Timbre-specific enhancement of auditory cortical representations in musicians

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Neural imaging studies have shown that the brains of skilled musicians respond differently to musical stimuli than do the brains of non-musicians, particularly for musicians who commenced practice at an early age. Whether brain attributes related to musical skill are attributable to musical practice or are hereditary traits that influence the decision to train musically is a subject of controversy, owing to its pedagogic implications. Here we report that auditory cortical representations measured neuromagnetically for tones of different timbre (violin and trumpet) are enhanced compared to sine tones in violinists and trumpeters, preferentially for timbres of the instrument of training. Timbre specificity is predicted by a principle of use-dependent plasticity and imposes new requirements on nativistic accounts of brain attributes associated with musical skill. *NeuroReport* 12:169–174 © 2001 Lippincott Williams & Wilkins.

Key words: Auditory cortex; Magnetoencephalography (MEG); Neural plasticity; Musical skill; Timbre specificity

INTRODUCTION

Recent functional brain imaging studies of musicians have shown that musical skill is associated with enhanced auditory cortical representations for notes of the musical scale [1], increased sensitivity of event-related potentials to disparities in melodic contour and pitch interval [2], and, in skilled violinists, enhancement of somatosensory representations of the fingering digits [3]. In each of these cases, functional enhancement was observed primarily for musicians who began to practice their instrument prior to the age of about 9 years. Neuroanatomical measurements taken from high resolution MR images have also revealed an enlargement of the anterior region of the corpus callosum in musician subjects who commenced practice at an early age [4], and a larger left-sided planum temporale (a posterior region of the auditory cortex believed to be important in the processing of complex sounds) in musicians with absolute pitch than in musicians with relative pitch or non-musicians [5]. Although it has been pointed out that brain attributes found in musicians may be influenced by a genetic code [6], experimental findings from animal [7–9] and human [10–12] studies suggest that these attributes may depend on neuroplastic mechanisms that modify synaptic connections [9] and/or neural growth processes [13–15] during musical training, so as to represent sensory inputs that are experienced during musical practice. Age-dependent effects may arise because musicians who commenced practice in their early years have on average practiced more than late starters, or because the brain is more plastic in the early years [16–18].

The present study was undertaken to test a neuroplastic account of enhanced auditory cortical representations for notes of the musical scale in musicians. We investigated whether cortical representations for notes of different timbre (violin and trumpet) are enhanced compared to sine tones in violinists and trumpeters, preferentially for timbres of the instrument on which the musician was trained. Timbre specificity is predicted by neuroplastic accounts of brain development, when musical training has been specific to one or the other of these instruments. In addition, timbre specificity portends new challenges for nativistic accounts of brain attributes associated with musical skill. In order to explain timbre specificity, nativistic accounts must be elaborated to propose that genetic mechanisms code for complex tones of specific spectral structure, and that the genetic code for spectral structure is sufficiently constraining as to determine who trains as a trumpeter and who as a violinist.

MATERIALS AND METHODS

Subjects: Seventeen highly skilled musicians (eight violinists and nine trumpeters, aged 23.8 ± 2.8 and 26.8 ± 3.0 years, respectively) were recruited from the Music Conservatory in Münster. Three of the trumpeters and seven of the violinists were women. Prior to the experiment subjects were screened for normal hearing by clinical audiometry (air conduction and bone conduction thresholds of no more than 10 dB hearing loss in the range from 250 to 8000 Hz) and were interviewed to collect information about their musical skills, listening habits, and the musical interests of their parents and siblings. All subjects reported playing either the violin or the trumpet as their principal instrument. Violinists had played their instrument for an average of 15.1 ± 3.3 years and trumpeters 15.3 ± 3.2 years at the time of the study, and reported that they practiced an average of 24.9 ± 13.1 and 18.4 ± 8.0 h/week, respectively, in the 5 years preceding the study. Although every subject had some experience playing secondary instruments, most frequently the piano (5.5 ± 3.5 years for violinists, 4.4 ± 1.6 years for trumpeters), none had ever played the trumpet or violin as a secondary instrument. All subjects, except one violinist with absolute pitch, reported that they had relative pitch. Subjects were informed of the experimental procedures and gave their written consent for participation.

Procedure: MEG was used to record the brain response to musical tones using a 37-channel BTi Magnes system. Magnetic sensors were placed in a spherical array 15 cm in diameter that covered one side of the head above the temporal cortex. Auditory stimuli were delivered by a non-magnetic and echo free acoustic delivery system to a silicon ear piece placed in the ear contralateral to the MEG sensors. In order to investigate responses of each hemisphere, the ear piece and sensor array were repositioned half way through the experimental session (left/right order randomized between subjects).

The auditory evoked field (AEF) corresponding to the major wave NI, having a latency of about 100 ms after stimulus onset, was recorded for each of five tonal stimuli. These stimuli consisted of two violin tones B4 and F4 (American notation, first harmonics of 465 and 353 Hz, respectively), two trumpet tones B4 and F4 (first harmonics 468 and 353 Hz, respectively), and a pure sine tone of 400 Hz between the fundamental frequencies of the B4 and F4 tones. The musical stimuli were digitally sampled natural tones from the violin and trumpet (see Fig. 1 for their envelope and spectra). The length of the pure sine tone was matched to the length of the musical tones (nominal duration about 400 ms), and its rise and fall times

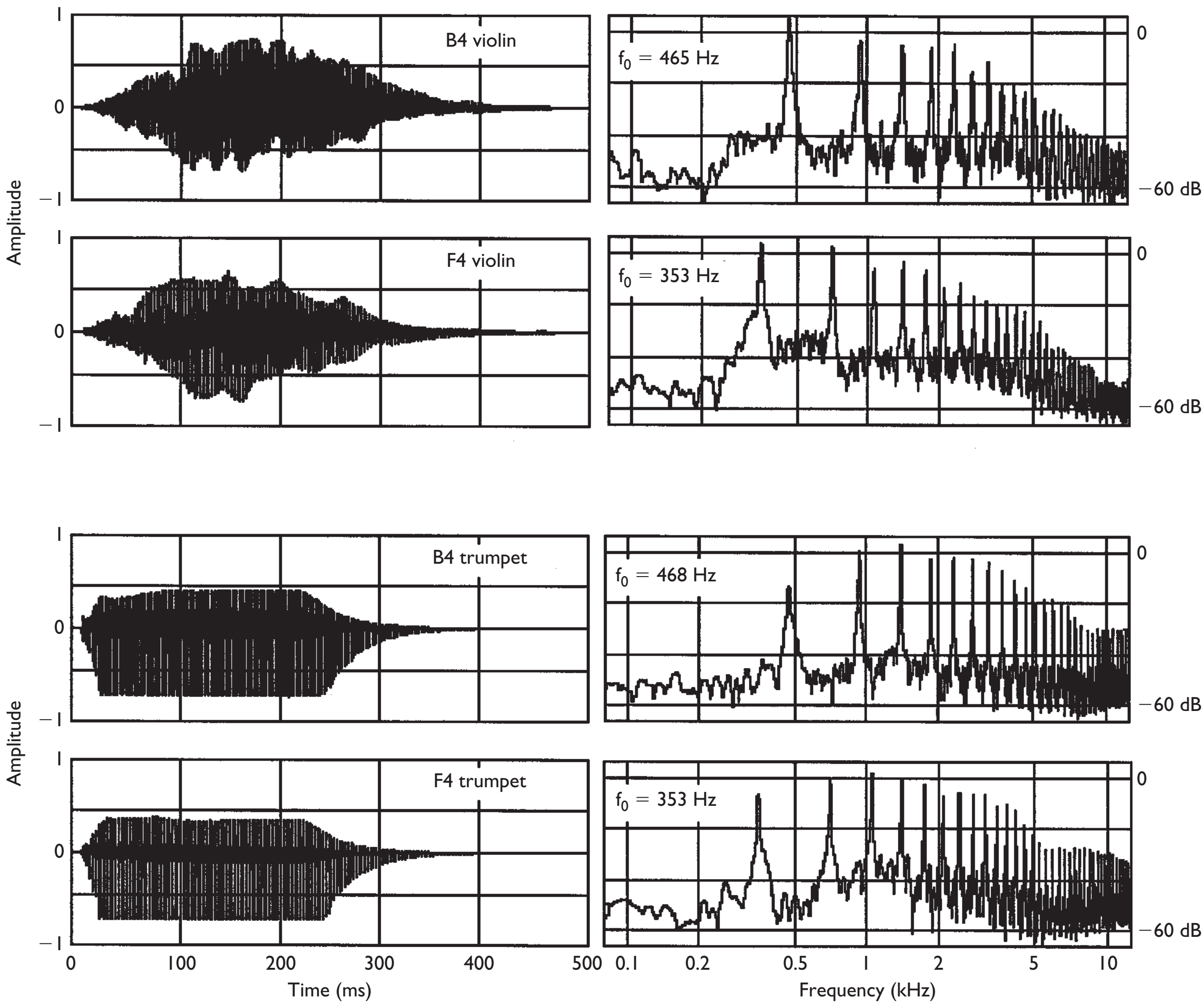

Fig. 1. Temporal envelope (left) and frequency spectrum (right) of the string (upper panel) and trumpet (lower panel) tones presented to trumpeters and violinists.

of 10 ms were almost the same as those for the trumpet tones. The five tonal stimuli were matched psychophysically for loudness by 20 non-musician control subjects in a separate preliminary study and were set individually at 60 dB above the threshold of the 400 Hz sine tone, which was measured for each musician subject at the beginning of the MEG session. The intensity of the musical stimuli adjusted with respect to threshold did not differ significantly between the two in groups ($F(1,15) = 1.10$, $p = 0.31$). Equal numbers of five stimuli were presented in a randomized sequence to each ear within a single block of 640 stimuli, using interstimulus intervals varying randomly between 3.5 and 4.5 s. The tones were presented while subjects watched silent cartoon videos of their individual choice which were intended to focus their attention. The subjects were explicitly instructed not to attend to the sequence of stimuli appearing in the ear.

Data analysis: AEFs were averaged and filtered within a 0.1–20 Hz bandwidth. Because the distribution of the N1 field component was highly dipolar, a single equivalent current dipole model (ECD) was used to explain the field distribution for each of the five stimulus conditions. The mean dipole moment was computed from time points within a 30 ms time interval around the maximum of the dipole moment. The coordinates of the dipole location were calculated as a mean of data points within the 30 ms time interval which satisfied the following requirements: (1) a goodness of fit of the ECD model to the measured field $> 95\%$; (2) variation of the source coordinates within the 30 ms interval < 15 mm; and (3) anatomical distance of the ECD to the midsagittal plane > 3 cm. The dipole moment indicates the total strength of cortical activation, i.e. the number of synchronously active neurons contributing to a cortical response. If this number increases, the dipole moment also increases [19].

Dipole moments calculated for each auditory stimulus were evaluated by analyses of variance (MANOVA). Significant main effects and interactions were evaluated by *t*-tests when preplanned or by Scheffé's method when *post-hoc*. We expected on the basis of previous studies of adult musicians [1–3], animal subjects [16] and children with cochlear implants [17,18] that changes in cortical representations are more readily induced by sensory experience in the young brain than in the adult brain. One-tailed tests were therefore accepted for age-related effects. All probabilities are two-tailed unless otherwise stated.

RESULTS

The time course of the strength of the cortical response evoked by violin and trumpet tones (averaged over B4 and F4) is portrayed separately for the two hemispheres in Fig. 2a, for one representative violinist and one representative trumpeter showing timbre specificity. A prominent peak corresponding to the AEF N1 component with a latency near 100 ms is seen in the responses to each of the musical stimuli. The amplitude of this peak was determined for each subject, stimulus, and hemisphere, and evaluated by ANOVA including musician (violinist/trumpeter), hemisphere, and musical stimulus (string/trumpet) as variables. An interaction of stimulus type with musician group was found ($F(1,15) = 28.55$, $p = 0.00008$) with no effect attributed to hemisphere (all Fs involving hemisphere were < 1). This interaction is depicted in Fig. 2b, where it can be seen that in each musician group N1 cortical strength was larger for timbres of the instrument of training. Preplanned comparisons collapsed over the hemispheres showed that trumpet tones evoked larger NI responses than did string tones in the trumpeters ($t(8) = 4.76$, $p = 0.001$), whereas the reverse pattern was seen for the violinists ($t(7) = -2.76$, $p = 0.028$). Main effects of musician group (trumpeter/violinist, $F(1,15) = 7.84$, $p = 0.013$) and type of tone (trumpet/string, $F(1,15) = 5.57$, $p = 0.032$) were also found in this analysis. These indicated larger cortical responses to the musical tones overall in the trumpeters compared to the violinists, and larger responses to trumpet tones than to string tones when the musician groups were combined.

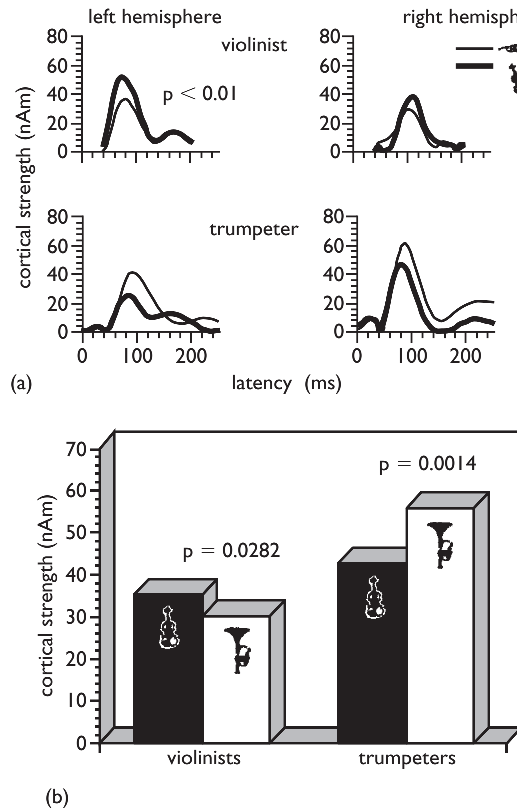

Fig. 2. (**a**) Timbre specificity. Cortical responses evoked by string tones and trumpet tones and measured as dipole moment are shown for a representative violinist (upper panel) and trumpeter (lower panel) for the left and right hemispheres separately. (**b**) Mean dipole moments evoked by the string tones and trumpet tones are shown for the trumpeter and violinist groups (hemispheres combined).

Effects of stimulus type on the strength of the NI response were investigated further in two subsidiary analyses. Women were more strongly represented in our violinist group (seven of eight subjects) than in our trumpeter group (three of nine subjects), which reflected student enrolment in conservatory training programmes for these instruments. To ensure that evidence for timbre specificity was not influenced by gender, we repeated the aforementioned analyses using female musicians only in the two instrumental groups. No main effects attributable to musician group, hemisphere, or musical stimulus were found, and interactions involving hemisphere were not significant. However, an interaction was found between musician group (violinist/trumpeter) and musical stimulus (string/trumpet), $F(1,8) = 14.98$, $p = 0.0047$, confining timbre specificity. Preplanned comparisons collapsed over the hemispheres showed that the string tones evoked a larger dipole moment than did the trumpet tones among the female violinists ($t(6) = 2.23$, $p < 0.05$, one-tailed), whereas the reverse pattern was obtained in the female trumpeters ($t(2) = -7.27$, $p < 0.01$). We also contrasted the two genders within the trumpeter group, including musical stimulus (string/trumpet) as a variable (hemispheres averaged). A main effect of musical stimulus was found, indicating larger mean responses overall to the trumpet stimulus ($F(1,7) = 18.2$, $p = 0.004$. However, neither the main effect of gender nor the interaction of gender with stimulus type reached significance.

The second analysis compared cortical activations evoked by the musical tones (string and trumpet) with activations evoked by the pure sine tone of 400 Hz. Tones were averaged over hemispheres and compared within the musician groups where gender was held constant. Dipole moments evoked by tones of the instrument of training were found to be larger than those evoked by the sine tones within the violinist group ($t(7) = 3.72$, $p = 0.007$) and within trumpeter group as well ($t(8) = 4.17$, $p = 0.003$). Cortical activations evoked by musical tones of the untrained instrument also differed from those of sine tones within the trumpeter group ($t(8) = 1.89$, $p < 0.05$, one-tailed) and when the trumpeter and violinist groups were combined ($t(16) = 2.20$, $p < 0.05$).

The latency of the N1 response (peak of the cortical activation, see Fig. 2a) was found to differ among the string, sine, and trumpet tones when averaged over hemispheres and musician groups ($F(1,30) = 13.49$, $p < 0.001$). N1 latency was shorter for the trumpet tone (85.3 ms) than for the string (91.9 ms) and sine (90.4 ms) tones ($p < 0.005$, Scheffé test), while N1 latency did not differ between the latter two stimuli. Response latency was about 3 ms shorter in the right than the left hemisphere for each tonal stimulus, but neither this difference, nor any interaction involving group, stimulus, or hemisphere, reached significance for the latency measure. The three-dimensional coordinates of ECDs fitted to the N1 field patterns were also determined for the violin, trumpet, and sine tones, separately for each hemisphere and musician group. No main effects attributable to type of tonal stimulus (string, trumpet, sine) were found. Overall, coordinates in the anterior posterior (x), medial-lateral (y), and inferior-superior (z) directions averaged 0.82 mm, 4.74 mm and 5.43 mm, respectively, in the left hemisphere, and 1.41 mm, 4.75 mm and 5.2 mm, respectively, in the right hemisphere.

Extensive data were gathered from the musicians regarding the age at which musical training commenced, years of instruction on their principal instrument, passive music listening habits, and the musical skills of their parents and family members. Five violinists and three trumpeters reported that one or both of their parents was a musician or musical hobbyist. Cortical activations evoked by tones of the principal instruments of these subjects did not differ significantly from those of subjects whose parents were non-musicians ($t < 1$). Within the violinist group, dipole moments for violin or trumpet tones did not correlate significantly with the age of inception of musical practice, years of training on the principal instrument, recent practice history, or music listening behavior. Among the trumpeters one correlation was found, which related instrument-specific enhancement of dipole moment for the trumpet tones (trumpet minus string) with the age of inception of musical practice ($r = -0.634$, $p = 0.026$, one-tailed). This correlation did not change appreciably when years of musical training was partialed out ($r = -0.639$). No other correlations reached significance within the violinist or trumpeter groups, or when the groups were combined into one musician sample.

DISCUSSION

Our findings indicate that highly skilled musicians exhibit enhanced auditory cortical representations for musical timbres associated with their principal instrument, compared to timbres associated with instruments on which they have not been trained. Timbre specificity is predicted by a principle of use-dependent plasticity when musical training has been given on one instrument but not another, which was the case in the subjects that we investigated. The augmented N1 dipole moment which we observed for timbres of the instrument of training imply either that more neurons were involved in representing and processing the musical sounds produced by this instrument, or that neurons serving these functions were firing more synchronously. Our findings on musician subjects are congruent with animal studies [7–9] and experiments with non-musicians [10–12] which have shown that auditory cortical representations are enhanced by neuroplastic processes, when behavioral training is given under controlled laboratory conditions. Animal studies have reported an increase in the cortical territory representing the trained stimuli as well as changes in the temporal response properties of neurons, which suggests that both the number of participating neurons and their temporal synchrony may be altered during cortical remodeling [7–9].

The spatial coordinates of ECDs fitted to the N1 field patterns are in broad agreement with earlier neuromagnetic localizations [20,21] and human intracortical recordings [22] which have situated N1 sources posterior and lateral to Heschl's gyrus, in secondary processing areas of the auditory cortex. Because only the center of cortical activation is depicted by source modeling, the boundaries of neural activity are unknown and we cannot preclude timbre specific modulation of wider auditory regions. The spatial coordinates of ECDs fitted to the two musical stimuli did not differ from those of sine tones in our study. However, the strengths of the cortical activations evoked by the musical and sine stimuli were found to differ, with the musical stimuli producing larger dipole moments than sine tones among trumpeters as well as violinists. There is evidence that this finding cannot be fully explained by the greater spectral complexity of the musical tones compared to the sine tones. In agreement with the present study, Pantev *et al.* [1] reported that larger dipole moments were evoked by piano tones than by sine tones matched in fundamental frequency in musicians. However, dipole moments for piano and sine tones did not differ from one another in non-musician control subjects. This suggests that enhanced representations for notes of the musical scale in musicians may be an experience-dependent effect. Auditory representations for notes of the unpractised instrument were also augmented compared to sine tones in our study. This may reflect partial generalization of the effects of musical practice on the principal instrument to other stimuli of the musical scale or the listening experience of our subjects during musical performance.

Overall, larger responses were recorded to the musical stimuli among the trumpeters of our study, particularly for the trumpet tones in this group. This finding could not be attributed to a preponderance of male trumpeters but appeared instead to be attributable to a robust timbre-specific enhancement of auditory cortical representations when the trumpet was the instrument of training. Augmentation of the cortical representation for trumpet tones in trumpeters could have arisen from the specific requirements of performance with this instrument. In contrast to string players, trumpet players do not use their instrument as a resonance body but utilize instead the pharynx, larynx, tongue, lip, and diaphragm to produce musical sounds. Cross-modal feedback arising from these structures (which are also involved in speech production) may have recruited more neurons into auditory representations evoked by trumpet tones. Trumpet tones are also typically played more loudly than are string tones, which may magnify the representation for these tones and other timbres that are heard during musical performance. Trumpeters tune their instruments to B3 and then to F4 prior to performance, which may have afforded preferential experience with the F4 stimulus compared to violin players whose tuning notes are typically G3, D4, A4, and E5 (American notation). The enhanced representations that we observed for trumpet and string tones among our trumpeters do not appear to be attributable to elevated hearing thresholds or louder stimuli among the trumpeters. The measured thresholds of all musicians at 400 Hz were within the normal range, and the intensity of the stimuli (which were adjusted with respect to threshold) did not differ significantly between groups.

Previous studies of adult musicians have reported negative correlations between the age of commencement of musical practice and functional cortical representations for several aspects of musical stimuli including sensory representations for piano tones [1], fingering digits of string players [3], and melody and interval [2]. In each of these studies, sensory representations were enhanced primarily among musicians who commenced training prior to the age of about 9 years. A similar relationship was observed among the trumpeters of the present study when instrument-specific enhancement was related to the age of commencement of practice, and it was not diminished when years of practice were partialed out. These findings are consistent with animal studies [16] and with recent studies of cochlear implants in children [17,18] which point to an influential role for early experience in remodeling of the sensory cortices by plastic mechanisms. However, this relation did not materialize among the violinists of the present study. In this respect it may be noteworthy that seven of our eight violinists commenced practice prior to age 8 or less, compared to six of nine trumpeters. Because fewer violinists commenced practice at later ages, the opportunity to detect age regressions may have been diminished in this group.

Our subjects listened to the auditory stimuli passively while they watched videos of their choice which we intended to fixate their attention. This procedure notwithstanding, one can question whether enhancement of the cortical response to tones of the trained instrument may have been caused by greater attention having been paid to these tones than to other stimuli in the test series. In this respect it may be noteworthy that sine tones were presented less frequently on our task (probability of occurrence on each trial of 0.2 compared to 0.4 for each of the musical tones). They were also comparatively novel in the sense that such stimuli are not encountered in the natural environment. Under these conditions the sine tone may have been more likely than the musical tones to have attracted attention, yet the dipole moment evoked by the sine tone was smaller than the dipole moments evoked by tones of either instrument type. Attentional modulation during testing also cannot explain why the degree of cortical activation observed among skilled musicians has been found to correlate with the extent of their musical experience gained several years prior to testing, unless it is proposed that the ability to command attention is itself a consequence cortical reorganization. If the neuromagnetic N1 response reflects an attentional process of the latter type, our findings indicate that this process can be timbre specific.

In principle, attributes of skill that distinguish musicians from non-musicians may derive from the genetic endowment of the musicians as well as from their musical practice or a combination of these factors. This question has become a subject of recent controversy owing to its pedagogic implications [6,23,24]. Our evidence for timbre specificity, and findings from other functional brain imaging studies documenting auditory [1,2,25] and somatosensory [3] representations unique to musicians, can be efficiently explained by neuroplastic mechanisms that appear to operate across sensory modalities, enhancing neural representations for stimuli that are experienced by the subject during musical training. The extent to which expression of these mechanisms is modulated by genetic factors that favor the development of musical skill is unknown. However, if genetic mechanisms are invoked to explain timbre specificity, it must be hypothesized that these mechanisms code for complex tones of specific spectral structure, and that the genetic code for spectral structure is sufficiently constraining as to determine who trains as a trumpeter and who as a violinist.

CONCLUSION

Recent brain imaging studies have shown that the brains of skilled musicians respond differently to musical stimuli compared to the brains of non-musicians, and that this effect is observed principally for musicians who commenced practice at an early age. Research on attributes of musical skill has attracted the interest of music educators and parents wishing to know whether musical training alters brain development in children [23,24]. Other scientists [6] have suggested that brain attributes observed in musicians may be innate, not learned, and if so, that musical training is not responsible for these brain attributes. Our current study informs the nature-nurture issue by showing that cortical representations for violin and trumpet tones (these tones differing in timbre) are enhanced preferentially in musicians, depending on whether the musician trained as a trumpeter or violinist. The results conform with use-dependent accounts of timbre specificity and constrain nativistic theories by imposing new requirements that increase their explanatory burden.

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