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Cognitive factors shape brain networks for auditory skills: spotlight on auditory working memory

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Musicians benefit from real-life advantages, such as a greater ability to hear speech in noise and to remember sounds, although the biological mechanisms driving such advantages remain undetermined. Furthermore, the extent to which these advantages are a consequence of musical training or innate characteristics that predispose a given individual to pursue music training is often debated. Here, we examine biological underpinnings of musicians' auditory advantages and the mediating role of auditory working memory. Results from our laboratory are presented within a framework that emphasizes auditory working memory as a major factor in the neural processing of sound. Within this framework, we provide evidence for music training as a contributing source of these abilities.

Keywords: hearing in noise; auditory working memory; experience-dependent plasticity; brainstem

Introduction

Listening to and understanding speech is an extraordinarily complex task involving a vast array of sensory and cognitive processes. The acoustic complexity of speech makes it particularly vulnerable to masking by other environmental sounds. Still, for the normal system, understanding speech in noise is something that our intricately tuned auditory system routinely accomplishes. Humans often face situations in which background noise impairs speech perception, yet musicians are less impeded by noise than the rest of us.[1–3] In standardized testing circumstances, accomplished musicians perform better in understanding speech in noise than their age- and hearing-matched peers. Aside from the implications that this result promotes regarding common music/speech physiological mechanisms, it also opens the question of the route by which musical training affords speech-in-noise processing advantages. Patel's OPERA hypothesis,[4] which is reviewed later, outlines conditions necessary for the successful transfer of learning from music to language domains. It addresses the convergence of the many levels of processing that music and speech share, and how musical training can enable us to capitalize on this overlap to enhance language function.

Hearing speech in noise

The ability to successfully listen to speech in noisy backgrounds involves both sensory- and cognitive-based skills. At the sensory end of the continuum, the auditory system must lock on to the target speech signal while excluding competing voices and ambient noise. This is accomplished by organizing disparate, overlapping auditory inputs into different streams by using grouping strategies based on shared characteristics such as location and acoustical similarity.[5] The relative stability of voice pitch, or fundamental frequency, over time in the course of running speech gives a speech stream an identity and aids in grouping it separately from other voices, even those close in pitch to the voice of interest.[6,7] In addition to voicing, other signal-based cues, such as timing, harmonics, and location, aid in group formation of speech.[8] At the cognitive end of the spectrum, a listener's attention and working

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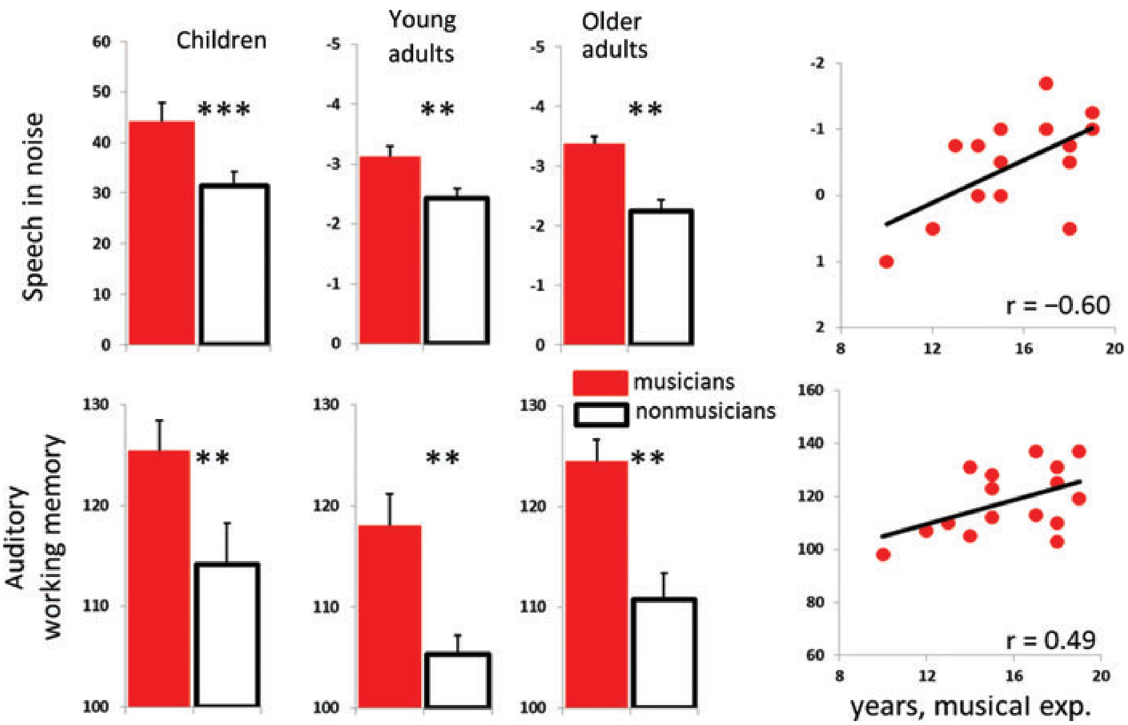

Figure 1. First three columns: musicians (solid, red) perform better than nonmusicians (open, black) in both hearing-in-noise ability (top) and auditory working memory (bottom). This is true for school-age children (left, age range 7–13; musician $n = 15$, nonmusician $n = 16$), young adults (center, age range 18–30; musician $n = 16$, nonmusician $n = 15$), and older adults (right, age range 45–65; musician $n = 18$, nonmusician $n = 19$). In all age ranges, groups were otherwise matched in IQ and audiometric thresholds. Child speech-in-noise scores are expressed in percentiles; young and older adult speech-in-noise scores expressed in threshold signal-to-noise levels (dB). Auditory working memory expressed as standardized scores. $^{**}P < 0.01$; $^{***}P < 0.001$. Right column: hearing-in-noise ability and working memory skill vary as a function of years of musical experience in young adults. These relationships also hold for children and older adults. Child, young adult, and older adult data adapted from Strait *et al.*[10] and Parbery-Clark *et al.*,[1,3] respectively.

memory skills, as well as knowledge about the world, are used to their utmost in the pursuit of a conversation in noise.[8,9] The better one's working memory and attention skills, the better the ability to hear speech in noise.[1]

Musicians, speech-in-noise perception, and auditory cognitive skills

In studies involving participants of all ages, our group is investigating the advantage musical training affords to hearing speech in noise (Fig. 1, top row). Both younger[1] and older[3] adult musicians outperform nonmusicians on standardized measures of speech-in-noise perception. School-age children (8 to 12 years) with musical backgrounds,[10] despite having enjoyed considerably fewer years of training than adult musicians, similarly outperform their peers. In these same age groups, auditory working memory has proven to be better in musicians (Fig. 1, bottom row).[1,3,10] Advantages may emerge at even younger ages, such as in preschool-age children embarking in Suzuki-Orff music training.[11] Indeed, auditory working memory and speech-in-noise perceptual abilities are correlated in all age groups and—relevant to the nature/nurture question discussed below—both track with years of musical experience (Fig. 1, right column). Although not reviewed here, musicians have demonstrated superior auditory attention skills as well.[12,13] In both children and adults, the cognitive enhancements exhibited in musicians tend to be auditory-domain specific.[1,12,14,15] It is noteworthy that rhythm skill is linked to auditory working memory and attention, and the ability of the nervous system to enhance stimulus regularities.[16]

The speech-in-noise advantage in musicians, given the importance of stream formation discussed previously, is unsurprising. A musician's auditory system is constantly tuned in to complex auditory streams, and the ability to separate and organize them is crucial to musical performance. This ability, in turn, translates to auditory perceptual advantages in other domains such as speech. The memory advantage in musicians, which we are not the first to report,[14,17] is postulated to have a basis in functional cortical activation: in a pitch memory task, nonmusicians rely more on auditory sensory areas, while musicians rely on areas of cortex more devoted to short-term memory.[18] The fact that musicians have an edge over nonmusicians in auditory memory is not entirely surprising given that much of music training involves memorization and short-term memory manipulations, such as those involved in working out a tough passage by listening to it, holding it in memory, and repeatedly executing the motor complexities of playing it. Improvisation also exercises memory, as the hook must be held in memory in order to successfully execute an improvisational flight. In addition, auditory memory is involved in the learning of notes and auditory patterns, instrumental fingerings and tuning, and remembering lyrics. Attention is likewise strongly involved in focusing on musical notation; sounds; body control, for example, fingering; and on tempi and dynamics of other musicians that you are playing with. This is akin to following a conversation in a noisy environment—memory of, and attention to, what was said a few seconds before is crucial to allowing you to make sense of what is being said at this moment.

The role of music training and a neurophysiological approach

As we have seen, musicians are better at speech-in-noise perception and auditory working memory than nonmusicians. We are working to identify the biological bases for this advantage. This section summarizes recent findings and posits a model of sensory–cognitive reciprocity accounting for the connections among neural processing, cognitive abilities, and the ability to decode speech in noisy backgrounds.

The auditory brainstem is a hub of sensory–cognitive interactions.[19] Once thought to be passive relay stations between the cochlea and the cortex, subcortical nuclei such as inferior colliculus are now understood to be highly reciprocally connected with cortical areas, affected by cognitive and emotional influences, and plastic in their response properties.[20–22] This plasticity can be wrought over different time scales—from online processing to weeks-long training to lifelong skill learning—and is accomplished via the massive efferent auditory connections that are active even out to the peripheral extreme—the hair cells of the cochlea.[23]

Our neurophysiological approach—recording auditory brainstem responses to complex sounds, the cABR—is not capable of arbitrating between bottom-up– and top-down–mediated plasticity—in other words, whether neurophysiological patterns visible in musician subcortical responses originated with hypertuned attention and memory or with locally sharpened response properties in the sensory structures. Our approach, however, provides a window into the functioning of a subcortical auditory system that is strongly affected by *both* sensory and cognitive influences. Therefore, it offers a powerful measure of the sensory–cognitive auditory system.

Accessing biology in humans

There is a long list of literature reporting biological changes following pervasive musical experience.[13,18,24–36] To better arm the reader to interpret the findings of the particular biological measure presented here, we need to say a few words about what a brainstem response to a complex sound looks like and some of the ways it can be analyzed. When stimulating with a complex sound, such as a speech syllable, the response of the auditory brainstem measured at the scalp is strikingly similar to the stimulating sound. In fact, a digitized cABR recording, played through a speaker, sounds very much like the original evoking stimulus. In the time domain, neural firing to transient events such as syllable onsets and offsets is readily visible in the response, as are the responses to the periodic voicing cycles of the vowel. In the frequency domain, a mirroring of spectral peaks is apparent, albeit with the auditory system's low-pass characteristic affecting higher-frequency amplitudes in the response. Unlike cortical responses that provide an abstract representation of the stimulus, the fidelity to the stimulus of the cABR and the resulting morphological richness lend themselves to a host of signal-processing techniques that permit examination of how stimulus attributes are biologically transduced.[37] In this review, the processing approaches used include correlation of the response to the stimulus; measuring noise-induced shifts in response timing; analyzing the frequency content of the response, especially the harmonics of voice pitch; and quantifying the timing/phase differences arising from frequency glides in consonant sounds.

Music training, speech in noise, working memory, and biological processing

The advantages that musicians have in hearing speech in noise and in cognitive processes, such as auditory memory, were examined with respect to the speech-evoked brainstem response. Using this approach enables us to determine the biological processing differences between musicians and nonmusicians and whether these differences relate to speech-in-noise perception and working memory. *Musicians*, in our studies, are defined as individuals who began their music training before the age of 9 years and have been playing at minimum three times weekly up to the time of enrollment in the study. *Speech-in-noise* tests require participants to repeat sentences that they hear in varying amounts of background noise until a threshold signal-to-noise ratio is determined.[38,39] Standardized *auditory working memory* tasks require the participant to remember, manipulate (e.g., reorder), and recite lists of words, numbers, or sentences.[40]

Response fidelity

The extent to which the nervous system generates a response that resembles the incoming sound reveals the fidelity with which the nervous system encodes sound. Correlating a digitized cABR waveform to the digitized stimulus waveform is one way to quantify this fidelity. The extent of similarity between the sound "da" and its evoked brainstem response is correlated with the ability to hear speech in noise on a standardized test (Fig. 2, top left), and this measure of biological processing, in turn, correlates with auditory working memory (Fig. 2, top center). Both child and adult musicians have responses that more

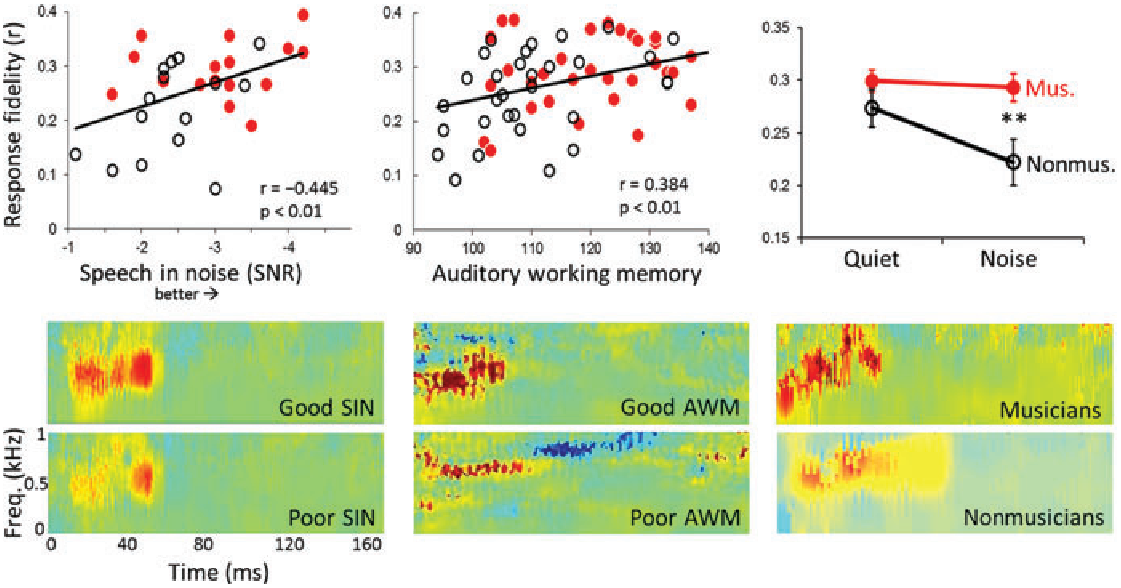

Figure 2. Two measures of neural processing, response correlation to stimulus (top row) and cross-phaseograms of responses to stop consonants ba and ga (bottom row), reveal biological underpinnings of behavior and experience. Left column: biological processing both correlates with speech-in-noise perceptual ability and reveals differences between good and poor speech-in-noise perceivers. Center column: auditory working memory patterns similarly with neural processing. In the two scatterplots, solid symbols are musicians, open symbols are nonmusicians. Right: musician and nonmusician groups also have different biological processing patterns, particularly when the evoking stimulus is masked by noise. To interpret the phaseograms, green indicates no phase differences between the two responses; warm colors, as seen in the 20–60 msec region in all cases, signify faster neural processing of ga than ba. This is the expected pattern based on the frequency content of the two syllables. $^{**}P < 0.01$.

highly reflect the acoustic properties of the evoking stimulus compared to their age-, IQ, and hearing-matched nonmusician peers (Fig. 2, top right).[10,42]

Noise-induced response delay

Background noise delays the timing of neural processing. It is thought that a better-tuned afferent auditory system will result in a response that is less delayed. To assess timing delays brought about by noise, we can either measure the timing of discrete response peaks or use cross-correlation procedures to compare responses to the same stimulus when presented in a quiet versus a noisy background.[41] The extent of the response shift between quiet and noisy backgrounds can serve as a metric of processing integrity. Indeed, in young adult musicians, the delay incurred by background noise is smaller than in otherwise-matched nonmusicians.[10,42] An almost identical pattern is seen in children who are either good or poor speech-in-noise perceivers.[43] In all of these populations, working memory is strongly correlated with both speech-in-noise perception and the degree of noise-induced cABR timing shift.

Response spectrum

The frequency composition of speech and music is preserved in the neural response, and the spectrum of the response yields a rich source of information regarding the encoding of a sound's frequency composition. The encoding of the harmonics, in particular, reveals a musician/nonmusician distinction. To a "da," the neural encoding of the syllable's harmonics is enhanced in musicians both when presented in quiet and in a noisy background.[10,42] This is seen both in children and young adults, and in both groups the extent of the harmonic enhancement is correlated with auditory working memory. We have also found that response spectrum depends on stimulus context, and the extent to which context (e.g., regular vs. random stimulus presentation) enhances the response spectrum is correlated with music and language abilities in children[16] and years of musical experience in adults.[44]

Timing

Speech and music are spectrotemporally dynamic signals and the processing of their rapid changes requires precise neural timing. Precise neural timing is essential for effective auditory-based communication, and timing breaks down with certain communication disorders.[45–47] Subtle differences between stimuli, such as the frequency content of a formant transition differentiating two stop consonants, result in quantifiable timing differences in the response. In addition to measuring the timing of discrete peaks, it is also possible to use cross-spectrum techniques to compute phase differences between two responses.[48] The cross-phaseogram produces a color representation of subtle timing differences between a pair of biological responses that may be difficult to quantify in the time-domain waveforms.[41,48] An example is the differentiation of responses evoked by differing stop consonants, such as /b/ and /d/. We have synthesized a trio of such sounds, ba, da, ga, such that they differ acoustically only in a subtle difference in the frequency sweep of the second formant. Although their time-domain responses are very similar, the differences in biological processing among them are readily apparent through the use of the cross-spectrum technique. Figure 2, bottom left, demonstrates that a poor speech-in-noise–perceiving cohort of subjects has a smaller phase difference between ba and ga than a good speech-in-noise–perceiving cohort (warm colors in the 0–60 msec range of the phaseograms represent neural differentiation between two sounds). Likewise, this timing precision is enhanced in good performers on a task of auditory working memory and in musicians (Fig. 2, bottom, center and right).

It must be mentioned that the complex auditory brainstem response is not monolithic in its response properties. The focus of this paper is to highlight that it differs between groups and relates to other phenomena, so a reader might have an impression that the response is depressed as a whole in poor speech-in-noise perceivers or nonmusicians. However, individual properties of the cABR are quite separable,[49] and there are many aspects of the response that do not differ between these groups. Nevertheless, in a variety of populations we have evidence of a three-way relationship between the subcortical processing of complex sounds, auditory working memory, and the ability to hear speech in noise.

How do we know that musical experience was the driving force behind improved outcomes on skills such as speech-in-noise perception and enhancements in subcortical auditory processing? Might it be the case that people with enhanced auditory processing and other skills are more inclined to persevere with music education? Evidence for "nurture" in this question comes from three sources:

longitudinal studies of individuals as they undergo musical training (e.g., Schlaug *et al.*[50]), cross-sectional studies of musicians with a range of years of experience (e.g., Forgeard *et al.*[51] and Fig. 1, right column[1]), and findings that musicians' brains react preferentially to their own instruments.[52–55] Research using these designs provides examples of anatomical, physiological, and behavioral development that coincide with degree of musical experience.[56–59] It is unlikely that such correlations would arise from preexisting conditions influencing the pursuit of musical expertise.

Discussion

Musical experience is a driving force in shaping biological responses to sound and, as we have seen, the benefits afforded by music transfer to other realms of auditory processing, including speech.[26,34,60,61] The recently proposed OPERA hypothesis[4] describes mechanisms by which music can lead to generalized learning. Among them is the *overlap* in biological resources available for the processing of these two types of sounds, along with the greater demands of *precision* that music, relative to speech, puts on these shared resources. Furthermore, music practice and performance elicits strong *emotions*. Emotion, in particular, is a strong driving force behind auditory learning in animals.[62,63] Finally, the *repetition* and the cognitive demands required by intensive music practice, such as *attention* and working memory, initiate enhanced cortical plasticity, which in turn strengthens subcortical circuitry and tunes the afferent system for signal processing of incoming speech.

Here, we present a model that describes the cortical, subcortical, and emotional mechanisms that interact to affect speech processing and how this reciprocally interactive network is influenced by musical experience (Fig. 3).[16] The relationships between musical skill and hearing speech in noise are no doubt mediated by cognitive factors such as memory, and the subcortical response patterns tying music, speech perception, and auditory memory together suggest a corticofugal-mediated shaping of sensory function. Auditory working memory and hearing in noise are intrinsically linked, and biological processing of sound, accessed by cABR, provides a biological basis for that link. It appears that cognitive function, such as working memory, is a force that drives the biological representation of sound.

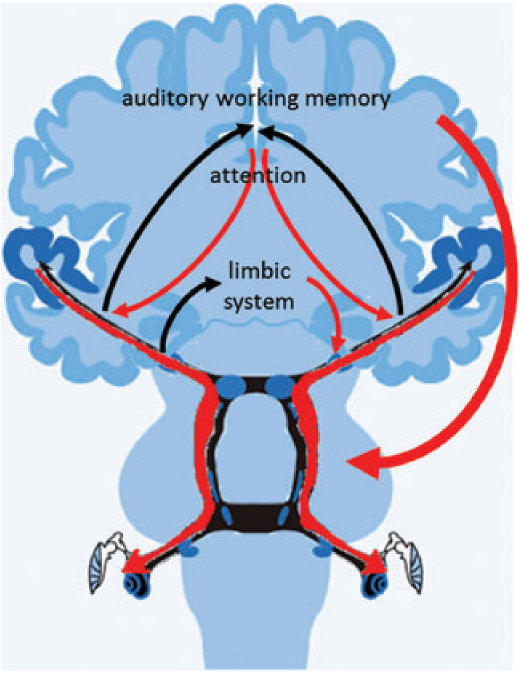

Figure 3. The afferent auditory pathway, from cochlea to cortex, is complemented by descending projections originating in brain regions responsible for executive and limbic functions. These corticofugal connections sharpen auditory processing. Auditory working memory, in particular, is stronger in musicians and drives strengthened auditory processing as well as perceptual benefits for following conversations in noise.

We propose that music training first drives cognitive enhancement that, in turn, shapes the nervous system's response to sound. Music training as a means of augmenting corticofugal auditory networks has the potential to enhance everyday communication.

In the last decade, we have moved away from the classical view of hearing as a one-way street from the cochlea to higher brain centers in the cortex. It is now accepted that cognition, once thought to play no role in hearing, has a dramatic influence on hearing and subsequent communication. Our approach—the convergent study of cognition, perception, and biological processing—is one means of understanding the mechanistic bases of cognition's role in auditory processing.

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Conflicts of interest

The authors declare no conflicts of interest.

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