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Letter to the Editor

Specialization among the specialized: Auditory brainstem function is tuned in to timbre

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1. Introduction

Evidence has mounted documenting widespread musician enhancements in an evolutionarily ancient subcortical structure, the auditory brainstem, highlighting the brainstem as a structure involved in learning-related brain plasticity (Banai and Kraus, 2007; Krishnan et al., 2009). Musicians not only show more precise subcortical encoding of music, but of speech and emotional communication sounds as well (Kraus and Chandrasekaran, 2010; Kraus et al., 2009). Though remarkable, such observations cannot disambiguate the source of this musician advantage. Does musical training shape subcortical auditory processing, or are individuals born with more refined auditory brainstem function predisposed to pursue musical training? Although neurobiological studies have employed correlational analyses to infer that functional differences between the brains of musicians and nonmusicians are a consequence of the extent of musical practice (Musacchia et al., 2007; Strait et al., 2009; Wong et al., 2007), causality cannot be derived from correlations. Given that experience-related and innate factors likely co-exist, we must clearly define their respective roles in shaping brain function in musicians. Here, we aimed to provide unambiguous evidence for musical training's impact on auditory brainstem function. The answer to this question bears great significance for sensory learning; if musical training has the power to fine-tune subcortical structures to better process sound, this would attest to the power of cognitive experience to shape basic sensory function.

Until now, subcortical investigations have approached musicians as a homogeneous population (Bidelman et al., 2009; Musacchia et al., 2007; Parbery-Clark et al., 2009; Strait et al., 2009; Wong et al., 2007). We asked whether or not musical training shapes human brainstem function by examining subgroups of musicians—specifically, musicians trained on different instruments. Guided by the hypothesis that subcortical precision in musicians is driven by extensive musical practice, we expected musicians' auditory brainstem responses to be uniquely tuned to their instrument of practice relative to other instruments.

2. Methods

2.1. *Participants*

Twenty-one accomplished adult musicians between the ages of 18 and 35 (mean age 25.2), including 10 pianists (females = 7) and 11 nonpianists (females = 7). Subjects gave informed consent in accordance with the Northwestern University Institutional Review Board and demonstrated normal audiometric thresholds (<15 dB HL pure-tone for

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octave frequencies from .125 kHz to 8 kHz) and normal auditory brainstem responses to 80 dB SPL 100 μsec click stimuli presented at 31.1 Hz.

All subjects had consistently practiced their primary instrument for a minimum of 10 years leading up to the time of testing. Nonpianists had no formal piano experience. Pianists and nonpianists did not differ in age ($t = 1.46$, $p = .16$), sex ($\chi^2 = .10$, $p = .76$), total years of musical practice ($t = 1.53$, $p = .15$) or age of musical practice onset ($t = .92$, $p = .50$).

2.2. Design and procedure

We recorded auditory brainstem responses from musicians to three musical sounds (piano, bassoon and tuba; 100 Hz, 200 msec). The sounds differed only in timbre, which is the quality of a sound that distinguishes it from other sounds of the same pitch and volume. Stimuli were presented separately in three blocks lasting ~30 min each, monaurally (right ear) via an insert earphone (ER-3, Etymotic Research, Elk Grove Village, IL, USA), at 80 dB SPL and at a rate of 3.33 Hz using Neuroscan Stim 2 (Compumedics, Charlotte, NC, USA). Stimuli were presented in alternating polarities and responses to each polarity were subsequently summed in order to limit contamination of the neural recording by the cochlear microphonic and stimulus artifact (Skoe and Kraus, 2010). During the recording session, subjects watched videos in order to maintain a still, wakeful state.

Brainstem responses were collected using Scan 4.3 (Compumedics, Charlotte, NC). Ag–AgCl electrodes were applied in a vertical, ipsilateral montage. Responses were filtered offline from 70 Hz to 2000 Hz with a 12 dB roll-off, epoched from −50 msec to 250 msec (stimulus onset at time zero) and digitally sampled at 20,000 Hz. Events with amplitude exceeding ±35 μV were rejected as artifacts, resulting in 5500 artifact-free responses to each stimulus for each subject.

2.3. Statistical analysis

Stimuli were band-pass filtered to match auditory brainstem response characteristics (70–2000 Hz) (Matlab, The Mathworks, Natick, MA, USA). Broadband amplitude envelopes were obtained by performing a Hilbert transform on the stimulus and response waveforms and low-pass filtering at 200 Hz. Each instrument's waveform demonstrated a unique amplitude envelope, which is known to differentiate instruments on the basis of perceptual timbre (Iverson and Krumhansl, 1993).

Stimulus and corresponding brainstem response envelopes were compared from 0 msec to 200 msec in 40 msec blocks that overlapped by 39 msec; each block was cross-correlated using the xcorr function in Matlab in order to generate a running stimulus-to-response cross-correlogram (Skoe and Kraus, 2010). Peak r values for each block, defined as the maximum correlation within the 6.5–10.5 msec lag range (the known subcortical response delay), were averaged to generate a single correlation coefficient for each subject to each stimulus. Prior to statistical analysis, averaged r values

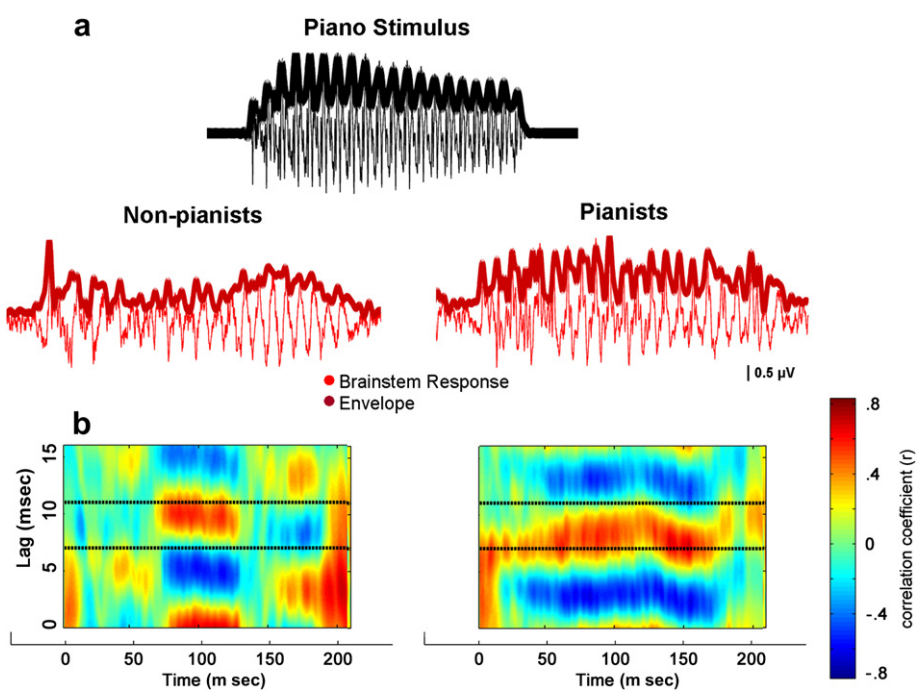

Fig. 1 – Pianists' auditory brainstem responses more closely reflect temporal characteristics of the piano sound than nonpianist musicians, (a) The piano stimulus and corresponding brainstem responses of pianists and nonpianists. Stimulus and brainstem response waveforms were rectified and low-pass filtered at 200 Hz to produce the amplitude envelopes. (b) The amplitude envelopes of pianists' brainstem responses to the piano sound correlate more strongly with the amplitude envelope of the piano stimulus than nonpianists' ($F = 6.97$, $p = .01$, two-tailed). Brainstem responses emerge 6.5–10.5 msec after the stimulus due to synaptic delay, resulting in the maximal correlations occurring within this demarcated lag range.

were Fisher transformed and normality for all data was confirmed by the Kolmogorov–Smirnov test for equality.

3. Results

Because the auditory brainstem response physically resembles the acoustic properties of incoming sounds (taking a neural "snapshot" of a sound's pitch, timing and timbre) (Tzounopoulos and Kraus, 2009), we were able to compare the precision with which musicians' auditory brainstem responses mimic the acoustic waveforms of piano, bassoon and tuba notes (see Fig. 1, panel a). By cross-correlating each subject's auditory brainstem response with the waveform of the eliciting stimulus, we discovered that pianists' auditory brainstem responses more closely reflected the morphology of the piano sound wave than nonpianists' (see Fig. 1, panel b). Pianists and nonpianists did not, however, differ for either of the other musical sounds (bassoon: $F = .08$, $p = .78$; tuba: $F = .07$, $p = .80$; $3_{stimulus} \times 2_{group}$ repeated measures analysis of variance interaction: $F = 3.3$, $p = .04$). Because only one of the nonpianists had bassoon experience and none had experience with the tuba, the potential for subcortical specialization to these two timbres could not be explored.

4. Discussion

By demonstrating timbre-specific subcortical tuning in musicians, we reveal that the human auditory brainstem is exquisitely more refined than previously assumed. This plasticity is likely driven by cortical-brainstem reciprocity (Suga and Ma, 2003) that is strengthened by musical practice. Although the biological mechanisms that drive this subcortical specialization remain under debate, our options are limited: either (a) local neural reorganization occurs within the auditory brainstem, or (b) top–down modulation via corticofugal (i.e., descending) neuronal tracts is driven by enhanced higher-level control over basic sensory processing (Krishnan and Gandour, 2009). Although both avenues likely contribute to subcortical specialization, involvement of corticofugal tracts has proven critical for auditory learning (Bajo et al., 2010). Here, we provide evidence for the direct sculpting of sensory function with musical training in humans using individual subjects as their own controls. Furthermore, we reveal, for the first time, an objective neural marker for sensory fine-tuning in musicians that unambiguously relates to specific instrumental training backgrounds. Although further work should explore subcortical specificity in other instrumentalists, the specificity of subcortical function in pianists demonstrated here suggests that musicians' and nonmusicians' auditory brainstem processing can be differentiated by use-dependent subcortical plasticity rather than hard-wired predispositions.

Overall, outcomes reveal that musical practice has the power to shape sensory circuitry, newly informing scientific understanding of the biological mechanisms that are fundamental to sensory learning. These mechanisms appear to depend, at least in part, on the corticofugal shaping of basic sensory function in that cognitive functions (here, musical learning) have the power to sculpt human experience of the sensory world.

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