THE MUSICIAN'S AUDITORY WORLD

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Introduction

Will listening to Radiohead make you smarter? Probably not. But according to noted Internet data miner Virgil Griffith,[1] the typical Radiohead fan scores about 110 points higher on the Scholastic Aptitude Test (SAT) than the typical Grateful Dead fan (Fig. 1). Of course as we all know, correlation does not equal causation. But, to quote Aniruddh Patel,[2] music is a "transformative technology of the mind," and we know that music does have a very real effect on skills outside the realm of air guitar. The quest to determine the mechanisms for this transference of musical skills has already begun.

"Brainstem evoked responses to music and speech alike are rich sources in the investigation of music training's role in shaping the nervous system."

In the Kraus lab at Northwestern University, the skills that interest us most are reading and speech-in-noise (SIN) perception. Significantly, musicians excel at these very activities. Our research has led us to measuring deep-brain electroencephalograph (EEG) in response to a variety of complex stimuli, and we have found correlates in this subcortical activity to reading and listening-in-noise skills. A logical step was to look at the interaction between SIN perception and reading and the changes in biology brought about by active engagement with music.

Background

Musicians' special skills

As interesting as questions of musical taste and the consequences of favoring one sort of music over another might be, in this report, we will focus on active musical practice. The extent to which musicians are or are not better than their non-musician peers at a variety of tasks that has received considerable attention.

For example, it appears that musicians have particularly good verbal memory[3,4] and auditory-attention skills[5] but not

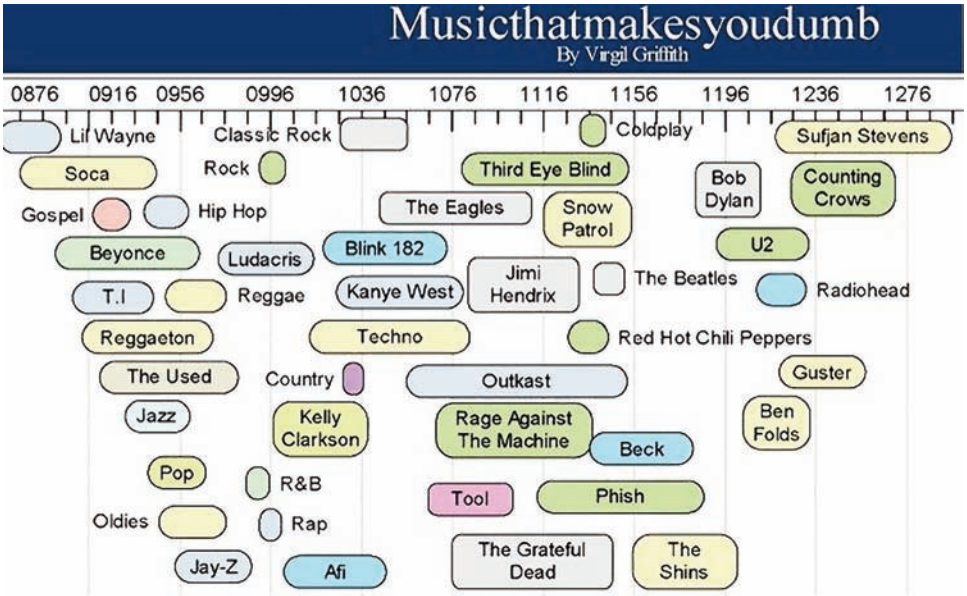

Fig. 1. Average SAT scores for college students who report a given artist or genre as a favorite. See musicthatmakesyoudumb.virgil.gr for additional data and an explanation of derivation. Reprinted with permission of author.

necessarily visual attention. Whether visual memory is superior in musicians is a matter of some debate.[3,6] The extent to which musicians identify emotion in voices or melodies exceeds that of non-musicians,[7] as does the ability to form distinct auditory streams from simultaneously-occurring sounds.[8] Visuospatial skills and certain math skills are also superior in young musicians,[9] as is their performance on executive-function tasks.[10]

Despite these findings, the chicken or egg question arises—does musical training stimulate prowess in these skills or are people who already excel in such arenas more likely to pick up an instrument? Some compelling evidence to support the former scenario comes from correlational studies. If inherent skill X leads to a predisposition toward music, there should be no particular relationship between extent of X prowess and years of musical study. However, such relationships indeed exist. To name a few, the length of musical training in children is predictive of vocabulary knowledge and nonverbal reasoning skills.[11] A variety of IQ measures are associated with duration of music lessons in primary-school children.[12] The other strong bit of evidence that music training leads to brain differences comes from longitudinal studies. After one year of musical training in children, auditory discrimination and fine motor skills increase,[13] and after three years, improvements in vocabulary and non-verbal reasoning skills are seen.[11] Even shorter periods of training result in increases in reading and pitch discrimination compared to children who were randomly selected to receive painting instruction.[14]

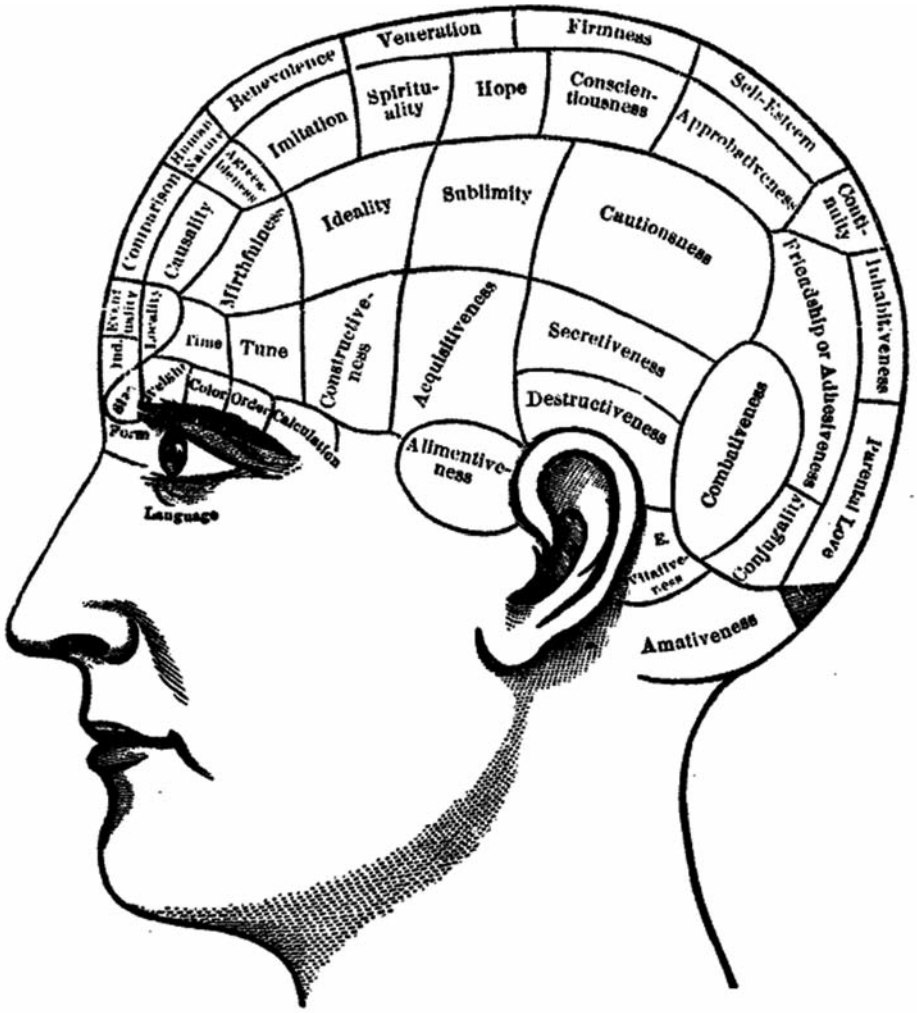

Fig. 2. The music organ, labeled "tune" here, is not far from "time" and "mirthfulness." People with very large tune organs, among other things, "learn tunes by hearing them sung once; sing in spirit and with melting pathos;…sing from the soul to the soul." From Fowler and Fowler, 1889.[144] Electronic resource courtesy of University of Michigan Library.

The musician brain

As we all know, the organ of music is "located immediately above the external angle of the eye and, when it is very developed, results in square foreheads,"—Franz Joseph Gall, quoted in Bentivoglio[15] (Fig. 2). Maybe. But foreheads aside, it stands to reason that, given the many behavioral advantages in musicians, there must be parts of the brain that—either structurally or functionally—differ in musicians. Efforts to localize and quantify these differences date back at least a hundred years,[15] with anecdotal accounts going back even further. The convolutions of Beethoven's brain were said to be "twice as numerous and the fissures twice as deep as in ordinary brains,"—Johann von Seyfried, quoted in Spitzka.[16]

More recently, imaging techniques have revealed structural differences in a variety of musician-brain regions. Just a few examples: gray matter volume of professional musicians is greater than in amateur musicians, who in turn have greater volume than non-musicians, in auditory, visuospatial and motor regions of the brain.[17] Somatosensory cortical areas mapped to the left hand are larger than those mapped to the right hand (and compared to either hand in non-musicians) in string-instrument musicians, tracking with the much larger demands for precise left-hand movement in string players.[18] White matter in the pyramidal tract is more structured in pianists than non-musicians.[19] A recent longitudinal study supports the idea that it is music training itself that induces structural brain enhancement in musicians, rather than existing brain differences encouraging certain individuals to take up music.[20]

Functional differences—measured by neurophysiological and functional imaging techniques—add more evidence of musicianship's role in shaping the brain. Oscillatory gamma-band activity in the brain, related to attention and memory, is enhanced in musicians.[21] A host of cortical evoked neurophysiological responses[22-24] and cortical activation patterns[25] are enhanced in musicians compared to non-musicians. Speeded maturation of cortical potentials is seen

in trained children, and seems to accelerate their development by about three years.[26] Additional evidence that music training is causing brain differences, rather than brain differences leading to musical proclivity comes from a study in which very young children in matched musically-trained and untrained cohorts were followed for a year and brain development between groups differed.[27] Research on instrumentalists who play different instruments reveals specialized activations. Gamma-band oscillatory activity in the brain is strongest when induced by the sound of a musician's own instrument.[28] Cortical evoked responses also are preferentially tuned to one's own instrument.[28,29]

Common and separate mechanisms

Turning back to reading and speech-in-noise perception, there are some noteworthy similarities in the skills required for these tasks and for playing a musical instrument. Two such skills, more on the cognitive end of the spectrum, are attention and working memory.

Another crucial need for all three endeavors is accurate processing of incoming auditory signals. The spoken word and music can be thought to consist of three fundamental components: *pitch, harmonics,* and *timing*. These three components of any acoustic signal can be differentiated by their time scales and carry different informational content. In speech, timing and harmonics convey the phonetic content—specific consonants and vowels—of non-tonal languages such as English, and thus are mainly responsible for the verbal message. Pitch conveys intent (e.g., question versus statement) and plays a large role in distinguishing one talker from another. In tonal languages such as Mandarin, pitch also carries linguistic information. In music, one could argue for similar divisions and classifications, but it is all to easy to be trapped into stretching a metaphor. What is information in music? What is intent? Suffice to say, music, even an individual note played by a single instrument, has a rich acoustical structure and is, by any definition, "complex." Thus, brainstem evoked responses to music and speech alike are rich sources in the investigation of music training's role in shaping the nervous system.[a]

Forming phonological representations of the sounds comprising words is a crucial building block of reading. A consonant that has a particular voicing onset (timing) and a spectrum of a particular shape (harmonics) is eventually associated by a young reader with, for example, the letter T. The pitch of this combination of sounds—was it spoken by mom, dad, or the funny-looking purple creature on television?—does not affect its phonetic identity. Timing and harmonic features in speech are especially vulnerable in poor readers and pose particular perceptual challenges[30-32] while pitch perception is generally intact.

Speech-in-noise perception, on the other hand, presents a different set of problems and a corresponding set of skills to accomplish it. Among these are keying in on location cues, stream segregation, and grouping of the acoustic scene.[33-44] Together, these are used to tag and follow the speaker's voice, and rely on pitch[43-48] as well as the timing and harmonic properties of the signal.

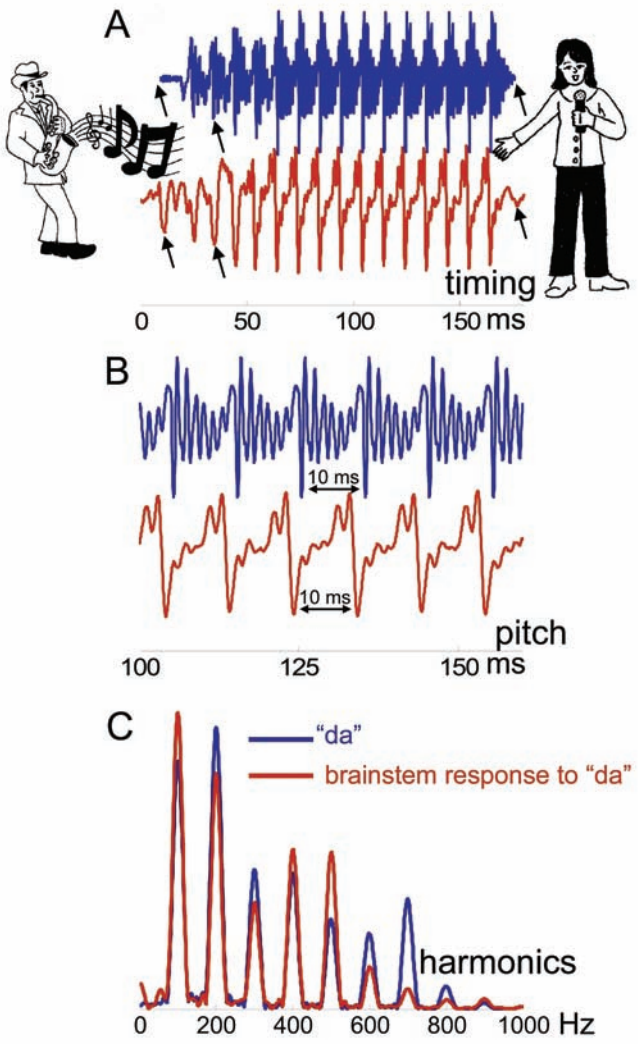

Fig. 3. Timing, pitch and harmonics describe complex acoustic signals: the acoustic waveform of "da" (blue) and its evoked brainstem response (red) on different time scales. A. Prominent timing landmarks of the stimulus, e.g., the onset, offset, and events during time-varying portions (arrows), evoke precisely synchronous and replicable electrical deflections in the auditory brainstem. For illustration purposes, the stimulus waveform in this figure has been delayed in time by 9 ms, to approximate the neural propagation time. This permits better visual coherence between stimulus and response. B. Several repeating periods of 10 ms each are shown. This imparts a pitch percept of 100 Hz, and this periodicity is mirrored in the response. C. Stimulus and response spectra in the frequency domain. Here, the stimulus has been filtered to mimic the response's low-pass characteristic. Spectrum peaks for the stimulus and its evoked auditory brainstem response are exactly aligned, representing their similarity in harmonics. (Artwork by Judy Song.)

Reading, SIN perception and music share a core set of skills—working memory, attention, perception of pitch, timing and harmonics—and each also requires some unique skills. Reading requires the use of phonology and the development of a vocabulary corpus. SIN perception relies on object formation and grouping, stream segregation, and voice tagging. Music involves knowledge of melody, harmony, and rhythm. The skill sets are a mix of low-level sensory processing and high-level cognitive proficiency. A strong *sensory-cognitive* link seems to be a factor in proficiency across domains, and each requires the formation of sound-to-meaning connections. The intersection of common skills, as well

as the unique skill sets required for the three, make reading, SIN perception and musical experience an interesting triumvirate to pursue in the investigation of processing of complex sounds in the auditory brainstem. Brainstem activity reflects the acoustical characteristics of signals very well—while plastic to language[49-51] and music[52-56] experience and short-term auditory training,[57,58]—making it well suited to provide objective physiological information about complex-sound encoding in populations with a range of reading, music and SIN perception skills (see Tzounopoulos and Kraus[59] and Skoe and Krause[145] for reviews). Encoding of pitch, timing, and harmonics is selectively diminished in certain clinical populations and selectively enhanced by expertise allowing us to examine specific, separable aspects of signal encoding. We are not observing simple gain effects; that is, overall response disruption or enhancement.

The approach: Music and speech evoked brainstem responses

In the past decade, the Kraus Lab has been a pioneer in the use of speech- and music-evoked auditory brainstem response (ABR) as an innovative objective marker of auditory function in a variety of populations.[49-58;60-113,131] Here, we will present a synopsis of this approach and some advantages over the more widely-studied cortical response and behavioral paradigms.[b]

Neural transcription of the acoustics of sound has been widely studied in the auditory cortex of humans and experimental animals for consonants,[114-116] vowels,[117] and pitch.[118] Structural and functional reorganization of auditory and sensorimotor cortex occur with musical training,[18;27;29;119-121,137] and non-sensory structures also appear to benefit.[122,123] Our focus, and the focus of this review, is on subcortical (auditory brainstem) processing of complex sounds such as speech syllables, musical notes, chords and melodies. Unlike the more abstract representation of sound in the cortex, the brainstem response *resembles and sounds like the evoking sound itself* (Fig. 3). Moreover, responses are reliably stable, interpretable, and meaningful in individuals. The brainstem response paradigm is passive, and its objectivity represents a significant advance over typical measures of complex-sound processing. Most such measures are behavioral in nature, with the person repeating the words that they heard, or making judgments about melodic or rhythmic properties of a musical snippet. Active engagement of processes such as attention, memory, and motor coordination is required to perform the task. Likewise, cortical physiological measures are susceptible to non-sensory factors such as state, motivation, etc. Therefore, our objective brainstem measure is a particularly effective tool at probing unadulterated auditory processing.

While objective, there is another property of the auditory brainstem that is crucial to its value as a window into auditory processing. As mentioned above, it is experience-dependent. On the surface, experience-dependency might seem a counterintuitive property if the principal purpose of the subcortical auditory system is the passive conveyance of acoustic information from receptor to auditory cortex for final and more complex processing. But, not only is there an obligatory system of afferent fibers carrying sensory information from the cochlea to the cortex, but there is also an extensive system of descending efferent fibers that synapse all the way down to the outer hair cells of the cochlea,[124] making plasticity in the brainstem not so implausible.

Now, back to the auditory signal. Many key perceptual ingredients of speech and music are driven by particular properties of the signal and have direct brainstem-response correlates. In response to syllables or musical notes, chords or melodies, the *timing* of the response provides information, on the order of fractions of milliseconds, about the onset and offset of the sounds (i.e., temporal envelope cues), and spectrotemporal patterns in the evoking signal are revealed in response timing and phase.[57,76,125] Analysis of the spectral content of the response provides information about the fundamental frequency, a major contributor to the perceived *pitch* of the signal as well as its *harmonics*, including the temporal fine structure of speech formants and the overtones of a musical note.[82,111,126]

To tie it all together, the components of the brainstem response that are measurably disrupted in poor readers and individuals with poor speech-in-noise perception are the very components that are enhanced in musicians. The connections among the three (music, reading, and speech-in-noise perception), as revealed by the auditory brainstem response, are covered in the next section.

What the brainstem has revealed about the musician's subcortical processing

In this mini-review of recent Kraus-lab investigations, a theme emerges. The subcortical processing augmentations in musicians are selective. Not every aspect of the brainstem response is enhanced, and enhancement does not occur to every stimulus. First, we start with a straight-forward investigation of subcortical processing differences between musicians and non-musicians to musical sounds. Then we look at the degree to which these processing advantages extend to speech, and then to non-speech vocalizations.

Enhancement to music I: Piano chords, Lee et al., 2009.[55] Two-note sampled-piano chords, G-E and F#-E, were used to elicit brainstem responses in a group of adult musicians and an otherwise-matched group of non-musicians. Some interesting aspects of brainstem responses are that they represent the pitch of the evoking signal in their spectra, and that they reveal nonlinear processes by exhibiting frequency components that are not present in the stimuli—namely distortion products or combination tones. These stimuli provided a wealth of response properties for the investigation of musical-signal processing in the rostral brainstem. Interesting findings arose from this investigation. First, of the two primary notes that compose the chord, only representation of the harmonics of the higher note—in both cases E—differed between groups (Fig. 4). Because the musician enhancement was selective, we interpreted the fact that the higher note revealed the group difference as indicative of the relatively greater importance that the upper note typically plays in music. A performing musician is tuned into the melody which is often the highest note of a score. This finding also

parallels cortical physiological findings of a larger mismatch response to changes in the upper note of a polyphonic melody.[127] A second finding is that the combination-tone responses, absent in the stimuli, also were enhanced in musicians, providing evidence that these responses probably are of a central origin, and not a result of cochlear non-linearities propagated up to the midbrain.

Enhancement to music II, Linguistic transfer I: Cello and speech. Musacchia et al 2007.[52] Musicians show enhanced processing to speech, not just music. In a design that tested musicians' responses to both music and speech, more evidence of selective enhancement in musicians' subcortical processing emerged. Two stimuli, a bowed cello note and a "da," revealed a musician enhancement. Musicians' phase-locked responses to the fundamental frequencies of both stimuli were enhanced and the extent of enhancement correlated with years of musical practice. This evidence of superior processing in the brainstem in musicians was the first indication of transfer to the speech domain. This study also investigated visual contributions to brainstem auditory processing because of musicians' known ability to better process dual-domain audiovisual stimuli.[128] Here, the two auditory stimuli were presented along with videos of the cello being bowed and a man speaking the syllable. In this presentation mode, similar phase-locking enhancements were seen in musicians, along with faster timing for an onset peak occurring at about 12 ms (Fig. 5). Thus processing of both music and speech and audiovisual interaction in the auditory brainstem appears to benefit from musical experience.

Linguistic transfer II, Tonal languages. Wong et al., 2007.[53] In tonal languages, a single phonetic combination, like "ma," has various meanings depending on the inflection with which it is spoken. In Mandarin, "ma" spoken with a high, level pitch, means "mother." Spoken with a dipping (down then up) pitch, it means "horse." Two other inflections, falling and rising, produce two additional words and these four tones round out the Mandarin repertoire. Other languages have even more tonal markers. It has been demonstrated that pitch-tracking to Mandarin words by the auditory brainstem is more accurate in native Mandarin speakers,[49] likely due to years of tuning engendered by the importance of pitch to their native language. We were interested to see if pitch tracking to Mandarin syllables is improved in individuals whose auditory systems were tuned to pitch for non-linguistic reasons. Non-tonal-language-speaking musicians were chosen for this investigation. Pitch, for musicians, is a critical dimension of their art, and both their auditory systems and their cognitive centers have been extensively honed to it. Brainstem responses to the syllable "mi" with high-level, rising and dipping tones were measured. Accuracy of pitch

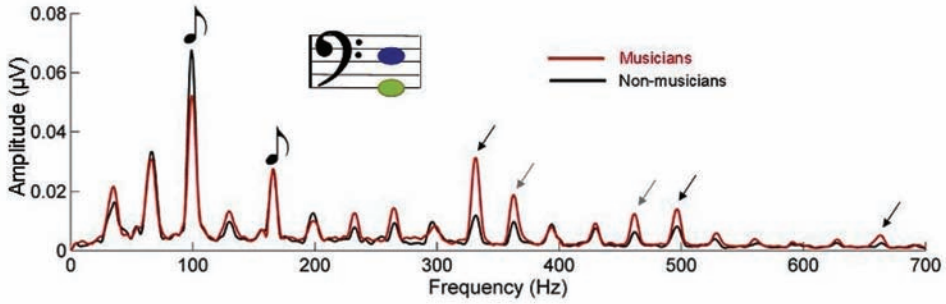

Fig. 4. Musicians have enhanced brainstem representation of the harmonics of the higher note in a chord. No encoding differences were seen at response frequencies corresponding to the two notes comprising the chord (G and E, labeled with musical notes). However, musicians have enhanced encoding at integer harmonics of the higher note (black arrows). Certain combination tones (not present in the chord) also are also more strongly represented in the musician response (gray arrows). Modified from Lee et al., 2009.[55]

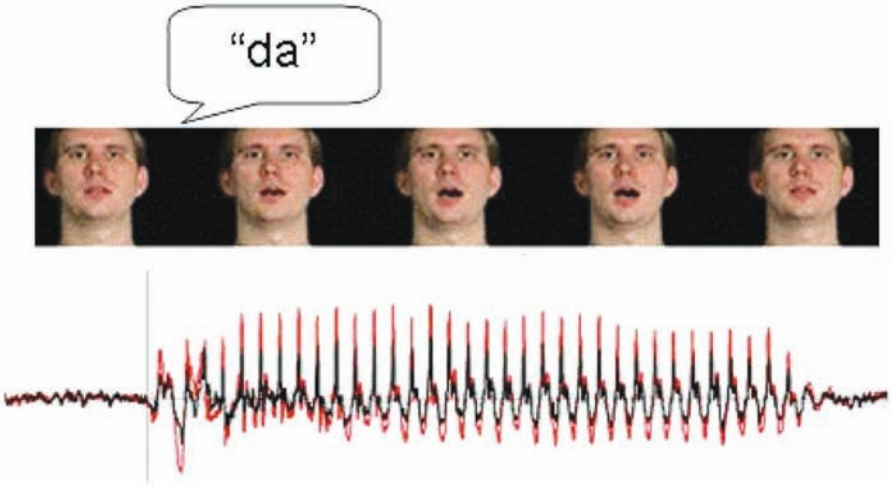

Fig. 5. Whether a "da" is heard by itself or with an accompanying video of its speaker uttering it, the evoked brainstem response is larger in musicians (red). This was the first evidence of linguistic transfer of the musician advantage. Modified from Musacchia et al., 2007.[52]

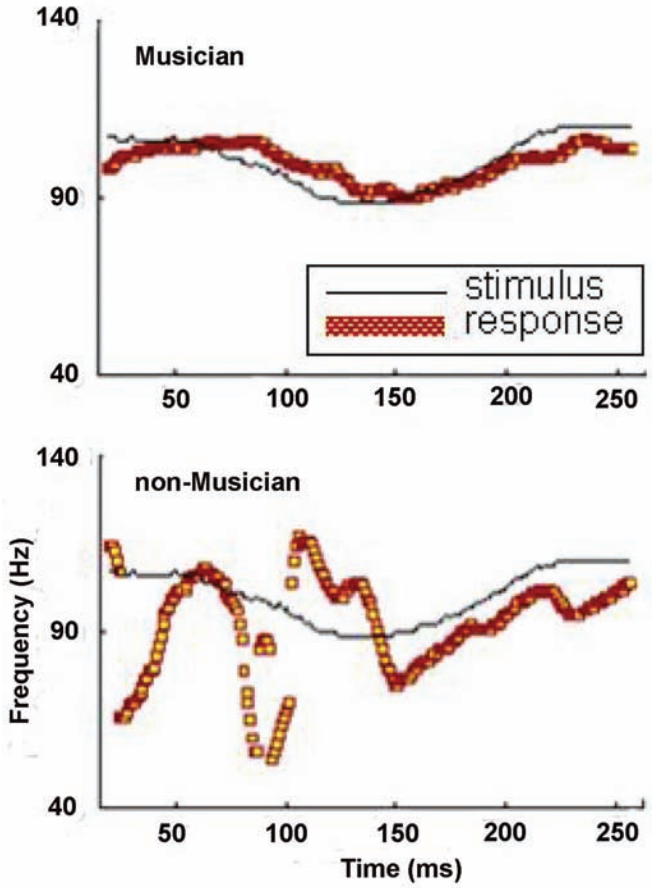

Fig. 6. The voicing contour of this stimulus, "mi," dipped from about 110 Hz, down to 90 Hz and then back up (thin black lines). The precision with which the brainstem response phase locked to the stimulus pitch (thick yellow) was superior in musicians. Modified from Wong et al., 2007.[53]

tracking, measured by how closely in frequency the phase locking in the response matched the changing pitch of the syllables, and strength of phase locking, measured by autocorrelation, both were greater in musicians than in nonmusicians. Notably, the musicians' advantage increased as the complexity of the tone increased (Fig. 6). The most complex, dipping, tone best distinguished the groups, while responses to the level tone differed little between groups. The accuracy of brainstem pitch-tracking of the dipping tone was correlated with the length of musical study, indicating that the differences between groups are likely due to musicianship rather than innate subject differences. This subcortical enhancement in musicians also may provide a mechanism to explain why musicians show a facility for learning foreign languages.[129]

Linguistic transfer III: Speech in noise, Parbery-Clark et al., 2009.[130] One of the biggest communication complaints, affecting school children, hearing impaired individuals, older adults, and everyone in between, is difficulty hearing conversations in noisy backgrounds. While many populations are affected, musicians, in whom stream segregation and object formation are required for parsing melodies from background harmonies, tend to cope with noisy backgrounds especially well. Musicians, in fact, are dramatically better in their ability to hear speech in noise as measured by standardized tests, and this advantage increases with extent of musical experience.[131] Musicians also excel in tasks that test working memory, and this ability relates to speech-in-noise perception. We reasoned that these performance advantages might manifest themselves in a brainstem that better maintains its synchrony in the presence of background noise. Using stimulus-to-response correlations as a metric of brainstem integrity in noise, this was the case. Responses to a speech syllable presented in a quiet background were relatively indistinguishable in normal-hearing adults regardless of their musical backgrounds. However, when the same syllable was masked by multispeaker babble, the musicians' responses maintained an extraordinary degree of robustness, while the nonmusicians' responses deteriorated (Fig. 7). Closer examination of the response spectra revealed that harmonics of the fundamental frequency of the syllable were a source of degradation in the non-musicians. Larger noise-induced delays in discrete peak timing were noted in non-musicians as well. It may be that enhanced processing of these higher-frequency components of sound facilitates the formation of auditory units and thus sets the stage for the stream segregation required for pulling sounds from noise. Thus, the precision in processing complex sounds in the auditory brainstem may be a precursor to successful SIN perception, and brainstem precision in musicians—likely driven by engagement with sound—may undergird their advantage in listening in noise.

Linguistic transfer IV: Regularity detection and reading, Chandrasekaran et al., 2009.[132] The ability to track regularities and to respond appropriately to change are hallmarks of the sensory systems. In the human auditory brainstem, we recently demonstrated that responses to a given sound differ depending on whether that sound is presented in a train by itself or embedded in a series of different sounds.[132] The specific difference, selective enhancements of harmonics two and four in the repetitive condition, has a relationship with behavior. In school-age children, the extent of these enhancements correlates dramatically with reading ability. The sound elements that result in brainstem deficiencies—poor readers in this study and others[88,89,113,125,132]—are the same aspects of auditory processing that are enhanced in musicians.[133,134] We speculate that some common mechanisms are at work. One mechanism might be proficiency at noise exclusion—the ability to extract relevant signals from a jumble of sounds.[135] Cognitive skills such as auditory memory and attention, enhanced in musicians, invoke corticofugal mechanisms that tune brainstem processing. The poorer engagement of cognitive skills in poor readers fails to solidify the corticofugal tuning of brainstem processing of complex sounds.

Vocal emotion, Strait et al 2009.[54] A baby's cry is a mix of harmonic and stochastic sounds strung together into an emotion-evoking signal. The acoustical variety packed into this short quarter-second sample makes this one of our most complex stimuli, and the pattern of response differences seen between musicians and non-musicians again speaks to the selective patterns of enhancement—and in this case also response suppression—engendered by musicianship. Zeroing in on the responses to a harmonic, relatively simple (112–142

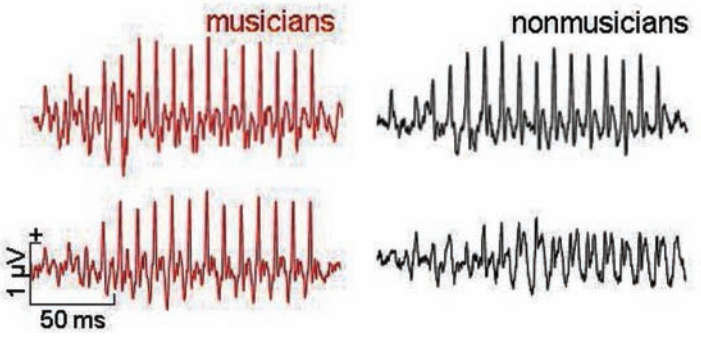

Fig. 7. Degradation in brainstem responses is common when the stimulus is embedded in background noise. While musicians' and non-musicians' responses are similar in quiet (top), the degradation of response morphology in noise (bottom) is minimized in musicians (red). Modified from Parbery-Clark et al., 2009.[130]

ms) segment and a complex non-harmonic (145–212 ms) segment, reveals an interesting pattern. Musicians' responses to the earlier segment are smaller than nonmusicians', while their responses to the later, complex, segment are larger (Fig. 8). This combination of processing strategies—both response efficiency and enhancement—to different types of acoustic stimulation has certain parallels to cortical studies in which musicians show an economy of response to harmonically simple sounds.[136] In contrast, the musician's enhancement to the more complex portion of the baby cry is in line with some of the other processing enhancements we have seen in musicians' auditory brainstems. The results of this investigation demonstrate that subcortical processing differences in musicians extend toward non-musical and non-speech vocal sounds.

Summary and conclusions

As we learn more about the auditory brainstem response to speech and musical sounds, one of the more interesting findings is that the same neural processes that are diminished in poor readers and individuals with difficulty hearing in noise are the same processes that are enhanced in musicians. Neither the deficits nor the enhancements are pan-response. In every case, with peripheral hearing as a strict control, only subtle response characteristics are affected while gross morphology is maintained. This speaks to the value of the brainstem response in the investigation of possible neural origins for reading and SIN perception problems and musical-experience-mediated processing advantages. Not only is the response powerful because of its suitability as an individual-subject probe, but it is many-faceted. That is, its components—each tied inextricably to components of the auditory landscape—are separable; it is not an undifferentiated phenomenon with little relationship to the evoking sound.[82] This gives the researcher a technique to look for selective enhancements or impairments that is unavailable in the more abstract realms of cortical physiology and imaging. The brainstem provides an exciting window into the *sensory-cognitive* reorganization that underpins the changes brought about by engagement with music. With it comes the promise of disambiguating the mechanisms through which these changes occur.

The behavioral, cognitive, cortical, and subcortical advantages bestowed by musical training, serve to promote musical training as a logical strategy for improving basic sound transcription via the reinforcement of reciprocal subcortical-cortical processing interactions brought about, at least in part, by the strengthening of auditory memory and attention. This improved sound transcription, in turn, is a building block of phonological processing, reading, and the extraction of speech from background noise. Further work also can address the extent to which musical practice may serve as protection and remediation against hearing-loss or age-induced communication difficulties and a means to engender the formation of sound-to-meaning relationships that are so critical to human communication.[137] The brainstem response can serve as a potent efficacy measure of music-based education due to its fidelity to the stimulus, its individual-subject reliability, its experience-dependent malleability and its selective nature. Supported by National Science Foundation grants SBE-0842376 and BCS-092275. **AT**

End notes

[a] We are using the terms pitch, timing and harmonics as shorthand throughout this report. We recognize that these constructs have other strict meanings, and that such a tidy differentiation among these three constructs in speech and music is an oversimplification. For our purposes, we refer to pitch as the fundamental frequency (f_0) of a note or an utterance. In speech, f_0 is a

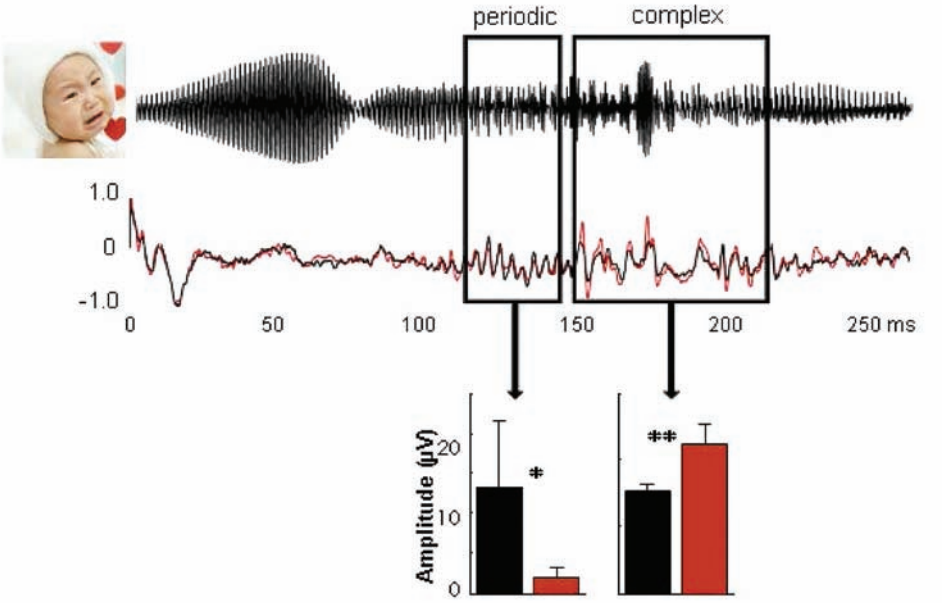

Fig. 8. Musicianship extends to brainstem processing advantages to non-linguistic vocal sounds. The selective nature of music training's impact on processing is revealed within the response to a single baby's cry (top). A complex region of the musician's response (red) is enhanced; a periodic part is reduced. From Strait et al., 2009.[54]

source characteristic and is directly related to the rate of vibration of the vocal folds; in music it is dictated by such things as string length. We recognize that the percept of pitch is not solely conveyed by the fundamental frequency, but pitch is our shorthand for the repeating period of the signal. We define harmonics as the overtones of the fundamental. We recognize that harmonics arise from the same source as the f_0 and also contribute to the percept of pitch. But in music, their relative amplitudes contribute to the identity of the instrument, and in speech, the identity of the particular vowel or consonant that is being spoken. These properties, not their shared origin with the fundamental, put harmonics into a different camp from pitch in our model. Timing refers to the major acoustic landmarks in the temporal envelope of the signal, in speech, arising from the alternating opening and closing of the articulators and from the interplay between laryngeal and supralaryngeal gestures, and in music the rhythmic structure of the phrase. In speech, timing also includes spectrotemporal features of speech such as the changing of formants over time. The three components of our model, pitch, timing and harmonics, as defined here, have direct and separable parallels in the speech- and music-evoked brainstem responses.

[b] How do we know that what we are recording does not arise from structures more central to the auditory midbrain? We acknowledge that our non-invasive (scalp electrode) technique prohibits certainty of source. We believe that the low-pass characteristic of the auditory system minimizes the possibility that the highly-filtered activity we measure is cortical afferent activity.[110] Moreover, the complex auditory brainstem response (cABR), especially its frequency-following response (FFR) component has been widely studied, and several converging lines of evidence point to a subcortical source. The FFR appears in response to tone pips that are shorter than the time required for cortical propagation.[138] The time delay of the individual FFR cycles, with respect to the evoking stimulus, is around six milliseconds, which is too early for cortical involvement.[139] Animal work[140] added two lines of evidence of a subcortical origin for FFRs: first, based on similarity of latencies of FFRs recorded from cat scalp and brainstem inferior colliculus, and second, from the abolition of surface-recorded responses with cryogenic cooling of inferior colliculus. Additionally, Galbraith[141;142] demonstrated that recordings from the scalp reflect a response of central brainstem origin. However, due to the length of our cABR stimuli—100 milliseconds and up, cortical influence can not be completely ruled out. More probable, is that the responses are a mix of afferent brainstem activity and cortically modulated efferent effects on brainstem function. It also bears mentioning that responses from putative deep-brain sources are less topographically variable than responses from more superficial cortical areas. Much insight on voltage sources is gained by a full topographical array of electrodes in the investigation of cortical responses. However, due to their long travel in propagation to the scalp, speech-ABRs lose site-specificity; hence, little is to be gained by studying their topographic distribution. A single vertex electrode is sufficient.[143]

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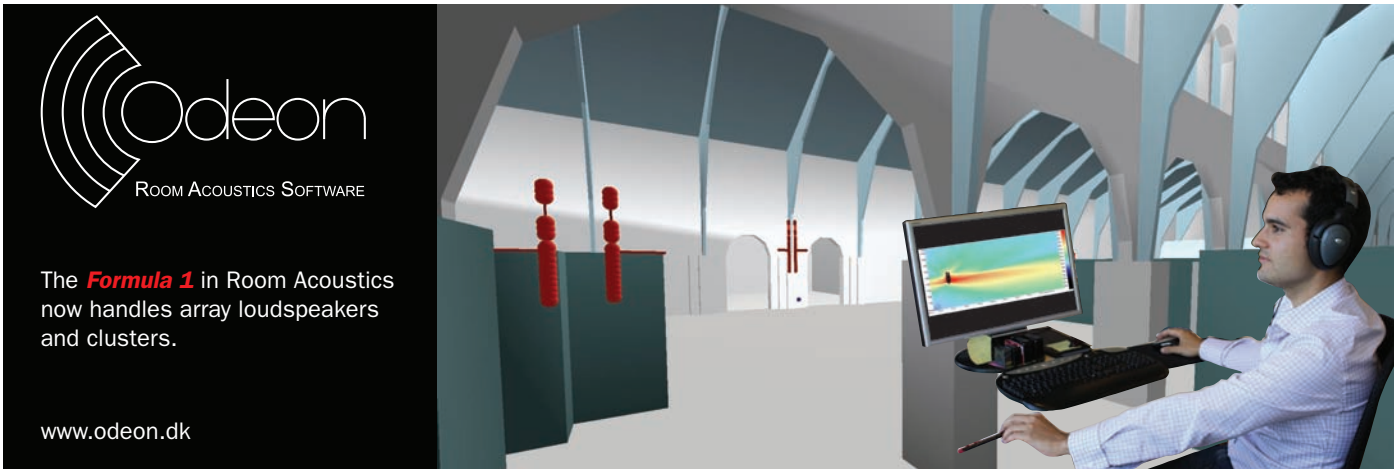

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