Research paper

Musical experience sharpens human cochlear tuning

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ABSTRACT

The mammalian cochlea functions as a filter bank that performs a spectral, Fourier-like decomposition on the acoustic signal. While tuning can be compromised (e.g., broadened with hearing impairment), whether or not human cochlear frequency resolution can be sharpened through experiential factors (e.g., training or learning) has not yet been established. Previous studies have demonstrated sharper psychophysical tuning curves in trained musicians compared to nonmusicians, implying superior peripheral tuning. However, these findings are based on perceptual masking paradigms, and reflect engagement of the entire auditory system rather than cochlear tuning, *per se*. Here, by directly mapping physiological tuning curves from stimulus frequency otoacoustic emissions (SFOAEs)—cochlear emitted sounds—we show that estimates of human cochlear tuning in a high-frequency cochlear region (4 kHz) is further sharpened (by a factor of 1.5×) in musicians and improves with the number of years of their auditory training. These findings were corroborated by measurements of psychophysical tuning curves (PTCs) derived via simultaneous masking, which similarly showed sharper tuning in musicians. Comparisons between SFOAE and PTCs revealed closer correspondence between physiological and behavioral curves in musicians, indicating that tuning is also more consistent between different levels of auditory processing in trained ears. Our findings demonstrate an experience-dependent enhancement in the resolving power of the cochlear sensory epithelium and the spectral resolution of human hearing and provide a peripheral account for the auditory perceptual benefits observed in musicians. Both local and feedback (e.g., medial olivocochlear efferent) mechanisms are discussed as potential mechanisms for experience-dependent tuning.

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1. Introduction

The mammalian cochlea functions as a filter bank that performs a spectral, Fourier-like decomposition on the acoustic signal (Dallos, 1996). Cochlear filters contribute to the primary organizational scheme (i.e., tonotopy) of the hearing pathway which is maintained at all subsequent stages of the auditory neuroaxis (Schreiner and Winer, 2007). Although initiated at the periphery, cochlear filtering is thought to influence the frequency and temporal resolution of hearing, and at least partially, account for the perceptual sensitivity for sounds (Evans, 1992). Although controversial (Ruggero and Temchin, 2005), estimates of human cochlear tuning are sharper compared to other mammals which may facilitate the specialized auditory skills and spectral acuity needed for

human speech communication (Joris et al., 2011; Shera et al., 2002). However, tuning is mature at birth (Abdala and Sininger, 1996) and thus, may be more immune to the neuroplasticity apparent at all higher stages of the auditory brain. This has bolstered the long-held view that early sensory processing is largely hard-wired and resistant to neuroplastic change resulting from auditory experience or learning.

The critical role of cochlear frequency selectivity in human communication is evident in normal aging and hearing impairments (Glasberg and Moore, 1986; Henry and Heinz, 2012; Lutman et al., 1991) where compromised inner ear function broadens the auditory filters and produces numerous perceptual deficits [e.g., hearing in noise (Badri et al., 2011; Henry and Heinz, 2012), poorer speech recognition (Baskent, 2006)]. Cognitive decline and speech-hearing deficits that emerge across the lifespan are often traceable to declines in cochlear function (Humes et al., 2013). Additionally, children with language-learning disorders show poorer auditory spectral resolution (Wright et al., 1997), suggesting that the

frequency resolving power of the cochlea plays an integral (but underappreciated) role in fortifying speech-language abilities early in life. While it is clear that frequency selectivity deteriorates (i.e., filters broaden) in cases of aberrant hearing disorders (Henry and Heinz, 2012; Lutman et al., 1991), whether or not human cochlear tuning is malleable and can be further enhanced through auditory learning or training has yet to be established.

Here, we investigated the hypothesis that salient forms of auditory listening experience can sharpen human cochlear tuning. Musicians represent an ideal model to understand the extent of auditory brain plasticity as musical aptitude has been shown to hone spectral processing across the auditory pathway (Herholz and Zatorre, 2012). Cochlear filtering represents a signal processing "bottle neck" through which all auditory information must pass prior to engaging these higher auditory brain structures. This raises the intriguing question of whether experience-dependent improvements in musicians' spectral acuity observed at behavioral (Bidelman et al., 2011a; Micheyl et al., 2006) and neural (Herholz and Zatorre, 2012; Munte et al., 2002) levels might actually be inherited from refinements in the sensory-receptor characteristics of the cochlea.

Presently, it is not possible to measure human cochlear tuning *in vivo* using gold standard approaches (e.g., basilar membrane measurements or auditory nerve fiber responses). However, indirect estimates of human cochlear tuning are possible via measurements of the suppression of stimulus frequency otoacoustic emissions (SFOAEs) (Charaziak et al., 2013; Keefe et al., 2008; Kemp and Chum, 1980). OAEs are bioacoustic sounds recorded in the ear canal originating from the cochlear outer hair cells (OHCs)—responsible for amplifying basilar membrane motion and providing the exquisite sensitivity/selectivity of mammalian hearing (Brownell, 1990; Dallos and Corey, 1991). OAE responses are generated exclusively within the sensory epithelium of the inner ear and offer a window into cochlear function at a pre-neural level (Abdala and Sininger, 1996). SFOAEs are desirable here as they are evoked by tonal stimuli and thus, are thought to provide the most accurate place-specific responses amongst the various classes of OAEs (Charaziak et al., 2013; Shera and Guinan, 1999). To investigate whether auditory experience sharpens peripheral cochlear tuning, we measured physiological frequency tuning curves derived via SFOAEs in listeners with and without formal musical training. Cochlear (i.e., SFOAE-derived) tuning was then compared with perceptual tuning in the same listeners measured via psychophysical tuning curves (PTCs) from simultaneous masking (Sek et al., 2005). We have previously reported sharper behavioral PTCs in trained musicians (Bidelman et al., 2014a). Here, we aimed to replicate and extend these perceptual results and identify if musicians also demonstrate superior physiological tuning at the level of the cochlea.

While previous studies have shown overall enhanced levels and efferent modulation of OAEs in musicians (Perrot and Collet, 2014), we are aware of no study that has assessed experience-dependent changes in *peripheral tuning* with these cochlear responses. Sharper physiological tuning in musicians would establish that the experience-dependent plasticity afforded by this and similar intense auditory experiences (Kraus and Chandrasekaran, 2010) might emerge even prior to engagement of the central nervous system, as peripheral as the cochlea.

2. Materials & methods

2.1. Participants

Twenty-seven young adults (age range: 18—33 years) participated in the experiment: 14 musicians (5 males, 9 females) and 13 nonmusicians (5 males, 8 females). Consistent with criteria of previous reports (Bidelman et al., 2014a; Micheyl et al., 2006; Parbery-Clark et al., 2009), musicians (Ms) were amateur instrumentalists who had received $\geq$ 8 years of continuous formal instruction on their principal instrument ($\mu \pm SD$; 14.4 $\pm$ 3.6 yrs), beginning prior to age 12 (7.3 $\pm$ 2.6 yrs), and were currently active in music practice or ensemble engagement. Nonmusicians (NMs) had $\leq$ 2 years of self-directed music training (0.2 $\pm$ 0.6 yrs) and no instruction within the past five years. All participants were native speakers of English, had normal audiometric thresholds (i.e., $\leq$20 dB HL between 250 and 8000 Hz), normal middle ear function (i.e., Type-A tympanograms), and reported no previous history of neuropsychiatric illnesses. Critically, both groups were well-matched in hearing acuity across the range of hearing thresholds tested (all p-values > 0.1). Besides musical training, the two groups were otherwise matched in age (Ms: 23.1 $\pm$ 3.4 yrs, NMs: 25.8 $\pm$ 3.3 yrs; $t_{25} = 2.04$, $P = 0.06$), formal education (Ms: 17.4 $\pm$ 3.15 yrs, NMs: 18.3 $\pm$ 2.5 yrs; $t_{25} = -0.94$, $P = 0.35$), and right-handedness laterality index (Ms: 87.2 $\pm$ 16.2%, NMs: 82.6 $\pm$ 19.6%; $t_{25} = 0.68$, $P = 0.51$) (Oldfield, 1971). Participants were paid for their time and gave written informed consent in compliance with a protocol approved by the Institutional Review Board of The University of Memphis.

2.2. Psychophysical tuning curves (PTCs)

All testing was carried out in an IAC sound attenuating chamber. Behavioral PTCs were measured in the right ear of each listener at a characteristic frequency (CF) of 4-kHz using simultaneous masking (for details, see Bidelman et al., 2014a; Sek et al., 2005). We restricted our analysis of tuning at 4-kHz given that our previous studies showed group differences in perceptual tuning (i.e., PTCs) only in high-frequency cochlear regions (Bidelman et al., 2014a). Briefly, listeners monitored a low intensity probe tone [4 kHz; 15 dB SPL ($\approx$20 dB SL)] concurrent with a narrowband masking noise (320 Hz) that was continuously varied according to a Békésy track on the masker's intensity (2 dB/s). The center frequency of the masker swept upward from a starting frequency of 1.5 below to 0.6 octaves above the 4-kHz probe frequency. Following a brief task familiarization, fast PTCs were measured twice for each listener and averaged across runs. A 2-point moving average was applied to raw fast PTCs prior to quantification to smooth the continuous thresholds obtained in the Békésy track. We then quantified the degree of tuning in listeners' behavioral auditory filters by measuring quality factor (Q_{10}), a normalized measure of filter "sharpness" [i.e., $Q_{10} = f_c/BW$, where f_c is the filter's CF and BW is the +10 dB bandwidth (BW)]. Auditory stimuli were delivered to the right ear through an insert earphone (ER-3A; Etymotic Research) that was calibrated using a Larson-Davis LxT SPL meter.

2.3. Physiological cochlear tuning curves (SFOAEs)

Physiological tuning was assessed by measuring the suppression of listeners' stimulus-frequency otoacoustic emissions (SFOAEs) using previously described procedures (Charaziak et al., 2013). It should be noted that SFOAE tuning curves are only an indirect (and likely under-) estimate of cochlear tuning. However, they provide a non-invasive assay to estimate basilar membrane tuning in humans (Shera and Guinan, 2003). SFOAEs are a particular class of emissions evoked by tonal stimuli and represent the OHC response at a specific cochlear place, at least at low stimulation levels (Shera et al., 2002). Briefly, SFOAEs were measured in the right ear using an ER-10C probe assembly (Etymotic Research) controlled by a Mimosa Acoustics Hear ID™ software, which both generated stimuli and acquired physiological responses (48 kHz sample rate). SFOAEs were evoked by a tone stimulus (f_{probe} = 4 kHz, ~420 ms

duration). The FFT buffer size for a subaverage was 85.33 ms (4096 samples). For one SFOAE average, the probe tone was output for the duration of four subaverages plus overhead for windowing (cosine ramping) the tone on/off to ensure the SFOAE was at steady state. The suppressor tone was output for a duration of two subaverages plus windowing overhead. The window was one-quarter the duration of the subaverage, and an additional one-quarter duration window was used to ensure steady state was achieved when the suppressor tone was turned on. Measurements were terminated following the completion of 16 SFOAE averages. The use of a 4-kHz stimulus ensured that physiological tuning curves were measured at the same cochlear place as behavioral PTCs and fell outside the evoking bandwidth (<2.8 kHz) of the middle-ear muscle reflex (MEMR) (Gelfand, 2002), which can negatively affect SFOAE recordings. Additionally, a high-frequency probe was desirable as low-frequency SFOAEs do not reflect place-specific basal membrane responses (Charaziak and Siegel, 2015). This would have rendered a direct comparison between physiological and behavioral tuning problematic as comparisons would reflect tuning at different cochlear locations.

We measured tuning curves at the 4-kHz location by presenting a concurrent suppressor tone (f_{supp}) of varying frequency (Charaziak et al., 2013; Keefe et al., 2008). The vector difference in response to the probe tone (f_{probe}) and to the probe tone paired with the suppressor signal (f_{supp}) results in an SFOAE residual, corresponding to the part of the SFOAE suppressed by f_{supp} (Charaziak et al., 2013). SFOAE residuals were calculated as the vector difference in ear canal pressure at the emission frequency (f_{probe}) with and without the presence of the suppressor tone.

Spontaneous otoacoustic emissions identified at frequencies less than 4 kHz are known to interact with certain external tones (Long, 1998), possibly affecting the measurement of PTCs and SFOAEs. However, spontaneous emissions are less commonly measured from normal-hearing ears near the 4 kHz probe used here compared to lower frequencies (Kuroda, 2007). Moreover, PTC Q_{10} values are not appreciably different in listeners with and without spontaneous OAEs (Baiduc et al., 2014) nor is PTC frequency selectivity measured at 4 kHz (Micheyl and Collet, 1994). Therefore, identification of spontaneous OAEs near 4 kHz was not performed in the present study.

We varied the probe tone level between 15 and 50 dB SPL to (i) account for listeners' individual auditory thresholds, (ii) guarantee SFOAE residual responses exceeded a signal-to-noise ratio (SNR) criterion of ≥ +9 dB in all participants (Lapsley-Miller et al., 2004), and (iii) ensure stimulus levels fell below the MEMR threshold (>85–90 dB SPL) and avoid inadvertent SFOAE attenuation (Gelfand, 2002). The noise floor was estimated from six FFT bins around the probe frequency in the combined probe + suppressor spectra. Artifact rejection criterion was set at 50 dB SPL. Prior to SFOAE tuning curve measurements, the baseline SFOAE level at the probe frequency was measured with the suppression method with the suppressor frequency fixed at a slightly higher frequency (~47 Hz) above the probe frequency at a ~50–60 dB SPL starting suppressor level (Berezina-Greene and Guinan, 2015; Shera and Guinan, 1999). The lowest probe level that would yield an SFOAE residual at a +9 SNR criterion was then established.

While audiometric thresholds did not differ between groups, it was necessary to vary presentation level to achieve adequate SNR of the SFOAE responses. However, the shapes of auditory filters are level dependent with stimulus intensity (Charaziak et al., 2013; Ruggero et al., 2000). Differences in presentation level between groups would render direct comparison of tuning spurious. Critically, we confirmed that the probe levels used to evoke cochlear emissions did not differ between musician and nonmusicians; on average, probe levels were <0.5 dB between groups (Ms:

34.6 ± 9.2 dB SPL, NMs: 34.2 ± 11.6 dB SPL; $t_{25} = 0.10$, $P = 0.92$). Moreover, tuning curve Q_{10}s were not correlated with probe level for either group (Ms: $r = -0.05$, $P = 0.86$; NMs: $r = -0.29$, $P = 0.32$). These controls rule out the possibility that differences in cochlear tuning between groups result from simple differences in stimulus intensity (Ruggero et al., 2000).

SFOAE tuning curves were measured as iso-residual curves. The suppressor tone frequency (f_{supp}) varied from $0.8f_{probe}$ to $1.2f_{probe}$, with a resolution of 16 points/octave (f_{supp} range: 3168–4832 Hz). For a given probe-suppressor condition, the probe level was fixed and the suppressor level was varied using a tracking procedure (5 dB step size). Note that this physiological procedure parallels the masking approach used to measure behavioral PTCs. Tracking was terminated when the SFOAE residual was within ±2 dB of a residual criterion of 0 dB SPL (Charaziak et al., 2013). The tracking procedure was terminated if the residual criterion was not met when the level of the suppressor reached 85 dB SPL. As with behavioral PTCs, we quantified the sharpness of physiological tuning by computing the Q_{10} of SFOAE tuning curves. SFOAE Q_{10} values were SQRT-transformed to improve homogeneity of variance assumptions prior to statistical testing. Both behavioral and SFOAE Q_{10}s were then compared between groups using independent samples t-tests.

While Q_{10} provides a quantification of the sharpness of tuning it fails to consider the overall shape of tuning curves. To directly assess the correspondence between perceptual and physiological measures, we measured the mutual information (MI) (Cover and Thomas, 1991) between PTC and SFOAE tuning curves. MI quantifies the statistical dependence between two signals and the amount of information, (i.e., reduction in uncertainty) that one tuning curve provides about the other. MI offers a means to detect both linear and nonlinear statistical dependencies between responses and is preferable here over correlations, which measure only linear dependencies (Jeong et al., 2001). Differences in MI were compared between groups using an independent samples t-test where higher values of MI indicate more robust correspondence between the overall shapes of cochlear and behavioral tuning (cf. brain-behavior consistency).

3. Results

Behaviorally, we found that musicians had more sharply tuned auditory filters than their nonmusician peers, replicating our prior studies (Bidelman et al., 2014a). PTC Q_{10} values (normalized measure of tuning) ranged from 5 to 10 (Bidelman et al., 2014a) but were ~1.5× sharper in musically trained ears ($t_{25} = 2.21$, $P = 0.036$) (Fig. 1A). Previous studies have suggested that musicians excel in detecting *speech* signals in noise (Bidelman and Krishnan, 2010; Parbery-Clark et al., 2009). However, PTC tip thresholds did not differ between groups ($t_{25} = 1.06$, $P = 0.29$), indicating that *simple* signal in noise detection was not influenced by musical experience. While PTCs are widely believed to reflect peripheral tuning (Evans, 2001; Pickles, 1979), central contributions (e.g., attention) cannot be ruled out given the use of an active listening task and thus, engagement of the entire auditory pathway. Sharper perceptual tuning in musicians may reflect higher peripheral frequency selectivity, increased spectral sensitivity at cortical levels (Schneider et al., 2002), or enhanced cognitive influences [e.g., auditory attention, efficiency of detection, or improved cognitive effort (Bianchi et al., 2016; Bidelman et al., 2014a; Fine and Moore, 1993; Strait et al., 2010)].

To directly assess whether musicians' increased frequency selectivity results from enhanced cochlear frequency selectivity rather than simply improved perceptual abilities, we mapped *physiological* tuning with *passively evoked* SFOAEs. Paralleling psychophysical tuning, we found that cochlear tuning was ~1.5×
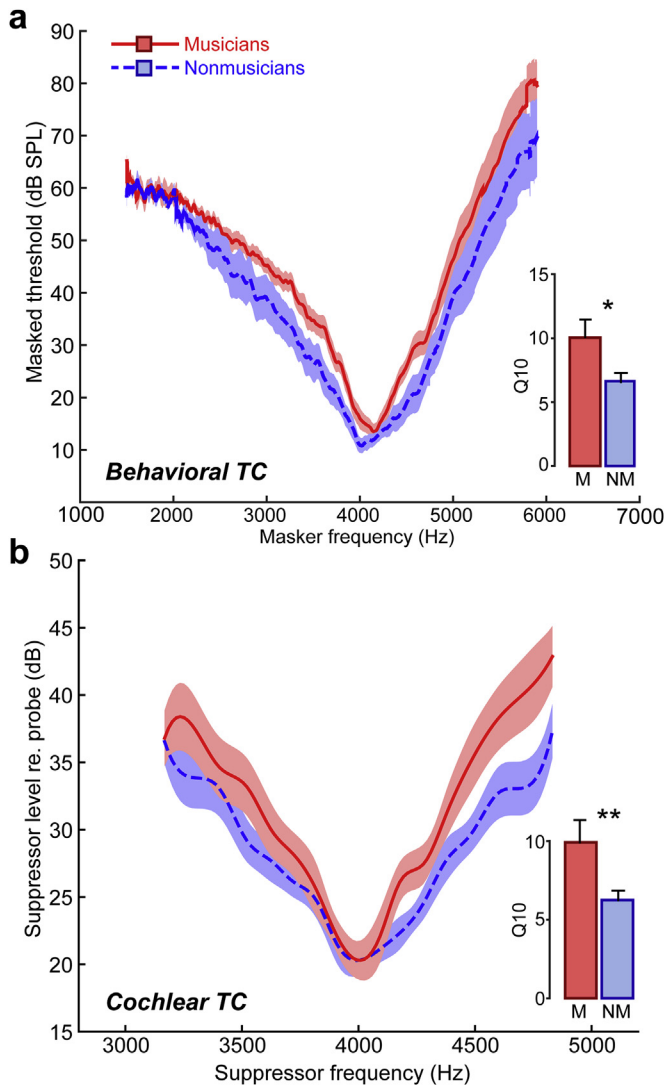
Fig. 1. Behavioral and cochlear tuning is sharper in musically trained ears. (a) Psychophysical tuning curves measured via simultaneous masking (Sek et al., 2005) show the threshold for detecting a 4 kHz probe signal in the presence of narrowband masking noise. Masking is more effective near the signal frequency compared to spectrally remote maskers. Sharper tuning in listeners with musical training is indicated by higher filter quality factor (Q_{10}), a normalized measure of tuning "sharpness" (inset). (b) Physiological tuning curves derived via suppression of SFOAEs corroborate behavioral results revealing sharper cochlear tuning in musicians. Suppressor levels are expressed relative to the probe level. Both behavioral and physiological tuning is ~1.5× better in musically trained ears. *P < 0.05, **P ≤ 0.01, errorbars = ±1 s.e.m.

sharper in musicians relative to nonmusicians ($t_{25} = 2.57$, $P = 0.01$). These results reveal that musicians' enhanced perceptual frequency selectivity observed behaviorally (Fig. 1A) can be directly attributed to sharper cochlear tuning (i.e., peripheral frequency selectivity). Furthermore, correlational analyses revealed strong positive associations between listeners' years of music experience and behavioral ($r = 0.53$, $P = 0.005$; Fig. 2A) and physiological ($r = 0.44$, $P = 0.02$; Fig. 2B) tuning such that longer extents of music engagement predicted sharper auditory filtering. Lastly, we found that mutual information between SFOAE and PTC curves was higher in musicians ($t_{25} = 1.90$, $P = 0.034$) (Fig. 2C), indicating better correspondence between the overall shapes of cochlear and behavioral tuning functions in trained listeners.

4. Discussion

Collectively, our findings indicate (i) musically trained individuals have sharper cochlear (and behavioral) tuning than their nonmusician peers at 4 kHz and (ii) enhancements in cochlear tuning vary according to the degree of listeners' experience/training. While a handful of previous studies have investigated potential links between musicianship and increased frequency selectivity (Bianchi et al., 2016; Fine and Moore, 1993; Soderquist, 1970), reports have been equivocal. Studies that have derived tuning estimates via *indirect* psychophysical paradigms such as notched-noise masking (Fine and Moore, 1993), critical bands (Soderquist, 1970), and pitch discrimination (i.e., transition point between resolved and unresolved harmonics; Bianchi et al., 2016), have failed to observe superior tuning in musicians. Here, by *directly* measuring peripheral and behavioral tuning via SFOAE and psychophysical tuning curves, our results provide the first direct evidence that protracted auditory experience can refine peripheral frequency selectivity in an experience-dependent manner, increasing the resolving power of the cochlea, and ultimately the spectral resolution of hearing. Musical training has long been recognized as a model of plasticity in central nervous system function (Herholz and Zatorre, 2012; Kraus and Chandrasekaran, 2010; Munte et al., 2002). Here we provide evidence that musical experience actually *improves* perceptual and physiological frequency selectivity at the level of the cochlea. It would be interesting to assess whether this musician advantage would mitigate the destructive effects of hearing loss on frequency selectivity, particularly as musicians are at greater risk of developing noise-induced hearing loss (Phillips et al., 2010), which tends to broaden the auditory filters (Glasberg and Moore, 1986; Henry and Heinz, 2012).

Musical aptitude is known to sensitize spectral processing at all levels of the auditory brain above the level of the cochlea (Kraus and Chandrasekaran, 2010; Schneider et al., 2002; Wong et al., 2010). Our findings thus offer a common, cochlear rather than perceptual-cognitive (Bianchi et al., 2016; Bidelman et al., 2014a), cortical (Schneider et al., 2002), or upper brainstem (Bidelman et al., 2011b; Wong et al., 2007) basis, *per se*, for musicians' increased auditory spectral acuity. By implicating a peripheral origin for music-related auditory perceptual advantages, our data suggest that functional changes in the musical brain previously observed at higher neural stages, e.g., brainstem (Bidelman et al., 2014b; Wong et al., 2007) and cortex (Bidelman et al., 2014b; Schneider et al., 2002), might be inherited from sensory-receptor characteristics of the cochlea. Moreover, musicians' superior cochlear tuning was observed under *passive* listening, suggesting that their enhancements in peripheral filtering do not depend on overtly controlled "top-down" factors (e.g., attention, listening effort; cf. Bianchi et al., 2016).

While we have confirmed that human experience and individual listening history can impact cochlear frequency selectivity, what might be the mechanisms driving such effects? One possibility is that musicians' experience-dependent sharpening of tuning results from local changes within the cochlea: either enhanced "pre-neural" receptor selectivity or changes to basilar membrane biomechanics (e.g., increased negative damping; Neely and Kim, 1983), both of which would increase cochlear tuning. Additionally, previously studies have shown plastic changes in the regulation of prestin—a motor protein responsible for OHC electromotility (Zheng et al., 2000)—with negative factors such as noise induced hearing loss (Xia et al., 2013) and ablation of efferent control (Lamas et al., 2015). It is conceivable that prestin regulation may also be driven by "positive" factors (e.g., auditory training) which could, in turn, change OHC motility in an experience-dependent manner and account for the observed differences in
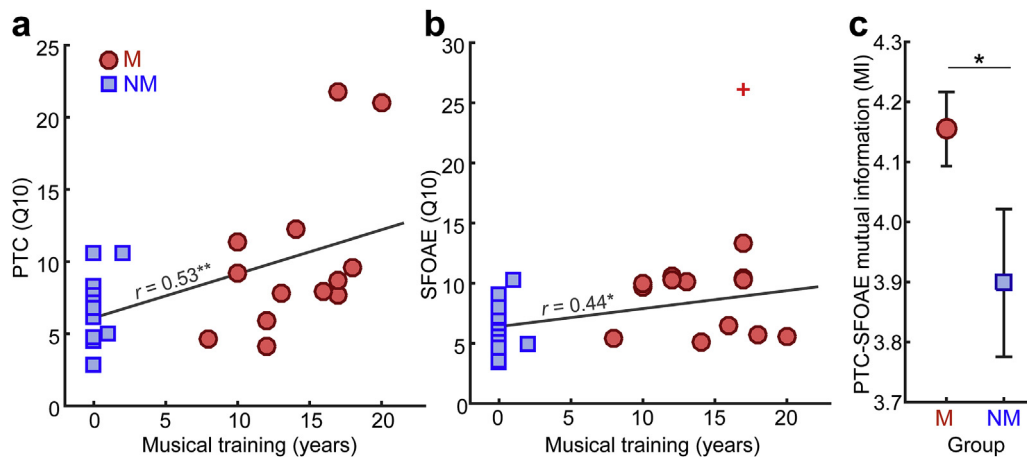
Fig. 2. Associations between tuning sharpness and musical training. Auditory filter sharpness (Q_{10}) of both (a) psychophysical and (b) cochlear tuning are predicted by listeners' years of formal musical training; longer musical engagement is associated with sharper behavioral and cochlear tuning reflecting central and peripheral frequency selectivity, respectively. +, influential observation excluded from regression (Cook's-D criterion) (Cook, 1979). (c) Higher mutual information between physiological and behavioral tuning curves in musicians indicates a closer correspondence between physiological and behavioral tuning in trained listeners. *$P < 0.05$, **$P \leq 0.01$; errorbars = ±1 s.e.m.

cochlear tuning observed here. Alternatively, sharper cochlear tuning could originate from training-related efferent feedback through the medial olivocochlear (MOC) fibers. Cochlear OHCs (responsible for OAE generation) are directly innervated by MOC neurons which originate in the lower brainstem and act as a modulatory gain control for cochlear amplification (Guinan, 2006) and auditory filter bandwidths (Francis and Guinan, 2010; Guinan and Gifford, 1988; Vinay and Moore, 2008). Yet, both sharper and broader tuning have been observed in auditory nerve fiber responses upon MOC stimulation (Guinan and Gifford, 1988) and in behavioral PTCs (Vinay and Moore, 2008), so explanations based on MOC changes in tuning remain speculative (see also, Bhagat and Kilgore, 2014).

A more plausible explanation for our findings are the putative roles of the MOC bundle in providing "antimasking" to the cochlea to improve signal detection in noise (Bhagat and Carter, 2010; de Boer et al., 2012) and successful auditory learning (de Boer and Thornton, 2008). Indeed, both the behavioral PTCs and SFOAE measures contained an additional masking signal concurrent with either the detection (PTC) or measurement (SFOAE) of the target probe signal which could act as an activator for the ipsilateral MOC pathway. Conceivably, goal-directed auditory experience(s) like musical training could act to strengthen efferent MOC antimasking and by proxy, cochlear frequency selectivity. In this regard, the central auditory nervous system would be continuously charged with sharpening tuning in the periphery through corticofugal feedback. This notion is supported by previous evidence from OAE recordings which suggests that musicianship strengthens MOC activation and efferent feedback to the cochlea (for review, see Perrot and Collet, 2014).

Additionally, while active engagement and attention are no doubt required during auditory learning and achieving musical aptitude, we note that OAEs were measured here under *passive* listening and are routinely recorded during sleep (Abdala and Sininger, 1996). This suggests that enhancements in musicians' cochlear frequency selectivity operate pre-attentively, without listeners consciously engaging with the acoustic signal. Under this notion, it may be the case that musical experience sensitizes spectral receptive fields of neurons in the brainstem (Bidelman et al., 2011a), and this is transmitted to the outer hair cells in a stereotyped, unconscious reflexive action through the MOC efferents in passive listening circumstances. In active listening

circumstances, musical training that improves cortical tuning (Bidelman et al., 2014b; Munte et al., 2002), may result in attention-driven feedback to the cochlea (Perrot et al., 2006) that also sharpens cochlear tuning.

Our study is restricted to examination of tuning at higher-frequency (4-kHz) regions of the cochlea. SFOAE filter estimates at low-frequency cochlear regions are questionable (Charaziak and Siegel, 2015) and our previous behavioral studies indicated that group differences in psychophysical tuning secondary to musical training emerge only in more basal (high frequency) cochlear regions (Bidelman et al., 2014a). Taken alongside our previous report (Bidelman et al., 2014a), it is conceivable that experience-dependent enhancements of cochlear tuning are restricted to high-frequency cochlear channels (i.e., >1 kHz). Greater effects of auditory experience at higher frequency regions of the cochlear partition could result from the known frequency-dependence of the cochlear amplifier, that is produced by the OHC motility and controls basilar membrane tuning (Dallos and Corey, 1991). Indeed, cochlear nonlinearities including level-dependent amplification and tuning are larger at higher (basal) relative to lower (apical) frequency regions of the cochlea (Abbas and Sachs, 1976). Enhanced high-frequency coding in and of itself would nevertheless be advantageous as higher spectral cues are critical for real-world listening including the differentiation of sound timbre (e.g., voice quality) and extracting speech from noise (Guinan, 2006)—skills at which musicians excel (Bidelman and Krishnan, 2010; Parbery-Clark et al., 2009). Along these lines, musicians may produce efferent activity that is shaped in frequency better than nonmusicians so as to make SFOAE tuning sharper (e.g., musicians recruit more efferent activity that turns down the gain at the masker frequency when far from the probe). Conceivably, musicians' auditory-perceptual benefits in these and similar complex spectral listening tasks could result from similar MOC "antimasking" and superior frequency selectivity at the level of the cochlea.

A limitation of the current study is the use of SFOAE suppression tuning curves, which provide only an indirect measure of cochlear tuning. Previous studies have shown good agreement between SFOAE estimates of tuning (based on group delay) and direct measurements from auditory nerve fibers in chinchillas (Shera et al., 2010). Nevertheless, it is important to note that SFOAE tuning curves as measured here require the use of a suppressor signal

in addition to the probe CF. This contrasts *in vivo* measurements of cochlear tuning (basilar membrane, auditory nerve fiber responses) which do not require a simultaneous suppressor (Ruggero et al., 2000). Given that suppression tends to broaden auditory filter bandwidths (e.g., Bidelman et al., 2014a; Moore, 1978; Oxenham and Shera, 2003), it is likely that tuning estimates observed here (via suppression of SFOAEs), actually *underestimate* true cochlear tuning. Additionally, as noted earlier, SFOAE suppression tuning curves probably also reflect influences from higher levels of the central auditory pathway (e.g., MOC efferents) in addition to pure "cochlear tuning." [Although this often cannot be ruled out in *in vivo* basilar membrane measurement either]. Nevertheless, what is clear is that we observe changes in *peripheral tuning* estimates in musically trained listeners. Whether or not these effects reflect local cochlear changes or influences from the central auditory pathway (e.g., MOC efferent) remains to be clarified in future experiments.

In conclusion, our results indicate that salient human experiences (i.e., musicianship) can sharpen peripheral tuning and the frequency selectivity of hearing. Our findings recast current understanding of auditory neuroplasticity by demonstrating experience-dependent enhancements as early as the sensory epithelium of the inner ear. However, while group differences are observable at the periphery, musicians' enhancements in cochlear function presumably result from central nervous system involvement and feedback from the brainstem MOC efferent pathway that would be engaged during the intensive auditory learning required of musical training (cf. de Boer and Thornton, 2008; Perrot and Collet, 2014). Nevertheless, by demonstrating beneficial plastic changes in human peripheral tuning our findings open the possibility for improving broadened cochlear tuning and auditory spectral acuity known to affect certain hearing and language-learning disorders (Wright et al., 1997).

Author contributions

G.M.B. and S.P.B. designed the experiment, C.N. collected the data, G.M.B. and C.N. analyzed the data, and G.M.B., C.N., and S.P.B. wrote the paper.

Acknowledgments

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