related changes in intensity discrimination because the two sounds of different intensity that are to be compared will both go through the child's middle ear and would be affected in the same way. Two types of immaturity likely contribute to poor intensity discrimination: inefficient neural processing in the auditory pathway and immature attentional processing. Myelination of the subcortical auditory pathways is largely complete by 6 to 12 months (Moore, Perazzo, & Braun, 1995), and the increase in processing speed enabled by this process is reflected in decreased latency of the ABR and middle latency responses of the auditory evoked potential (see Moore & Linthicum, 2007). This development likely accounts in part for the rapid development of intensity discrimination in infancy. Indeed, behavioral thresholds in infants for intensity are correlated with ABR latencies (Werner, Folsom, & Mancl, 1993a,b).

In general, thresholds obtained through behavioral methods are influenced by the infant's or child's ability to attend to the stimulus. Modeling studies have shown, however, that such inattention cannot account for most of the difference between children and adults (Schneider & Trehub, 1992; Viemeister & Schlauch, 1992; Werner, 1992; Wightman &

Allen, 1992). However, infants are immature in another respect. Adults have lower thresholds if they know the frequency of the sound to listen for, whereas infants appear to be unable to engage in selective listening (Bargones & Werner, 1994). This difference likely reflects immaturity in auditory cortex and beyond, immaturities that remain until at least 12 years of age (Moore & Linthicum, 2007; Ponton, Eggermont, Kwong, & Don, 2000; Shahin, Roberts, & Trainor, 2004).

In sum, thresholds for hearing and intensity difference thresholds are substantially elevated in early infancy. There is rapid improvement over the first year after birth. Adult levels are reached earlier for sounds of high than of low frequency, with overall adult levels not obtained until about 10 years of age. This developmental profile is consistent with maturational timetables for conductive efficiency in the middle ear and for the development of subcortical and cortical pathways. To date there have been no studies of the influence of experience on intensity perception, so the question of the role of the environment remains unknown.

Frequency Resolution and Frequency Discrimination

The vast majority of sounds in the natural world have complex vibration patterns made up of many frequencies. The basilar membrane in the inner ear acts as a sort of Fourier analyzer, separating the incoming signal into its frequency components. This is accomplished through variation in the stiffness of the membrane along its length, such that low frequencies move the membrane maximally at one end and high frequencies at the other. Inner hair cells along the length of the basilar membrane move when the membrane moves. This mechanical motion is transduced into electrical signals in auditory nerve fibers. Thus the inner ear contains a tonotopic frequency map. This frequency organization is referred to as the “place code” and is maintained in the auditory nerve, through subcortical nuclei, and into primary auditory cortex. There is also a “temporal code” for frequency. Because auditory nerve fibers fire when the basilar membrane is maximally displaced, the rate of firing over a population of adjacent nerve fibers is inversely related to the frequency of the incoming sound signal.

“Frequency resolution” refers to the ability of the place code to discriminate between different frequencies. This is generally measured in masking studies. The ability of a person to detect a target tone of a particular frequency (or a narrow band of noise centered at a particular frequency) is tested in the presence of a masking tone (or noise). The general finding in adults is that detection of the target tone is affected by the presence of the masker only when it falls within a critical band (about a quarter of an octave for most of the frequency range) of the target tone.

Behavioral studies indicate that frequency resolution (i.e., the size of the critical bandwidth) is mature for low frequencies at birth and for high frequencies by 6 months of age. Studies of cochlear function suggest that the cochlea is mature at birth, and ABR studies suggest that the early limitations in high-frequency resolution before 6 months are due to immature processing of high frequencies in the brainstem (Abdala & Folsom, 1995a,b; Folsom & Wynne, 1987), as discussed earlier in the section "Thresholds for Hearing and Intensity Discrimination."

(p. 315) Although frequency resolution appears mature at 6 months, the ability to discriminate two frequencies continues to improve until about 10 years of age (Jensen & Neff, 1993; Maxon & Hochberg, 1982; Thompson, Cranford, & Hoyer, 1999). This is likely because the place code is too coarse to account for adults' ability to detect fine differences in pitch, which rely on the temporal mechanism. Discrimination for high frequencies matures earlier than for low frequencies, perhaps reflecting the fact that low-frequency discrimination depends to a greater extent on the temporal mechanism. The temporal mechanism might be expected to mature later as it depends on precise temporal firing patterns. Despite the long developmental trajectory, it should be noted that thresholds in infancy are still sufficiently good to support musical perception. For example, at 1,000 Hz, 6-month-olds can detect a 1.5% to 3.0% change in frequency under conditions where adults detect a 1.0% change.

The protracted development of frequency discrimination probably reflects the protracted development of auditory cortex. Studies of human auditory cortex from autopsy cases indicate that in early infancy, subcortical input appears to go only to layer I and does not contain frequency-specific information (Moore & Linthicum, 2007). Neurofilament is not yet expressed in the other layers, indicating that mature, fast connections between neurons are not yet present. Between 6 months and 5 years of age, neural connections proliferate in the deeper cortical layers (IV, V, VI, and lower III) and myelination is gradually completed. This development supports frequency-specific input to layer IV and processing of that information within cortical columns in auditory cortex. Only after age 5 does this anatomical maturation begin in the upper layers (II and upper III) and adult levels of maturation are not reached until age 12. The maturation of auditory evoked potentials follows this anatomical maturation, with the emergence of the N1 response around 5 years of age and an increase in its amplitude until about age 12 (Ponton et al., 2000; Shahin et al., 2004). The upper layers contain the main connections to other cortical areas, so it is likely not until they begin to mature that top-down attentional processes can be fully brought to bear on auditory discrimination tasks.

Animal studies indicate that auditory experience is critical for the development of tonotopic organization in the auditory neural pathways. Cortical plasticity is evident even in adult animals. For example, lesioning an area of the cochlea of an adult guinea pig leads to a reorganization of tonotopic maps in auditory cortex, such that areas that formerly represented the lesioned frequencies came to respond to adjacent frequencies instead (Robertson & Irvine, 1989). Indeed, simple training of frequency discrimination at a particular frequency in owl monkeys leads to an expansion of the representation of that frequency in cortical tonotopic maps (Recanzone, Schreiner, & Merzenich, 1993). Recently, EEG studies in humans have also shown larger responses to frequencies trained in the laboratory than untrained frequencies, suggesting that the discrimination training led to more neurons dedicated to representing the trained frequencies (e.g., Bosnyak, Eaton, & Roberts, 2004). Of most interest from a developmental perspective are studies indicating that animals exposed only to pulsed white noise (which contains all frequencies in the absence of any pattern) during the critical period for cortical tonotopic organization develop very abnormal cortical tonotopic maps where neurons respond broadly to many frequencies (Zhang, Bao, & Merzenich, 2002).

It is of course not ethical to conduct controlled deprivation studies in humans. However, a recent study indicates that extensive active participation in music classes between 6 and 12 months of age results in more mature auditory cortical responses to sound compared to an equal amount of passive exposure to music (hearing music in the background) at infant classes (Trainor, Marie, Gerry, Whiskin, & Unrau, 2012).

In sum, frequency resolution reflecting the spatial mechanisms reaches adult levels by 6 months, whereas more fine-grained frequency discrimination takes many years to reach adult levels. The early maturation of the place mechanism reflects the early maturation of the cochlea. The protracted development of frequency discrimination reflects the protracted development of auditory cortex. Animal studies indicate that experience with tonal sounds appears to be crucial for the development of normal tonotopic maps and normal frequency discrimination. Recent research suggests that extensive exposure to music in humans may lead to enhanced frequency representations.

Pitch and Timbre

Sounds containing only one frequency component are very rare in the natural environment. Sounds perceived to have pitch typically contain energy at a fundamental frequency (which corresponds to the perceived pitch) and at integer multiples (harmonics) of that frequency. For example, a (p. 316) sound perceived to have a pitch of 440 Hz (concert A) would also contain energy at 880, 1320, 1,760, 2,200 Hz., etc. Although the basilar membrane separates at least the lower (resolvable) harmonics into different frequency channels, adults do not perceive a separate sound for each harmonic. Rather, the harmonics are fused into a single percept at a later stage of processing. Primary auditory cortex contains frequency (tonotopic) maps but does not contain pitch representations, even at a neural population level (Fishman, Reser, Arezzo, & Steinschneider, 1998). Pitch appears to be first represented in a region adjacent to primary auditory cortex in marmoset monkeys (Bendor & Wang, 2005). Studies using fMRI (Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002; Penagos, Melcher, & Oxenham, 2004; Schneider et al., 2005) and analyses of lesion cases (Schönwiesner & Zatorre, 2008) confirm generalization of this finding to humans.

That the brain integrates the harmonics, and does not simply use the fundamental frequency when determining the pitch, is clear from a phenomenon known as the pitch of the missing fundamental. If the fundamental frequency of a tone is removed, the pitch is not affected (although the timbre does change). Indeed, the repetition period of the complex sound wave does not change. This phenomenon enables study of the development of pitch perception. In a series of studies, Clarkson and colleagues (Clarkson & Clifton, 1985, 1995; Clarkson & Rogers, 1995; Montgomery & Clarkson, 1997) showed that 7-month-old infants hear the pitch of the missing fundamental.

However, given the immaturity of auditory cortex, especially prior to 6 months of age, as discussed above, and given the fact that auditory cortex appears to be necessary for pitch processing, it might be expected that very young infants cannot integrate harmonics into a single sound with pitch. He and Trainor (2009) tested this using EEG responses. They presented sequences of trials where each trial consisted of a rising pair of tones, both with fundamentals and several harmonics present. Each harmonic rose in pitch from the first to second tone, but the starting pitch and amount of pitch rise varied from trial to trial. Occasionally, the harmonics in the second tone lined up so as to produce a missing fundamental that was lower than the pitch of the first tone. If infants could hear the pitch of the missing fundamental, they would show a brain response indicating violation of expectation for a rising pitch. However, if they could not integrate the harmonics, each harmonic still rose from the first to the second tone, so there would be no violation of expectation. They found that adults, 7-month-olds, and 4-month-olds heard the pitch of the missing fundamental, but no evidence that 3-month-olds were able to do so. In sum, it appears that the ability to integrate harmonics into a percept of pitch emerges between 3 and 4 months of age as cortex matures. It remains unknown as to whether specific experience affects the emergence of this ability.

The perception of pitch is intimately tied to the perception of timbre or sound quality. Timbre is defined negatively as the perceptual difference between sounds with the same pitch, duration, and loudness that nonetheless sound different. Examples include musical sounds, such as a violin versus a flute; one human voice versus another; and one vowel sound versus another. In each case, even when equated for pitch, duration, and loudness, a difference in sound quality remains. The perception of timbre is multidimensional, but the main physical correlates are the frequency spectrum (the relative amounts of energy at each frequency present in the sound) and sound onset characteristics (e.g., a violin has a slow onset whereas a piano has a fast onset). Because of its multidimensional nature, timbre is difficult to study, and there are few studies of its development. It appears that infants can discriminate between sounds with different spectral shapes (i.e., different relative intensities of different frequency regions) (Clarkson, Clifton, & Perris, 1988; Trehub, Endman, & Thorpe, 1990), but their resolution compared to adults has not been tested. There is some evidence in children that discrimination of spectral shape differences does not reach adult levels until 9 years of age (Allen & Wightman, 1992).

Few studies have examined the role of experience in timbre perception. However, Tsang and Trainor (2002) showed that infants are better at spectral shape discrimination for sounds with spectral shapes that are typical of speech and music compared to those that are not. Voices and musical instruments have negative spectral slopes (i.e., intensity fall-off with increasing frequency) between −4 and −12 dB/octave. Tsang and Trainor (2002) found that infants were better able to discriminate tones with spectral slopes in this region compared to sounds with positive or highly negative spectral slopes. A question for future research is whether this sensitivity for spectral slopes that are relevant in the human environment is innate or the result of experience with human voices. However, one recent study indicates that a small amount of experience with particular timbres can modify cortical EEG responses (Trainor, Lee, (p. 317) & Bosnyak, 2011). Infants who listened for 20 a minutes day for a week to children's songs, played in either guitar timbre or marimba timbre, showed larger responses to tones and pitch changes in the trained timbre.

Temporal Resolution

The adult auditory system is capable of resolving timing differences of a few milliseconds and also of integrating information in time windows of 200 to 300 ms. The former ability is very useful, for example, in speech perception, where differences of a few milliseconds can change perception from one speech sound category (phoneme) to another. Almost all developmental work in this area has been directed at temporal resolution. Although there is some variation depending on methodology, the consensus is that when other factors are controlled, temporal resolution is relatively mature early on. At the same time, many factors affect performance on temporal resolution tasks, and adult levels on many tasks are not reached until well into childhood.

One of the most common ways to measure temporal resolution is gap detection, where the smallest silent interval between two sound markers that can be detected is determined. Performance on gap detection tasks is affected by a number of factors (see

Phillips, 1999). Performance is worse for longer sound markers, probably because the first marker creates forward masking of the silence and the second marker creates backward masking. Performance is also worse for cross-channel gap detection, a situation in which the two markers are in different frequency regions and therefore processed in different spatial frequency channels (see the section “Frequency Resolution and Frequency Discrimination” above). Performance can also be adversely affected by band-limited noise markers because such stimuli naturally contain amplitude fluctuations that can be confused with the gap. Using behavioral methods and short 500-Hz tone pips (with Gaussian on and off ramps), Trehub, Schneider, and Henderson (1995) found that 6-month-old infants’ gap thresholds were about 12 ms, in comparison to adult thresholds of 6 ms. Using objective EEG measures and stimuli similar to Trehub and colleagues (1995), Trainor and colleagues (2003) measured event-related EEG responses to occasional presentations of gap stimuli in sequences of 2,000-Hz no-gap stimuli matched in duration and intensity. They found that both infants and adults exhibited reliable responses to gaps as small as 4 ms. This result indicates that temporal resolution is quite mature by 6 months of age.

In contrast, using continuous noise markers, Werner, Marean, Halpin, Spetner, and Gillenwater (1992) found that infant gap detection thresholds (50 ms) were much worse than those of adults (10 ms). This suggests that infants are particularly disadvantaged by the noise markers, whether by increased masking or by amplitude fluctuations in the markers. Indeed, several studies indicate that even much older children are very susceptible to backward masking (Buss, Hall, Grose, & Dev, 1999; Hartley, Wright, Hogan & Moore, 2000; Rosen, van der Lely, Adlard, & Manganari, 2000). For example, Hartley and colleagues (2000) found that compared to adults a 1,000-Hz tone had to be 34 dB more intense at 6 years and 20 dB more intense at 10 years in order to be detected in the presence of backward masking.

Infants are also particularly affected by cross-channel gap detection. In contrast to thresholds close to adult levels by 6 months when the sound markers are short and have the same frequency content (Trainor, McFadden, et al., 2003; Trehub et al., 1995), when the sound markers must be processed in different frequency channels, infant thresholds are 30 to 40 ms under conditions where adult thresholds are 10 to 20 ms (Smith, Trainor, & Shore, 2006). This suggests that infants have particular problems comparing timing across different channels. However, this ability is probably very important for speech perception, where small temporal silences often occur between voiced segments of different frequencies (Phillips, 1999).

Another approach to measuring temporal resolution that, like gap detection with short tone pips, gets around confounds of masking is to measure the temporal modulation transfer function (Viemeister, 1979). Sounds are presented with and without Gaussian amplitude modulation (i.e., periodic fluctuations in loudness) and listeners indicate the presence or absence of the amplitude modulation. The rate of modulation is varied, typically from about 4 Hz to beyond 60 Hz. The depth (size of the modulation in dB) that can be detected is determined at each modulation rate. Typically for adults, the threshold (size of modulation that can just be detected) is similar between 4 Hz and 50 to 60 Hz, after which much larger modulation is needed. This indicates that adults can perceive modulations of up to about 50 to 60 Hz, which corresponds to a temporal rate of about 17 to 20 ms. Although 4- to 7-year-old children need larger modulations in general (indicating poorer intensity discrimination; 9- to 10-year-olds are adultlike), (p. 318) they also show consistent thresholds until about 50 to 60 Hz. Thus, temporal resolution itself appears to be adultlike in children as young as 4 years. One study in infants using temporal modulation transfer functions suggests that by this measure, infants are also quite mature in temporal resolution (Levi & Werner, 1996).

In sum, temporal resolution appears to mature quite early. However, situations involving intensity comparison, the presence of masking, and the need to compare timing across frequency channels can all lead to poor performance on temporal resolution tasks well into childhood. The effects of experience during childhood on these factors remains largely unknown, but one study in adults shows that gap detection thresholds improve substantially with training (Smith, Trainor, Gray, Plantinga, & Shore, 2008).

Sound Localization

The ability to localize sounds in space is very useful, in that knowing the location of a predator or speeding car aids survival. Locating the source of sounds is also helpful for detecting and identifying objects when more than one is sounding at the same time. The main cues for localizing sounds in the horizontal plane involve comparing the intensity level (interaural level difference [ILD]) or timing difference (interaural timing difference [ITD]) between the ears. Sounds to the right of midline will be louder and arrive earlier at the right than left ear, and vice versa for sounds to the left of midline. Cues to location in the vertical plane primarily involve changes in the frequency spectrum as sounds from different elevations hit the pinna (outer ear) at different angles, causing differential filtering of different frequencies. Sound localization is not as good in the vertical plane as in the horizontal plane, and it relies to a greater extent on familiarity with the sounds to be located because this information is needed to determine the extent of frequency distortions caused by the pinna.

Most studies of sound localization in infants have measured infants' ability to make a head turn to the location of a sound. Muir and Field (1979) first showed that newborns will turn their head to the right or left to localize broadband sounds. Interestingly, head turning to sound location follows a J-shaped function. Newborn head turning is very slow and imprecise (Muir, Clifton, & Clarkson, 1989). Around 12 weeks, the response disappears entirely, and when it returns at around 16 weeks, it is faster and more accurate and is accompanied by visual search for the object (Muir et al., 1989). Clifton (1992) proposed that the early head turn response is reflexive and driven by subcortical structures; that as cortex matures, it inhibits subcortical processing but is not yet able to perform sound localization; and that by 4 months, sound localization abilities return as cortex takes over this function. However, despite the lack of head turn responses at 3 months, event-related EEG responses to a change in sound location can be seen at this age (Sonnadara & Trainor, 2005). This suggests that infants are still able to localize sounds during the time in which they do not make head turn responses, but that cortical sensorimotor integration between location and head turns has not yet been achieved.

Sound localization has a fairly protracted development. In the horizontal plane, the minimum audible angle (the smallest difference in sound location that can be detected, measured in degrees) is about 27 degrees at 1 month and reaches 5 degrees at 18 months and adult levels of 1 to 2 degrees at 5 years (Ashmead, Clifton, & Perris, 1987; Clifton, Morrongiello, Kulig, & Dowd, 1981; Morrongiello, 1988; Morrongiello, Fenwick, & Chance, 1990; Morrongiello, Fenwick, Hillier, & Chance, 1994; Morrongiello & Rocca, 1987a, 1990). In the vertical plane, high-frequency sounds are easier to localize than low-frequency sounds as they are more affected by the pinna. Few studies have examined the development of localization in the vertical plane; however, for an 8- to 12-kHz noise band, the minimum audible angle is about 16 degrees at 6 months and improves to 4 degrees at 18 months, which is comparable to that of adults (Morrongiello & Rocca, 1987b,c). Sounds reflect off surfaces such as walls and furniture, resulting in multiple copies actually reaching the ear. Infants learn to ignore these reflections in a process known as the precedence effect (Clifton, Morrongiello, & Dowd, 1984). However, even though sound localization in nonreverberant spaces appears mature by age 5 years, children perform more poorly in reverberant spaces containing more reflections (Litovsky, 1997). It remains unknown as to when sound localization reaches adult levels in all environments, but in general children perform more poorly on many tasks in the presence of background noise (Werner & Marean, 1996).

In part, development of accurate sound localization is protracted because, with increasing age, the head becomes bigger, the ears become further apart, and interaural cues become larger. Not only do representations for ILD and ITD need to be (p. 319) recalibrated as the head grows, but they become more reliable as well (Clifton, Gwiazda, Bauer, Clarkson, & Held, 1988). However, this increased reliability is not enough to account entirely for the poor performance of infants (Ashmead, Davis, Whalen, & Odom, 1991). Furthermore, infants are much better at discriminating ITDs between 16 and 28 weeks of age than would be predicted by their localization performance (Ashmead et al., 1991). ITD and ILD cues are known to be processed in subcortical nuclei, specifically the medial superior olive and the lateral superior olive, respectively (King, Parsons, & Moore, 2000). However, in adults at least, maps of space are found in auditory cortex, and these are necessary for localization of sounds in space (e.g., Al'tman, 1983; Clarke et al., 2002; Cornelisse & Kelly, 1987; Efron, Crandall, Koss, Divenyi & Yund, 1983; Zatorre, Bouffard, Ahad, & Belin, 2002). Thus, it appears that much of the sound localization limitations early in development are probably due to immaturities in cortical maps of space rather than to processing of localization cues.

Because the cues to sound location change as the head grows, auditory maps of space must remain plastic for an extended period. Interestingly, Sonnadara and Trainor (2005) found that event-related brain responses to changes in location remain immature past 8 months of age although responses to changes in pitch and timing take on an adult morphology between 4 and 6 months of age. There is evidence from animal studies for a sensitive period for the development of auditory maps of space (e.g., Binns, Withington, & Keating, 1995; Gray, 1992; Knudsen, 1988; Moore, 1983). The same appears to be true for humans, who, if deprived of binaural hearing during development, do not develop spatial hearing as adults even if binaural hearing is restored (Wilmington, Gray, & Jahrsdorfer, 1994). Furthermore, auditory maps of space must converge with visual maps of space as our perception of objects involves the integration of information from different senses into a unified perception of an object and its location. Typically, visual information to location is dominant, but auditory cues to location can override visual cues if the visual cues are sufficiently degraded (Alias & Burr, 2004; Battaglia, Jacobs, & Aslin, 2003). To date, few studies have addressed the role of experience in human development of sound localization abilities, and the extent and timing of a sensitive period remains largely unknown.

Auditory Scene Analysis

Natural auditory environments are typically complex, containing multiple objects that emit sounds that change over time and overlap with each other. For example, there may be several people talking, cars driving by, music playing in the background, a baby crying, and a washing machine churning. The sound waves produced by these objects simply sum as they travel through the air and bounce off various objects, such that what impinges on the ear is a complex waveform in which the information about separate objects is jumbled together. Unlike in the visual system, where the two-dimensional shapes of objects and their relative distances from each other are mapped in some fashion onto the receptors in the retina, the auditory periphery encodes spectral (frequency) information along the length of the basilar member and temporal information through firing patterns in the auditory nerve. Objects and their locations are not given directly in this mapping as each object likely contains many frequency components that may overlap and change over time. Extracting information about what objects are present and where they are requires considerable complex processing, which is likely the reason why the subcortical auditory pathway is so much more extensive than the visual subcortical pathway.

The process of determining the number, identity, and location of objects is referred to as “auditory scene analysis,” and it depends on the basic abilities described in the previous sections of frequency and pitch processing, intensity discrimination, temporal resolution, and sound localization (Bregman, 1990). There are two basic complementary processes in auditory scene analysis, one being integration of components that belong to the same object and the other being the segregation of components that belong to different objects. Both of these processes apply to both sequences of sounds and simultaneous sounds. For example, the successive notes of a melody or the successive phonemes of a person talking need to be integrated and perceived as coming from one object, and they need to be segregated (or streamed) from other sounds such as another melody or the phonemes coming from a different person. Similarly, the simultaneous harmonics of a sound with pitch (e.g., a musical tone or a vowel) need to be integrated into a percept of a single object, and they need to be separated from other harmonics that may belong to a different auditory object that is sounding at the same time.

Almost all of the small amount of developmental work on auditory scene analysis has focused on (p. 320) streaming, or sequential integration and segregation. Whether the elements of a sequence of sounds are heard as being in one stream (emanating from one object) or two streams (emanating from two objects) depends on a number of factors, the most important being frequency or pitch differences between elements, rate of presentation, and timbre differences between elements. Specifically, if some elements are high in pitch while others are low, the high elements will tend to be heard as one stream and the low elements as another. If the sequence is played more rapidly, it is more likely that the high and low tones will segregate. This is consistent with objects in the real world, which typically do not jump about rapidly in pitch. Similarly, if some elements have one timbre and other elements have another timbre, the elements of similar timbre will tend to integrate into streams and segregate from the elements with different timbre, and this becomes more likely the faster the presentation rate. Again this is consistent with objects in the natural world, which tend not to jump back and forth rapidly between timbres.

Developmentally, one of the most interesting questions is whether the heuristic rules, described above, as to when elements will integrate and when they will segregate are learned through experience with sounds in the world or whether they are innate. Bregman (1990) suggested that, although there are rules that do depend on learning, those described above do not depend a great deal on experience; rather, they are bottom-up and only partially amenable to conscious control. In this case, they would be expected to operate in infancy, and indeed several studies show that infants can segregate sequences of sounds into two streams (Demany, 1982; Fassbender, 1993; McAdams & Bertoncini, 1997). These studies make use of the fact that the auditory system keeps good track of the temporal order of elements within a stream but rather poor track of the temporal order of elements in different streams. Thus, if one hears a particular sequence of four elements that repeat in a given order as coming from one source, one will easily detect a change in the order of its elements. However, if every other element is low in pitch and the remaining alternating elements are high in pitch, then two streams will be perceived, one consisting of the low-pitched elements and the other consisting of the high-pitched elements. The temporal order of the low-pitched tones will be encoded accurately, as will the temporal order of the high-pitched tones. However, the temporal order of the high and low tones relative to each other will not be encoded accurately. Winkler and colleagues (2003) made use of this fact to show that 2- to 5-day-old infants can do stream segregation.

As far as integrating simultaneous components into a single percept, one study indicates that infants can do this at 7 months of age (Folland, Butler, Smith & Trainor, 2011). If a set of harmonics are all integer multiples of a common fundamental frequency, adults will typically integrate the components into a single complex sound with pitch equal to that of the fundamental frequency. If one harmonic is mistuned, it will not be integrated into the complex, and two simultaneous sounds will be heard, one higher pitched tone at the frequency of the mistuned harmonic, and one lower pitched tone at the frequency of the fundamental. Folland et al. (2011) showed that 6-month-old infants are quite good at detecting mistuned harmonics. Furthermore, as discussed above, from 4 months of age, infants perceive the pitch of the missing fundamental, which also implies that they can integrate the harmonics into a single percept.

While the studies described above demonstrate that auditory scene analysis is present in very young infants, they do not indicate whether such abilities improve with age or are dependent on experience. Sussman and colleagues (Sussman, Čeponienė, Shestakova, Näätänen, & Winkler, 2001; Sussman, Wong, Horváth, Winkler, & Wang, 2007) conducted studies in children using similar stimuli as Winkler and colleagues (2003). They found that although children between 5 and 11 years all demonstrated stream segregation, the younger children were less efficient than the older children and adults.

Although no training studies on auditory scene analysis have been conducted in children, comparing adult musicians and nonmusicians provides a natural experiment of the effects of musical training. Fujioka, Trainor, Ross, Kakigi, and Pantev (2005) found that when two simultaneous melodies (polyphonic music) were presented to adults, MEG brain responses indicated that musicians were able to form more robust representations of the two melodies compared to nonmusicians. This suggests that experience likely plays a significant role in the efficiency of auditory scene analysis processes.

Summary of Basic Auditory Development and Neural Correlates

In general, basic auditory-processing abilities improve greatly during infancy but do not fully mature until around 10 years of age. The early improvements are likely associated with maturation (p. 321) of auditory cortical areas. In particular, myelination and the expression of neurofilament in the deeper cortical layers during the first couple of years after birth enables input of specific auditory information from subcortex to layer IV, and processing of this information internal to auditory areas. However, the upper layers that contain the majority of connections to cortical areas beyond auditory cortex do not begin to show mature neural connections until after age 5 years. The maturation of these layers is associated with improvements in attention, the ability to filter out certain sounds and listen selectively. These abilities are likely achieved through connections from higher cortical areas back to auditory areas. Such connections likely enable selective priming of auditory cortical neurons in order to direct processing to particular sound features of interest. Event-related potential studies indicate that auditory evoked potentials continue to mature until about 18 years of age (Ponton et al., 2000; Trainor, Shahin, & Roberts, 2003). For example, the N1 and P2 components of the evoked potential, occurring about 100 ms and 170 ms after onset of an isolated sound, respectively, are obligatory responses in adults. They likely reflect recurrent activations in auditory areas that are influenced by connections from other cortical areas. However, in children, they are not seen robustly until after about 4 years of age. Thereafter, they increase in amplitude with age, reaching a maximum around 10 to 12 years of age, the point at which neurofilament development matures. After age 12, these responses decrease in amplitude, probably reflecting fewer, more efficient connections for processing sound, and they reach stable adult levels around 18 years of age. Also of interest is the maturation of oscillatory activity seen in the EEG in response to sound. Shahin, Roberts, Chau, Trainor, and Miller (2008) have shown that induced gamma-band activity, which is associated with top-down processing, attention, and memory, also matures rather late. Finally, although direct tests of the effects of auditory experience on these ERPs have not been done, several studies show that N1 and P2 (Shahin et al., 2004), N2 (a component related to attentional processing; Fujioka, Ross, Kakigi, Pantev, & Trainor, 2006), and induced gamma-band activity (Shahin et al., 2008) are all larger in preschool children engaged in music lessons compared to children engaged in nonmusical activities. These studies suggest that the development of auditory cortex is greatly influenced by specific auditory experience during childhood.

Musical Development

Music is produced by instruments that create sound vibrations, including the striking of percussion instruments, the plucking or bowing of strings, the blowing of air columns in wind instruments, and the vibrating of vocal cords in singing. The ability to perceive the individual sounds from which music is composed depends on the ability to process the basic sound features of intensity, frequency, pitch, timbre, duration, and location outlined in the previous section. However, meaning in music arises largely from how the individual sounds are put together, both sequentially and simultaneously. Musical structure has two basic aspects, a temporal (rhythmic) aspect and a pitch (melodic and harmonic) aspect. The perception of music relies intimately on the general principles of auditory scene analysis outlined in the section "Auditory Scene Analysis" above. Some sound events are perceived as being grouped together, while different groups of sounds are perceived as being segregated from each other. For example, to perceive a melody, successive tones from one sound source (voice or stream) must be grouped into a coherent whole. Similarly, to perceive the different colors or timbral qualities of different chords, the relationships between simultaneous tones must be perceived in an integrated manner. On the other hand, to hear the different parts (voices or streams) of polyphonic music, each part or melody must be segregated from each other melody.

Musical behavior is found in all human societies, past and present, and, like language, music is a defining characteristic of the human species. People spend a tremendous amount of time and resources engaging in musical activity. For example, the male Mekranoti Indians of the Amazon sing for 1 to 2 hours every morning before dawn (see Huron, 2003). In modern Western society, much time and money is also devoted to music, as can be seen by the fact that the United States makes more money exporting music than pharmaceuticals (Huron, 2003). Music engages sensory, perceptual, and cognitive systems, but it also has direct effects on the emotions (see Huron, 2006; Sloboda, 1991; Trainor & Schmidt, 2003). Music serves important social functions and is found at birthday parties, weddings, religious ceremonies, and political rallies, and in rallying armies for warfare. In adults, singing and playing music together appears to have the effect of engendering a common emotional feeling across people and increases people's willingness to cooperate (Wiltermuth & Heath, 2009). Singing is also an everyday activity among young children, who (p. 322) incorporate music into their games. It is likely not by chance that music is an integral part of daycare and preschool programs everywhere. Perhaps most interesting is that caregivers around the world communicate with their preverbal infants through singing (Trehub, 2009). Across cultures, infant-directed singing is distinguishable from other types of singing (Trehub & Trainor, 1998; Trehub, Unyk, & Trainor, 1993a,b). In keeping with infants' processing limitations, infant-directed singing uses simple structures and a lot of repetition and is often somewhat conversational in that caregivers will modify what they sing based on the infants' reactions (Smith & Trainor, 2008; Unyk, Trehub, Trainor, & Schellenberg, 1992). The communicative intent of infant-directed singing is evident in the fact that caregivers sing in different styles when attempting to achieve different parenting goals—for example, singing in a quiet, slow, lower-pitched voice with an airy timbre when putting infants to sleep, and in a faster, higher-pitched, and more enunciated voice when playing with infants (Trainor, Clark, Huntley, & Adams, 1997).

Infants are very responsive to music (Trehub, 2009). For example, they prefer to listen to renditions of songs that are sung in an infant-directed style compared to the same songs sung in an adult-directed style (Trainor, 1996), particularly preferring the loving tone and the higher pitch (Trainor & Zacharias, 1998) of the infant-directed versions. Infants also react differently to different types of infant-directed singing, focusing inward and looking downward during the presentation of lullabies and actively looking outward at people in the room during the presentation of play songs (Rock, Trainor, & Addison, 1999). Speech directed to preverbal infants contains musical features such as exaggerated pitch contours and rhythmic patterning, leading to the suggestion that infant-directed music and speech serve similar functions related to emotional regulation and social bonding (Dissanayake, 2000). Music and language development also appear to be related during childhood. For example, Anvari, Trainor, Woodside, and Levy (2002) showed that musical abilities and early reading abilities are correlated in preschool children, even after other factors such as memory, vocabulary, and phonological awareness are factored out. Furthermore, participation of school-aged children in musical activities appears to improve early reading ability (Magne, Schon, & Besson, 2006; Moreno & Besson, 2006) and general intelligence (Schellenberg, 2004).

In the following sections, we examine the development of sensitivity to musical pitch and rhythmic structure. In both cases, there are universal or near-universal features, but, as is the case with language, some aspects of musical structure vary considerably between musical systems. Different musical systems use different scales (set of notes from which musical compositions are formed), different melodic conventions, and different predominant rhythmic structures, and they may or may not use complex harmonic structure. Thus, as with language, children must acquire the specific musical system to which they are exposed, and adults, even those without specific musical training, process music through mental structures that were sculpted by the music to which they were exposed as children. In the following sections we consider early musical abilities and how specific musical pitch and rhythmic structures are acquired through everyday exposure to music, a process known as "enculturation." We then examine the research evidence for effects of enriched early musical training on musical acquisition and development in general.

Development of Musical Pitch Organization

Some aspects of musical pitch structure are near universal, whereas others vary greatly from musical system to musical system. It might be expected that near-universal aspects reflect general brain mechanisms for processing auditory information, including how sound is represented in cortical tissue, basic memory limitations, and the integration and segmentation processes involved in auditory scene analysis. Sensitivity to near-universal aspects of musical pitch structure might be expected to appear early in development. On the other hand, the fact that musical system-specific aspects have evolved in only some musical systems suggests that these aspects may reflect processing that is less dependent on general auditory mechanisms and may require more experience with a particular musical system to be acquired by children. In the following, we first consider early-developing musical capabilities and their relation to near-universal musical features, then later-developing capabilities and their relation to enculturation, and, finally, effects of enriched musical training.

Early Abilities for Perceiving Musical Pitch Organization

Consonance and dissonance. To adults, when the ratio between the fundamental frequencies of two tones can be expressed as a small integer ratio (p. 323) (e.g., intervals of an octave, 1:2 and perfect fifth, 2:3) they are perceived to sound consonant (smooth, pleasant, without roughness) to adults, but when the ratios are more complex (e.g., major seventh, 8:15, tritone, 32:45) they sound dissonant (rough, unpleasant) (e.g., see Plomp & Levelt, 1965; Terhardt, 1984; Tramo, Cariani, Delgutte, & Braida, 2001). This perception is thought to arise from both the spatial and the temporal mechanisms. The more consonant the perception of two tones, the more the frequencies of the harmonics tend to be either identical or more than a critical band apart so that their vibration pattern representations on the basilar member are separated and do not interact. On the other hand, the more dissonant the perception of two tones, the greater the chance that there are harmonics whose frequencies are nonidentical but within a critical band. In this case, there is interference in the spatial neural representation of these frequency components. Studies have shown that the temporal mechanism is also involved. Small versus large integer frequency ratios set up firing patterns in the auditory nerve fibers that are distinct (Tramo et al., 2001).

The consonance/dissonance continuum is commonly used as an organizing structural feature for musical pitch. For example, in Western musical structure, a dissonant interval creates tension, which is typically subsequently resolved by a following consonant interval, giving rise to an emotional experience of ebb and flow of tension. Given its origin at relatively peripheral levels of the auditory system, one would expect sensitivity to consonance and dissonance to be present early in life. Indeed, a number of studies in 6-month-olds show that infants of this age can categorize consonant and dissonant intervals (Trainor, 1997) and that they find two consonant intervals to sound more similar than a consonant and a dissonant interval, even when the pitch distance between the two consonant intervals is larger than that between the consonant and dissonant interval (Schellenberg & Trainor, 1996). Furthermore, infants between 2 and 6 months of age prefer to listen to consonance compared to dissonance, whether with isolated intervals or in the context of a simple piece of music (Trainor & Heinmiller, 1998; Trainor, Tsang, & Cheung, 2002; Zentner & Kagan, 1998). Even hearing newborns of deaf parents prefer consonance to dissonance (Masataka, 2006). Given the fundamental importance of consonance and dissonance in musical pitch structure and its early development, we propose that the perceptual continuum between consonance and dissonance might provide the starting point for the development of musical pitch systems.

Octave equivalence. Another basic feature of sound representation that is related to consonance is octave equivalence. Tones an octave apart (1:2 ratio of fundamental frequencies) are perceived as very similar. Indeed, because of their small-integer ratio relation, all of the harmonics in the higher tone are contained within the lower tone. In terms of musical structure, a near-universal feature of musical systems is that tones an octave apart are considered structurally identical (Burns, 1999). In Western music, tones an octave apart are given the same note names (e.g., there are seven *A*s on the piano keyboard). When males and females sing together and their voice ranges do not overlap, they commonly sing octaves apart. Infants also appear to be sensitive to octave relations (Demany & Armand, 1984).

Unequal interval scales. Music is not typically composed using continuous pitch. Rather, the octave is divided into a small set of pitch intervals, and the notes formed by these intervals are used to make melodies and harmonies. This near-universal convention is probably related to memory constraints of the human auditory system, which make continuous pitch compositions difficult to encode and remember. While different musical systems use different scales (e.g., pentatonic, *ragas* of Indian classical music, Western major and minor), the vast majority of scales have the characteristic that they contain two (or more) sizes of intervals. For example, the Western major scale contains intervals of a semitone (1/12th octave) and a tone (1/6th octave). Use of more than one interval size gives rise to the possibility of making unique sets of relations between each note of the scale and every other note of that scale (Balzano, 1980). This structure allows for different notes to take on different functions. For example, in the Western major scale, the tonic is the most stable pitch, and compositions that end on this note sound most complete. The fifth tone of the scale, the dominant, and the seventh note, the leading tone, require resolution to the tonic. Although infants need to learn the intervals in the scales used in their culture (see below), even before they have done this they show processing advantages for scales with two interval sizes compared to scales with one interval size (Trehub, Schellenberg, & Kamenetsky, 1999).

Transpositional invariance. One universal aspect of musical pitch structure is that of transpositional invariance. A melody maintains its identity (p. 324) regardless of the absolute pitch of the starting note as long as the pitch distances (intervals) between notes are correct. For example, *Happy Birthday* is recognizable whether transposed to a higher or lower pitch range. Indeed, most adults do not readily remember the absolute pitches of a melody, but favor a representation in the nervous system where the distances between notes are encoded. The ability to compare the pitch distance between one set of two tones and another set of two tones is called *relative pitch*. The fragility of absolute pitch representations in long-term memory in most adults is evident in studies showing that the ability to judge whether two tones have the same or different pitch deteriorates rapidly as more distracter tones with random pitch are placed between them, although a very small percentage of people do readily remember absolute pitch and are not affected by such distracter tones (Ross et al., 2004).

Infants may also process absolute pitch under some circumstances (Saffran & Griepentrog, 2001; Volkova, Trehub, & Schellenberg, 2006), but, like adults, they favor relative pitch representations (Plantinga & Trainor, 2005, 2008; Trehub, Bull, & Thorpe, 1984). Also similar to adults, infants' memory for absolute pitch fades rapidly. Infants' ability to determine whether two pitches are the same or different deteriorates as the number of distracter tones placed between them increases (Plantinga & Trainor, 2008). On the other hand, infants readily process relative pitch. Several studies show that infants can detect a change in one note of a melody, even when the comparison melody is transposed with respect to the original (e.g., Trainor & Trehub 1992; Trehub et al., 1984). Infants' long-term memory representations also favor relative pitch. Plantinga and Trainor (2005) exposed infants to one of two melodies every day for a week. After this exposure, infants showed a novelty preference, preferring to listen to whichever of the two melodies they had not heard previously. Of most interest here, this preference for the novel melody remained as strong when the melodies at test were transposed up or down by either a perfect fifth (7/12ths of an octave) or tritone (1/2 octave) compared to their presentation during familiarization the prior week. However, infants showed no preference for the melody of exposure presented at the pitch level heard during the week of exposure compared to that same melody presented at a different pitch level. These results are interesting because relative pitch representations are more complex than absolute pitch representations in that the former require the comparison of pitch distances whereas the latter require simple encoding of isolated pitches. These results are particularly interesting when it is considered that absolute frequency representations are present already on the basilar membrane in the inner ear and are maintained through subcortical tonotopic maps and into primary auditory cortex. Yet melodic representations largely discard this absolute pitch information in favor of relative pitch representations. This attests to the usefulness of the relative pitch representations. Different people speak and sing at different pitch levels, and therefore relative pitch representations are essential for recognizing musical input across such variation.

Enculturation to Specific Musical Pitch Systems

Although infants show some precocious musical processing abilities as indicated in the previous section, these abilities appear to concern near-universal aspects of musical pitch structure. Just as it takes time for children to acquire a particular language, it takes time for them to acquire a musical system. Yet, for both music and language, implicit knowledge of the structure is acquired without any formal instruction. Indeed, some have argued that, when given appropriate implicit behavioral tests that do not require explicit music knowledge, nonmusicians show considerable knowledge of the musical system of their culture (e.g., Bigand & Poulin-Charronnat, 2006; Tillmann, Bigand, Escoffier, & Lalitte, 2006). For example, Trainor, McDonald, and Alain (2002) found that Western nonmusicians show preattentive automatic brain responses to changes to a note that violate Western musical structure (out-of-key notes) in an unfamiliar melody, indicating that they have internalized the structure of Western music and process music through representations that instantiate these expectations.

There are two basic aspects of musical pitch structure that vary considerably from musical system to musical system: scale (or key) structure and harmonic structure. Lynch, Eilers, Oller, and Urbano (1990) showed that Western adults are much better at detecting changes to Western scales than to unfamiliar Balinese scales, whereas Western infants are equally good at detecting changes to both. Trainor and Trehub (1992) showed that Western adults, whether formally musically trained or not, process melodies in terms of Western major scale structure. Specifically, they are much better at detecting changes to an unfamiliar Western melody that go outside the notes of the key of the melody (p. 325) compared to changes that remain within the key of the melody. Thus, they have implicit knowledge of Western key structure. Infants, on the other hand, detect both types of changes equally well, and even perform better than adults under some conditions on within-key changes, indicating that they have not yet learned what notes belong in the Western major scale. EEG studies indicate that event-related potential measures of cortical representations for melodies take on an adultlike morphology later than representations for individual pitches (He, Hotson, & Trainor, 2007, 2009; Tew, Fujioka, He, & Trainor, 2009), indicating that processing melodic information develops more slowly than processing the pitch of individual tones. The exact age at which children acquire scale knowledge is not known; however, it is certainly present by age 4 or 5 years (Corrigall & Trainor, 2009; Trainor, 2005; Trainor & Corrigall, 2010; Trainor & Unrau, 2012; Trehub, Cohen, Thorpe, & Morrongiello, 1986).

Although the vast majority of musical systems use some kind of scale structure for melodic composition, elaborate harmonic structure is relatively rare across musical systems. Interestingly, harmonic structure is acquired rather late in development and, at least in the absence of musical training, does not reach adult levels until around 12 years of age (Costa-Giomi, 2003). However, younger children do show some sensitivity to harmony. Schellenberg, Bigand, Poulin-Charronnat, Garnier, and Stevens (2005) showed that when harmonic progressions ended on the expected tonic chord, 6-year-olds were faster to make judgments about that chord (e.g., which of two vowels was sung on the chord) compared to when the harmonic progression ended on an unexpected subdominant chord (based on the fourth note of the scale), even though the tonic and subdominant chords are structurally identical in isolation (i.e., composed of the same intervals). They take on different roles only in the context of a key. Koelsch and colleagues (2003) used EEG to demonstrate that children as young as 5 years show a brain response to harmonically very unexpected chords. And Corrigall and Trainor (2009) demonstrated that 4-year-old children rate sequences that end on the tonic chord as sounding “good” significantly more often than sequences that end on the subdominant chord.

Even when chords do not accompany a melody in Western music, the notes of the melody alone imply a harmonic accompaniment. Trainor and Trehub (1994) investigated the development of sensitivity to implied harmony. They found that adults and 7-year-olds readily detected changes to a melody that remained within the key of the melody (and so did not violate scale-based expectations) but that violated harmonic expectations at that point in the melody. This result indicates that these age groups are processing melodies according to a sophisticated implied harmonic representation. On the other hand, 5-year-olds did not detect changes that violated the implied harmonic structure better than changes that did not, indicating that at this age they do not have a well-developed sense of implied harmony.

In sum, although infants show early development of sensitivity to near-universal musical features, it takes many years to fully acquire system-specific musical pitch processing. Yet, as in language, such processing is learned through everyday exposure to music in the absence of formal training. Interestingly, the earlier acquisition of scale (key) knowledge and the later acquisition of harmonic knowledge parallels how commonly these music features are seen across the world's musical traditions. Scale structure is very common, whereas elaborate harmonic structure is relatively rare. One caveat to these conclusions, however, is that almost all of the research evidence to date comes from the study of the acquisition of Western musical structure, and we can only speculate that acquisition of other musical systems follows similar patterns.

Effects of Formal Musical Training on Musical Pitch Development

In contrast to language, where syntax (grammar), vocabulary, semantics (meaning), and the ability to read written words are trained in all children in school, musical training in Western societies varies considerably from individual to individual, from no formal training to decades of intensive practice for hours a day. Thus, there is the possibility to examine the effects of extensive musical training. Most studies in this area have compared adult musicians and nonmusicians. This provides a starting point for this line of inquiry, although it can be difficult to disentangle genetic from experiential factors in these studies (see discussion below).

A number of MRI studies indicate structural brain differences between musicians and nonmusicians that extend across a wide network of areas (e.g., Koelsch & Siebel, 2005). In particular, musical training is associated with enlarged areas in auditory cortex, particularly on the right side (Bermudez, Lerch, Evans, & Zatorre, 2009; Schneider et al., 2002), Broca's area (Sluming et al., 2002), cerebellum (p. 326) (Hutchinson, Lee, Gaab, & Schlaug, 2003), and motor areas (Bangert & Schlaug, 2006; Gaser & Schlaug, 2003). Musical performance places great demands on fast encoding, memory, retrieval, multisensory integration, and executive functions such as attention and inhibition, and this network of brain differences likely reflects the training of these functions.

While MRI studies give information about brain structures, when sounds are presented the stages of musical information processing can be tracked in detail with EEG and MEG (see Näätänen et al., 2007, and Trainor & Zatorre, 2009, for reviews). Functional differences between musicians and nonmusicians have been found at virtually every stage of sound processing. Auditory brainstem responses occurring within 12 ms of sound onset are already enhanced in musicians (Musacchia, Sams, Skoe, & Kraus, 2007). Likewise, middle latency responses originating in primary auditory cortex are also enhanced (Schneider et al., 2002). Several responses from secondary auditory cortex are earlier and larger in musicians, including the N1b occurring around 100 ms after stimulus onset, the N1c around 170 ms, and the P2 around 200 ms (Kuriki, Kanda, & Hirata, 2006; Pantev et al., 1998; Shahin, Roberts, Pantev, Trainor, & Ross, 2005). Finally, P3a responses indicating attentional capture of sounds in an unattended stream (e.g., Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004, 2005; Trainor, McDonald, & Alain, 2002) and P3b responses reflecting memory and conscious attending to the sound (e.g., Tervaniemi, Just, Koelsch, Widmann & Schröger, 2005; Trainor, Desjardins, & Rockel, 1999) are also larger in musicians. Another ERP response that has been studied with respect to musical training is MMN. Musicians show larger and/or earlier MMN responses to occasional note changes in a single melody presented in transposition (Fujioka et al., 2004), to occasional changes in each of two simultaneously presented melodies in a polyphonic musical texture (Fujioka et al., 2005), and to unexpected harmonies in chord progressions (Koelsch, Schmidt, & Kansok, 2002). A study by Shahin and colleagues (2008) also indicates larger induced gamma-band (40- to 100-Hz oscillation) responses in musicians compared to nonmusicians. The evoked gamma-band response is phase-locked to the sound stimulus and occurs primarily between about 50 and 100 ms after sound onset (e.g., Pantev et al., 1991). However, the induced gamma-band response is more long lasting and is not phase-locked to the incoming sound (e.g., Kaiser & Lutzenberger, 2003). It is therefore thought to reflect the entrainment of intrinsic oscillatory networks in the brain to the incoming sound. Induced gamma-band activity likely reflects top-down executive processes (e.g., Fujioka, Trainor, Large, & Ross, 2009; Gurtubay, Alegre, Valencia, & Artieda, 2006; Snyder & Large, 2005), and its enhancement in musicians suggests that musical training might influence general attentional and executive functions (Trainor, Shahin, & Roberts, 2009).

Are these musician/nonmusician differences related to musical experience or do they reflect innate factors such that musicians simply have a genetic endowment that favors good sound processing? The only way to definitively show effects of experience is to examine children and randomly assign them to musical training or not, an expensive and time-consuming enterprise. However, a number of factors point to a large role of experience in the adult comparison data. First, the amount of musical training is often correlated with the extent of the brain enhancement, including for structural differences (e.g., Schneider et al., 2002) and ERP differences (e.g., Pantev et al., 1998; Trainor, Desjardins, et al., 1999). Second, enhancements are greatest for sounds in the timbre of the instrument of practice in comparison to timbres of other instruments (e.g., Pantev, Roberts, Schulz, Engelien, & Ross, 2001). Third, components that are enhanced in musicians can also be affected even in adulthood through laboratory training (e.g., Bosnyak et al., 2004; Lappe, Herholz, Trainor, & Pantev, 2008).

Effects of musical experience can be measured most directly by studying children, but because such studies are difficult to carry out, few have been completed. Most of these studies compare children taking music lessons to those not taking music lessons at one point in time without random assignment to groups, so the conclusions must be treated with caution. However, these studies consistently find enhanced processing in musician children. As discussed above, ERP responses to sound (including N1, P2, N2, and induced gamma band) do not reach adult levels of maturity until well into the teenage years (Ponton et al., 2000; Trainor, Shahin, & Roberts, 2003; Shahin et al., 2004), but musician children appear to be advanced along this trajectory (Fujioka et al., 2006; Jentschke, Koelsch, & Friederici, 2005; Shahin et al., 2004, 2008).

A few studies have used longitudinal designs to compare children at two time points. Differential gains by musician and nonmusician children over the time period lend support that musical (p. 327) experience is involved. Corrigall and Trainor (2009) examined how musical processing develops in two groups of 4- to 5-year-old children, one engaging in musical training and the other not. They found no differences between groups at the first measurement. However, by the second measurement 8 months later, the group engaging in musical training showed superior ability to detect harmonically unexpected chords. Fujioka and colleagues (2006) measured MEG responses to sound in 4- to 5-year-old children, first when they were about to start music lessons and then every 3 months for a year during musical training. The responses of these children were compared to those of a control group engaging in other activities such as athletic training. The largest differences between groups in how the ERP responses changed over the year were in the N2 component, which likely reflects greater attentional and memory gains in the musician group compared to the nonmusician group. Similarly, Shahin and colleagues (2008) examined the development of induced gamma-band responses in 4- to 5-year-old children, measuring musician and nonmusician children twice separated by a year. They found that none of the children showed induced gamma-band responses at the first measurement and that only those engaged in musical training did so at the second measurement. These results also strongly suggest that musical training enhances executive functions such as memory and attention. Finally, in one of the few studies randomly assigning children to either music or drama lessons, Schellenberg (2004) found that after a year of experience, those in music lessons showed greater improvement in IQ scores than those in drama lessons.

In sum, although even nonmusicians develop brains specialized for processing the structure of the music in their environment, musical training greatly enhances structural and functional aspects of the brain for musical processing. Furthermore, musical training in the preschool period results in superior musical abilities and, perhaps most interesting, in superior executive functioning as well, which may well lead to benefits for other cognitive domains (see Moreno, et al., 2011; Schellenberg, 2011; Trainor & Corrigall, 2010; Trainor & Unrau, 2012 for reviews).

Development of Musical Rhythmic Organization

Musical pitch structure must be realized over time, so the temporal structure of music is in a sense the most basic aspect of musical structure. Indeed, a considerable amount of music has only rhythmic structure, with little or no pitch variation. Brain representations for rhythm appear to involve two aspects that are closely linked to general auditory scene analysis processes. The first is *metrical structure*, whereby listeners abstract a steady beat (and its subdivisions and superdivisions) from a presented series of sound events. The metrical structure is not given in the stimulus directly. Indeed, perceived beats of a steady metrical structure may occur at places where there is no actual sound event. The perception of a steady beat depends on regularities in the sequence of sound event onset-to-onsets as well as on the durations, relative intensities, and pitches of the sound events. The metrical structure is hierarchical, usually with an obvious tactus (or tempo at which one would tap along) on which most people agree (Drake, Penel, & Bigand, 2000; Repp, 2005; Snyder & Krumhansl, 2001). In Western music, beats are typically evenly spaced and successive levels of the hierarchy divide each beat of the previous level into two or three beats. The second aspect of rhythmic structure is *grouping*, whereby sequences of sound events are divided or grouped into phrases and subphrases and segregated from surrounding phrases and subphrases.

Most research has been conducted on the perception of metrical structure, so that will be the focus of the following sections. Metrical perception in music has been linked closely with motor rhythms (Grahn & Brett, 2007; Grahn & Rowe, 2009; Phillips-Silver & Trainor, 2005, 2007, 2008; Repp, 2005; Trainor, Gao, Lei, Lehtovarara, & Harris, 2009). Indeed, rhythmic music makes people want to move and dance. A close connection between auditory and movement rhythms also underlies people's ability to synchronize when singing together or playing musical instruments together, a coupling that is not required by speech. Few species appear to have this ability to synchronize movement to an external auditory beat, but those that do also appear to be capable of vocal imitation (Patel, Iversen, Bregman, & Schulz, 2009; Schachner, Brady, Pepperberg, & Hauser, 2009). Some of these species are evolutionarily distantly related, such as humans and cockatoos, suggesting that this ability evolved independently in different species. Although metrical structure is a near-universal organizing principle in music, the details of metrical organization differ substantially across musical systems. Thus, as with musical pitch structure, learning is necessary for rhythmic enculturation. In the following, we first consider early-developing rhythmic capabilities, (p. 328) then enculturation to the predominant rhythms of one's culture, and finally effects of enriched musical training.

Early Abilities for Perceiving Rhythmic Organization

As with musical pitch perception, young infants show considerable sensitivity to rhythmic structure. Winkler, Háden, Ladinig, Sziller, and Honing (2009) used EEG to demonstrate that newborn infants show surprise when a downbeat is omitted in a rhythmic context that sets up an expectation for that downbeat. By 2 months of age infants are best at tempo discrimination around 600 ms onset-to-onset (Baruch and Drake, 1997), which is in the optimal range for adults across cultures. Infants of this age can also discriminate simple rhythmic patterns (Demany, McKenzie, & Vurpillot, 1977). By 6 months, Western infants use duration to extract grouping structure, perceiving relatively longer sound events as the ends of groups (Trainor & Adams, 2000). At this age, infants can also distinguish metrical structures where successive levels of the metrical hierarchy involve groups of three beats (as in a waltz) from those that involve groups of two beats (as in a march) (Hannon & Johnson, 2005; Hannon & Trehub, 2005a; Morrongiello, 1984; Phillips-Silver & Trainor, 2005). At least as young as 7 to 9 months, infants can generalize across pitch and tempo and recognize a rhythm across variation in these aspects (Trehub & Thorpe, 1989).

Infants are motorically immature. However, Phillips-Silver and Trainor (2005) showed that for infants as young as 7 months of age, the way that they are moved affects how they perceive musical rhythms. The researchers created a repeating six-beat rhythm pattern that was ambiguous in that it had no physical accents, but could readily be *perceived* either with accents on every second beat (as in a march) or with accents on every third beat (as in a waltz). They played this ambiguous rhythmic pattern for infants, while bouncing half of the infants on every second beat and the other half on every third beat. After this training, they found that infants bounced on every second beat preferred to listen to a version of the rhythmic pattern with physical accents added on every second beat over a version with accents on every third beat, whereas infants bounced on every third beat showed the opposite pattern of preferences. Because the infants did not move themselves, this suggests that motor planning may not be necessary for the interaction between movement and auditory rhythm perception. Indeed, subsequent studies with adults indicate that vestibular input, which is necessary for balance and movement in a gravitational field, is crucial for this interaction (Phillips-Silver & Trainor, 2008; Trainor, Gao, et al., 2009).

There is rather little research on the development of rhythmic abilities in children, and much of it has been conducted in the laboratory of Carolyn Drake. With respect to the reproduction of rhythm patterns, at age 7, but not at age 5, children are as accurate as musically untrained adults in reproducing short rhythms (Drake, 1993). Younger children, like adults, find duple meters easier than triple meters, rhythms with fewer different note durations easier, and rhythms with intensity accents easier. With respect to metrical perception, young children have difficulty moving in time with an external beat, whether by tapping or using whole-body movement (Eerola, Luck, & Toiviainen, 2006). However, the ability to tap to a beat improves dramatically between ages 4 and 11 years (Drake, Jones, & Baruch, 2000). Finally, children's preferred tapping tempo decreases with age and with musical training, suggesting that they are able to deal with longer spans of time as they get older (Drake, Jones, & Baruch, 2000; McAuley, Jones, Holub, Johnston, & Miller, 2006).

In sum, young infants show precocious abilities to discriminate rhythmic patterns, and their auditory perception of rhythm is influenced by movement. However, the motor skills needed to produce musical rhythms take considerable time to develop.

Enculturation to the Rhythmic Structure of Specific Musical Systems

Western music predominantly contains simple metrical structures (Fraisse, 1982), and those who have grown up listening to Western music find simple metrical structures such as those with duration ratios of 1:1 or 1:2 (as in a march) easier to process than those with more complex rhythms, such as ratios of 2:3 (i.e., a group of two beats followed by a group of three beats) (Hannon & Trehub, 2005a; Repp, London, & Keller, 2005; Snyder, Hannon, Large, & Christiansen, 2006). A privileged status for simple rhythmic structures might reflect the simple ratios involved in human movements, such as heartbeats and walking. However, many musical systems, such as those in Bulgaria and Macedonia, use more complex rhythms in their folk music, and adults in these cultures have no difficulty in perceiving these complex rhythms (Hannon & Trehub, 2005a).

(p. 329) As with the development of system-specific scale structure discussed above, Hannon and Trehub (2005a,b) have shown that at 6 months infants are able to perceive both simple and complex rhythms, but that they lose the ability to process complex rhythms by 12 months if these rhythms are not present in their musical system of exposure. They presented Western adults and infants of 6 and 12 months, as well as Bulgarian and Macedonian adults, with musical excerpts that had either simple or complex metrical structures. They found that Western 6-month-olds and Bulgarian and Macedonian adults could detect timing changes in rhythms with both types of structures, but that Western adults and Western 12-month-olds could do so only for rhythms with simple metrical structures. In sum, the brain appears to become specialized by 12 months of age for the metrical structures that are predominant in the musical system of one's culture.

Effects of Formal Musical Training on Rhythmic Development

Very few studies have directly examined effects of musical training on rhythmic development. However, a large range of rhythmic abilities exist in the general population, and these individual differences extend to motor manifestations of rhythm such as dancing. fMRI studies show that rhythmic stimuli activate a network of auditory and motor regions in the brain that are similar in musicians and nonmusicians (Limb, Kemeny, Ortigoza, Rouhani, & Braun, 2006). At the same time, several studies show differences between adult musicians and nonmusicians, and it is reasonable to speculate that these differences are caused at least in part by their different musical experiences in childhood. For example, when five beats in a row are occasionally omitted in an isochronous beat sequence, musicians are more accurate than nonmusicians at tapping at the point where they thought the fifth tone should occur (Jongsma, Desain, Honing, 2004). Musicians' ERPs are also temporally less variable than those of nonmusicians. Both fMRI studies (Limb et al., 2006) and EEG studies measuring MMN (Vuust et al., 2005) indicate that musicians show greater left activation when engaging in rhythmic processing compared to nonmusicians. The right hemisphere may be necessary for sequencing, but the left hemisphere is likely better for precise timing (Zatorre, 2001), so these studies suggest that musical training may have its greatest effect on rhythm processing in the networks of the left hemisphere for precise timing.

It remains unknown as to exactly how rhythms are encoded in cortex. However, theoretical models have shown that rhythmic entrainment can be accomplished by a bank of oscillators, each flexible but maximally driven by a particular best frequency (e.g., Large & Jones, 1999). Recent evidence suggests that this type of model may be biologically plausible. The past decade has seen an increased interest in oscillatory activity at various frequencies that is present in EEG and MEG recordings. Some of this activity is directly driven by the stimulus in that it is precisely phase-locked to the onset of the presented sound, such as the evoked gamma-band response (Pantev et al., 1991). However, some of this activity increases in response to the presented stimulus but is not precisely phase-locked to the stimulus, such as the induced gamma-band response (between 40 and 100 Hz). The induced gamma-band response can occur when no sound is actually present, but when there is an expectation for a sound at a certain point in a rhythmic pattern (Snyder & Large, 2005). With respect to effects of musical training, gamma-band responses are larger in musicians than in nonmusicians (Bhattacharya, Petsche, & Pereda, 2001) and develop earlier in children taking music lessons than in children not taking formal music lessons (Shahin et al., 2008). Relations between activity in various frequency bands is likely important as well. For example, Fujioka and colleagues (2009) found that activity in the beta band (15 to 30 Hz) followed each sound event in a regular sequence of presented sound beats but did not respond to omitted beats, whereas activity in the gamma band increased after each presented beat as well as after omitted beats. Furthermore, oscillatory activity is likely related to rhythmic coupling between auditory and motor networks. Fujioka, Trainor, Large, and Ross (2012) used source analysis techniques on MEG data to demonstrate that presentation of an auditory beat in the absence of any motor movement or instruction to imagine movement leads to similar modulation of oscillatory beta band activity across auditory and motor regions that follows the tempo of the auditory beats.

There are very few scientific studies examining the effects of musical training on rhythmic development. However, Drake and her colleagues have consistently found that compared to children not taking music lessons, children training musically are better at reproducing rhythmic patterns and are more flexible in their ability to tap the beat at different levels of the metrical hierarchy (Drake, 1993; Drake, Jones, & Baruch, 2000). To date there is one study of the (p. 330) effects of music experience in infancy on rhythm development. Gerry, Faux, and Trainor (2010) used the methods of Phillips-Silver and Trainor (2005) discussed above (see the section “Early Abilities for Perceiving Rhythmic Organization”) to compare infants enrolled in parent-and-infant Kindermusik classes with infants not engaged in formal musical classes. Specifically, this method was developed to measure the influence of movement on whether an ambiguous rhythmic pattern is perceived as a march or as a waltz. Infants in Kindermusik classes get a lot of experience being walked and swayed to musical rhythms, and this study examined whether such enriched auditory-movement experience would influence metrical development. Gerry and colleagues found that infants in Kindermusik tended to listen longer to the rhythm patterns in general in the preference test phase, suggesting a greater interest in musical rhythms. The music used in the Kindermusik classes is predominantly in duple rather than triple meter, following conventions of Western music. Of most interest with respect to enculturation was the finding that the effects of movement on auditory disambiguation of the metrical structure were much stronger when infants were moved on every second bet of the ambiguous pattern compared to when they were moved on every third beat for the Kindermusik group but not for the group not engaged in formal musical training. Thus, Kindermusik training is associated with an earlier processing bias for the dominant duple rhythm patterns of Western music.

In sum, although there are few studies directly addressing this issue, musical training likely has a large effect on the level of rhythmic accomplishment achieved. However, little research to date addresses the ages at which formal training has the largest effects on rhythmic perception and production.

Conclusions

Some common themes apply to the discrimination of sound features of isolated sounds, the perception of auditory objects, and the perception of music with complex spectrotemporal structure. First, for each of these levels of auditory processing, young infants show some sophisticated processing abilities. Second, mature adult levels of processing, however, are not usually achieved until well into childhood or even, in many cases, into the teenage years. Third, through exposure to specific sounds with specific structures, children's processing becomes refined and specialized for the structure of their auditory input. For example, exposure to sounds with pitch is necessary for the development of tonotopic representations and the ability to discriminate different frequencies of sound. Similarly, enculturation—development of specialized brain representations—to the specific melodic, harmonic, and rhythmic structure of the musical system of a person's culture depends on considerable exposure to that musical system. Fourth, specific intense experience has a profound effect on perception. For example, early exposure to complex rhythms appears to be necessary for fluent processing of those rhythms, and brain representations for musical pitch structure are considerably different in both child and adult musicians compared to nonmusicians.

It can be readily argued that auditory scene analysis and the representation of sounding objects developed under evolutionary pressure, as there is survival value in being able to identify which conspecifics and predictors are present in the environment and where they are located. This pressure in turn could easily translate into pressure for better encoding of basic sounds features such as frequency, pitch, timbre, timing, and sound location as they are all necessary for optimal auditory scene analysis. The perception of musical structure also depends on basic sound processing and on auditory scene analysis, but music presents more of a puzzle in terms of survival value. However, music serves important communication functions in preverbal infants and continues to be important in childhood and adulthood for emotional regulation and social bonding. Thus, it is possible that the social/emotional functions of music confer survival value, and that music, in turn, has led to evolutionary pressure for better basic pitch processing and auditory scene analysis.

Questions for Future Research

General issues that remain for future research include the following:

1. Why does basic auditory processing take many years to reach adult levels?
2. How does auditory plasticity differ at different ages?
3. What are the sensitive periods in humans for processing different sound features?
4. How are physiological and behavioral auditory development related?
5. Are there sensitive periods for the acquisition of musical skills?
6. Does the orderly acquisition of musical skills in Western children apply to the acquisition of other musical systems?

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