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Opinion paper

Reply to Manley: Is there more to cochlear tuning than meets the ear?

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ABSTRACT

Enhanced psychophysical and cochlear tuning observed in musicians is unlikely to be explained by mere differences in human cochlear length. A parsimonious account of our 2016 data is improved efferent feedback from the medial olivocochlear efferent system that adjusts masking and tuning properties of the cochlea and is subject to attentional modulation—all functions reported to be enhanced in musically trained ears. Still, new experiments are needed to tease out "nature" vs. "nurture" effects in music-related brain plasticity and move beyond cross-sectional studies and definitions of "musicians" based solely on self-report.

While cochlear tuning is broadened by maladaptive plasticity in hearing (e.g., hearing loss), whether it can be sharpened through listening experience to improve the frequency resolving power of the cochlea was an open question. In Bidelman et al. (2016), we mapped physiological tuning curves using stimulus frequency otoacoustic emissions (SFOAEs) to provide the first comparisons of cochlear tuning in musicians and nonmusicians. We reported tuning was, on average, sharper in musicians compared to nonmusicians and scaled with their number of years of self-reported music training. These *physiological* findings corroborated several behavioral studies reporting sharper psychophysical tuning curves (PTCs) in musicians estimated via both forward and simultaneous masking paradigms (Fig. 1A) (Bidelman et al., 2016, 2014; Kakar et al., 2021). The also converged with a number of prior OAE studies demonstrating enhanced emissions in musicians (Brashears et al., 2003; Main and Skoe, 2024; Micheyl et al., 1997; Perrot and Collet, 2014; Perrot et al., 1999). The SFOAE tuning findings were especially provocative because they suggested that brain plasticity and at least some of musicians' enhanced spectral acuity observed in behavioral pitch discrimination tasks (Bidelman et al., 2011, 2013; Micheyl et al., 2006; Zarate et al., 2012) and sensory encoding (Herholz and Zatorre, 2012; Moreno and Bidelman, 2014) might begin at a surprisingly early stage of the auditory system—the cochlea.

In his editorial opinion, Manley (2025) questions our findings and refutes the notion that listening experience could sharpen cochlear and neural tuning selectivity. His chief complaints rest in (i) the lack of correspondence between SFOAE and PTC measures, (ii) the assertion that changes in cochlear selectivity as the result of (music) experience "lack both any known anatomical substrate and precedent" and thus render our interpretations as being "not-parsimonious," and (iii) the correlational nature of our data and what constitutes the definition of a "musician." We welcome such commentary on our work.

To the first point, it is not clear that cochlear/neural and behavioral tuning are necessarily isomorphic properties of auditory frequency resolution. As noted by Bergevin et al. (2017), "OAEs provide means to characterize the cochlear mechanical filter peripheral to the perceptual auditory filter and the exact relationship between OAE-derived tuning measures, auditory nerve tuning curves, and perceptual auditory filters is not entirely established (p. 304)." Similar conclusions were drawn by Charaziak et al. (2013). Behavioral PTC and OAEs differ by non-trivial factors, notably attention, that could produce disparate results between measures. While Q10 (a singular metric of tuning) was not correlated between PTCs and SFOAEs, musicians did show higher mutual information between their behavioral and physiological responses (Bidelman et al., 2016), suggesting better correspondence in the overall shape of their tuning curves.

In his second critique, Manley argues that musicians may constitute "a subgroup of humans whose cochlear development was influenced by genetic and epigenetic factors." His central claim is that musicians (i.e., or individuals that pursue music in the first place) might be endowed with extraordinarily long cochleae that enables more refined frequency resolution. The argument that humans become or at least are drawn to becoming musicians because of their cochlea seems highly restrictive, and it is entirely auditory in formulation. People drawn to music might have much more than hearing aptitudes. Better skills to learn the motor

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patterns to play an instrument compared to people who lack those abilities comes to mind. Still, from a strictly auditory standpoint, longer cochleae could, in theory, produce sharper tuning (Shera and Charaziak, 2019). In support of his assertion, Manley cites anatomical studies that have shown several millimeter variation in human basilar membrane (BM) length (e.g., Ulehlová et al., 1987; Würfel et al., 2014). Are individual differences in BM length substantial enough to explain the empirical data on musicians' tuning?

We tested the plausibility of this argument by compiling published data across several mammalian species for which both cochlear length and auditory nerve fiber Q10 tuning data are available (or estimable in the case of humans) (Fig. 1B). Across species, we confirmed tuning is in fact easily predicted from BM length via a simple linear relation: $Q_{10} = 0.14\,BM + 1.91$ (Eq. 1). However, within humans, the range of plausible Q10 based on human BM length (estimated via the 95% CI of Eq. 1) is considerably smaller than SFOAE Q10 s observed in some musician listeners (Bidelman et al., 2016) (Fig. 1C). Musicians' tuning (Bidelman et al., 2016) also appears sharper than the general population as reported in other human studies using similar OAE methodology (Charaziak et al., 2013). Thus, it appears that regardless of definition, "musician" tuning is better than what would be expected from normal variation in human BM length alone.

While we agree cochlear dimensions probably influence certain aspects of mammalian hearing (Braga et al., 2015; Manley and van Dijk, 2016) (e.g., high- and low-frequency limits; Echteler et al., 1989; Kirk and Gosselin-Ildari, 2009; West, 1985), the notion that a subset of humans labeled as "musicians" have longer cochlea relative to their peers seems doubtful. A musician-effect in tuning, while small, was observed whether we consider music as either a categorical or continuous variable (Bidelman et al., 2016). A strict anatomical argument would also imply that the correlation between music engagement and tuning (Fig. 1C) is driven not by experience but by increasingly longer BMs in listeners with more years of training. Ever elongating BMs also seems dubious. Moreover, males have longer cochleae than females (Baguant et al., 2022) but we find no such sex difference in our data [$t(25)=0.08, p = 0.94$]. As another counter example, the human cochlea is almost twice as long in humans as in chinchillas despite almost identical hearing ranges (Kirk and Gosselin-Ildari, 2009). Thus, although an octave occupies nearly twice as much space in humans (and likely also enjoys more dense hair cell packing), the sharpness of frequency tuning appears similar in the two species (Ruggero and Temchin, 2005; their Fig. 6A). Clearly, there is more to tuning than meets the ear.

On the contrary, recent studies have corroborated our experience-dependent interpretation, revealing that other auditory experiences besides musicianship (e.g., tone-language experience) might also enhance cochlear tuning. Liu et al. (2020) showed that Mandarin Chinese speakers—who in many ways have similar spectral acuity as musicians (Bidelman et al., 2011, 2013)—also have sharper SFOAE suppression tuning curves than non-tone language listeners (Liu et al., 2020). Asians also have slightly smaller cochlear lengths (Grover et al., 2018) compared to Western listeners (cf. Ulehlová et al., 1987) further weakening a BM length argument. Instead, these findings suggest that sharper cochlear filtering in humans may not be an evolutionary spandrel (Gould et al., 1979), but might be a functional trait that is tunable by auditory experience(s) that place heavier perceptual demands on spectral and pitch processing.

If *anatomical* differences are insufficient to account for musicians' improved tuning, what other mechanisms might explain such effects? We offered several parsimonious, *functional* mechanisms in our original report (Bidelman et al., 2016). One possibility could be differences in the expression of the motor protein prestin (Zheng et al., 2000), which could alter OHC motility to improve tuning. Prestin regulation degrades with otopathologies (Solis-Angeles et al., 2021; Xia et al., 2013) but is upregulated in individuals exposed to higher environmental sound levels (Parker et al., 2021). Musicians typically experience louder sound levels than their nonmusician peers (McBride et al., 1992) which could lead to stronger prestin-related OHC motility and more refined OAE responses (Main and Skoe, 2024). Alternatively, we favor and account whereby sharper cochlear tuning originates from plasticity in efferent feedback through the medial olivocochlear (MOC) system. OHCs are responsible for OAE generation and are directly innervated by MOC neurons which originate in the lower brainstem and act as a modulatory control for cochlear amplification and adjusting auditory filter bandwidths (Guinan and Gifford, 1988; Vinay and Moore, 2008). Indeed,

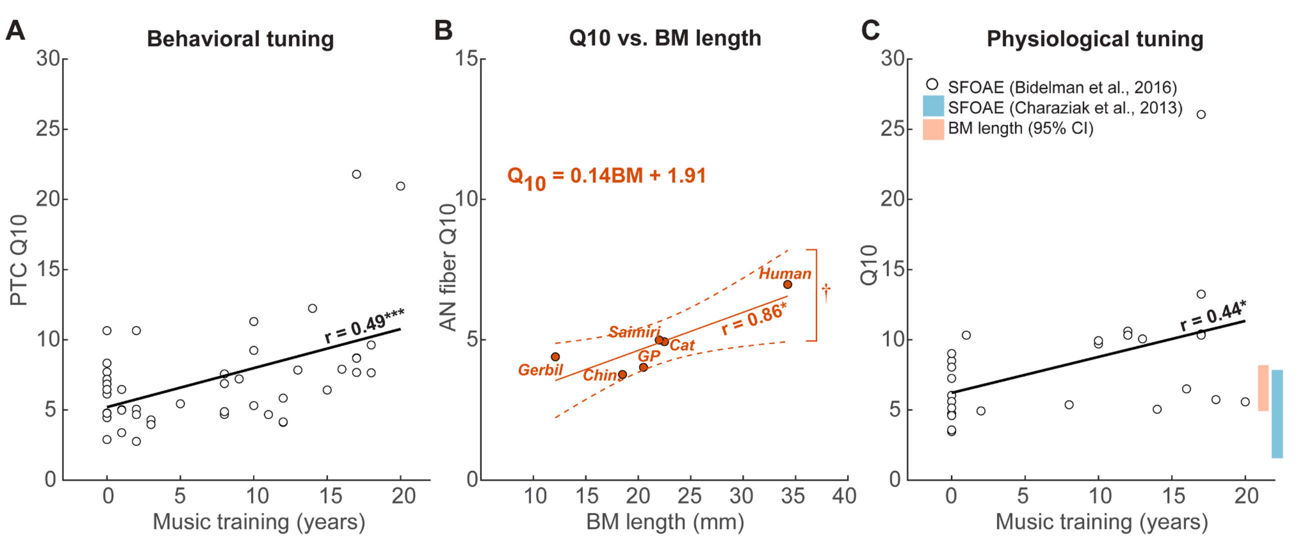

Fig. 1. Tuning in musicians is difficult to explain by individual differences in cochlear length alone. (A) Psychophysical tuning curve (PTC) filter Q10 sharpness measured at 4 kHz in two studies ($n = 46$ listeners) as reported by Bidelman and colleagues (Bidelman et al., 2016, 2014). Musicianship positively correlates with PTC tuning; listeners with more extended self-reported music training show sharper behavioral PTCs. (B) Relation between BM length and auditory nerve (AN) fiber Q10 tuning. Data reflect the 4 kHz place aggregated across several physiological studies (Heffner and Heffner, 2010; Kirk and Gosselin-Ildari, 2009; Verschooten et al., 2018). Across several mammalian species, longer BMs are associated with sharper AN tuning. Q10 tuning is predicted from cochlear length via simple regression ($Q_{10} = 0.14\,BM + 1.91$). Dotted lines = 95% CI. † = denotes the 95% CI for estimated human cochlear tuning based on BM length in humans. (C) Correlation between physiological SFOAE tuning curves at 4 kHz and self-reported musical training as reported in Bidelman et al. (2016). Listeners with more music training show sharper tuning. SFOAE Q10 in most musicians (Bidelman et al., 2016) appears sharper than the general population (Charaziak et al., 2013) and what would be expected from normal variation in human BM length alone (see †, panel B). $^*p < 0.05$, $^{***}p < 0.0001$.

there is ample evidence from both loudness adaptation and OAE studies that musicians have stronger ipsilateral and contralateral MOC efferent feedback to the cochlea (Bidelman et al., 2017; Brashears et al., 2003; Bulut et al., 2019; Kumar et al., 2016; Micheyl et al., 1995, 1997; Perrot and Collet, 2014; Perrot et al., 1999)—but see Tarnowska et al. (2020). Stronger efferent control could also produce less masking in musician ears (e.g., Coffey et al., 2017; Mankel and Bidelman, 2018) and thus alter suppression SFOAE tuning widths. Furthermore, the MOC system is also modulated by attention (de Boer et al., 2012) and musicians are known to show enhanced auditory attentional deployment (Strait et al., 2010; Yoo and Bidelman, 2019). These factors could drive musicians' more refined SFOAE responses.

Manley's third critique is well grounded. The data reported in Bidelman et al. (2016) are strictly correlational in nature. As was common in the literature at the time, we used a cross-sectional sample to maximize the potential of observing differences in frequency selectivity between "musician" (~10 years of *self-reported* training) and "nonmusician" listeners (< 2 years training). Thus, it is entirely possible that enhanced cochlear tuning we observed in musicians is not due to musical experience/training, per se, but preexisting factors (i.e., "nature" vs. "nurture"). As Manley asserts, differences between musician and nonmusician listeners' SFOAE tuning curves could be "…explained not by an influence of experience on cochlear tuning, but that the cochleae of those who take up music seriously have from birth cochleae that are more sharply tuned (Manley, 2025)." We could not agree more.

Fortunately, the field has since taken a more nuanced approach to understanding music and brain plasticity over the past decade. It is now well-recognized that innate differences in auditory system function could masquerade as plasticity in cross-sectional studies on music-related plasticity (Bidelman and Mankel, 2019; Brown and Bidelman, 2022; Mankel and Bidelman, 2018). For example, our group has shown that among the normal population, individuals considered "musical sleepers" (i.e., nonmusicians with a high level of receptive musicality but whom lack any formal musical training) have enhanced electrophysiological responses to spectrally rich sounds like speech that rival those of trained musicians (Bidelman and Mankel, 2019; Mankel and Bidelman, 2018). Musical skills such as pitch and timing perception also develop very early in infancy (i.e., 6 months of age; Trehub, 2003) and may even be linked to certain genetic markers (Park et al., 2012; Pulli et al., 2008; Tan et al., 2014; Ukkola et al., 2009). As we and others have suggested (Corrigall et al., 2013; Mankel and Bidelman, 2018; Moreno and Bidelman, 2014), musicians might also differ from their peers on latent perceptual (Mankel and Bidelman, 2018), cognitive (Corrigall et al., 2013; Schellenberg, 2004), personality (Corrigall et al., 2013), or other social factors (e.g., socioeconomic status) (Schellenberg, 2019) that could drive differences between "musician" and "non-musician" groups. Such studies highlight the importance of recognizing musicianship as a *continuum*, rather than categorical demographic variable. In the nature versus nurture debate of music and the brain, distinguishing between innate and experience-dependent effects can only accomplished through longitudinal studies (which are costly and often impractical for assessing decades-long training effects) or utilizing objective measures of listening skills (Law and Zentner, 2012) that can identify people with highly acute (i.e., musician-like) auditory-sensory function (Mankel and Bidelman, 2018). Several randomized controlled studies have shown that enriched music training programs can boost auditory processing in children and adults (Dubinsky et al., 2019; Kraus et al., 2014). Still, whether or not music experience *causally* relates to sharper cochlear tuning remains to be tested.

New experiments could tease apart the nature vs. nurture conundrum. In addition to studies with larger sample sizes and longitudinal experiments, and obvious experiment would be to test listeners who have inherently good music perceptual skills by objective listening tasks but lack any formal music training (e.g., "musical sleepers"; Mankel and Bidelman, 2018). In this vein, large-scale pre-registered replication studies are in the works to assess the robustness of tuning enhancements observed in musicians' behavioral PTCs (Whiteford, 2019) so we may know the answer soon enough. In vivo imaging of cochlear duct lengths in individuals with varying levels of musicality as well as categorically defined "musicians" and "nonmusicians" could be another fruitful approach. Lastly, it is worth noting that mapping suppression SFOAE tuning curves is inherently a masking paradigm. There is some evidence that musicians perform better in figure-ground noise tasks and experience better "antimasking" than their nonmusician peers (Coffey et al., 2017; Mankel and Bidelman, 2018). Thus, an alternate interpretation of our OAE and PTC data (Bidelman et al., 2016) is that musicians do not have better cochlear tuning, per se, but better signal-in-noise analysis. Suppressive effects (Bentsen et al., 2011) could be mitigated entirely by utilizing different SFOAE measures of cochlear tuning (e.g., group delay; Shera et al., 2002). This might reveal even larger differences in tuning among musicians. Regardless, we concur with Manley that the list of questions is long and more research should be carried out.

CRediT authorship contribution statement

Gavin M. Bidelman: Writing – original draft.

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Data availability

Data will be made available on request.

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