MUSIC TRAINING: LIFELONG INVESTMENT TO PROTECT THE BRAIN FROM AGING AND HEARING LOSS

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Age-related declines in the auditory system contribute strongly to older adults' communication difficulties, especially understanding speech in noisy environments. With the aging population growing rapidly there is an expanding need to discover means to offset or remediate these declines. Music training has emerged as a potential tool to set up the brain for healthy aging. Due to the overlap between neural circuits dedicated to speech and music, and the strong engagement of cognitive, sensorimotor, and reward circuits during music making, music training is thought to be a strong driver of neural plasticity. Comparisons of musicians and non-musicians across the lifespan have revealed that musicians have stronger neural processing of speech across timescales, ranging from the sentence and word level to consonant features on a millisecond level. These advantages are also present in older adult musicians, and they generalise to advantages in memory, attention, speed of processing, and understanding speech in noise. Excitingly, even older adult musicians with hearing loss maintain these neurophysiological and behavioural advantages, outperforming non-musicians with normal hearing on many auditory tasks. Delineating the neurophysiological and behavioural advantages associated with music experience in older adults, both with normal hearing and hearing loss, can inform the development of auditory training strategies to mitigate age-related declines in neural processing. These prospective enhancements can provide viable strategies to mitigate older adults' challenges with everyday communication.

INTRODUCTION

Older adults often have difficulty communicating in noisy or reverberant listening environments. This temporal processing deficit is compounded by presbycusis, meaning that older adults with hearing loss find speech comprehension in noise especially challenging. These communication challenges are not trivial: from talking on the telephone to ordering in a noisy restaurant, poor speech understanding in degraded listening environments can contribute to stress, social isolation, and depression [1]. In 2009 there were approximately 37 million adults over age 65 in the United States alone, a figure expected to double by 2030 [2]. And it is estimated that nearly two-thirds of adults over age 70 have hearing loss [3]. Therefore, there is an expanding need to develop strategies to mitigate older adults' communication challenges. More generally, there is a burgeoning interest in tools to promote "healthy aging" – investments made at any age to bolster cognition, health, and quality of life in senescence – including through diet, exercise, and vocational activities [4].

Music training has emerged as an exciting candidate for this prevention and remediation. Due to the overlap between neural circuits dedicated to speech and music, and the distributed network of cognitive, sensorimotor, and reward circuits engaged during music making, it would appear that music training is a potent driver of experience-dependent plasticity [5–7]. For the majority of studies discussed herein, music training is operationalized as engaging in active music training regularly, for a minimum of 20 minutes twice a week since childhood. These individuals are described as "musicians" as a shorthand, however the benefits for auditory processing associated with music training are likely observed in many individuals who have pursued training less rigorously [8,9], and those who may not self-identify as "musicians" in a formal sense [10,11]. This training is associated with neurophysiological benefits for encoding speech that cascade to heightened auditory-cognitive skills across the lifespan [12,13]. Therefore, music training may hold special promise to set up the communicating brain for healthy aging.

THE AGING AUDITORY SYSTEM: IMPACT ON COMMUNICATION

Pervasive age-related changes occur in the auditory system, which degrade the precision and stability of signal processing. These changes compound age-related declines in cognitive functions (speed of processing, memory, attention, etc.) that, taken together, create challenges for everyday communication [14,15]. In cases of age-related hearing loss, these communication challenges are even greater [16]. A large series of behavioural and neurophysiological studies has characterized the maladaptive plasticity incurred by aging and presbycusis (see [17] for an authoritative review).

Age-related declines in the auditory system

Most age-related changes that occur irrespective of hearing loss affect the fine temporal resolution required for coding fast-changing elements in speech, such as consonants. Age-related declines in temporal processing have been observed in psychophysical studies that have pinpointed a loss of temporal resolution as a hallmark of auditory aging [18–20]. Neurophysiologically, this temporal processing deficit is likely due to a pervasive reduction in inhibitory neurotransmitter function throughout the auditory neuraxis [for review, see 21]. This inhibitory loss is compounded by an increased postsynaptic recovery time [20] and likely a loss of ribbon synapses [22]. These declines cause a reduction in the *neural synchrony* that is required for speech perception in noise [23].

Anderson and her colleagues used the auditory brainstem response to complex sounds (cABR) to investigate age-related changes in the neural precision of speech encoding in older adults with normal hearing [24]. The cABR is a variant of the auditory brainstem response that is elicited in response to complex sounds such as speech or music. By using these sounds, cABR can measure the neural processing of both transient and sustained acoustic elements, providing unique insight into submillisecond temporal processing (neural phaselocking occurring predominantly between 100-1000 Hz). This rapid neural processing is important to encode details in speech such as formants and temporal fine structure that provide perceptual clarity and convey information about phonemic categories and sounds' locations. These features also support listening in the "dips" of certain kinds of maskers [16,25,26]. Five age-related declines in neural processing were described by Anderson *et al*. (see Table 1; Figures 1 & 2). In older adults, responses were *smaller*, including for representation of the fundamental frequency and harmonics in speech. Responses were more *variable* on a trial-by-trial basis, and there was an increase in timing jitter across frequencies. Older adults exhibited a *selective timing delay* on the order of a few milliseconds. This timing delay was only present for time regions of the response corresponding to the onset and consonant-vowel transition in speech; importantly, there was no neural timing delay for the vowel. cABR timing bears strongly on speech-in-noise perception and communicative skills broadly, with sub-millisecond timing differences distinguishing performance on speech perception tasks between groups [27,28]. Finally, there was an age-related increase in *spontaneous neural activity*, putatively representing more "neural noise." These findings have been replicated by a variety of studies [29–31], and conform well to complementary investigations in humans and animals [18,19,32,33].

Hearing loss

Presbycusis exacerbates the communication challenges posed by central auditory aging [16,34]. Although it is difficult to disentangle the effects of aging from those of age-related hearing loss, some of the classic age-related declines in auditory processing are exaggerated, such as the loss of inhibitory neurotransmitter function and misbalance of excitatory and inhibitory neurotransmitters [21,35]. Distinct cochlear pathologies, such as loss of outer hair cells and spiral ganglion cells, likely contribute strongly to age-related hearing loss as well [36]. These losses can modulate cochlear filter properties, eventually leading to downstream changes that may cause maladaptive gain mechanisms in peripheral and central structures [37–39].

A hot topic is how hearing loss exacerbates cognitive decline. Operating under the hypothesis that effective and active engagement with sound supports the maintenance of cognitive skills in older adults, Lin and his colleagues have demonstrated that age-related hearing loss can speed up the rate of cognitive decline in older adults [40]. The same group has found that older adults with better hearing thresholds have larger brain volumes, suggesting retention of cytoarchitectonic integrity through the active and meaningful engagement with sound that is facilitated by good hearing [41]. These studies illustrate two important points. For one, hearing loss affects more than the ear and, in fact, affects more than auditory system function. Changes in the *quality and consistency* of auditory experiences—theoretically, for the better or the worse—can propagate to cognitive functions. But for two, these studies are cases in point that the declines in central processing that are associated with aging and presbycusis may not be *fait accompli*: active engagement with sound can reinforce auditory-cognitive skills, potentially bolstering communicative abilities despite aging and hearing loss.

MUSIC TRAINING ACROSS THE LIFESPAN

Myriad correlational and cross-sectional studies have evaluated the impact of music training on the nervous system and associated behavioural functions. A recurring theme is that music training has a profound impact on *auditory* perception and cognition, in addition to its underlying neurophysiology. Although debates persist as to innate vs. trained differences in studies of music training [42], it would appear that irrespective of intelligence and other personality factors music training can effect changes in nervous system function (although in most cases music training likely interacts with several other factors to dictate final behavioural outcomes). These benefits are grounded in enhanced neural processing of speech [6], occurring across timescales, from slower features such as sentence-level processing, to syllable-level features such as pitch contours and phonemic cues such as voice onset time, to very rapid processing of millisecond features such as formant changes [43–48].

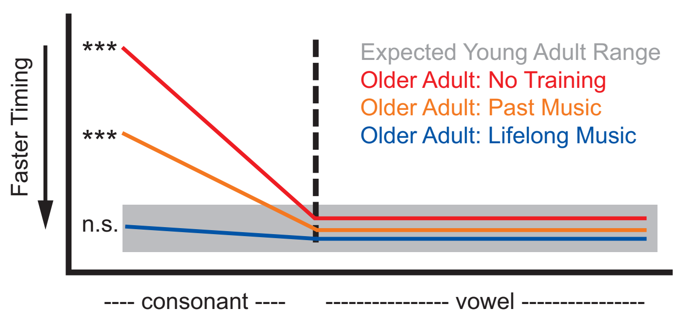

Figure 1. Schematic illustrating neural timing in older adults with no music training (red), past music training (orange), and lifelong music training (blue). Aging slows neural responses to consonants, however music training mitigates this effect. Lifelong musicians have neural timing within a typical young adult range.

The Kraus Laboratory has conducted a series of studies investigating the biological impact of music training on the nervous system across the lifespan, once again using the cABR. By measuring the precision of millisecond-level neural encoding of speech features, these techniques have pinpointed which acoustic aspects of speech processing are enhanced through music training, delineating a *neural signature* [5,12,49]. Briefly, musicians have faster neural timing in response to consonants, enhanced neural encoding of speech harmonics, more synchronous responses to speech, and more resistance to noise degradation (see Table 1).

But these benefits are not solely reflected in neural processing. In fact, these neural enhancements likely underlie a series of behavioural advantages in auditory perception and cognition. Compared to their non-musician peers, musicians have better speech understanding in noise, refined auditory temporal resolution, and heightened auditory memory and attention skills [5,12]. These enhancements combine to make the musician's brain a powerful canvas for auditory processing, tuned into behaviourally relevant sounds and primed to encode them precisely. Importantly, all of the domains where child and young-adult musicians outperform their non-musician peers are areas of decline in aging. This raises the question: can a life of music training mitigate age-related loss?

OLDER ADULTS: MUSIC, AGING, AND HEARING LOSS

A smaller number of studies have considered the biological impact of music training on the older adult's brain. Most of these have considered lifelong musicians, and have asked whether a life of playing music abates age-related declines in auditory processing. The answer is a resounding yes. Both behaviourally and neurophysiologically, older adult musicians do not exhibit many of the age-related declines in auditory function commensurate with typical aging.

Musicians and aging

Parbery-Clark and her colleagues conducted a series of studies of older adult musicians (ages 45-65) to describe the age-related changes—or lack thereof—that occur in neural speech processing. The first set of studies considered older adult musicians with normal hearing. Unlike their non-musician peers, older adult musicians do not exhibit the age-related neural timing delay in response to consonants in speech [50]. In fact, older adult musician's neural timing matches young adult *non-musicians* (see Figure 1). These musicians also had more robust representation of speech harmonics, more consistent responses to speech, and more resilient responses to noise degradation [51]. All told, four of the five signature aging effects on the neural encoding of speech appear to be absent in lifelong musicians (see Table 1; Figure 2). Impressively, these older adult musicians also outperform their non-musician peers on behavioural tests of speech understanding in noise, auditory temporal processing, and auditory working memory [52, see also 53,54]. Therefore, these biological enhancements appear to be linked to advantages in auditory perception and cognition as well.

Table 1. Summary of aging effects and whether they are offset by lifelong music training in older adults with normal hearing or hearing loss.

	Is the aging effect offset by music training in older adults with …	
Aging effect	**… normal hearing?**	**… hearing loss?**
Lower cognitive and perceptual performance	**YES**	**YES**
Neural timing delays in response to consonants	**YES**	**YES**
Decreased response magnitude for fundamental frequency	**NO**	**YES**
Decreased response magnitude for spectral harmonics	**YES**	**NO**
Decreased neural synchrony	**YES**	**YES**
Less precise encoding of the temporal envelope	**YES**	**NO**
Increased in spontaneous neural activity ("neural noise")	**NO**	**NO**

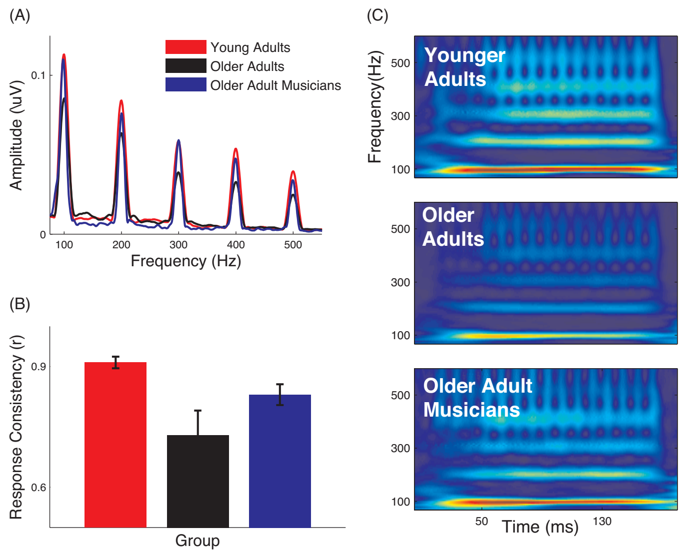

Figure 2. Aging effects that are offset by lifelong music training. (A) Older adult musicians have stronger encoding of the fundamental frequency and harmonics of speech, in line with young adults. (B/C) Age-related declines in neural synchrony are absent in lifelong musicians. This is reflected in the trial-by-trial stability of the neural response to speech overall (B) and on a frequency-specific basis (C).

A complementary series of studies has come from Zendel and Alain, who have compared auditory processing and attentional allocation in musicians and non-musicians throughout the lifespan. In a cross-sectional comparison of musicians and non-musicians (ages 18-91) Zendel and Alain found consistent lifelong advantages in central auditory processing in musicians irrespective of hearing thresholds [13]. Subsequent neurophysiological studies, considering auditory processing occurring predominantly below 100 Hz, demonstrated that older adult musicians had enhanced temporal processing at slower time scales, including for auditory stream segregation [55] and compensatory attention-dependent activity [56].

Taken together, these studies are consistent with the idea that lifelong music training can set up the brain for healthy aging. This is true for auditory tasks requiring processing across seconds and minutes all the way to sub-millisecond neural processing of very fine speech features. Given the gamut of slow-to-fast processing that appears enhanced in older adults, one may extrapolate to additional advantages that may be present in older musicians but have yet to be characterized biologically. For example, aging degrades the neural processing of voice onset time [57], a temporal cue in speech that informs phonemic categorization; music training, however, enhances this processing [44]. By making timing sensitivity behaviourally relevant to the listener, music training may engender biological enhancements particularly tailored to counteract the older adult's temporal resolution deficit.

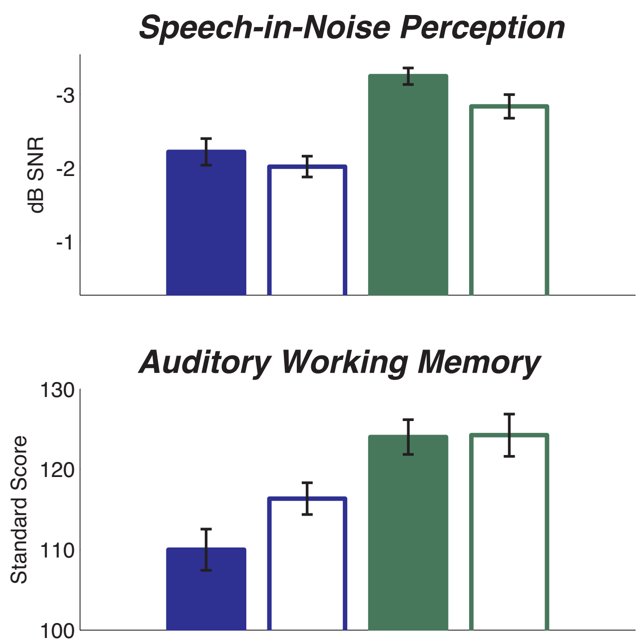

Figure 3. Behavioral advantages found in older adult non-musicians (blue; grouped on left) and musicians (green; grouped on right) musicians with normal hearing (solid bars) and hearing loss (open bars). Musicians outperform their non-musician peers on tests of speech perception in noise and auditory working memory. In fact, musicians with hearing loss even outperform non-musicians with normal hearing on the same tasks.

Musicians with hearing loss

Building upon their work in older musicians with normal hearing, Parbery-Clark and her colleagues considered the impact of music training on older adults with mild age-related hearing loss [58]. Older adult musicians with hearing loss exhibited several of the same biological enhancements as their normal-hearing peers, namely: faster neural timing in response to rapidly-changing sounds, more synchronous responses to speech, and greater resistance to noise degradation. However, in their neural responses older musicians with hearing loss had greater amplitudes at the fundamental frequency of speech as opposed to the enhanced harmonics seen in normal-hearing musicians. This unique neural signature is thought to be a compensatory mechanism developed to maintain robust encoding of sound despite a loss of peripheral function. Remarkably, these musicians with hearing loss outperformed normal hearing non-musicians on behavioural tests of speech-in-noise perception and auditory working memory (see Figure 3). These musicians' enhanced encoding of the fundamental frequency of speech may underlie their maintained behavioural advantage; indeed, in non-musician older adults robust neural encoding of the fundamental frequency supports speech perception in noise [15,59].

DOES MUSIC TRAINING HAVE TO BE LIFELONG?

The studies discussed so far have focused on individuals who played an instrument for their entire lives. This is a rare breed, especially in the context of senescence; it is much more common to encounter individuals who played music for a number of years as children and adolescents but then stopped as young adults. This raises an intriguing question: does the brain continue to benefit from these early experiences?

Skoe and Kraus [10] compared young adults (ages 18-31 yr) with varying levels of music training during childhood. More years of music lessons were associated with a higher signal-to-noise ratio in the neural response to sound, reflecting "cleaner" and more robust neural processing. Inspired by this work, White-Schwoch and colleagues [11] evaluated older adults (ages 55-76 yr) who played instruments from 1-14 years as children but had not touched an instrument for decades. Despite an intervening 40-50 years without training, older adults with past music experience had faster neural responses to consonants in speech than their peers—counteracting older adults' hallmark age-related temporal processing deficit [24].

Anderson and her colleagues [15] further investigated the impact of past music training on auditory perception, namely, the ability to understand speech in noise. They used structural equation modelling to elucidate the cognitive, central, peripheral, and lifestyle factors that contributed to older adults' abilities to understand speech in noisy listening environments. They dichotomized their subjects into two groups: one with no music training and a second with any amount (1-71 yr). The older adults with past music training relied more on cognitive functions such as working memory and attention to achieve the same performance on the speech-in-noise perception tasks, *irrespective of the amount of music training* and *irrespective of hearing status*. In older adults with no past music experience, life experience still informed mechanisms of hearing in noise, with socioeconomic status affecting hearing in noise and central auditory functions playing a stronger role.

These experiments are in line with animal studies that have demonstrated a lifelong impact of early sensory experience on auditory processing see, for example, [60]. A theme of these studies is that past auditory training—especially music training—may teach listeners to listen more meaningfully to sound. By directing attention to the most salient and acoustically complex elements in a soundscape, music training may subtly change the substrate mechanisms a listener uses to process novel sounds, even after said training has stopped. An intriguing possibility is that these listeners, even if they do not outperform peers on a cognitive or perceptual task [61], have achieved a different mode of *automatic* auditory processing that may "set the stage" for future auditory experiences [11]. If so, these individuals may be good candidates for auditory training to remediate challenges in auditory perception or cognition.

CONCLUSIONS

Taken together, the work reviewed here revolves around three general themes:

1. Age-related declines in auditory processing are not inevitable. They may be offset by the quality and consistency of everyday auditory experience.
2. Music training appears to be a powerful strategy to support meaningful interactions with sound, mitigating age-related decline in nervous system function.
3. Early auditory experiences, such as through music, are investments in healthy aging that pay lifelong dividends for auditory processing.

But why music? Music training directs special attention to meaningful acoustic features in the environment while engaging motor, cognitive, and emotional circuits. This rich series of networks combine into a powerful driver of experience-dependent neural plasticity. By allowing a listener to make sound-meaning connections, these listening activities can refine the *automatic* state of auditory processing, even during future listening tasks. This neural remodelling primes the musician's brain for effective and efficient auditory processing.

Despite the many accomplishments made with respect to aging, hearing loss, and music training, there remain open questions. Answering these questions can further inform the use of music training as a tool to remediate age- and hearing loss-related declines:

1. What is the impact of music training resumed or initiated early in life? In light of evidence that the nervous system retains substantial potential for plasticity into older age [see, for example, 62-64], and the large series of aforementioned benefits conferred by lifelong and early music, music training later in life may have special potential to engender improvements in auditory processing. Although there are some promising early studies [65,66], to date there have been no systematic investigations, and there have been no studies of biological changes following music training later in life. *Community-based* interventions are particularly appropriate for large-scale interventions in senior centres and retirement communities. Music would seem an especially suitable training regimen for these settings because music lends itself to group performance in choirs and ensembles.
2. How does music training compare to other training strategies for auditory rehabilitation, and what predictions can be made about who is a good candidate for which training strategy? Music training may not be a panacea, especially because there are some people who simply are not drawn to music. Understanding the pros and cons of different training strategies can inform clinicians interested in using auditory training as a part of their practice. Dosage studies can lead to best-practice protocols to identify candidates not just for auditory training in general, but for *particular kinds* of training.
3. What is the role of social and emotional engagement in music-related neuroplasticity? Listening to and performing music engages a large series of emotional networks, and it is thought that the emotional salience and motivation of a training regimen can bolster its neuroplastic potential.

Nevertheless, there is resounding evidence that music training can set up the brain for healthy aging. By bolstering the very aspects of auditory processing that decline with aging and hearing loss, music may prevent or mitigate the challenges that aging and hearing loss pose to spoken communication. Hopefully, music training at any point across the lifespan may lead to improvements in the quality of older adults' lives by bolstering everyday communication, grounded in improved auditory perception and cognition.

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REFERENCES

[1] Heine C and Browning C 2002 Communication and psychosocial consequences of sensory loss in older adults: overview and rehabilitation directions *Disabil. Rehabil.* **24** 763–73

[2] US Census Bureau 2011 *2008 National Population Projections* (Washington, D.C.: US Census Bureau)

[3] Lin F R, Thorpe R, Gordon-Salant S and Ferrucci L 2011 Hearing loss prevalence and risk factors among older adults in the United States *J. Gerontol. A. Biol. Sci. Med. Sci.* **66** 582–90

[4] Paganini-Hill A, Kawas C H and Corrada M M 2011 Activities and mortality in the elderly: The Leisure World Cohort Study *J. Gerontol. A. Biol. Sci. Med. Sci.* **66A** 559–67

[5] Kraus N and Chandrasekaran B 2010 Music training for the development of auditory skills *Nat. Rev. Neurosci.* **11** 599–605

[6] Patel A D 2011 Why would musical training benefit the neural encoding of speech? The OPERA hypothesis *Front. Psychol.* **2**

[7] Herholz S C and Zatorre R J 2012 Musical training as a framework for brain plasticity: Behavior, function, and structure *Neuron* **76** 486–502

[8] Putkinen V, Tervaniemi M and Huotilainen M 2013 Informal musical activities are linked to auditory discrimination and attention in 2–3-year-old children: an event-related potential study *Eur. J. Neurosci.* **37** 654–61

[9] Tierney A, Krizman J, Skoe E, Johnston K and Kraus N 2013 High school music classes enhance the neural processing of speech *Front. Psychol.* **4** 855

[10] Skoe E and Kraus N 2012 A little goes a long way: How the adult brain is shaped by musical training in childhood *J. Neurosci.* **32** 11507–10

[11] White-Schwoch T, Woodruff Carr K, Anderson S, Strait D L and Kraus N 2013 Older adults benefit from music training early in life: Biological evidence for long-term training-driven plasticity *J. Neurosci.* **33** 17667–74

[12] Strait D L and Kraus N 2014 Biological impact of auditory expertise across the life span: musicians as a model of auditory learning *Hear. Res*. **308**, 109-121.

[13] Zendel B R and Alain C 2012 Musicians experience less age-related decline in central auditory processing. *Psychol. Aging* **27** 410

[14] Salthouse T A 1985 *A theory of cognitive aging* Amsterdam: North Holland

[15] Anderson S, White-Schwoch T, Parbery-Clark A and Kraus N 2013 A dynamic auditory-cognitive system supports speech-in-noise perception in older adults *Hear. Res.* **300** 18–32

[16] Lorenzi C, Gilbert G, Carn H, Garnier S and Moore B C 2006 Speech perception problems of the hearing impaired reflect inability to use temporal fine structure *Proc. Natl. Acad. Sci.* **103** 18866–9

[17] Gordon-Salant S 2014 Aging, hearing loss, and speech recognition: stop shouting, I can't understand you *Perspectives on Auditory Research* Popper, Arthur, Fay, Richard R. (Eds.), New York: Springer. pp. 221-228.

[18] Gordon-Salant S and Fitzgibbons P J 1993 Temporal factors and speech recognition performance in young and elderly listeners *J. Speech Lang. Hear. Res.* **36** 1276

[19] Pichora-Fuller M K, Schneider B A, MacDonald E, Pass H E and Brown S 2007 Temporal jitter disrupts speech intelligibility: A simulation of auditory aging *Hear. Res.* **223** 114–21

[20] Walton J P 2010 Timing is everything: Temporal processing deficits in the aged auditory brainstem *Hear. Res.* **264** 63–9

[21] Caspary D M, Ling L, Turner J G and Hughes L F 2008 Inhibitory neurotransmission, plasticity and aging in the mammalian central auditory system *J. Exp. Biol.* **211** 1781–91

[22] Sergeyenko Y, Lall K, Liberman M C and Kujawa S G 2013 Age-related cochlear synaptopathy: an early-onset contributor to auditory functional decline *J. Neurosci.* **33** 13686–94

[23] Kraus N, Bradlow A R, Cheatham M A, Cunningham J, King C D, Koch D B, Nicol T G, McGee T J, Stein L and Wright B A 2000 Consequences of neural asynchrony: a case of auditory neuropathy *JARO-J. Assoc. Res. Otolaryngol.* **1** 33–45

[24] Anderson S, Parbery-Clark A, White-Schwoch T and Kraus N 2012 Aging affects neural precision of speech encoding *J. Neurosci.* **32** 14156–64

[25] Smith Z M, Delgutte B and Oxenham A J 2002 Chimaeric sounds reveal dichotomies in auditory perception *Nature* **416** 87–90

[26] Moore B C 2008 The role of temporal fine structure processing in pitch perception, masking, and speech perception for normal-hearing and hearing-impaired people *JARO-J. Assoc. Res. Otolaryngol.* **9** 399–406

[27] Anderson S, Skoe E, Chandrasekaran B and Kraus N 2010 Neural timing is linked to speech perception in noise *J. Neurosci.* **30** 4922

[28] Banai K, Hornickel J, Skoe E, Nicol T, Zecker S and Kraus N 2009 Reading and subcortical auditory function *Cereb. Cortex* **19** 2699–707

[29] Vander Werff K R and Burns K S 2011 Brain stem responses to speech in younger and older adults *Ear Hear.* **32** 168

[30] Clinard C G and Tremblay K in press Aging degrades the neural encoding of simple and complex sounds *J. Am. Acad. Audiol.*

[31] Bidelman G M, Villafuerte J W, Moreno S and Alain C 2014 Age-related changes in the subcortical-cortical encoding and categorical perception of speech *Neurobiol. Aging* in press.

[32] Parthasarathy A and Bartlett E 2011 Age-related auditory deficits in temporal processing in F-344 rats *Neuroscience* **192** 619–30

[33] Ruggles D, Bharadwaj H and Shinn-Cunningham B G 2012 Why middle-aged listeners have trouble hearing in everyday settings *Curr. Biol.* Vol 22, pp. 1417–1422.

[34] Dubno J R, Dirks D D and Morgan D E 1984 Effects of age and mild hearing loss on speech recognition in noise *J. Acoust. Soc. Am.* **76** 87–96

[35] Kotak V C, Fujisawa S, Lee F A, Karthikeyan O, Aoki C and Sanes D H 2005 Hearing loss raises excitability in the auditory cortex *J. Neurosci.* **25** 3908–18

[36] Engle J R, Tinling S and Recanzone G H 2013 Age-related hearing loss in rhesus monkeys is correlated with cochlear histopathologies *PloS ONE* **8** e55092

[37] Schaette R and McAlpine D 2011 Tinnitus with a normal audiogram: physiological evidence for hidden hearing loss and computational model *J. Neurosci.* **31** 13452–7

[38] Henry K S and Heinz M G 2012 Diminished temporal coding with sensorineural hearing loss emerges in background noise *Nat. Neurosci.* **15** 1362–4

[39] Anderson S, Parbery-Clark A, White-Schwoch T, Drehobl S and Kraus N 2013 Effects of hearing loss on the subcortical representation of speech cues. *J. Acoust. Soc. Am.* **133** 3030–8

[40] Lin F R, Yaffe K, Xia J, Xue Q-L, Harris T B, Purchase-Helzner E, Satterfield S, Ayonayon H N, Ferrucci L, Simonsick E M and others 2013 Hearing loss and cognitive decline in older adults *JAMA Intern. Med.* **173** 293–9

[41] Lin F R, Ferrucci L, An Y, Goh J, Metter E J, Davatzikos C, Kraut M and Resnick S (2013) Hearing loss and changes in brain volume in older adults. *Assoc. Res. Otolaryngol. Abs*. **312**

[42] Corrigall K A, Schellenberg E G and Misura N M 2013 Music training, cognition, and personality *Front. Psychol.* **4**

[43] Parbery-Clark A, Skoe E and Kraus N 2009 Musical experience limits the degradative effects of background noise on the neural processing of sound *J. Neurosci.* **29** 14100–7

[44] Chobert J, François C, Velay J-L and Besson M 2012 Twelve months of active musical training in 8-to 10-year-old children enhances the preattentive processing of syllabic duration and voice onset time *Cereb. Cortex*

[45] Strait D L, O'Connell S, Parbery-Clark A and Kraus N 2013 Musicians' enhanced neural differentiation of speech sounds arises early in life: Developmental evidence from ages three to thirty *Cereb. Cortex* in press

[46] Strait D L and Kraus N 2011 Can you hear me now? Musical training shapes functional brain networks for selective auditory attention and hearing speech in noise *Front. Psychol.* **2**

[47] Bidelman G M, Gandour J T and Krishnan A 2011 Cross-domain effects of music and language experience on the representation of pitch in the human auditory brainstem *J. Cogn. Neurosci.* **23** 425–34

[48] Zuk J, Ozernov-Palchik O, Kim H, Lakshminarayanan K, Gabrieli J D, Tallal P and Gaab N 2013 Enhanced syllable discrimination thresholds in musicians *PloS One* **8** e80546

[49] Kraus N and Nicol T 2014 The cognitive auditory system *Perspectives on Auditory Research* Springer Handbook of Auditory Research ed R Fay and A Popper (Heidelberg: Springer-Verlag) pp 299–319

[50] Parbery-Clark A, Anderson S, Hittner E and Kraus N 2012 Musical experience offsets age-related delays in neural timing *Neurobiol. Aging* **33** 1483.e1–1483.e4

[51] Parbery-Clark A, Anderson S, Hittner E and Kraus N 2012 Musical experience strengthens the neural representation of sounds important for communication in middle-aged adults *Front. Aging Neurosci.* **4**
[52] Parbery-Clark A, Strait D L, Anderson S, Hittner E and Kraus N 2011 Musical experience and the aging auditory system: Implications for cognitive abilities and hearing speech in noise *PLoS ONE* **6** e18082
[53] Hanna-Pladdy B and MacKay A 2011 The relation between instrumental musical activity and cognitive aging. *Neuropsychology* **25** 378
[54] Amer T, Kalender B, Hasher L, Trehub S E and Wong Y 2013 Do older professional musicians have cognitive advantages? *PloS ONE* **8** e71630
[55] Zendel B R and Alain C 2013 The influence of lifelong musicianship on neurophysiological measures of concurrent sound segregation *J. Cogn. Neurosci.* **25** 503–16
[56] Zendel B R and Alain C 2014 Enhanced attention-dependent activity in the auditory cortex of older musicians *Neurobiol. Aging* **35** 55–63
[57] Tremblay K L, Piskosz M and Souza P 2003 Effects of age and age-related hearing loss on the neural representation of speech cues *Clin. Neurophysiol.* **114** 1332–43
[58] Parbery-Clark A, Anderson S and Kraus N 2013 Musicians change their tune: How hearing loss alters the neural code *Hear. Res.* **302**, 121–131.
[59] Anderson S, Parbery-Clark A, Yi H-G and Kraus N 2011 A neural basis of speech-in-noise perception in older adults *Ear Hear.* **32** 750
[60] Zhou X and Merzenich M M 2008 Enduring effects of early structured noise exposure on temporal modulation in the primary auditory cortex *Proc. Natl. Acad. Sci.* **105** 4423–8
[61] Gaab N and Schlaug G 2003 The effect of musicianship on pitch memory in performance matched groups *NeuroReport* **14** 2291–5
[62] Anderson S, White-Schwoch T, Parbery-Clark A and Kraus N 2013 Reversal of age-related neural timing delays with training *Proc. Natl. Acad. Sci.* **110** 4357–62
[63] Anderson S, White-Schwoch T, Choi H J and Kraus N 2013 Training changes processing of speech cues in older adults with hearing loss *Front. Syst. Neurosci.* **7**
[64] Anguera J, Boccanfuso J, Rintoul J, Al-Hashimi O, Faraji F, Janowich J, Kong E, Larraburo Y, Rolle C, Johnston E and others 2013 Video game training enhances cognitive control in older adults *Nature* **501** 97–101
[65] Bugos J, Perlstein W, McCrae C, Brophy T and Bedenbaugh P 2007 Individualized piano instruction enhances executive functioning and working memory in older adults *Aging Ment. Health* **11** 464–71
[66] Johnson J K, Louhivuori J, Stewart A L, Tolvanen A, Ross L and Era P 2013 Quality of life (QOL) of older adult community choral singers in Finland *Int. Psychogeriatr.* 1–10