

Chapter 12

Music and language: relations and disconnections

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INTRODUCTION

Above all, music and language are forms of human communication. Since sensory function is ultimately shaped by what is biologically important to the organism, the human urge to communicate has been a powerful driving force in both the evolution of auditory function and the ways in which it can be changed by experience within an individual lifetime. The ability to extract meaning from sound requires that all aspects of the auditory system work together in concert: by considering human auditory function in the context of communication, we hope to emphasize the highly interactive nature of the auditory system as well as the depth of its integration with other sensory and cognitive systems. Through consideration of relations and dissociations between music and language we will explore key themes in auditory function, learning and plasticity.

First we will look to the origins of music and language: we shall not attempt to resolve the ongoing debate regarding their evolutionary status, but we will consider what their structural characteristics and functional origins reveal about the human relationship with sound. Then we will focus on the role of temporal structure in music and language, and how temporal patterns provide a framework for information processing in the brain. Next we will consider how music and language are learned, emphasizing interactions between the auditory system, cognition, and emotion and reward centers in the brain. The final section of this chapter will focus on the biology of sound processing and how experience with music and language influences underlying neural function. We will show that auditory expertise strengthens

some of the very same aspects of sound encoding that are deficient in impaired populations and discuss the implications for clinical and social contexts.

MUSIC AND LANGUAGE: STRUCTURAL AND FUNCTIONAL ORIGINS

Structure rooted in sound

Both music and language are complex communication systems, in which basic components are combined into higher-order structures in accordance with rules. Whether music was an evolutionary precursor to language (Mithen, 2005) or merely a byproduct of cognitive faculties that developed to support language (Pinker, 1999), music is pervasive across human cultures and throughout history, with evidence of prehistoric bone and ivory flutes dating back over 42,000 years (Higham et al., 2012). The capacity of music to convey emotion is driven not only by cultural conventions but by the underlying psychophysical properties of sound and cochlear mechanics (Balkwill and Thompson, 1999; Tramo et al., 2001; Gomez and Danuser, 2007). For example, the perception of consonance and dissonance arises at least in part from the different vibration patterns generated by combinations of frequencies and their harmonics on the basilar membrane, where consonant intervals comprise simple frequency ratios and generate less interference than dissonant intervals (Von Helmholtz, 1912). Consonant intervals are typically considered to be pleasing to the ear (Trainor, 2008), which may reflect a relationship between ease of perceptual processing and positive emotional state (Reber et al.,

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1998, 2004). Children's innate receptivity to music from a very young age, including their ability to perceive consonance and dissonance (Trainor and Heinmiller, 1998; Zentner and Kagan, 1998; Trehub, 2003), reinforces the idea that musical structure is rooted in fundamental characteristics of sound and sensory perception.

An important distinction between music and language is in their differing degrees of semantic specificity. While language can be used to convey precise semantic content between individuals, precision can also lead to disagreement; music lacks semantic specificity but plays an important role in promoting social bonding (Cross, 1999; Trehub, 2003), as demonstrated experimentally by an increase in cooperative behavior in young children following joint music making (Kirschner and Tomasello, 2010). In this sense, language enables articulation of what is within us, whereas music strengthens what is shared between us.

Communication in context

While we are largely focused on music and language as forms of auditory communication, it is important to acknowledge that the auditory system does not function in isolation, especially within the context of communication. Other sensory modalities, such as vision, help the brain to construct a percept of sound object (Schutz and Lipscomb, 2007; Musacchia et al., 2008) and can influence speech perception. This is demonstrated by the McGurk effect, in which a video presenting repeated utterances of the syllable [ba] dubbed on to the lip movements for [ga] result in normal-hearing adults perceiving a hybrid percept, the syllable [da] (McGurk and MacDonald, 1976). In the case of music and language, this cross-modal integration is important in helping to determine the communicative intent which produced a sound, and thereby determining its meaning, thus: "Speech is processed both as a sound and as an action" (Scott and Johnsrude, 2003). Similarly, it has been shown that the perception of musical performances can be significantly influenced by non-auditory cues, such as body movements (Tsay, 2013).

Music and language are likely to have evolved in conjunction with important shifts in the emergence of human cognition, and while the exact sequences and interdependence of these evolutionary trajectories are debated (Cross, 1999; Mithen, 2005; Fitch, 2006), it is clear that processing of music and language relies upon cognitive capacities, such as working memory. There is evidence that expertise such as musical training is associated with greater auditory working-memory capacity across the lifespan (Bugos et al., 2007; Kraus et al., 2012), which also relates to better performance on everyday listening tasks such as perceiving speech in a noisy

background (Parbery-Clark et al., 2009b; Kraus and Chandrasekaran, 2010; Anderson et al., 2013). Taken together, these outcomes emphasize that the ability to make sense of sound in a communication context relies heavily upon integration between the auditory system and other cognitive and sensory systems. We will provide further discussion of how these relationships are mediated by experience with music and language in the final section of this chapter.

TEMPORAL PROCESSING IN MUSIC AND LANGUAGE

The auditory system plays a unique role as the temporal processing "expert" in the nervous system, with micro-second precision required for the localization of sounds (Mauk and Buonomano, 2004). The ability to lock on to temporal patterns is a fundamental aspect of auditory processing, and is especially important for the perception of communication sounds: meaningful information unfolds simultaneously over multiple timescales in both speech and music, from overarching rhythms and stress patterns, to the fine-grained timing differences which differentiate consonants and characterize the distinctive timbre of a voice or musical instrument.

The timing precision of the auditory system is also important for sensorimotor coordination, with a study of 16 normal adults showing that synchronization of finger tapping to an auditory stimulus is more accurate than to a visual stimulus (Repp and Penel, 2002), and a study from our laboratory with 124 typically developing adolescents showing that the ability to synchronize with a beat tracks with more consistent subcortical neural timing in the auditory system in response to speech sounds (Tierney and Kraus, 2013a).

The integration between auditory and motor systems is especially strong in vocal learning species, with co-activation of comparable motor and auditory brain regions in both humans and songbirds during vocal learning tasks (Brown et al., 2004). Rhythm perception involves activation of motor regions of the brain (Zatorre et al., 2007; Chen et al., 2008), and it has been proposed that the ability to synchronize to a beat may rely upon the same auditory-motor neural infrastructure that evolved to support vocal learning (Patel, 2006; Patel et al., 2008, 2009; Patel and Iversen, 2014). This ability has been observed in humans and other vocal learning species but is otherwise very rare in non-human animals, however, individual cases of beat-keeping abilities in non-vocal-learning species such as the sea lion (Cook et al., 2013) leave this a matter of continuing research.

The motor system is not only involved in the production of linguistic and musical sounds (Zatorre et al., 2007; Nasir and Ostry, 2009); motor areas are also

activated during the perception of speech and music, when no explicit movement is involved (Zatorre et al., 2007; Chen et al., 2008). In particular, motor regions of the brain such as the cerebellum and basal ganglia are activated during the perception of rhythm (Grafton and Brett, 2007; Chen et al., 2008), which is unsurprising given the direct origins of rhythm in physical movement. Together, these findings emphasize that auditory processing does not happen in isolation: the neural networks involved in the acquisition and production of communication sounds also play a role in their perception. Further, the involvement of other brain areas can be influenced by an individual's previous experience with specific sounds, as demonstrated by a study with 15 adult pianists in which experimenters observed greater excitability in motor regions of the brain while listening to a rehearsed piece of music compared with an unfamiliar piece (D'Ausilio et al., 2006).

Rhythm as a “temporal map”

In the perception of both music and language, rhythm provides a “temporal map” with signposts to the most likely locations of meaningful input. The ability to anticipate based on prior experience can help to streamline attention and processing resources; for example, timing regularities in speech may help a listener develop temporal expectations about when important phonetic information is likely to occur (Pitt and Samuel, 1990; Quene and Port, 2005; Schmidt-Kassow and Kotz, 2008, 2009; Roncaglia-Denissen et al., 2013). Sensitivity to temporal patterns is critical to language acquisition, since it assists in the detection of word boundaries in a continuous speech stream (Nakatani and Schaffer, 1978; Cutler and Butterfield, 1992). These parsing mechanisms are critical to developing accurate representations of meaningful sound elements which can then be mapped to written language, and the ability to make use of rhythmic cues when perceiving speech has been linked to reading ability (Wood and Terrell, 1998; Whalley and Hansen, 2006; Gutiérrez-Palma and Palma Reyes, 2007; Holliman et al., 2008, 2010). One study found that performance on a metric perception task strongly predicted reading ability and phonologic awareness across a population of normal and dyslexic subjects (Huss et al., 2011) and a longitudinal study in a sample of 695 French children showed that rhythm reproduction skills in kindergarten were predictive of reading ability in second grade (Dellatolas et al., 2009). A recent study with preschoolers revealed that those who were able to synchronize with a beat performed better on tests of pre-reading skills, including phonologic awareness, and demonstrated more precise neural encoding of the temporal modulations in speech than those who were unable to synchronize (Woodruff

Carr et al., 2014). Impaired rhythmic abilities have been associated with language disorders such as dyslexia (Overy et al., 2003; Thomson and Goswami, 2008; Corriveau and Goswami, 2009; Huss et al., 2011) and there has been some success in using rhythm-based interventions to address reading difficulties in children (Bhide et al., 2013). Music-based therapies, such as melodic intonation therapy, have been used to facilitate the rehabilitation of speech function in aphasic patients by emphasizing “musical” features of speech and thereby engaging neural networks normally involved in the processing of music, to compensate for damaged language-processing regions (Schlaug et al., 2008). Interestingly, a recent study with 17 aphasic patients revealed that rhythmic speech improved articulatory quality in patients whereas melodic intonation alone did not, suggesting that rhythm may play a critical role in the effectiveness of this therapy (Stahl et al., 2011).

In the musical realm, a 2010 study looked at how rhythm influences attention during the process of stream segregation while listening to interleaved melodies, showing that subjects more effectively suppressed a distractor melody when the distractor was rhythmically regular (Devergie et al., 2010). The authors highlight this as evidence for the importance of rhythmic attention in auditory scene analysis, within the framework of the dynamic attending theory (Large and Jones, 1999; Jones et al., 2002). Another study demonstrated that musical training improved performance in a lexical stress-processing task (Kolinsky et al., 2009), suggesting a transfer of rhythmic expertise to speech perception. These studies support the idea that, despite its natural irregularities, metric structure is an important organizing principle for language as well as music, that our perceptual systems are tuned to take advantage of this, and that attention plays a significant role in that tuning process (Kotz et al., 2009; Schmidt-Kassow and Kotz, 2009).

Temporal predictability also serves an important function in communication by facilitating interpersonal synchrony (Phillips-Silver et al., 2010): from the exchange between a mother and her newborn (Censullo et al., 1985) to the exquisitely choreographed complexities of conversational turn taking (Auer et al., 1999) and the interplay of improvisational jazz (Berkowitz, 2010), the ability to coordinate human behavior in time not only streamlines the flow of information, but also engenders greater affiliation between individuals (Hove and Risen, 2009; Cirelli et al., 2012; Launay et al., 2013).

REGULARITY AND VARIABILITY IN TEMPORAL STRUCTURE

One notable difference between music and language is that music typically contains a regular beat, whereas

the temporal patterns of natural speech are less regular and more free-flowing (Patel, 2006, 2010). It has been proposed that much of the emotional power of music stems from the creation (and violation) of temporal expectancies within a metrically predictable framework (Huron, 2006). It is also important to note that, although music is formulated around a regular pulse, live music performances contain significant timing fluctuations and exhibit more complex temporal patterns, closer to the free-flowing rhythms of speech (Repp, 1992; Palmer, 1997; Large et al., 2002; Ashley, 2002; Levitin et al., 2012).

Despite the tempo fluctuations of live performances, listeners have no difficulty perceiving the underlying pulse of music (Large and Snyder, 2009; Rankin et al., 2009), indicating that the ability to extract a beat does not rely upon rigid predictability but rather can be conveyed through more subtle timing cues. Analyses of musical excerpts have revealed that the timing variations in musical performance exhibit fractal characteristics (Rankin et al., 2009; Levitin et al., 2012) that are found in many other naturally generated time series, from heart beats (West and Shlesinger, 1989) to the dynamic oscillations of neuronal populations (Engel et al., 2001; Linkenkaer-Hansen et al., 2001; Large and Snyder, 2009). Human sensory systems have an inherent preference for signals that exhibit these fractal characteristics (Gilden et al., 1995; Yu et al., 2005), and naturally generated movement sequences, such as gait (Hausdorff, 2007) and tapping to a beat (Torre and Delignières, 2008) vary over time according to the same underlying mathematic relations.

Neural basis of temporal processing: oscillatory rhythms

In recent years there has been increased interest in the role of oscillatory brain rhythms in the coordination of activity across cortical regions and in establishing temporal binding and prediction mechanisms in the brain (Engel and Singer, 2001; Engel et al., 2001; Buzsaki and Draguhn, 2004; Sauseng and Klimesch, 2008; Buzsaki, 2009; Uhlhaas et al., 2009). It is argued that predictable variations in the balance of ongoing neuronal activity increase the efficiency of information processing (Buzsaki, 2009) and that some degree of noise in the nervous system may, in fact, confer processing benefits (Faisal et al., 2008). The dynamic attending theory mentioned above proposes that attention can be modulated over time based on temporal expectancies that are tracked by neuronal oscillatory activity (Large and Jones, 1999). Recent research into the neural bases of rhythm perception indicates that neural oscillatory activity also plays an important role in encoding musical

rhythm (Fujioka et al., 2009, 2012; Large and Snyder, 2009; Levitin, 2009; Grahn, 2012; Nozaradan et al., 2012).

The brain's ability to make use of temporal patterns in extracting meaning from speech may also be driven by underlying oscillatory activity, which allows the brain to "entrain" to various aspects of temporal structure (Luo and Poeppel, 2007; Schmidt-Kassow and Kotz, 2008; Ghitza and Greenberg, 2009; Giraud and Poeppel, 2012), with different frequency bands of brain activity concurrently synchronizing to different components. It has further been suggested that poor reading skills and language-based learning impairment may result from deficient oscillatory mechanisms (Abrams et al., 2009; Goswami, 2011; Kraus, 2012). If the brain cannot lock on to underlying temporal information patterns, the efficiency of information processing is greatly reduced. This causes disruption in attention and memory resources and impedes coordination between brain regions, as is evidenced in impaired multisensory integration common in dyslexics (Facoetti et al., 2010; Goswami, 2011). The cerebral hemispheres show specialization in their encoding of different temporal integration windows based on distinct frequency bands of dominant oscillatory activity, with the left hemisphere specialized for fast acoustic processing and the right hemisphere specialized for slower temporal processing (Belin et al., 1998). Stronger reading abilities have been linked to stronger lateralization of relevant timing rates within the speech signal, such as right-hemisphere specialization for the slower syllable rate of speech (Poeppel, 2003; Abrams et al., 2009; Goswami, 2011). Oscillatory mechanisms may therefore play an important role not only in integrating activity across disparate regions of the brain, but in melding the activity within more specialized local networks.

As with the rhythmicities of speech and music, neuronal entrainment is happening simultaneously on multiple timescales. This increases the information-processing capacity by using pattern extraction and prediction to allocate neural resources as efficiently and effectively as possible (Fig. 12.1). We have seen that deficiencies in oscillatory mechanisms may result in language-related difficulties; further, musical training has the potential to strengthen oscillatory function (Trainor et al., 2009). This is an exciting area of research in which there is much work still to be done, with great potential for informing the use of music as a means of strengthening language abilities.

In summary, despite greater variability in the rhythms of natural language compared with the perceived musical beat, both exhibit complex temporal structure. Neural oscillations across different frequency bands provide an important mechanism by which the brain is able to lock

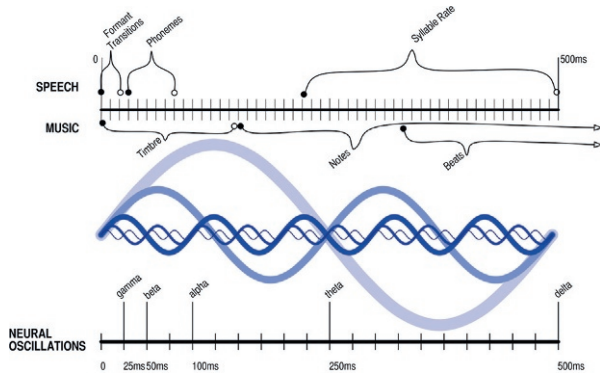


Fig. 12.1. Timescales of speech and music characteristics: different frequencies of neural oscillatory activity lock on to meaningful temporal patterns in speech and music.

on to underlying temporal patterns in both music and speech. Taken together, these findings show that the communicative systems of music and language are exquisitely in tune (or in time!) with the temporal processing mechanisms of the human brain.

MUSIC AND LANGUAGE: MODELS OF LEARNING AND PLASTICITY

Rule-based learning

Mastery of both music and language depends upon rule-based learning, which involves an ongoing process of perception, prediction, feedback, and correction. A comparison of grammar acquisition in human infants and non-human primates suggests that human learning mechanisms are distinctively tuned to complex predictive patterns (Saffran et al., 2008), and while there is some evidence of recursive sequence generation in non-human communication such as birdsong (Gentner et al., 2006), the degree of complexity of grammatic structure in human communication may be unique. As infants acquire language, they are able to implicitly extract statistical regularities to help guide the segmentation of a continuous acoustic stream into syllables and words, thereby constructing a framework from which they can begin to map sounds to meaning (Saffran et al., 1996, 2001; Conway and Pisoni, 2008; Conway et al., 2010; Romberg and Saffran, 2010).

Motivation plays an important role in learning, and activation of reward centers in the brain has been associated with neural plasticity (Wise, 2004; Day et al., 2007). As the brain starts to build predictions based on experience, the reward pathways are activated not only by the reward itself, but in anticipation of likely reward (Knutson et al., 2001), with the degree of activation reflecting the statistical probabilities derived from prior experience (Morris et al., 2004). Release of the neurotransmitter dopamine provides a chemical mechanism

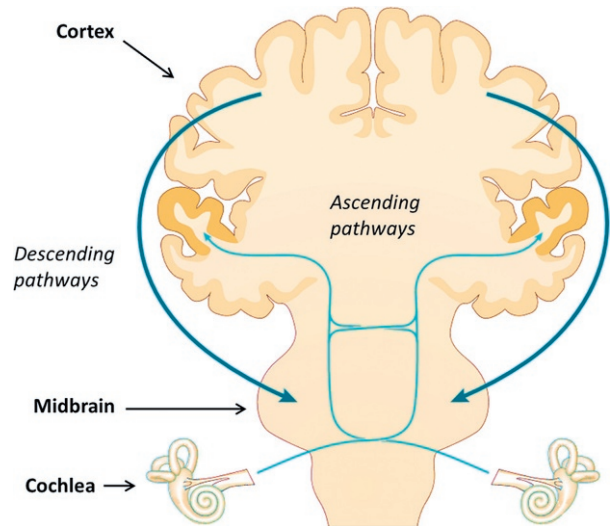


Fig. 12.2. Patterns and predictability are important for processing both speech and music. Neural responses to speech sounds are enhanced under predictable conditions in good readers, but not in poor readers, and this enhancement tracks with rhythm skills.

by which patterns, predictions, and feedback are tracked within the brain (Salimpoor and Zatorre, 2013), and the same chemical signal is involved in the implicit learning functions of the basal ganglia, which are implicated in the acquisition of linguistic and musical grammar (Ullman, 2001, 2005; Conway and Pisoni, 2008; Ettlinger et al., 2011).

Evidence of relationships between rapid auditory processing skills and neural indices of implicit learning (McNealy et al., 2006) suggest that basic temporal processing abilities may provide the foundation for more complex, rule-based learning. There is ongoing debate as to whether the same neural processes underlie learning in both music and language (Rogalsky et al., 2011), but there is evidence of some overlap in the neural resources involved in the processing of linguistic and musical syntax (see Patel, 2003, for a review), and that musical expertise results in improved implicit learning abilities for both musical and linguistic structures (Ettlinger et al., 2011; Francois and Schön, 2011; François et al., 2013; Skoe et al., 2013).

Further, there is evidence that the statistical context of a sound influences neural encoding in the auditory brainstem (Skoe et al., 2013), and that the extent of this neural enhancement relates to language-related skills such as speech-in-noise perception (Chandrasekaran et al., 2009; Parbery-Clark et al., 2011), as well as reading abilities and rhythm-related skills (Strait et al., 2011). These outcomes suggest that common underlying pattern detection abilities are involved in the extraction of meaning from sound in both music and language (Fig. 12.2).

LEARNING TRAJECTORIES IN MUSIC AND LANGUAGE

While the developmental trajectory of native language acquisition is relatively consistent, at least within a given culture, there is much greater diversity in the extent of musical participation and style of musical training: from none at all, to a lifetime of intensive instruction and practice. Given evidence for some degree of commonality between music and language learning, the greater diversity in musical experience can provide invaluable insight into the underlying mechanisms of learning and in illuminating how training and experience interact with development. In particular, while it is widely acknowledged that acquiring a second language or learning to play a musical instrument is much easier at a young age, there is ongoing debate regarding the existence of so-called “sensitive periods” and what they reflect about the underlying neural circuitry of learning. It has been shown that, while infants are able to differentiate phonetic categories in a non-native language, this ability diminishes within the first year of life (Werker and Tees, 1984). Similar constraints are evident in the acquisition of musical structure; for example, infants are able to differentiate metrical categories from another musical culture while adults only respond to those which exist in their own culture (Hannon and Trehub, 2005). However these constraints may not be set in stone, as there is evidence to suggest that enriched experience such as musical training can heighten the nervous system’s receptivity to learning during these sensitive periods (Skoe and Kraus, 2013).

Children are natural improvisers: it is notable that young children will often create their own songs before they can reproduce learned songs (Trehub, 2003), and research into childhood play behavior suggests that high-quality play is important for the development of abstract thinking, as well as social and linguistic competence (Bergen, 2002). Adult second-language instruction provides an interesting contrast with native-language learning since typically it involves greater emphasis on explicit learning of rules and memorization of phrases, with less experimentation and play than occurs in childhood language acquisition. There is evidence that the balance of learning style may shift over development, from implicit procedural-based learning in childhood (Kuhl, 2004) to more explicit, declarative learning styles in adulthood, and that this reflects a shift in the underlying memory systems involved in learning between childhood and adulthood (Ullman, 2005).

There is much still to be discovered about how we learn to communicate through music and language, and the wide range of musical learning styles and experiences present within the normal population presents a rich opportunity for further investigation. This area of research is of particular interest to educators and

clinicians given that musical experience can strengthen aspects of brain function which also support language-related skills (Patel, 2011; Strait and Kraus, 2014), and may thereby offer a framework for the remediation of language difficulties. Since music making integrates brain activity across sensory, motor, and reward regions, engagement in musical activities strengthens neural networks that benefit other non-musical activities and promotes neural plasticity throughout the lifespan (Wan and Schlaug, 2010; Herholz and Zatorre, 2012); in other words, music may help prime the nervous system for learning, in part by “exercising” the reward systems which are critical to plasticity (Salimpoor and Zatorre, 2013). In the case of expert musicians, the drudgery of daily practice may not offer immediate positive reward but still represents emotional engagement in the task, and the longer-term goal of skilled communication and expression through music provides a motivational framework that is critical to the attainment of expertise (Ericsson et al., 1993).

NEURAL PLASTICITY: THE INTERACTIVE AUDITORY SYSTEM

In this section we will look at relations between music and language from the perspective of how sound is represented by the nervous system. Many aspects of the neural encoding of speech and music have been covered in previous chapters, with the first chapter focused on ascending auditory pathways: it is perhaps fitting that this chapter will close the section by emphasizing the great importance of the descending pathways. In particular, we will examine how experience can fine-tune the auditory system’s ability to extract meaning from sound through the interaction of sensory and cognitive processing (Suga and Ma, 2003; Bajo et al., 2009) (see Figs 1.10 and 1.15 in Chapter 1).

There has been extensive and important debate regarding the degree to which music and language functions are distinct within the brain (Patel and Peretz, 1997; Peretz and Hyde, 2003; Patel, 2010). Rather than reviewing the cortical areas and neural networks that are involved in specialized aspects of sound processing, we will focus on the underlying subcortical representation of sound, where sensory and cognitive influences converge. We shall summarize evidence for neural plasticity resulting from music and language experience, as well as showing that many of the same aspects of sound processing that are selectively enhanced through expertise are deficient in populations with language-based impairments such as dyslexia. We will end the section with a discussion of the clinical implications of these findings for the remediation of language and learning disorders.

The auditory brainstem: hub of auditory information processing

The brainstem auditory nuclei are highly specialized for very precise neural signaling, which underlies the complex temporal processing necessary for biologically critical functions such as sound localization (Oertel, 1999). Importantly, the auditory system is not a one-way street: the extensive network of efferent pathways enables dynamic modulation of signal processing, as well as long-term tuning of sensory function with experience (Suga and Ma, 2003; Bajo et al., 2009) (see Fig. 1.15 in Chapter 1). The inferior colliculus in the brainstem is a critical information-processing hub in which top-down cortical influences converge with multiple bottom-up sensory inputs to compile an integrated and comprehensive representation of the auditory scene. On this basis, the role of the inferior colliculus has been described as the auditory analog to the primary visual cortex in the visual system, generating a “whiteboard” of all available information from which higher processing pathways diverge (Nelken, 2008). There are also direct connections between the inferior colliculus and brain regions important for motor control and coordination, including output to the cerebellum and input from the basal ganglia (Casseday et al., 2002), which also play an important role in pattern learning, as discussed above (see Fig. 1.15 in Chapter 1).

In our lab, investigation of the evoked auditory brainstem response to complex sounds (of which the

inferior colliculus is a primary generator) has proved an extremely fruitful approach in exploring mechanisms of experience-based plasticity (Kraus and Chandrasekaran, 2010; Skoe and Kraus, 2010). The evoked brainstem response preserves fundamental characteristics of the incoming signal such as its timing, fundamental frequency, and harmonics, allowing direct comparison between the response and its evoking stimulus. By comparing stimulus and response characteristics in both time and frequency domains, it is possible to assess the neural representation of spectral characteristics important for the perception of pitch and timbre, as well as neural response timing and consistency across trials. The evoked responses has also been shown to be sensitive to experience (Krishnan et al., 2005; Tzounopoulos and Kraus, 2009; Krizman et al., 2012; Kraus and Nicol, 2014) and therefore offers an objective biologic snapshot of how sound is processed in an individual. We have used this approach to explore how music and language are processed by “auditory experts” such as bilinguals and musicians, as well as in individuals with language impairments (Fig. 12.3).

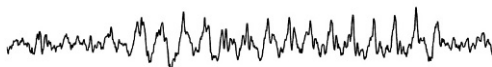
Selective enhancement: neural signatures of auditory expertise

MUSICAL EXPERTISE

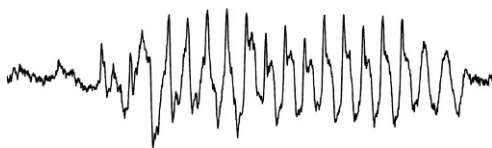
Experience does not shape auditory function with a simple volume knob effect: rather, the effect is more like a mixing board, boosting important components, attenuating irrelevant inputs, and exploiting patterns in the incoming signal to reduce redundant processing. In combination these modulations help to bring out what is meaningful with the greatest possible clarity and efficiency. Of course, what is meaningful to any given individual will depend upon their specific type of experience, resulting in distinct “neural signatures” of expertise (Kraus and Nicol, 2014). Musicians’ neural responses can be enhanced specifically for the sound of their own instrument: pianists demonstrate more robust subcortical representation of a piano sound than of a bassoon or cello tone (Strait et al., 2012a), and there are timbre-specific effects on cortical evoked responses (Pantev et al., 2001) as well as neural oscillatory activity (Shahin et al., 2008) based on the instrument of practice. The style of music played may also influence plasticity effects, with jazz musicians demonstrating greater sensitivity to acoustic features in their preattentive brain responses to sound (Vuust et al., 2012).

In addition to the selective enhancement of the sounds or patterns that are meaningful to an individual, extended experience also shapes the automatic processing of sound, and thereby influences perception in auditory domains beyond the specific area of expertise. Musicians demonstrate more robust brainstem encoding

Language-Impaired Child



Normal Adult



Musician

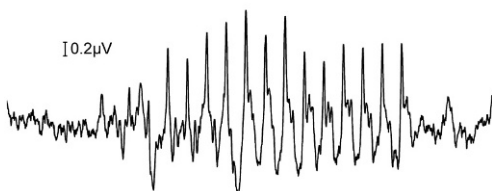


Fig. 12.3. Representative waveforms showing individual variation in brainstem responses to speech. Auditory expertise such as musical training has been shown to strengthen many of the same aspects of the neural encoding of sound that are deficient in individuals with language impairment.

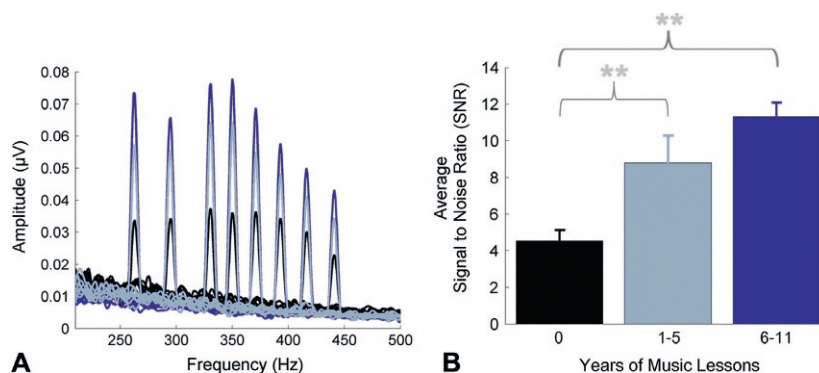


Fig. 12.4. Musical practice during childhood is associated with more robust neural responses to sound in adulthood, years after training has stopped. Adults with no past musical experience (in black) have smaller-amplitude brainstem responses (smaller signal-to-noise ratios (SNRs)) relative to adults who played a musical instrument from around the age of 9, and continued to play for either 1–5 (light blue) or 6–11 (dark blue) years. (A) Frequency-following responses to eight sounds of varying frequency. (B) Average SNR across the eight sounds for each group (mean $\pm$ 1 SEM). $^{***}P < 0.01$. (Adapted from Skoe and Kraus, 2012.)

of speech sounds in noise (Parbery-Clark et al., 2009a; Strait et al., 2012b, 2013b) and less degradative effects of reverberation on neural encoding of the harmonic information in speech sounds (Bidelman and Krishnan, 2010) compared with non-musician counterparts. Musicians also demonstrate enhanced neural representation of the emotion-carrying portion of a baby's cry (Strait et al., 2009), more accurate brainstem encoding of linguistic pitch patterns in an unfamiliar tonal language (Wong et al., 2008), and a greater benefit of audiovisual integration in their encoding of music and language sounds (Musacchia et al., 2007).

Neural representation of meaningful timing characteristics is also more precise in musicians; for example, they show greater neural differentiation of contrastive consonant sounds than non-musicians across the lifespan (Parbery-Clark et al., 2012c; Strait et al., 2013a; Kraus et al., 2014a). There is evidence that musical experience offsets age-related delays in neural timing in older adults and increases the consistency of neural responses (Parbery-Clark et al., 2012a, b). Further, musicians' subcortical encoding of sound is influenced by harmonic context (Bidelman and Krishnan, 2009; Lee et al., 2009; Marmel et al., 2011) as well as by statistical predictability (Parbery-Clark et al., 2011; Skoe et al., 2013), suggesting that musical experience may strengthen the ability of the nervous system to benefit from underlying patterns in sound in both musical and linguistic contexts.

Taken together, these findings indicate that auditory expertise such as musical experience tunes the auditory system so that it can more effectively pull out a meaningful signal from a complex soundscape. Recent studies from our lab demonstrate that just a few years of musical training in childhood can influence the neural encoding of sound in adulthood, years after the training has ceased (Skoe and Kraus, 2012; White-Schwoch et al., 2013) (Fig. 12.4), emphasizing that attention to sound

in the past can result in more efficient automatic processing of sound in the present, even many years later.

There is much work still to be done in further understanding the parameters of plasticity across the lifespan. It seems plausible that similar overall “information processing” benefits could result from very different types of musical expertise, each with their own underlying neural signatures: a vocalist may tune into pitch and a drummer may tune into timing, but both may be better at “tuning in” to meaningful sound in general (Slater et al., 2014). This is reflected in behavior, with musicians showing enhanced speech-in-noise perception across the lifespan (see Strait and Kraus, 2014 for a review). Much of the work so far in the field of musical experience-based plasticity has focused on the comparison between musicians and non-musicians; further investigation into the distinct effects of different types of musical activity on plasticity and learning presents a promising area for future research and would advance understanding of how selective neural enhancements relate with more general perceptual benefits.

BILINGUALISM

In the language domain, bilinguals represent another example of auditory expertise: there is converging evidence that bilingual experience engenders functional and structural changes in cortical language networks (Kim et al., 1997; Crinion et al., 2006). Bilingual experience also strengthens cognitive function (Bialystok et al., 2012) and may counteract age-related cognitive decline, with bilinguals demonstrating later onset of dementia than monolingual peers matched for potentially confounding factors such as education and socioeconomic background (Bialystok et al., 2007; Alladi et al., 2013).

Recent work from our lab reveals more robust subcortical representation of a speech syllable in bilingual adolescents compared with age-matched monolinguals (Krizman et al., 2012, 2014). Specifically, bilinguals show a selective enhancement in the encoding of the fundamental frequency, which has particular salience for bilinguals in helping to identify a language switch (Altenberg and Ferrand, 2006), and this enhanced subcortical representation is related to stronger attention skills (Fig. 12.5).

Both music and language expertise have been shown to strengthen cognitive function, such as auditory attention, working memory, and executive control (Bialystok, 2012; Bugos et al., 2007; Kraus et al., 2012). It is proposed that the observed enhancements in the neural

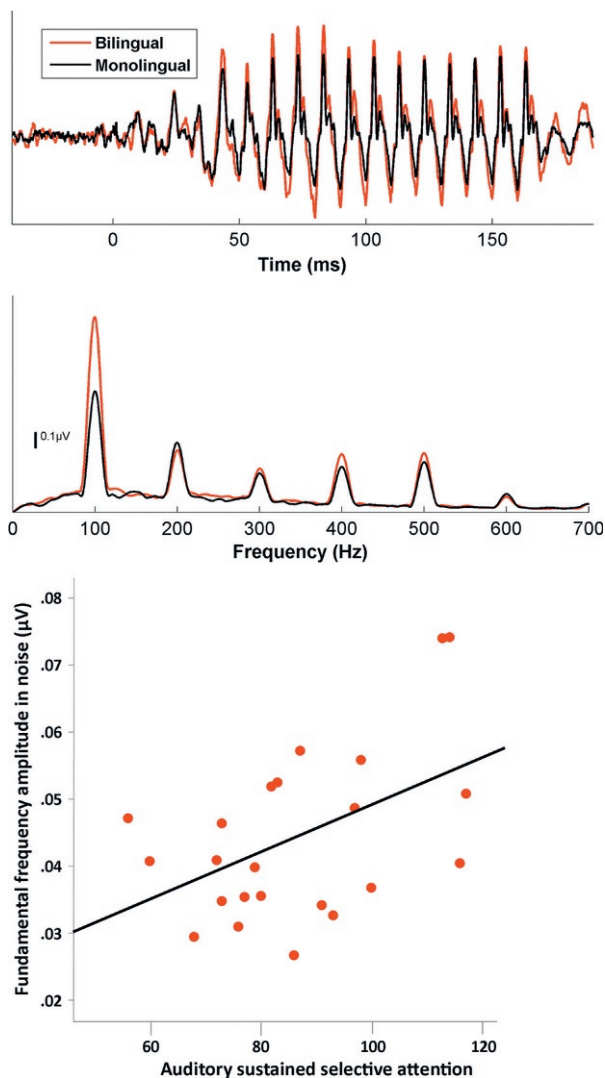


Fig. 12.5. Bilinguals (red) show a larger neural response to the fundamental frequency (100 Hz) of a speech sound than monolinguals (black). Within the bilingual group only, sustained selective attention ability correlated with the amplitude of the fundamental frequency encoding ($r=0.483$, $P=0.02$). (Adapted from Krizman et al., 2012.)

encoding of sound may be driven in a top-down manner by this strengthened cognitive function (Nelken and Ulanovsky, 2007; Ahissar et al., 2009; Conway et al., 2009; Kraus and Chandrasekaran, 2010; Kraus et al., 2012) by more effectively homing in on relevant aspects of the signal, as well as by coordinating underlying neural activity, thereby promoting more consistent and robust neural responses (Krizman et al., 2012; Parbery-Clark et al., 2012b; Skoe and Kraus, 2013).

Neural underpinnings of language ability and impairment

In this section we will consider the relationship between reading and the neural encoding of sound in both typically developing and impaired populations. While it is not always intuitive to think of reading as an auditory skill, the first internal representations of linguistic meaning in a typically developing child will come from exposure to speech; the accurate mapping of orthographic representations to meaning is therefore dependent upon these sound-based representations, and auditory processing skills in infants have been shown to predict later reading performance (Benasich and Tallal, 2002; Boets et al., 2007, 2008, 2011; Corriveau et al., 2010). An important characteristic of speech is that the most meaningful parts of the signal are carried by the fastest-changing components, namely the consonants. The ability to encode these subtle timing differences is critical to developing accurate phonologic representations and therefore essential for the development of strong reading skills, with more precise subcortical timing linked to better reading abilities (Fig. 12.6) (Banai et al., 2009; Hornickel et al., 2009),

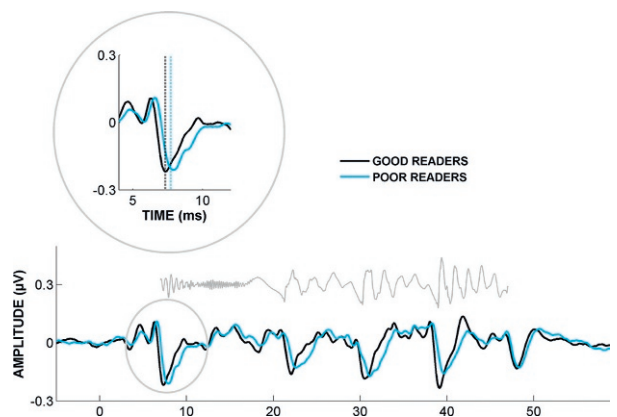


Fig. 12.6. Subcortical timing in response to speech is delayed in poor (blue) readers compared with good (black) readers. Grand average waveforms of responses to the syllable /da/. The stimulus is presented in gray, shifted by 8 ms to align stimulus features with the response. Magnified peak is shown. Standard errors surrounding the mean latency of each group are denoted by the dashed lines. (Modified from Banai et al., 2009.)

and reading difficulties associated with less consistent timing in neural responses to speech (Hornickel and Kraus, 2013).

As discussed above, oscillatory activity plays an important role in coordinating neural synchrony within different temporal frameworks which are important for speech perception, and there is evidence of links between abnormal oscillatory activity and reading impairments such as dyslexia (Nagarajan et al., 1999; Goswami, 2011; Heim et al., 2011; Kraus, 2012). The left-hemispheric specialization which supports rapid acoustic processing is predicted by the precision of brainstem encoding of speech sounds, suggesting that accurate timing in the brainstem is an important foundation for higher-level processing of the fast acoustic properties of speech which are critical to the development of reading skills (Abrams et al., 2006; Tierney and Kraus, 2013b).

Clinical implications

We have shown that auditory expertise with music and language can strengthen many of the same aspects of neural sound encoding that are found to be deficient in populations with language-related disorders (see Tierney and Kraus, 2013b for review) (Fig. 12.7). A number of studies have demonstrated that deficient neural processing of speech can be strengthened by short-term training in children with language-based learning problems (see Kraus and Hornickel, 2012 for review), such as a study of children with clinical diagnoses of language-based learning difficulties (e.g., dyslexia), in which 9 children underwent 3 months of computer-based training, while a control group of 10 children did not participate in any remediation program. The children who received training showed a significant improvement in the fidelity of their neural response to the evoking stimulus, while the control children showed no such improvement (Russo et al., 2005). Another study with 38 dyslexic children showed that use of an assistive-listening device (classroom-based FM system) for 1 year increased the consistency of neural responses to speech and that these neural changes were associated with improvements in phonologic awareness and reading skills (Hornickel et al., 2012). Taken together, the evidence for strengthened neural processing in musicians and the potential for improved speech processing following short-term training suggest that music-based interventions may also be effective in the treatment of language disorders, and this is an important area for future research.

Recent longitudinal assessments of existing music education programs provides support for the educational merits of musical training in fostering the development of critical language and learning skills (Slater et al., in press; Kraus et al., 2014b; Tierney et al.,

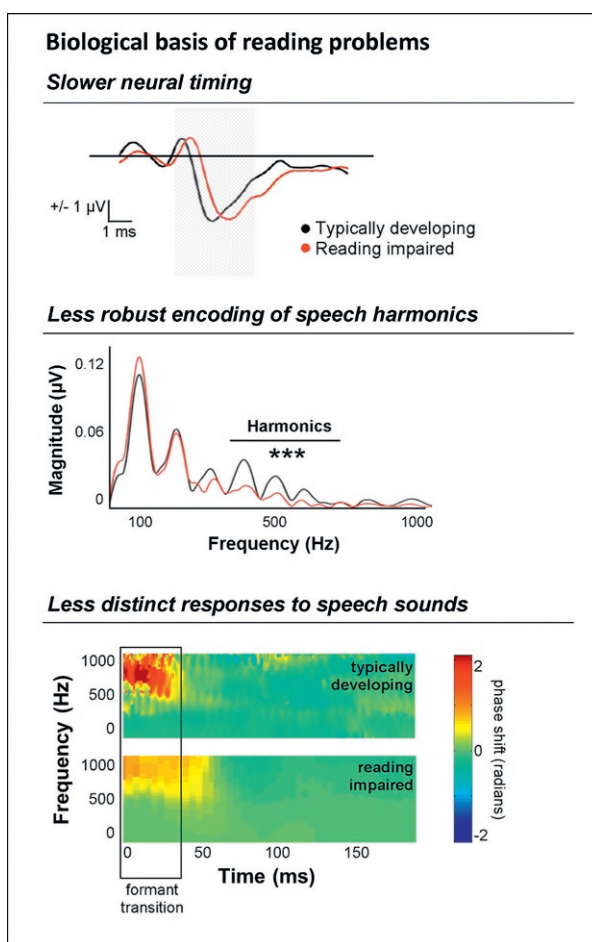


Fig. 12.7. Reading problems are associated with deficits in the neural encoding of sound. Many of the same aspects of sound processing that are deficient in populations with language-based impairments are strengthened in auditory experts such as musicians. (For review, see Tierney and Kraus, 2013b.)

2013c). Given that music can play an important role in promoting social development, interpersonal skills, and community building, the integration of music-based programs offers particular value in at-risk settings. Real world education programs, in combination with laboratory-based research, there is still a great need for longitudinal assessments to begin differentiating which aspects of musical training are driving language-related benefits. Certainly the accumulating evidence for shared temporal processing mechanisms underlying musical rhythm and language skills offers a promising avenue for future research.

CONCLUSIONS

Music and language are two sides of the human communication coin: while language is effective for semantically precise communication, the great strength of

music lies in its facilitation of social bonding and shared emotion. Both systems of communication are derived from the fundamental building blocks of sound, its inherent harmonic properties, and its temporal patterns. In many senses music and language are sewn from the same cloth, but their complementary strengths may have played distinct and important roles in the emergence of human cognition and learning.

A dominant theme in this chapter has been that of temporal processing: from the temporal structure of music and language, to the role of anticipation, prediction, and reward in learning, to the oscillatory rhythms which orchestrate perception and action. The exquisite temporal precision of the auditory system provides the biologic basis for sophisticated information processing, enabling the extraction of meaning from a complex soundscape. Through the convergence of sensory and cognitive influences, auditory function is not only shaped by the immediate demands of the environment but fine-tuned by experience over the course of a lifetime. We have demonstrated the significant impact of experience with language and music on the neural encoding of sound, and highlighted the potential for auditory training to support the development of language and listening skills, and in the remediation of language deficits.

While many ingredients of sound processing are common across species, examination of music and language reveals a degree of sophistication in both communication and underlying cognition which may be uniquely human. These rich connections illuminate our understanding of human auditory function and present many exciting avenues for future research in further disentangling the myriad rhythms of music, language and the brain.

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