



Research paper

Musicians change their tune: How hearing loss alters the neural code

Alexandra Parbery-Clark^{a,b}, Samira Anderson^{a,b,1}, Nina Kraus^{a,b,c,d,*}^a Auditory Neuroscience Laboratory, Northwestern University, 2240 Campus Drive, Evanston, IL 60208, USA^b Department of Communication Sciences, Northwestern University, Evanston, IL, USA^c Neurobiology and Physiology, Northwestern University, Evanston, IL, USA^d Otolaryngology, Northwestern University, Evanston, IL, USA

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ABSTRACT

Individuals with sensorineural hearing loss have difficulty understanding speech, especially in background noise. This deficit remains even when audibility is restored through amplification, suggesting that mechanisms beyond a reduction in peripheral sensitivity contribute to the perceptual difficulties associated with hearing loss. Given that normal-hearing musicians have enhanced auditory perceptual skills, including speech-in-noise perception, coupled with heightened subcortical responses to speech, we aimed to determine whether similar advantages could be observed in middle-aged adults with hearing loss. Results indicate that musicians with hearing loss, despite self-perceptions of average performance for understanding speech in noise, have a greater ability to hear in noise relative to nonmusicians. This is accompanied by more robust subcortical encoding of sound (e.g., stimulus-to-response correlations and response consistency) as well as more resilient neural responses to speech in the presence of background noise (e.g., neural timing). Musicians with hearing loss also demonstrate unique neural signatures of spectral encoding relative to nonmusicians: enhanced neural encoding of the speech-sound's fundamental frequency but not of its upper harmonics. This stands in contrast to previous outcomes in normal-hearing musicians, who have enhanced encoding of the harmonics but not the fundamental frequency. Taken together, our data suggest that although hearing loss modifies a musician's spectral encoding of speech, the musician advantage for perceiving speech in noise persists in a hearing-impaired population by adaptively strengthening underlying neural mechanisms for speech-in-noise perception.

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1. Introduction

Daily communication rarely occurs in quiet environments; background noise is often present, degrading the acoustic signal and interfering with the neural transcription of sound (Kujala and Brattico, 2009). While hearing in noise is challenging for everyone, hearing loss exacerbates the negative effects of background noise (Dubno et al., 1984; Helfer and Wilber, 1990). Within

the United States alone, approximately 36 million people have a hearing loss (NIDCD, 2012). As such, determining ways to enhance hearing in noise abilities in a hearing-impaired population would have widespread impact on public health; musical training may represent a viable strategy.

Normal-hearing musicians have lifelong hearing advantages in noise (Parbery-Clark et al., 2009b, 2011; Zendel and Alain, 2011) and a greater neural resistance to the deleterious effects of background noise (Parbery-Clark et al., 2009a, 2012b; Strait et al., 2012). We do not know, however, whether these musician advantages are maintained in a population with hearing loss. Sensorineural hearing loss has a profound impact on the auditory system, affecting both peripheral and central structures. For example, auditory deprivation associated with hearing loss can lead to changes in central auditory processing (Aizawa and Eggermont, 2006; Reed et al., 2009; Bureš et al., 2010), compromising auditory perception (Dubno et al., 1984; Blair, 1985; Crandell, 1993) and quality of life (Dalton et al., 2003). Hearing loss also results in tonotopic remapping (Willott, 1991; Harrison et al., 1998; Barsz et al., 2007)

Abbreviations: ABR, auditory brainstem response; dB, decibel; F_0 , fundamental frequency; Hz, Hertz; IQ, intelligence quotient; Ms, millisecond; NAL-R, National Acoustic Laboratory-Revised; NIDCD, National Institute on Deafness and other Communication Disorders; RMANOVA, repeated measure analyses of variance; SIN, speech in noise; SNR, signal-to-noise ratio; SSQ, Speech, Spatial and Qualities

* Corresponding author. Auditory Neuroscience Laboratory, Northwestern University, 2240 Campus Drive, Evanston, IL 60208, USA. Tel.: +1 847 491 3181.

E-mail address: nkraus@northwestern.edu (N. Kraus).

URL: <http://www.brainvolts.northwestern.edu>

¹ Present address: Department of Hearing and Speech Sciences, University of Maryland, College Park, MD 20742, USA.

and a widening of auditory filters (Tyler et al., 1984; Glasberg and Moore, 1986; Moore, 2007), reducing how spectral information is encoded (Plyler and Ananthanarayan, 2001) and, thus, an individual's ability to analyze the frequency content of sounds (Leek et al., 1987; Summers and Leek, 1994). These changes may account for the speech perception difficulties experienced by hearing-impaired individuals (Dubno et al., 1982; Boothroyd, 1984; Strouse et al., 1998). Since normal-hearing older musicians have heightened auditory perceptual skills as well as enhanced neural encoding of temporal and spectral features of speech (Zendel and Alain, 2011; Parbery-Clark et al., 2012a,b), establishing whether musical training in a hearing-impaired population enhances the perception and neural encoding of speech in noise has important rehabilitative and clinical implications.

Here, we asked whether musicians' advantages for the perception and neural encoding of speech in noise are maintained with hearing loss. To address this question, we assessed hearing-in-noise abilities with standardized clinical tests and self-report, in addition to speech-evoked auditory brainstem responses in quiet and noisy backgrounds. We focused our analyses on neural timing, spectral encoding, and the precision of neural encoding (i.e., neural response fidelity and consistency) – all measures that have previously distinguished normal hearing children, young adult and middle-aged musicians from their nonmusician counterparts (Parbery-Clark et al., 2009a, 2012a,b; Strait et al., 2012) and that are known to decline with age and hearing loss (Clinard et al., 2010; Vander Werff and Burns, 2011; Anderson et al., 2012). We were especially interested in determining whether hearing loss diminishes known musician biological advantages or, alternatively, whether new musician neural signatures emerge in the face of hearing loss. We hypothesized that hearing-impaired musicians maintain hearing benefits in noise over nonmusicians and that these advantages are undergirded by more resilient neural encoding of speech.

2. Methods

2.1. Participants

Thirty-four middle-aged adults with mild or moderate sensorineural hearing loss (Fig. 1) participated (45–65 years, mean age 58 ± 4 years). Seventeen subjects were categorized as musicians, having started musical training before the age of nine and were engaged in musical activities a minimum of three times a week since then. Seventeen subjects were categorized as nonmusicians, with 11 having had no musical training and 6 having fewer than 5 years of accrued musical experience; (Table 1).

Participants had no history of neurological or learning disorders nor reported a history of chemotherapy or ototoxic medication, major surgeries or head trauma. Octave frequencies between 0.125 and 12.5 kHz were tested including 3 and 6 kHz. All participants had symmetric pure-tone thresholds (defined as ≤ 15 dB difference at two or more frequencies between ears). All participants had normal click-evoked auditory brainstem responses (defined as a wave V latency of ≤ 6.8 ms at 80 dB SPL presented at a rate of 31.25 Hz). In addition, all participants were native English speakers and had normal non-verbal IQ, as assessed by the Abbreviated Wechsler's Adult Scale of Intelligence's matrix reasoning subtest (Wechsler, 1999). All experimental procedures were approved by the Northwestern University Institutional Review Board; all participants provided informed written consent.

Musician and nonmusician groups were matched on hearing thresholds (0.125–12.5 kHz including 3 and 6 kHz; $F_{(1,33)} = 0.733$; $p = 0.743$; Fig. 1). No participant reported sudden hearing loss; 7 musicians and 4 nonmusicians indicated that they had bilateral tinnitus. No participants reported a history of hearing aid usage. Groups were equated on measures of age, click wave V latency and IQ (all $P > 0.4$; Table 2).

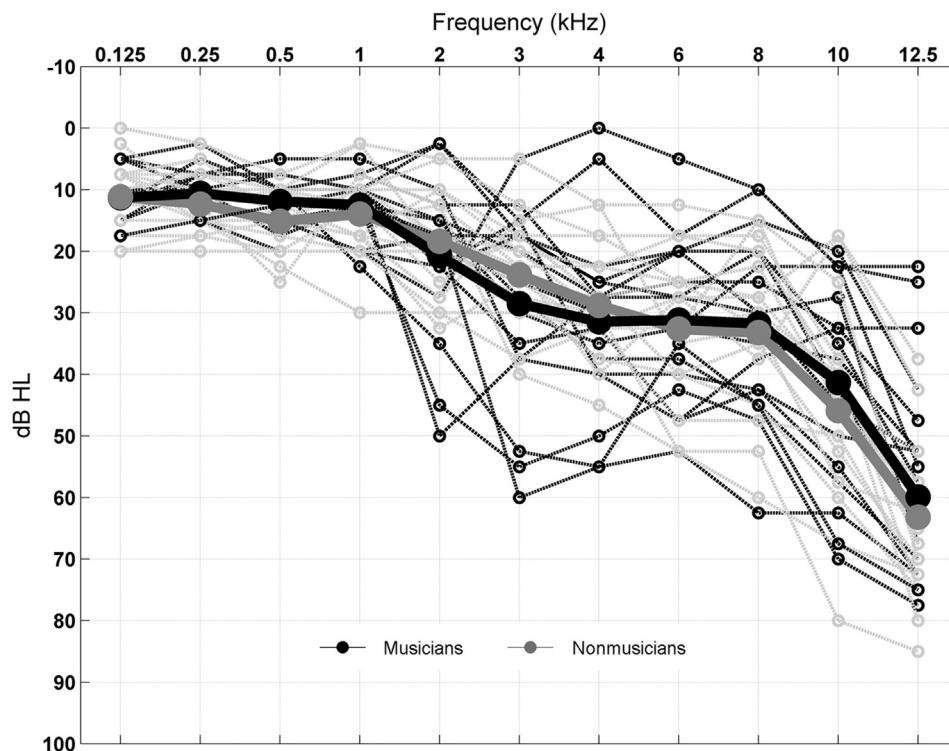


Fig. 1. Audiometric profiles. Mean pure-tone thresholds (average of right and left ears) for musicians (black) and nonmusician (grey) from 0.125 to 12.5 kHz. Dashed lines indicate individual data. Musician and nonmusician groups demonstrated equal hearing sensitivity ($F_{(1,33)} = 0.733$; $p = 0.743$).

Table 1

Participants' musical practice histories. Age at which musical training began, years of musical training and major instrument(s) are indicated for all participants with musical experience. Means for years of musical training and age at onset for the nonmusicians were calculated from the six participants who had musical experience.

	Years of musical experience	Age onset, years	Instrument
<i>Musicians</i>			
1	44	7	Trumpet
2	49	9	Flute
3	56	4	Piano/Trumpet
4	51	4	Piano/French Horn
5	51	7	Piano/Clarinet
6	49	5	Piano/Bass
7	52	8	Piano/Bassoon
8	42	9	Piano/Saxophone
9	55	8	Piano
10	49	6	Piano
11	54	5	Piano
12	51	6	Piano
13	53	7	Piano
14	47	8	Piano
15	61	3	Piano
16	49	3	Piano
17	45	9	Piano
Mean	50	6.3	
<i>Nonmusicians</i>			
1	3	14	Trumpet
2	2	14	Piano
3	4	25	Piano
4	3	10	Piano
5	4	8	Clarinet
6	2	12	Clarinet
7–17	NA	NA	NA
Mean	3	13.8	

2.2. Electrophysiology

2.2.1. Stimulus

The evoking speech stimulus was a 170 ms six-formant speech syllable /da/ synthesized at a 20 kHz sampling rate. The stimulus has a steady fundamental frequency ($F_0 = 100$ Hz) except for an initial 5 ms (*onset*) burst. For the first 50 ms (*transition* between the stop burst /d/ and the vowel /a/), the lower three formants change over time (F_1 , 400–720 Hz; F_2 , 1700–1240 Hz; F_3 , 2580–2500 Hz) but stabilize for the 120 ms *vowel*. The upper three formants are constant throughout the syllable (F_4 , 3300 Hz; F_5 , 3750 Hz; F_6 , 4900 Hz). The /da/ was chosen for 2 reasons: first, because it combines a transient (the /d/) and periodic (the /a/) segment and second, because of the perceptual challenges posed by stop-consonants (Miller and Nicely, 1955) over vowels (Ohde and Abou-Khalil, 2001). Therefore, using this syllable enables us to separately assess the neural encoding of these two acoustic aspects.

To equate audibility of the stimulus to the fullest extent possible across participants, the /da/ was selectively amplified with the NAL-R algorithm (Byrne and Dillon, 1986) over the 0.250–6 kHz range based on the individual's audiogram. The algorithm was only

applied when a threshold exceeded 20 dB. We used routines coded in MATLAB (The Mathworks, Inc., Natick, MA) to create binaural stimuli that were customized to each ear's thresholds. This frequency-specific amplification procedure improves response morphology in hearing-impaired individuals, while maintaining the neural transcription of stimulus timing and spectral information (Anderson et al., 2013).

2.2.2. Electrophysiologic recording parameters and procedures

Auditory brainstem responses (ABRs) were differentially recorded at a 20 kHz sampling rate using Ag–AgCl electrodes in a vertical montage (Cz active, FPz ground and linked-earlobe references) in Neuroscan Acquire 4.3 (Compumedics, Inc., Charlotte, NC). Contact impedance was 2 k Ω or less across all electrodes. Stimuli were presented binaurally in alternating polarities at 80 dB SPL with an 83 ms inter-stimulus interval (Scan 2, Compumedics, Inc.) through ER-3 insert earphones (Etymotic Research, Inc., Elk Grove Village, IL). During the recording session (26 ± 2 min), subjects watched a muted, captioned movie of their choice to facilitate a restful state. Six thousand artifact-free trials were collected.

2.2.3. Data reduction

Responses were offline, band-pass filtered from 70 to 2000 Hz (12 dB/octave, zero phase-shift) in MATLAB and epoched using a –40 to 213 ms time window with the stimulus onset occurring at 0 ms. Any trial with amplitude outside the range of ± 35 μ V was considered artifact and rejected. The responses of the two polarities were added to minimize the influence of cochlear microphonic and stimulus artifact on the response (Aiken and Picton, 2008). Lastly, responses were amplitude-baseline corrected to the prestimulus period.

2.2.4. Timing

To analyze the effects of musicianship on neural timing, prominent response peaks were manually identified. Peaks were labeled according to stimulus onset at time 0 ms such that a peak occurring around 33–34 ms after onset would be called *Peak 33*. The onset peak was identified as Peak 9, transition peaks were 33, 43, 53, and vowel peaks were 63, 73, 83...163 ms. Two peak-pickers, blind to participant group, identified each peak of interest. Inter-peak identification between the first two peak-pickers was highly reliable (96.9%). A third peak-picker confirmed peak identification and reconciled any disagreements between the first two.

All participants had identifiable transition and vowel peaks for both the quiet and noise conditions. For the onset peak, one participant (nonmusician) had non-observable peaks in the quiet condition and four participants (1 musician, 3 nonmusicians) had non-observable peaks in the noise condition. Statistical analyses for onset peak latency only included those participants who had clearly discernible peaks in both quiet and noise ($n = 29$). For correlational analyses between response timing and speech-in-noise perception, composite peak timing scores were created separately for the responses to transition and the vowel. These composite scores were calculated by taking the average latency of the three transition peaks and the eleven vowel peaks (Fig. 2).

2.2.5. Stimulus-to-response fidelity

To quantify the precision of neural encoding in the quiet and noise conditions, we cross-correlated the stimulus and response waveforms using the *xcorr* function in MATLAB. The stimulus was band-pass filtered from 70 to 2000 Hz to match the brainstem response characteristics and was shifted over a 7–12 ms range relative to the response until a maximum correlation value was found. We restricted this analysis to the vowel as this portion of the response bears the greatest resemblance to the evoking stimulus.

Table 2

Participant characteristics. Means (with standard deviations) for the musician and nonmusician groups. Only hearing-in-noise ability and auditory working memory differed between the groups. * $p \leq 0.05$, ** $p \leq 0.01$.

	Musicians ($N = 17$)	Nonmusicians ($N = 17$)
Age (years)	57.2 (3.86)	59.0 (4.24)
Click (ms)	5.86 (0.25)	5.98 (0.34)
Wave V		
IQ (percentile)	83.35 (22.96)	85.02 (23.56)
HINT (dB SNR)**	–2.92 (0.73)	–2.02 (0.64)
Auditory working memory (standard score)*	124.24 (10.83)	116.35 (8.17)

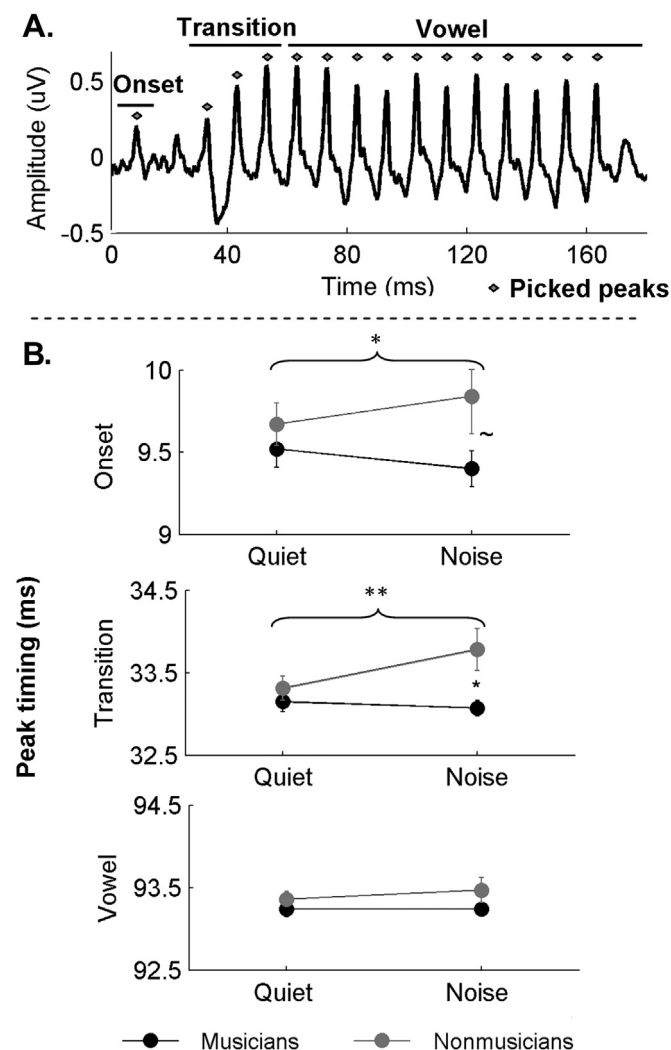


Fig. 2. Musical training offsets the negative effects of noise on neural response timing. (A) Group average response for the musicians with hearing loss in the quiet listening condition. Diamonds indicate which peaks were assessed. (B) In quiet, musicians and nonmusicians demonstrate similar response timing for the most perceptually challenging aspects of the stimulus – the onset and the formant transition – but musicians experience a smaller timing delay than nonmusicians with the introduction of background noise. Neural timing in response to the vowel is stable across quiet and noise conditions and showed no musician enhancement. While all of the major prominent, positive peaks were picked between 33–53 ms (transition) and 63–163 ms (vowel), for simplicity of visualization one representative peak from each region is plotted. ~ $p < 0.1$, * $p < 0.05$, ** $p < 0.01$.

The 7–12 ms time lag was chosen based on the observed time lag between the stimulus and the neural responses due to the stimulus transmission delay (from the ER-3 transducer and ear insert ~1.1 ms) and the neural lag between the cochlea and the rostral brainstem (Fig. 3). Justification for this time range can be found by calculating the difference between a representative peak in the acoustic waveform and its corresponding peak in the neural response. For example, in these data the stimulus peak at ~75 ms corresponds to the neural response peak at 83.249 ms in quiet (S.D.: ± 0.37 ; lag range: 7.4–9.2 ms) and 83.288 ms in noise (S.D.: ± 0.47 ; lag range: 7.5–10.47 ms). Therefore, using a sliding window of 7–12 ms encapsulates the timing lags for all individuals in both conditions. Average r -values were Fisher transformed for statistical analysis. Higher r -values indicate greater degrees of similarity between the stimulus and the response.

2.2.6. Spectral representation: fundamental frequency and harmonics

The neural encoding of the stimulus spectrum was calculated using a fast Fourier transform in MATLAB. The average spectral amplitudes relating to the transition (20–60 ms) and the vowel (60–170 ms) were determined by averaging spectral response amplitude over 20 Hz bins centered around the frequencies of interest, which included the fundamental frequency (F_0 , 100 Hz) and its integer harmonics up to 600 Hz (H_2 – H_6). A composite overall harmonic score (average of H_2 to H_6 values) was used in correlations with speech-in-noise ability (Fig. 3).

2.2.7. Response consistency

Inter-trial response consistency over the length of the recording period (i.e., across the 6000 trials) was calculated for each subject. Specifically, we created 300 pairs of sub-averages, with each sub-average comprising 1500 randomly-selected trials of each polarity. Each pair of sub-averages was correlated to determine their degree of similarity. This process was performed for each of the 300 pairs. The final response consistency value represents the average of the 300 correlation r -values. R -values were Fisher transformed to z -scores for statistical analyses. Response consistency was computed for the two time regions of interest: the transition and the vowel.

2.2.8. Neural response magnitude

The magnitude of the neural response during the prestimulus (–40–0 ms) and stimulus period (5–170 ms) was quantified using a root mean square (RMS) measurement.

2.3. Speech-in-noise (SIN) measures

2.3.1. Speech-in-noise perception

The Hearing in Noise Test (HINT, Biologic Systems Corp; Mundelein, IL; Nilsson et al., 1994) is an adaptive test of speech recognition that measures speech perception ability in noise. Participants repeat short, semantically and syntactically simple sentences presented in speech-shaped background noise. Speech stimuli consist of Bamford-Kowal-Bench (Bench et al., 1979) sentences (12 lists of 20 sentences) spoken by a male and presented in free field. Target sentences and noise were delivered from a loud-speaker placed 1 m from the participant at 0° azimuth. The noise presentation level was fixed at 65 dB SPL and the program adjusted perceptual difficulty by increasing or decreasing the intensity level of the target sentences until the threshold signal-to-noise ratio (SNR) was determined. Threshold SNR was defined as the level difference (in dB) between the speech and the noise presentation levels at which 50% of sentences are correctly repeated. Lower SNRs indicates better performance.

2.3.2. Self-reported SIN perception

To assess an individual's self-perceived hearing ability in everyday settings, we administered the Speech subscale of the Speech, Spatial and Qualities Questionnaire (Gatehouse and Noble, 2004). The Speech subscale consists of 14 questions (Table 3) relating to hearing performance in various environments, ranging from quiet one-on-one listening situations to multiple talkers in background noise. Individuals rate how well they can hear in such situations using a 10-point Likert scale.

2.3.3. Auditory working memory

The auditory working memory subtest of the Woodcock–Johnson III Test of Cognitive Abilities (Woodcock et al., 2001) requires participants to reorder a dictated series of digits and nouns by first repeating the nouns and then repeating the digits in

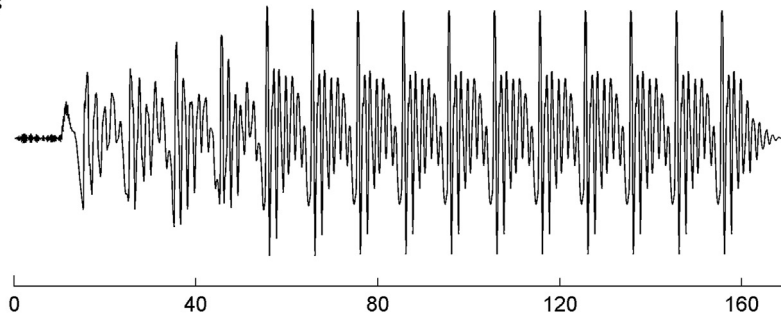
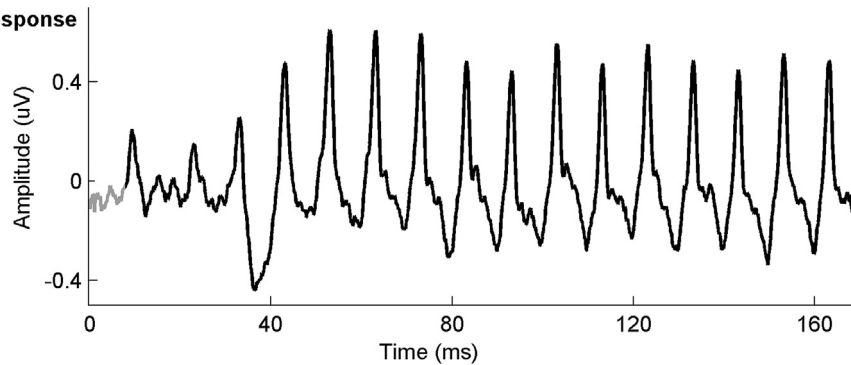
A Stimulus**B Response**

Fig. 3. Stimulus and group average response. (A) The acoustic waveform and (B) the corresponding grand average response from musicians with hearing loss. The delay from the onset of the stimulus to the onset of the response is also indicated (grey). This time lag comprises the stimulus transmission delay as well as the neural transmission time from the cochlea and the rostral brainstem. Note the stimulus has been forward-shifted by ~ 8 ms to account for this delay to align with the onset of the response.

Table 3

Self-assessment of hearing in noise ability. Means (with standard deviations) and significance values for the musician and nonmusician groups' self-assessment of their speech-in-noise abilities. These questions are part of the Speech, Spatial and Qualities Assessment questionnaire. Note that not all of the above questions pertain to speech-in-noise perception.

Question	Musician	Nonmusician	<i>p</i> -value
You are talking with one other person and there is a TV on in the same room. Without turning the TV down, can you follow what the person you're talking to says?	7.85 (1.97)	7.21 (2.29)	0.393
You are talking with one other person in a quiet, carpeted lounge-room. Can you follow what the other person says?	9.41 (0.79)	9.67 (0.56)	0.297
You are in a group of about five people, sitting round a table. It is an otherwise quiet place. You can see everyone else in the group. Can you follow the conversation?	9.29 (1.05)	9.19 (0.85)	0.748
You are in a group of about five people in a busy restaurant. You can see everyone else in the group. Can you follow the conversation?	7.76 (2.11)	7.49 (1.55)	0.666
You are talking with one other person. There is continuous background noise, such as a fan or running water. Can you follow what the person says?	8.53 (2.03)	8.22 (1.59)	0.628
You are in a group of about five people in a busy restaurant. You cannot see everyone else in the group. Can you follow the conversation?	6.95 (2.49)	6.29 (2.29)	0.428
You are talking to someone in a place where there are a lot of echoes, such as a church or railway terminus building. Can you follow what the other person says	7.76 (2.41)	8.18 (1.68)	0.567
Can you have a conversation with someone when another person is speaking whose voice is the same pitch as the person you're talking to?	8.01 (2.03)	7.74 (2.17)	0.674
Can you have a conversation with someone when another person is speaking whose voice is different in pitch from the person you're talking to?	8.3 (2.11)	8.32 (1.86)	0.973
You are listening to someone talking to you, while at the same time trying to follow the news on TV. Can you follow what both people are saying?	6.67 (2.44)	6.78 (2.28)	0.885
You are in conversation with one person in a room where there are many other people talking. Can you follow what the person you are talking to is saying?	7.97 (2.09)	7.55 (2.01)	0.552
You are with a group and the conversation switches from one person to another. Can you easily follow the conversation without missing the start of what each new speaker is saying?	8.18 (2.29)	8.52 (1.34)	0.606
Can you easily have a conversation on the telephone?	9.41 (1.23)	9.11 (0.98)	0.428
You are listening to someone on the telephone and someone next to you starts talking. Can you follow what's being said by both speakers?	6.88 (2.53)	6.96 (2.48)	0.930

sequential order (e.g., the correct ordering of the following sequence, “4, salt, fox, 7, stove, 2, 9, boot” is “salt, fox, stove, boot” and “4, 7, 2, 9”). Age-normed standard scores were used for all statistical analyses. Higher scores indicate better performance.

2.3.4. Statistical analyses

All statistical analyses were conducted in SPSS Version 20.0 (SPSS Inc., Chicago, IL). For each dependent measure, repeated measure analyses of variance (RMANOVA) were used for group (musician vs. nonmusician) \times condition (quiet vs. noise) comparisons. Dependent measures included timing, spectral representation (i.e., F_0 and harmonics), stimulus-to-response fidelity, and response consistency. Univariate analyses of variance were used for behavioural measures. Post-hoc tests were used when appropriate. For relationships between variables, Pearson- r correlations were used. In all cases, p -values reflect two-tailed tests. Levene's test was used to ensure homogeneity of variance for all measures; Kolmogorov–Smirnov test was used to ensure that all variables were normally distributed. The self-reported measure of SIN ability (SSQ) violated the assumption of normality. Neither log nor reciprocal transforms rendered these data normal; as such, these data were only used to quantify group differences (non-parametric test – Mann–Whitney); correlations with other variables were not explored.

3. Results

Middle-aged musicians with hearing loss demonstrated more precise neural encoding of speech in both quiet and background noise as measured by stimulus-to-response fidelity and response consistency. In addition, musicians had greater neural encoding of the fundamental frequency and smaller neural timing delays with the addition of background noise. However, no musician advantage for spectral encoding was found. Musicians scored higher on a standardized measure of speech-in-noise ability and auditory working memory but did not self-rate themselves as having better hearing in noise than nonmusicians.

3.1. Speech-in-noise and cognitive measures

In addition to having better auditory working memory ($F_{(1,33)} = 5.735$, $p = 0.023$), musicians with hearing loss had better speech perception in noise than nonmusicians (HINT: $F_{(1,33)} = 14.687$, $p = 0.001$; Table 2). However, despite better SIN perception, musicians with hearing loss did not perceive themselves as having a heightened ability to hear in the presence of background noise (self-rated assessment of hearing in noise ability, Table 3).

3.1.1. Neural timing

Musical experience in older individuals with hearing loss limits the degradative effects of noise on neural timing in response to the onset and formant transition of a speech syllable, as reflected by a significant condition \times group interaction (onset: $F_{(1,28)} = 4.075$, $p = 0.05$; transition: $F_{(1,33)} = 7.561$, $p = 0.01$). Although musicians and nonmusicians had equivalent response timing in quiet (onset: $F_{(1,28)} = 0.701$, $p = 0.410$; transition: $F_{(1,33)} = 1.031$, $p = 0.318$), musicians were less delayed by the addition of background noise (onset: $F_{(1,28)} = 3.416$, $p = 0.076$; transition: $F_{(1,33)} = 6.538$, $p = 0.016$). For the vowel, there was no effect of noise ($F_{(1,33)} = 0.708$, $p = 0.406$), no timing differences between groups ($F_{(1,33)} = 1.378$, $p = 0.249$), nor a significant condition \times group interaction ($F_{(1,33)} = 2.507$, $p = 0.123$) (Fig. 2).

Table 4

Impact of musical training on measures of neural precision. Neural precision as calculated by stimulus-to-response correlations and response consistency scores: means (with SDs) and significance values for the musicians and nonmusicians across the transition (20–60 ms) and vowel (60–170 ms) region of the response.

Time range	Musicians	Nonmusicians	p -value
Neural precision (stimulus-to-response correlations)			
Quiet:			
Vowel	0.27 (0.05)	0.22 (0.06)	0.016
Noise:			
Vowel	0.28 (0.05)	0.23 (0.06)	0.016
Response consistency			
Quiet:			
Transition	0.85 (0.09)	0.68 (0.22)	0.003
Vowel	0.82 (0.11)	0.63 (0.21)	0.005
Noise:			
Transition	0.81 (0.10)	0.54 (0.33)	0.004
Vowel	0.83 (0.11)	0.58 (0.31)	0.003

3.1.2. Stimulus-to-response correlations

Musicians demonstrated more precise neural representation of the vowel in both quiet and noise, as evidenced by a greater degree of similarity between the stimulus and the corresponding neural response ($F_{(1,33)} = 6.730$, $p = 0.014$; Table 4). The addition of background noise degraded neural response morphology ($F_{(1,33)} = 5.571$, $p = 0.025$) to an equal extent in both groups, indicated by an absent condition \times musicianship interaction ($F_{(1,33)} = 2.488$, $p = 0.761$).

3.2. Spectral representation

3.2.1. Fundamental frequency (F_0)

In response to the formant transition, musicians had greater encoding of the F_0 in both quiet and noise ($F_{(1,33)} = 6.627$, $p = 0.015$). Noise reduced the neural representation of the F_0 ($F_{(1,33)} = 10.401$, $p = 0.003$), however, no condition \times group interaction was present ($F_{(1,33)} = 0.416$, $p = 0.502$). Alternately, in response to the vowel, there was no main effect of musicianship ($F_{(1,33)} = 1.486$, $p = 0.232$), noise ($F_{(1,33)} = 0.002$, $p = 0.962$), nor an interaction between the two ($F_{(1,33)} = 0.001$, $p = 0.991$) (Figs. 4 and 5).

3.2.2. Harmonics

In contrast to their F_0 encoding advantage, musicians did not have greater harmonic encoding than the nonmusicians across the two conditions (transition: $F_{(1,33)} = 1.372$, $p = 0.265$; vowel: $F_{(1,33)} = 0.665$, $p = 0.653$). Noise reduced the harmonic encoding of both the formant transition and the vowel portion of the neural response (transition: $F_{(1,33)} = 4.511$, $p = 0.004$; vowel: $F_{(1,33)} = 2.375$, $p = 0.065$). There was no condition \times group interaction (transition: $F_{(1,33)} = 0.814$, $p = 0.550$; vowel: $F_{(1,33)} = 0.584$, $p = 0.712$) indicating similar effects of noise on both groups for harmonic encoding (Figs. 4 and 5).

3.2.3. Response consistency

Musicians had greater neural response consistency in both quiet and noise conditions in response to the vowel ($F_{(1,33)} = 11.204$, $p = 0.002$). Noise did not reduce response consistency ($F_{(1,33)} = 0.056$, $p = 0.815$) and no significant condition \times group interaction was present ($F_{(1,33)} = 1.095$, $p = 0.303$). In response to the formant transition, again musicians had more consistent responses relative to the nonmusicians in both quiet and noise conditions ($F_{(1,33)} = 12.456$, $p = 0.001$). Although noise resulted in a decline in response consistency ($F_{(1,33)} = 5.816$, $p = 0.022$), the decline was equivalent for both groups ($F_{(1,33)} = 0.345$, $p = 0.516$) (Table 4).

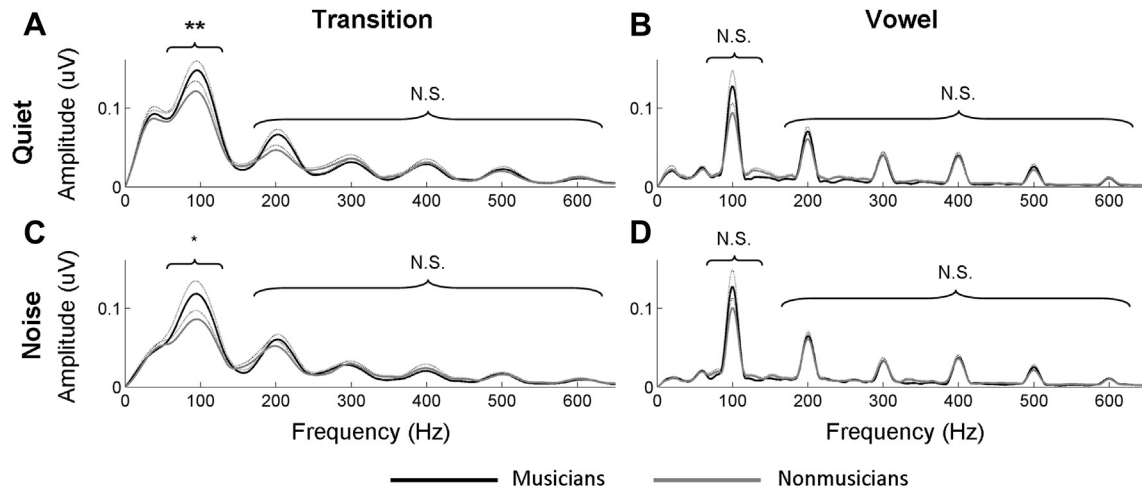


Fig. 4. Impact of musical training on measures of spectral encoding. Spectral encoding for the transition (A and C) and vowel (B and D) in quiet (A and B) and noise (C and D). Musicians (black) demonstrated enhanced spectral encoding for the fundamental frequency (100 Hz) in both quiet and noise for the transition relative to the nonmusicians (grey); the groups were equivalent for all other spectral measures. Dashed lines indicate one standard deviation. * $p < 0.05$, ** $p < 0.01$.

3.2.4. Neural response magnitude

Musicians had less prestimulus activity across conditions ($F_{(1,33)} = 6.157$, $p = 0.019$), but they did not have greater neural response amplitude ($F_{(1,33)} = 0.450$, $p = 0.507$). Noise resulted in smaller response amplitudes during prestimulus and stimulus periods (Entire response: $F_{(1,33)} = 5.844$, $p = 0.022$; prestimulus: $F_{(1,33)} = 9.287$, $p = 0.005$) but no condition \times musicianship interactions were found (Entire response: $F_{(1,33)} = 0.036$, $p = 0.850$; prestimulus: $F_{(1,33)} = 0.977$, $p = 0.330$).

3.2.5. Relationships between perceptual and neural measures of hearing in noise

Performance on the Hearing in Noise Test related with neural encoding of the F_0 but only in quiet, with greater encoding of the F_0 corresponding to better hearing in background noise (Table 5). Hearing in noise also related to response consistency, again with better hearing in noise associated with greater response

consistency. This relationship was stronger in quiet than in noise. Neither peak timing, stimulus-to-response fidelity, nor harmonic encoding correlated with SIN perception (all $p > 0.1$).

4. Discussion

We reveal that middle-aged musicians with hearing loss have better hearing in noise than their age- and hearing-matched nonmusician counterparts. However, they do not rate their hearing in noise ability as better than nonmusicians, indicating a disconnect between their actual performance and how they perceive their abilities. Similar to normal-hearing adult musicians, musicians with hearing loss have more precise neural responses (i.e., stimulus-to-response correlations) and faster neural timing in noise (i.e., onset and formant transition). Unlike normal-hearing adult musicians, hearing-impaired musicians demonstrate greater encoding of the fundamental frequency (F_0) but not its harmonics.

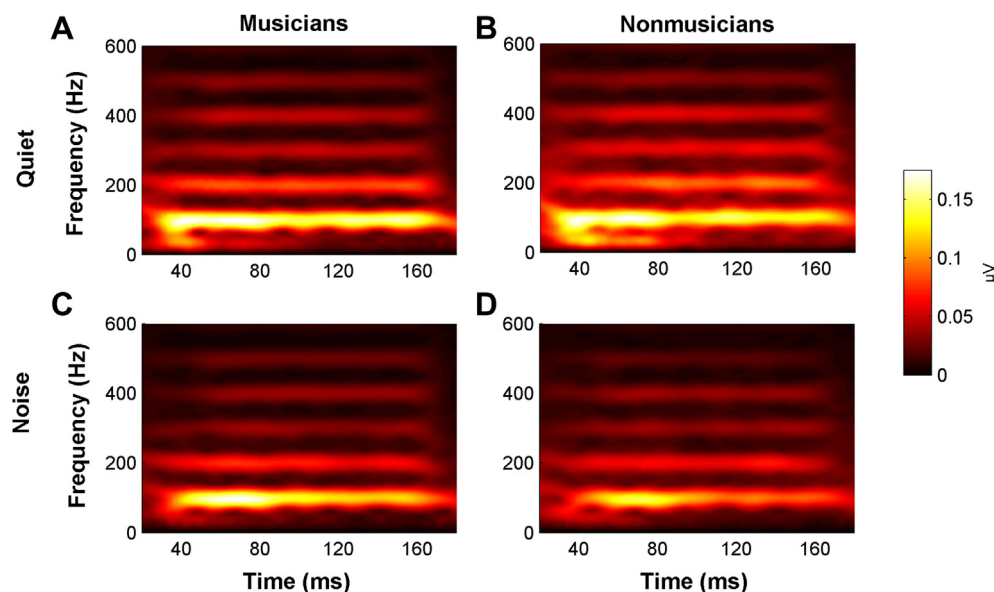


Fig. 5. Group differences in spectrotemporal encoding. The musicians' strength of spectral encoding is evidenced in quiet and noise conditions (A and C respectively) relative to nonmusicians (B and D). While the harmonics are equivalent between the groups, note the greater encoding of the fundamental frequency (i.e., brighter colour) that is especially prominent in the earliest part of the neural response (i.e., the response to the transition).

Table 5
Relationships between neural measures and hearing in noise ability. Correlations, *Pearson-r values* (*p*-values), between performance on the Hearing in Noise Test and the neural measures of F_0 encoding and response consistency over the two time regions of interest in the two conditions. $\sim p < 0.1$; $*p < 0.05$; $**p < 0.01$.

	Quiet		Noise	
	Transition	Vowel	Transition	Vowel
HINT- F_0 encoding	−0.421 (0.013)*	−0.355 (0.039)*	−0.219 (0.213)	−0.254 (0.147)
HINT-Response consistency encoding	−0.376 (0.029)*	−0.449 (0.008)**	−0.318 (0.067)~	−0.348 (0.044)*

These results demonstrate that while hearing loss reduces the nervous system's ability to represent the harmonic complexity of sound, musical experience continues to provide both perceptual and neural benefits for hearing in noise.

4.1. Impact of sensorineural hearing loss: spectral implications

Here, we found musician enhancement for the F_0 in response to the formant transition portion of the syllable. Pitch, which is the perceptual correlate of the F_0 , is an important component for speech-in-noise perception. The auditory system uses pitch as a cue to promote auditory object formation and speaker identification (Clarke and Becker, 1969; Kreiman et al., 1992; Baumann and Belin, 2010), two elements required for extracting a voice from a noisy environment (Oxenham, 2008; Shinn-Cunningham and Best, 2008). Indeed, when two auditory streams are presented to a listener, increased pitch differences facilitate their segregation and the subsequent perception of their content (Brokx and Nootboom, 1982; Assmann and Summerfield, 1987; Culling and Darwin, 1993; Bird and Darwin, 1998; Drullman and Bronkhorst, 2004), although aging and hearing loss decrease the ability to use such cues (Summers and Leek, 1998). Until recently, the relationship between the F_0 and hearing in noise was limited to the psychoacoustic domain, but we now have physiological evidence from children and adults documenting greater subcortical encoding of the F_0 being associated with better speech-in-noise perceptual ability (Anderson et al., 2010b, 2011; Song et al., 2011). Exceptions to this pattern occur in normal hearing musician children and adults, where greater harmonic encoding and faster neural timing relate with their enhanced ability to hear in noise (Parbery-Clark et al., 2009a, 2012b; Strait et al., 2012). For the first time, however, we

show that the relationship between the strength of F_0 encoding and hearing in noise ability is present in an older, hearing-impaired musician population.

While middle-aged musicians with hearing loss demonstrate enhanced F_0 encoding, the traditional musician hallmark for increased harmonics representation (Parbery-Clark et al., 2009a, 2012b,c; Strait et al., 2012) was not maintained, highlighting the profound impact of hearing loss on the neural representation of spectral cues (see Table 6 for a summary of previous spectral results between musicians and nonmusicians in younger and older normal age groups). Auditory deprivation, such as that associated with hearing loss, alters the response properties of neurons (Willott, 1984, 1986; Yang et al., 1992; Wang et al., 1996) as well as their tonotopic organization (Willott, 1991; Harrison et al., 1998; Barsz et al., 2007) and, in animal models, the effects of auditory deprivation are evidenced as an increase in low-frequency encoding (Syka, 2002; Willott, 2005). Because none of our subjects wore or had worn hearing aids, we can assume that they had all experienced varying levels of auditory deprivation. Therefore, our reported reduction of harmonic representation but increase in pitch encoding in hearing-impaired musicians may be indicative of musicians compensating for the loss of their previously noted spectral advantage. Of note, none of our musicians were string players; given the need for focused listening to harmonic vibrations in string players, future research should consider whether the spectral changes reported here are consistent across string players. Future work aimed at determining whether hearing aids that increase the salience of the spectral components of the signal can restore the musicians' neural advantage for the encoding of speech harmonics. An alternative line of research might examine whether musicians can benefit from a short-term auditory training program focused on improved spectral encoding.

Table 6

Musicians' neural signatures. Summary table detailing the known effects of musicianship on the auditory brainstem responses to the speech sound used in this study in three different populations: young adults (Parbery-Clark et al., 2009a), older adults with normal hearing (Parbery-Clark et al., 2012a, b) and older adults with hearing loss. In all significant cases, musicians demonstrate a neural advantage for these measures relative to nonmusicians except for the F_0 encoding in quiet for the transition (*), where older, normal-hearing nonmusicians had greater F_0 representation. $\sim p < 0.1$; $* = p < 0.05$; $** = p < 0.01$; $*** = p < 0.001$.

		Musician-nonmusician group differences					
		Young adults		Older adults – NH		Older adults – HL	
		Quiet	Noise	Quiet	Noise	Quiet	Noise
F_0 encoding	Transition	–	–	* ₁	–	**	*
	Vowel	–	–	–	–	–	–
Harmonic encoding	Transition	–	–	–	–	–	–
	Vowel	–	**	**	**	–	–
Response consistency	Transition	–	–	–	–	**	**
	Vowel	–	–	**	**	**	**
Peak timing	Onset	–	**	*	**	–	~
	Transition	–	**	***	***	–	*
	Vowel	–	–	–	~	–	–
Neural precision (i.e., stimulus-to-response fidelity)	Vowel	–	**	**	**	*	*

4.2. Maintenance of temporal enhancements

In the timing domain, older hearing-impaired musicians demonstrate enhanced neural encoding of speech in noise, the more challenging of the two conditions, a finding similar to that reported in young adult musicians (Parbery-Clark et al., 2009a). Compared to older normal-hearing musicians, who have enhanced temporal encoding in both quiet and noise (Parbery-Clark et al., 2012b), musicians with hearing loss seem to have lost their advantage in quiet yet maintain the enhancement in noise (see Table 6 for a summary of musician–nonmusician temporal differences in young and older normal hearing adults). There is a known correlation between earlier peak timing in noise and better hearing in noise in children (Anderson et al., 2010a; Strait et al., 2012), young adults (Parbery-Clark et al., 2009a), and older adults (Parbery-Clark et al., 2012b) that was, however, not observed here. Hearing loss impacts subcortical neural timing with the majority of studies documenting varying degrees of delayed neural timing, although experimental protocols differed (i.e., monaural/binaural, suprathreshold levels, compensation for hearing loss, degree of hearing loss, age of subjects), complicating generalization across studies (Otto and McCandless, 1982; Boettcher, 2002; Vander Werff

and Burns, 2011; Konrad-Martin et al., 2012). Here, we did not find a correlation between peak latencies and hearing in noise in a hearing-impaired population, which may reflect the fact that hearing loss breaks down the typical relationship between peak timing and hearing in noise.

4.3. Fidelity and stability of neural encoding

In addition to faster neural timing in response to speech in noise, hearing-impaired musicians exhibited greater trial-by-trial neural response consistency and more precise encoding of the stimulus in both quiet and in the presence of background noise, suggesting more stable representation of stimulus elements. The auditory system is dependent on synchronous neural firing to accurately encode sound (Kraus et al., 2000; Wang, 2007). Concordant with the notion that response stability is a basic function of the nervous system, reductions in response consistency are seen with aging (Anderson et al., 2012), dementia (Hultsch et al., 2000), attention-deficit hyperactivity disorder (Castellanos and Tannock, 2002; Bellgrove et al., 2005) and dyslexia (Hornickel et al., 2012). Furthermore, recent evidence indicates that response consistency can be improved with auditory training such as wearing assistive listening devices for dyslexic children (Hornickel et al., 2012) or lifelong musical experience in older adults (Parbery-Clark et al., 2012b).

4.4. Mechanisms underlying the musician advantage

Our reported higher levels of response consistency and neural precision in musicians potentially signify more synchronous neural phase-locking and, hence, greater accuracy in the neural transcription of sound. Top-down processes are a known vehicle for promoting plasticity in the auditory brainstem. Work from animal models indicates that cortical activity modulates brainstem response patterns via the corticofugal system (Suga, 2008) and that the corticofugal pathway is important for auditory learning (Bajo et al., 2010). This interaction between cortical and subcortical sites is especially pronounced for stimuli that bear behavioural significance (Suga and Ma, 2003). Musical training involves actively listening to behaviourally relevant signals and by the age of 60 older musicians have accumulated approximately 60,000 hours of this intense auditory activity (Krampe and Ericsson, 1996). Therefore it may be the case that musicians have enhanced top-down control of subcortical response properties, resulting in greater encoding of the most behaviourally-relevant features (for review see Kraus and Chandrasekaran, 2010). We also found that musicians have less prestimulus activity – that is, decreased spontaneous neural activity in the absence of sound. Again, this finding supports the notion of greater top-down control in musicians in that the known effects of hearing loss, which result in increased excitability in the auditory pathway (Kotak et al., 2005; Dong et al., 2009), are potentially controlled to a greater degree in the musician system.

4.5. Music as auditory rehabilitation

Participation in social activities relates to a higher quality of life (Guse and Masesar, 1999); however, hearing loss can create communication barriers, leading to social isolation (Christian et al., 1989; Heine and Browning, 2002; Dalton et al., 2003; Heine and Browning, 2004). Consequently, addressing such concerns in a hearing-impaired population is crucial for the health and well-being of a large segment of the population. Musicians with hearing loss demonstrate clear advantages for hearing in noise over their nonmusician peers as well as concomitant cognitive and

neural enhancements; therefore, we believe that musical training offers a potential rehabilitative tool for an older, hearing-impaired population. In addition, musical activities (i.e., orchestra, choir, music lessons) often include a social component, which may help combat the feelings of social isolation associated with hearing loss. While a recent study assessing quality of life in older musicians did not specifically address hearing loss, it did find that musical participation was a source of enjoyment and contributed to greater life satisfaction (Johnson et al., under review). Future work assessing the effects of short-term musical training in older nonmusician individuals is needed to validate the therapeutic effects of musical training initiated later in life. In addition to including the behavioural and neural measures reported here, quantifying changes in quality of life will also likely prove fruitful in judging the full range of benefits that musical training can provide.

4.6. Clinical management of musicians with hearing loss

We previously showed that older musicians with normal hearing rate their hearing in noise performance higher than age- and hearing-matched nonmusicians (Parbery-Clark et al., 2012b); here we find that musicians with hearing loss do not perceive themselves as able to hear better than nonmusicians with hearing loss in background noise. Therefore, it may be the case that musicians with hearing loss, given their heightened auditory skills, are more sensitive to subtle decrements in their performance. For this reason, it would be important for clinicians to closely attend to a musician's stated symptoms. Because of the high auditory demands of musicianship, their perception of hearing difficulties may be greater than would be predicted from the traditional audiological work-up and they may need more intensive intervention to regain what they perceive to be normal performance.

5. Conclusions

We reveal that older musicians with hearing loss have enhanced hearing in noise abilities relative to nonmusicians. In musicians, we also document strengthened neural encoding of several key acoustic features important for speech perception. Together, these neural enhancements may drive the older musicians with hearing loss' advantage for hearing in noise. Hearing loss does, however, eliminate the musician's harmonic enhancement that is characteristic of normal-hearing young and middle-aged musicians. Given that hearing in noise is a primary complaint of older, hearing-impaired individuals, these results suggest that musical training may be a useful remediation tool for age- and hearing-related deficits.

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