# Cortical music selectivity does not require musical training

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## ABSTRACT

Recent work has shown that human auditory cortex contains neural populations anterior and posterior to primary auditory cortex that respond selectively to music. However, it is unknown how this selectivity for music arises in development. To explore the role of musical training, we measured fMRI responses to 192 natural sounds in 10 people with extensive musical training and 10 with almost none. When voxel responses were decomposed into underlying components, both groups exhibited a music-selective component that was very similar in response profile and anatomical distribution to that previously seen in individuals with moderate musical training. We also found that musical genres that were less familiar to our participants (e.g., Balinese *gamelan*) produced strong responses within the music component of both groups. Our findings demonstrate that the signature properties of neural music selectivity are present in individuals at both extremes of musical training, suggesting that they are widespread in humans.

## INTRODUCTION

Music is uniquely and universally human (Mehr et al., 2019) and musical abilities arise early in development (Trehub, 2003). Recent evidence has revealed neural populations in bilateral non-primary auditory cortex that respond selectively to music and thus seem likely to figure importantly in musical perception and behavior (Leaver and Rauschecker, 2010; Rogalsky et al., 2011; Fedorenko et al., 2012; Tierney et al., 2013; LaCroix et al., 2015; Norman-Haignere et al., 2015, 2019). How does such selectivity arise? Most members of Western societies have received at least some explicit musical training in the form of lessons or classes. However, most Western individuals, including non-musicians, also implicitly acquire knowledge of musical structure from a lifetime of exposure to music (Bigand, 1983; Bigand and Pineau, 1997; Koelsch et al., 2000; Tillmann et al., 2000; Tillmann, 2005; Bigand and Poulin-Charronnat, 2006). The roles of these two forms of musical experience in the neural representation of music are not understood. Here, we directly test whether explicit musical training is necessary for the development of music-selective neural responses, by testing whether music-selective responses are robustly present – with similar response characteristics and anatomical distribution – in individuals with little or no explicit training as well as individuals with very extensive training.

Why might explicit musical training be necessary for neural tuning to music? In animals, exposure to specific sounds can elicit long-term changes in auditory cortex, such as sharper tuning of individual neurons (Recanzone et al., 1993; Fritz et al., 2003; Lee and Middlebrooks, 2011) and expansion of cortical maps (Recanzone et al., 1993; Polley et al., 2006; Bieszczad and Weinberger, 2010). These changes occur primarily for behaviorally relevant stimulus features (Ahissar et al., 1992, 1998; Fritz et al., 2005; Ohl and Scheich, 2005; Polley et al., 2006) related to the intrinsic reward value of the stimulus (Bakin and Weinberger, 1996; Fritz et al., 2005; David et al., 2012), and thus are closely linked to the neuromodulatory system (Bao et al., 2001; Kilgard et al., 2001; Blake et al., 2006). Additionally, the extent of cortical map expansion is correlated with the animal's subsequent improvement in behavioral performance (Recanzone et al., 1993; Rutkowski and Weinberger, 2005; Polley et al., 2006;

Bieszczad and Weinberger, 2010, 2012; Reed et al., 2011). Musical training in humans meets virtually all of these criteria for eliciting functional plasticity: playing music requires focused attention, fine-grained sensory-motor coordination, and is known to engage the neuromodulatory system (Blood and Zatorre, 2001; Salimpoor et al., 2011, 2013). And expert musicians often begin training at a young age and hone their skills over many years.

Although many prior studies have measured neural responses in musicians and non-musicians (Ohnishi et al., 2001; Pantev et al., 2001; Shahin et al., 2003; Fujioka et al., 2004, 2005; Besson et al., 2007; Wong et al., 2007; Dick et al., 2011; Lee and Noppeney, 2011; Ellis et al., 2012, 2013; Angulo-Perkins et al., 2014; Doelling and Poeppel, 2015; Lappe et al., 2016), it remains unclear whether any tuning properties of auditory cortex depend on musical training. Previous studies have found that fMRI responses to music are larger in musicians compared to non-musicians in posterior superior temporal gyrus (Ohnishi et al., 2001; Dick et al., 2011; Angulo-Perkins et al., 2014). However, these responses were not shown to be selective for music, leaving the relationship between musical training and cortical music selectivity unclear.

Music selectivity is weak when measured in raw voxel responses using standard voxel-wise fMRI analyses, due to spatial overlap between music-selective neural populations and neural populations with other selectivities (e.g. pitch). To overcome these challenges, Norman-Haignere et al. (2015) used voxel decomposition to infer a small number of component response profiles that collectively explained voxel responses throughout auditory cortex to large set of natural sounds. This approach makes it possible to disentangle the responses of neural populations that overlap within voxels, and has previously revealed a neural population with clear selectivity for music compared to both other real-world sounds (Norman-Haignere et al., 2015) and synthetic control stimuli matched to music in many acoustic properties (Norman-Haignere and McDermott, 2018). These results have recently been confirmed by intracranial recordings, which show individual electrodes with clear selectivity for music (Norman-Haignere et al., 2019). Although Norman-Haignere et al. (2015) did not include actively practicing musicians, many of the participants had substantial musical training earlier in their lives.

Here, we test whether music selectivity is a widespread property of the human brain, or whether it arises only after explicit musical training. To this end, we probed for music selectivity in two groups at the extremes of musical training. Music selectivity might be expected to differ at either end of this spectrum, so we tested both. First, we tested the hypothesis that explicit musical training is necessary for the existence of music-selective neural populations, in which case music selectivity should be weak or absent in non-musicians. Second, because musical training is one of the most pronounced examples of human auditory expertise, we might expect extensive musical training to modify the responses of auditory cortex such that highly-trained musicians would show qualitatively distinct music selectivity. Thus we also test for any such differences, which might be manifested as substantially higher music component weights, a fractionation of the music-selective component into multiple components, concentration of music-selective neural populations in different regions of non-primary auditory cortex, or an increase in lateralization with training. Using these same methods, we were also able to test whether the inferred music-selective neural population responds strongly to less familiar musical genres (e.g. Balinese *gamelan*), and to drum clips with rich rhythm but little melody.

## RESULTS

Our primary question was whether cortical music selectivity is present in people with almost no musical training. We also asked whether music selectivity is altered functionally or anatomically in those at the other end of the spectrum of musical expertise: highly trained musicians. To that end, we scanned ten people with extensive musical training and ten with almost none (**Table 1**), and used voxel

decomposition to isolate music-selective neural populations. First, we asked whether the response components across all of auditory cortex reported by Norman-Haignere et al. (2015) replicate in both non-musicians and highly trained musicians when analyzed separately. Second, we examined the detailed characteristics of music selectivity in particular, to test whether its previously documented key properties are present in both non-musicians and highly trained musicians. Third, we compared the stimulus tuning and anatomical location of music-selective cortical responses between non-musicians and highly trained musicians. And lastly, we took advantage of our expanded stimulus set to look at additional properties of music selectivity, such as the response to musical genres that are less familiar to our Western participants.

| | Subject # | Instrument | Age of Onset (Years) | Years of Lessons | Years of Regular Practice | Years of Training | Hours of Weekly Practice | Hours of Daily Music Listening |
|---|---|---|---|---|---|---|---|---|
| MUSICIANS | 1 | violin | 7 | 11 | 11 | 11 | 2 | 2 |
| | 2 | piano, French horn | 5 | 7 | 18 | 12 | 6 | 4 |
| | 3 | piano, bass | 6 | 12 | 18 | 18 | 2 | 2 |
| | 4 | piano | 3 | 15 | 15 | 15 | 2 | 2.5 |
| | 5 | piano, violin, viola | 5 | 17 | 19 | 20 | 3 | 4 |
| | 6 | piano, flute | 5 | 13 | 13 | 13 | 12 | 3 |
| | 7 | flute | 7 | 12 | 13 | 15 | 15 | 3 |
| | 8 | piano, cello, flute | 4 | 19 | 15 | 18 | 25 | 1 |
| | 9 | violin | 3 | 18 | 18 | 18 | 4 | 10 |
| | 10 | violin, clarinet | 4 | 13 | 8 | 23 | 4 | 5 |
| | | mean | 5.2 | 13.7 | 14.8 | 16.3 | 7.1 | 3.65 |
| NON-MUSICIANS | 11 | | | 0 | 0 | 0 | 0 | 0 |
| | 12 | | 20 | 1 | 0 | 1 | 0 | 2 |
| | 13 | | | 0 | 0 | 0 | 0 | 0.25 |
| | 14 | | | 0 | 0 | 0 | 0 | 5 |
| | 15 | | | 0 | 0 | 0 | 0 | 1 |
| | 16 | | | 0 | 0 | 0 | 0 | 1.5 |
| | 17 | | 10 | 1.5 | 0 | 1.5 | 0 | 1 |
| | 18 | | | 0 | 0 | 0 | 0 | 0.1 |
| | 19 | | | 0 | 0 | 0 | 0 | 0.5 |
| | 20 | | | 0 | 0 | 0 | 0 | 5 |
| | | mean | 24.4 | 0.3 | 0 | 0.3 | 0 | 1.64 |
| | | grand mean | 14.8 | 7 | 7.4 | 8.3 | 3.55 | 2.64 |

**Table 1**. Details of participants' musical backgrounds and training, as measured by a self-report questionnaire.

### ***Replication of functional components of auditory cortex from Norman-Haignere et al. (2015) in musicians and in nonmusicians***

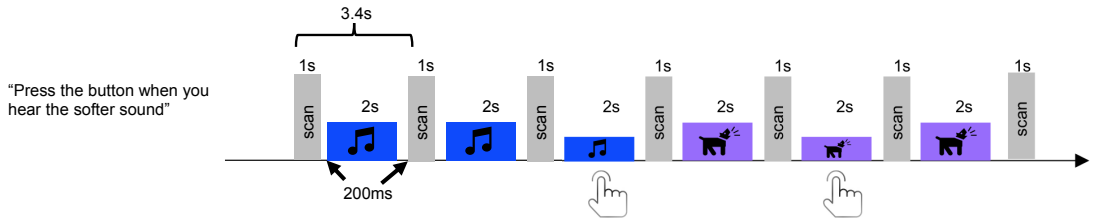
Replication of previous voxel decomposition results

We first tested the extent to which we would replicate the overall functional organization of auditory cortex reported by Norman-Haignere et al. (2015) in our groups of musicians and non-musicians, using the voxel decomposition method introduced in that paper. Specifically, in every participant, we measured the response of voxels within auditory cortex to 192 natural sounds (**Figure 1A** & **B;** the average response of each voxel to each sound was estimated using a standard hemodynamic response function). These 192 sounds included the 165 sounds used in the original study along with additional music clips to further explore brain responses to foreign music and drumming. Then, separately for musicians and non-musicians, we used voxel decomposition to model the response of these voxels as the weighted sum of a small number of canonical response components (**Figure 1C**). This method factorizes the voxel responses into two matrices: one containing the components' response profiles across the sound set, and the second containing voxel weights specifying the extent to which each component contributes to the response of each voxel. The method searches for components that have maximally non-Gaussian weight distributions (**Supplemental Figure 1**). The logic of this approach is that independent non-Gaussian variables become more Gaussian when they are linearly mixed, and thus non-Gaussianity provides a statistical signature that can be used to detect the unmixed components. Similar to standard algorithms for independent components analysis (ICA), the method maximizes non-Gaussianity by minimizing entropy, since the Gaussian distribution is maximally entropic.

**A.** Stimulus Set of Commonly Heard Natural Sounds

| | | | | |
|---|---|---|---|---|
| 1. Man speaking | 11. Running water | 21. Cellphone vibrating | 31. Computer startup | 41. Splashing water |
| 2. Flushing toilet | 12. Breathing | 22. Water dripping | 32. Background speech | 42. Computerized speech |
| 3. Pouring liquid | 13. Keys jangling | 23. Scratching | 33. Songbird | 43. Alarm clock |
| 4. Tooth brushing | 14. Dishes clanking | 24. Car windows | 34. Pouring water | 44. Walking with heels |
| 5. Woman speaking | 15. Ringtone | 25. Telephone ringing | 35. Pop song | 45. Vacuum |
| 6. Car accelerating | 16. Microwave | 26. Chopping food | 36. Water boiling | 46. Wind |
| 7. Biting and chewing | 17. Dog barking | 27. Telephone dialing | 37. Guitar | 47. Boy speaking |
| 8. Laughing | 18. Walking (hard surface) | 28. Girl speaking | 38. Coughing | 48. Chair rolling |
| 9. Typing | 19. Road traffic | 29. Car horn | 39. Crumpling paper | 49. Rock Song |
| 10. Car engine running | 20. Zipper | 30. Writing | 40. Siren | 50. Door knocking |
| | | | | … |

**B.** Scanning Procedure and Task Structure




**C.** Voxel Decomposition Procedure

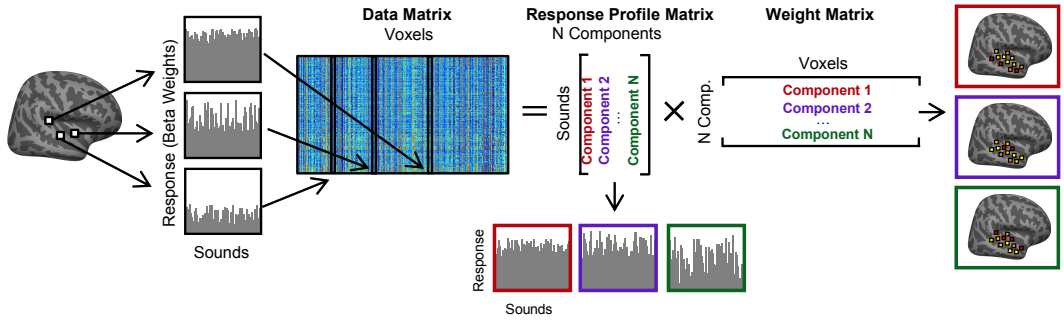



**Figure 1. Experimental design and voxel decomposition method.** (**A**) Fifty examples of the original set of 165 natural sounds used in Norman-Haignere et al. (2015), ordered by how often participants' reported hearing them in daily life. An additional 27 music stimuli were added to this set of 165 for the current experiment. (**B**) Scanning paradigm and task structure. Each 2-second sound stimulus was repeated three times consecutively, with one repetition (the second or third) being 12 dB quieter. Subjects were instructed to press a button when they detected this quieter sound. A sparse scanning sequence was used, in which one fMRI volume was acquired in the silent period between stimuli. (**C**) Diagram depicting the voxel decomposition method, reproduced from Norman-Haignere et al. (2015). The average response of each voxel to the 192 sounds is represented as a vector, and the response vector for every voxel from all 20 subjects is concatenated into a matrix (192 sounds x 26,792 voxels). This matrix is then factorized into a response profile matrix (192 sounds x N components) and a voxel weight matrix (N components x 26,792 voxels).

Since the only free parameter in this analysis is the number of components recovered, the optimal number of components was determined by measuring the fraction of the reliable response variance the components explain. In the previous study (Norman-Haignere et al., 2015), six components were sufficient to explain over 80% of the reliable variance in voxel responses. We found the same to be true in both participant groups of the current study: six components were needed to optimally model the data from the 10 participants in separate analyses of each group. The six components explained 88.09% and 88.56% of the reliable voxel response variance for musicians and non-musicians respectively, after which the amount of explained variance for each additional component plateaued (**Supplemental Figure 2**).

Next, we examined the similarity of the components inferred from musicians and non-musicians separately to the components from our previous study, comparing their responses to the 165 sounds common to both experiments. Because the order of the components inferred using ICA holds no significance, we first used the Hungarian algorithm (Kuhn, 1955) to optimally reorder the components, maximizing their correlation with the components from our previous study. For comparisons of the response profile matrices of two groups of subjects, we matched components using the weight matrices; conversely, for comparisons involving the voxel weights, we matched components using the response profile matrices (see Methods). In practice, the component matches were identical regardless of which matrices were used for matching.

For both groups, corresponding pairs of components were highly correlated with those from our previous study, with r-values for non-musicians' components ranging from 0.63 to 0.99 (**Figure 2A** & **B**) and from 0.66 to 0.99 for musicians' components (**Figure 2C** & **D**).

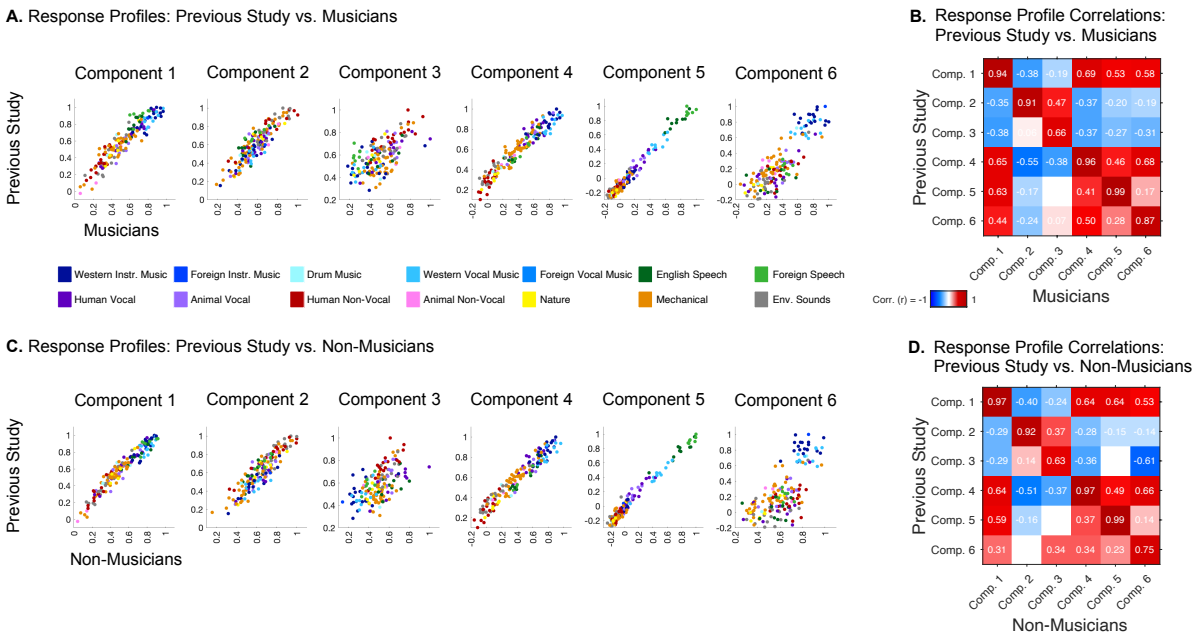



**Figure 2. Replication of components from Norman-Haignere et al. (2015).** (**A**) Scatterplots showing the correspondence between the component response profiles from the previous study (y-axis) and those inferred from musicians (x-axis). Sounds are colored according to their semantic category, as determined by raters on Amazon Mechanical Turk. Note that the axes differ slightly between groups in order to make it possible to clearly compare the pattern of responses across sounds independent of the overall response magnitude. (**B**) Correlation matrix comparing component response profiles from the previous study (y-axis) and those inferred from musicians (x-axis). (**C, D**) Same as **A & B** but for non-musicians.

<u>Component responses are similar between musicians and non-musicians</u>

The sets of six components inferred from the musician and non-musician participant groups were also similar to each other (assessed here with their responses to the full set of 192 sounds; **Figure 3A**), with pairs of corresponding response profiles from musicians and non-musicians being highly correlated (r-values between 0.77 to 0.99; r = 0.90 for the music-selective component; **Figure 3B**). We calculated 95% confidence intervals (CIs) around the correlations between corresponding pairs of response profiles (**Figure 3B**, diagonals), using bootstrapping. For each of the six components, the correlations between mis-matched response profiles (**Figure 3B**, off-diagonals) fell far below the lower bound of these CIs (see Methods for more details about this analysis). This result confirms that the response

profiles inferred from musicians and non-musicians are in fact very similar to each other, and not simply an artifact of the matching procedure. Further, the observed response profile correlation for the music-selective component is about as high as it could be given the reliability of the component (it was not significantly lower than the correlation between components of 1,000 random splits of all 20 participants, $p = 0.93$, mean correlation of such splits = 0.95).

Anatomical distributions of components are similar between musicians and non-musicians

The two sets of components were also similar in the anatomical distribution of their weights. We quantified this similarity by correlating the voxel weights of the components inferred from musicians and non-musicians separately. We averaged voxel weights across participants within each group and then correlated these group-averaged weights between groups, yielding r-values between 0.73 and 0.93; $r = 0.73$ for the music-selective component (**Figure 3C**). Bootstrapped 95% CIs determined that the correlations between corresponding pairs of voxel weights (**Figure 3D**, diagonals) were significantly higher than the correlations between mis-matched pairs (**Figure 3D,** off-diagonals; see Methods for more details about this analysis). Although the correlation was lowest for the music component, it is still about as high as can be expected given the reliability of the component itself (not significantly lower than the correlation between components of 1,000 random splits of all 20 participants, $p = 0.17$, mean correlation of such splits = 0.69).

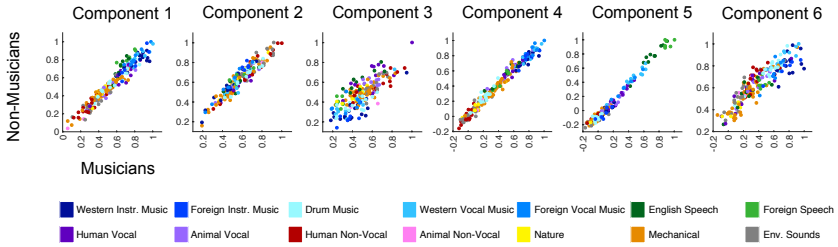
The extent of this similarity can also be seen in the groups' cortical weight maps (**Figure 3E**) and the distribution of weights across a standardized set of anatomical parcels (Glasser et al., 2016), both of which showed a strong resemblance between groups in the pattern of weights for all six components (**Figure 3G**). We note that the components were inferred without any information about the sounds or the anatomy of the voxels and so the fact that our method infers similar functional and anatomical response patterns suggests a strong resemblance between the musician and non-musician groups, and also provides two fully independent replications of our prior results.

Component response profiles and selectivity for sound categories

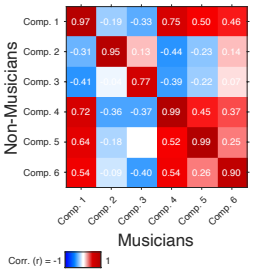
Four of the six components from our previous study captured expected acoustic properties of the sound set (e.g. frequency, spectrotemporal modulation; see **Supplemental Figure 3A** for analyses relating the responses of these components to audio frequency and spectrotemporal modulation) and were concentrated in and around primary auditory cortex (PAC), consistent with prior results (Chi et al., 2005; Schönwiesner and Zatorre, 2009; Humphries et al., 2010; Da Costa et al., 2011; Herdener et al., 2013; Santoro et al., 2014; Hullett et al., 2016; Norman-Haignere and McDermott, 2018). The two remaining components responded selectively to speech (**Figure 4A**, left column) and music (**Figure 4B**, left column), respectively, and were not well accounted for using acoustic properties alone (**Supplemental Figure 3A**). The corresponding components inferred from musicians (**Figure 4A** & **B**, middle columns) and non-musicians (**Figure 4A** & **B**, right columns) also show this category selectivity.

We also found similarities in the anatomical distribution of speech- and music-selective component weights between the previous study and both groups in the current study. The weights for the speech-selective component were concentrated in the middle portion of the superior temporal gyrus (midSTG, **Figure 4C**), as expected based on previous reports (Scott et al., 2000; Hickok and Poeppel, 2007; Overath et al., 2015). In contrast, the weights for the music-selective component were most prominent anterior to PAC in the planum polare, with a secondary cluster posterior to PAC in the planum temporale (**Figure 4D**) (Ohnishi et al., 2001; Margulis et al., 2009; Dick et al., 2011; Fedorenko et al., 2012; Angulo-Perkins et al., 2014; Armony et al., 2015; Norman-Haignere et al., 2015).

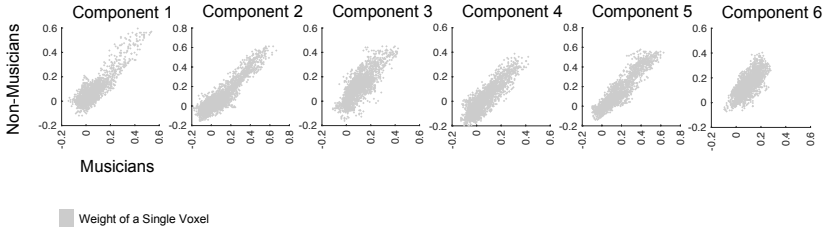
**A.** Response Profiles: Musicians vs. Non-Musicians



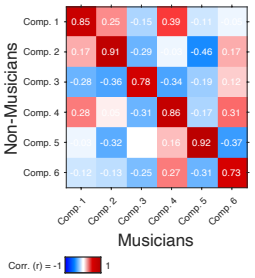

**B.** Response profile correlations



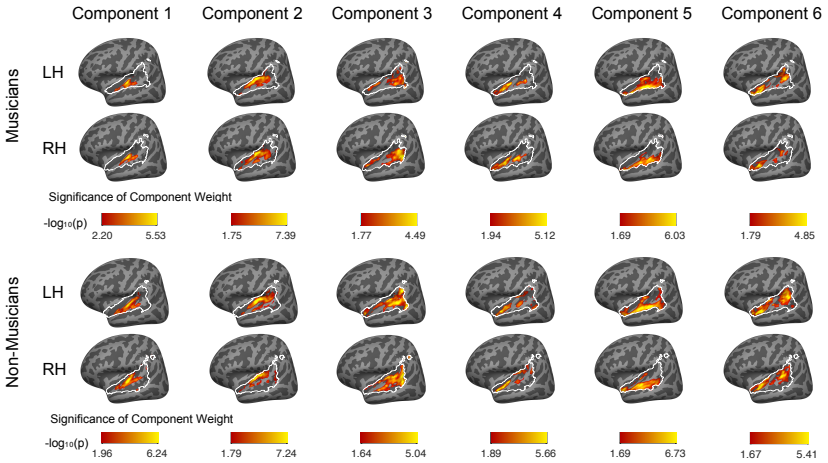

**C.** Voxel Weights: Musicians vs. Non-Musicians



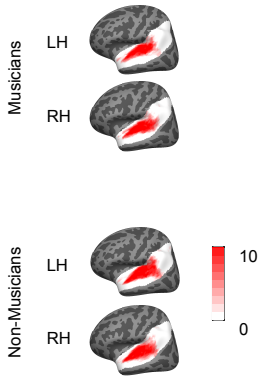

**D.** Voxel weight correlations



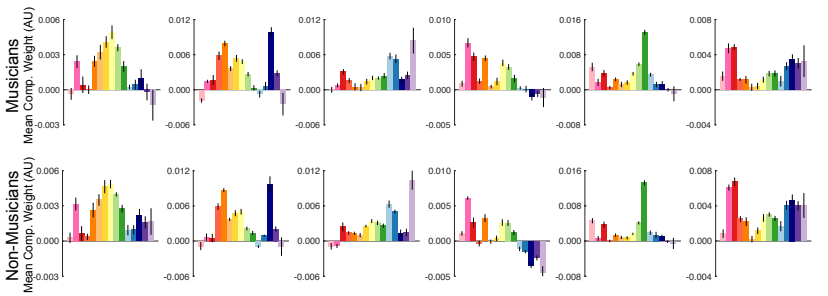

**E.** Anatomical Distribution of Component Weights: Musicians vs. Non-Musicians




**F.** Voxels Selected for ICA




**G.** Mean Component Weights in Anatomical ROIs: Musicians vs. Non-Musicians




**H.** Anatomical ROIs

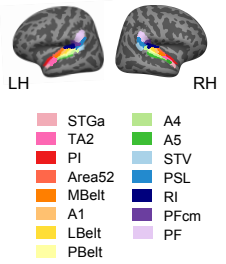


**Figure 3. Comparison of components inferred separately in musicians and non-musicians.** (**A**) Scatterplots showing the correspondence between the component response profiles inferred from musicians and non-musicians. Sounds are colored according to their semantic category, as determined by raters from an online study. (**B**) Correlation matrix comparing component response profiles inferred from musicians and non-musicians. (**C**) Scatterplots showing the correspondence between the component voxel weights inferred from musicians (x-axis) and non-musicians (y-axis), measured by averaging voxel weights across subjects within each group and then plotting these group-averaged weights against one another. (**D**) Correlation matrix comparing group-averaged component voxel weights from musicians and non-musicians. (**E**) Spatial distribution of component voxel weights from musicians and non-musicians. Color denotes the statistical significance of the weights, computed using a random effects analysis across subjects comparing weights against 0; p values are logarithmically transformed ($-\log_{10}[p]$). The white outline indicates the voxels that were both sound-responsive (sound vs. silence, $p < 0.001$ uncorrected) and split-half reliable ($r > 0.3$) at the group level (see Methods for details). The color scale represents voxels that are significant at FDR $q = 0.05$, with this threshold computed for each component separately. Voxels that do not survive FDR correction are not colored, and these values appear as white on the color bar. The right hemisphere (bottom rows) is flipped to make it easier to visually compare weight distributions across hemispheres. (**F**) Subject overlap maps showing which voxels were selected in individual subjects to serve as input to the voxel decomposition algorithm for both musicians (top) and non-musicians (bottom). To be selected, a voxel must display a significant ($p < 0.001$, uncorrected) response to sound (pooling over all sounds compared to silence), and produce a reliable response pattern across stimuli between scanning sessions (see equations in Methods section). The white area shows the anatomical constraint regions from which voxels were selected. (**G**) Mean component voxel weights within standardized anatomical parcels from Glasser et al. (2016). Error bars plot one standard error of the mean across participants. (**H**) Selected anatomical parcels from Glasser et al. (2016), chosen to fully encompass the superior temporal plane and superior temporal gyrus (STG).

Together, these findings show that we are able to twice replicate the overall component structure underlying of auditory cortical responses described in our previous study (once for nonmusicians and once for musicians), and that similar component structures underlie auditory cortical responses in musicians and non-musicians. Further, both musicians and non-musicians show the same category-selective components as in our previous study, including a single component that appears to be selective for music.

### *Characterizing music selectivity in musicians and non-musicians separately*

We next asked whether each group exhibited the signature response characteristics of music selectivity documented in our prior paper: (1) the music component response profile showed a high response to both instrumental and vocal music and a low response to all other categories, including speech, (2) music component voxel weights were high in anterior and posterior superior temporal gyrus (STG), and low in both PAC and lateral STG, and (3) music component voxel weights had a largely bilateral distribution. We examined whether each of these properties was present in the components separately inferred from musicians and non-musicians.

<u>Response profiles show selectivity for both instrumental and vocal music</u>

The defining feature of the music-selective component from Norman-Haignere et al. (2015) was that its response profile showed a very high response to stimuli that had been categorized by humans as "music", including both instrumental music and music with vocals, relative to non-music stimuli, including speech (**Figure 4B**, left column). The category-averaged responses of the music-selective component showed similar effects in non-musicians and highly trained musicians (**Figure 4B**, center and right columns).

To quantify this music selectivity, we measured the difference in mean response profile magnitude between music and non-music sounds, divided by their pooled standard deviation (Cohen's d). So that we could compare across our previous and current experiments, this was done using the set of 165 sounds that were common to both studies. We measured Cohen's d separately for several different pairwise comparisons: (1) instrumental music vs. speech stimuli, (2) instrumental music vs. other non-music stimuli, (3) vocal music vs. speech stimuli, and (4) vocal music vs. other non-music stimuli

(**Figure 5**). In each case, the significance of the separation of the two stimulus categories was determined using a nonparametric test permuting stimulus labels 10,000 times. All four of these statistical comparisons were highly significant for non-musicians when analyzed separately (all p's < $10^{-5}$, **Table 2**). This result shows that the music component is highly music selective in non-musicians, in that it responds highly to both instrumental and vocal music, and significantly less to both speech and other non-music sounds. Similar results were also found for musicians (all p's < $10^{-5}$, **Table 2**).

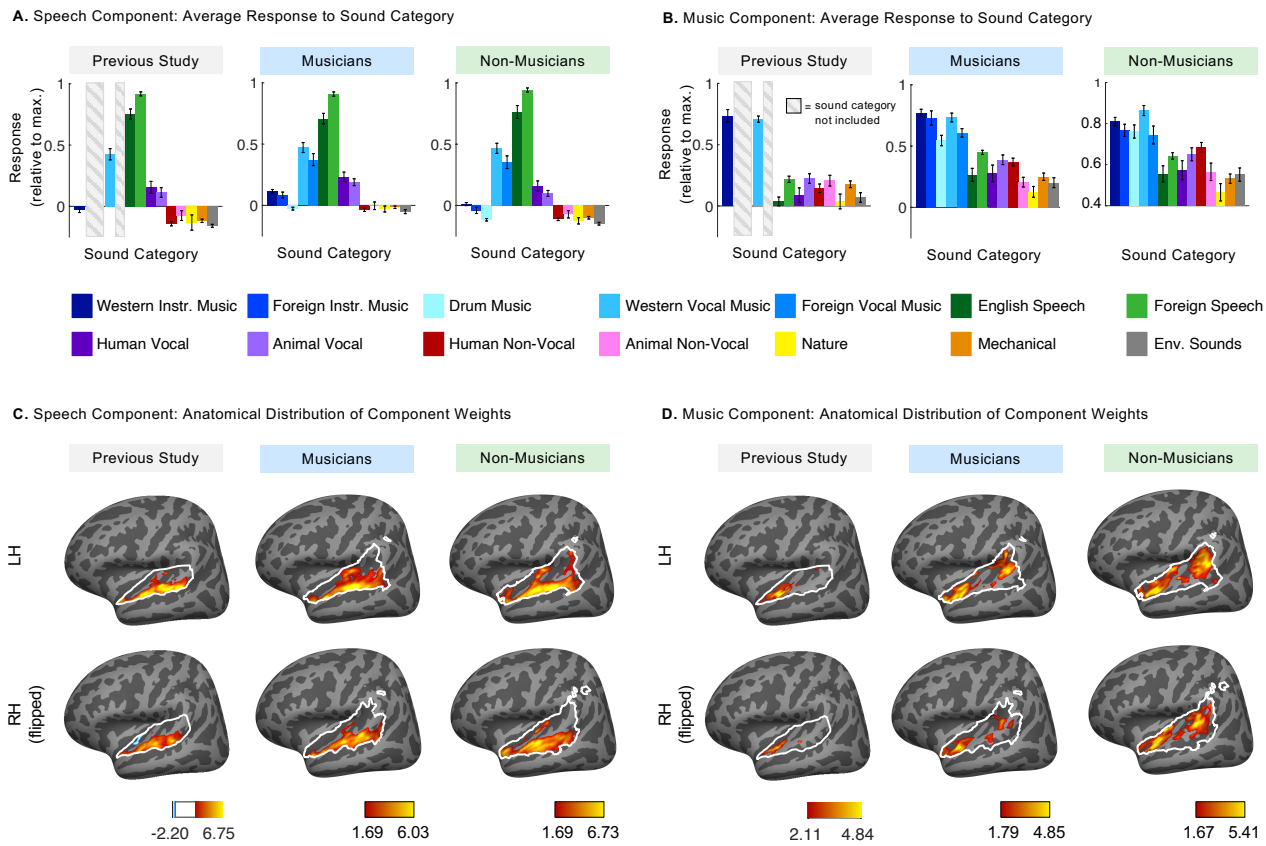



**Figure 4. Comparison of speech-selective and music-selective components for participants from previous study, musicians, and nonmusicians**. Component response profiles averaged by sound category (as determined by raters on Amazon Mechanical Turk). (**A**) The speech-selective component responds highly to speech and music with vocals, and minimally to all other sound categories. Shown separately for the previous study (left), musicians (middle) and non-musicians (right). Note that the previous study contained only a subset of the stimuli used in the current study, so some conditions were not included and are thus replaced by a gray rectangle. (**B**) The music-selective component (right) responds highly to both instrumental and vocal music, and less strongly to other sound categories. Note that "Western Vocal Music" stimuli were sung in English. Note the different axis limits for the two groups to accommodate different 'DC' offsets. For both **A** and **B**, error bars plot one standard error of the mean across sounds from a category, computed using bootstrapping (10,000 samples). (**C**) Spatial distribution of speech-selective component voxel weights in both hemispheres. (**D**) Spatial distribution of music-selective component voxel weights. Note that the cortical maps shown here follow the same plotting conventions as those in **Figure 3E**, and that the cortical maps for musicians and non-musicians in both **C** and **D** are the same as those in **Figure 3E**.

We note that the mean response profile magnitude for the music-selective component differed between groups, being lower in musicians than non-musicians (note different axes in **Figure 4B**). However this effect is unlikely to be a consequence of musical training because mean response magnitude was lower still in the previous study, whose participants had substantially less musical training than the musicians in the current study.

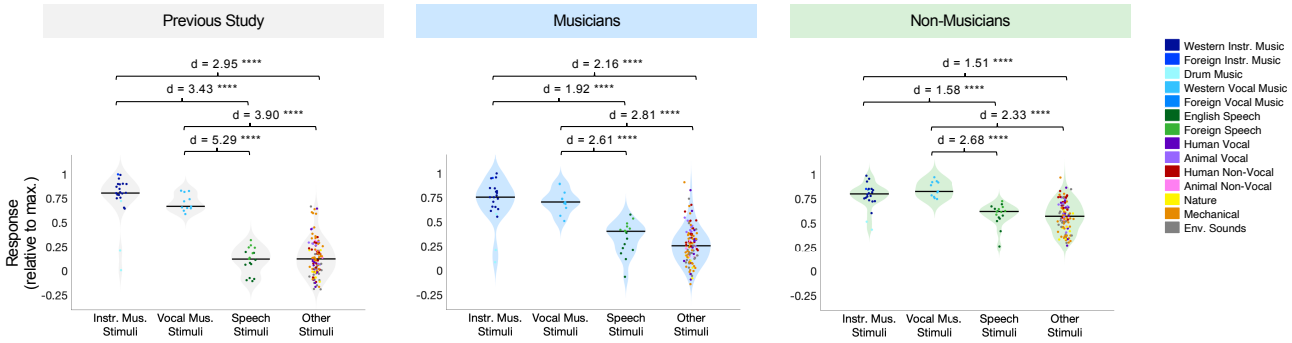



**Figure 5. Separability of sound categories in music-selective components of musicians and non-musicians.** Distributions of (1) instrumental music stimuli, (2) vocal music stimuli, (3) speech stimuli, and (4) other stimuli within the music component response profiles from our previous study (left, grey shading), as well as those inferred from musicians (center, blue shading) and non-musicians (right, green shading). The mean for each stimulus category is indicated by the horizontal black line. The separability between pairs of stimulus categories (as measured using Cohen's d) is shown above each plot. Individual sounds are colored according to their semantic category. See **Table 2** for results of pairwise comparisons indicated by brackets; **** = significant at $p < 0.0001$ two-tailed.

| | | Stimulus Category | Mean | SD | Cohen's d | p-value |
|---|---|---|---|---|---|---|
| MUSICIANS | 1 | Instrumental Music | 0.72 | 0.22 | 1.92 | 1.19e-08 |
| | | Speech | 0.34 | 0.16 | | |
| | 2 | Instrumental Music | 0.72 | 0.22 | 2.16 | 7.40e-20 |
| | | Other | 0.27 | 0.19 | | |
| | 3 | Vocal Music | 0.72 | 0.12 | 2.61 | 8.38e-11 |
| | | Speech | 0.34 | 0.16 | | |
| | 4 | Vocal Music | 0.72 | 0.12 | 2.81 | 3.62e-18 |
| | | Other | 0.27 | 0.19 | | |
| NON-MUSICIANS | 1 | Instrumental Music | 0.78 | 0.13 | 1.58 | 2.14e-06 |
| | | Speech | 0.59 | 0.11 | | |
| | 2 | Instrumental Music | 0.78 | 0.13 | 1.51 | 1.88e-10 |
| | | Other | 0.57 | 0.15 | | |
| | 3 | Vocal Music | 0.85 | 0.08 | 2.68 | 4.54e-11 |
| | | Speech | 0.59 | 0.11 | | |
| | 4 | Vocal Music | 0.85 | 0.08 | 2.33 | 1.87e-12 |
| | | Other | 0.57 | 0.15 | | |

**Table 2.** Results of pairwise comparisons between stimulus categories shown in **Figure 6B**. The significance of the separation of the two stimulus categories was determined using a nonparametric test permuting stimulus labels 10,000 times.

Music component weights concentrated in anterior and posterior STG

A second notable property of the music component from Norman-Haignere et al. (2015) was that the weights were concentrated in distinct regions of non-primary auditory cortex, with prominent clusters in anterior and posterior STG. Conversely, music component weights were low in primary auditory cortex (PAC) and non-primary lateral STG.

To assess whether these anatomical characteristics were evident for the music components inferred from our musician and non-musician participants, we superimposed standardized anatomical parcels (Glasser et al., 2016) on the data, and defined anatomical regions of interest (ROIs) by selecting four sets of these anatomically-defined parcels corresponding to anterior non-primary, primary, and lateral

non-primary auditory cortex (**Figure 6A**). We then calculated the average music component weight for each individual participants within each of these four anatomical ROIs, separately for each hemisphere (**Figure 6B**). This was done separately for musicians and non-musicians, using their respective music components. We did not perform this analysis on the data from our previous study because its anatomical coverage was more restricted than the data we collected here.

For each group, a 4 (ROI) x 2 (hemisphere) repeated measures ANOVA on these mean component weights showed a significant main effect of ROI for both musicians ($F(3, 27) = 20.00$, $p = 4.98e\text{-}07$, $\eta_p^2 = 0.70$) and non-musicians ($F(3, 27) = 50.51$, $p = 3.32e\text{-}11$, $\eta_p^2 = 0.85$). Planned pairwise comparisons showed that for each group, component weights were significantly higher in the anterior and posterior non-primary ROIs than both the primary and lateral non-primary ROIs when averaging over hemispheres (**Table 3**; musicians: all p's < 0.02, non-musicians: all p's < 0.003).

These results show that in both musicians and non-musicians, music selectivity is concentrated in anterior and posterior STG, and present to a lesser degree in lateral STG, and only minimally in PAC.

<u>Music component weights are bilaterally distributed</u>

A third characteristic of the previously described music selectivity is that it was similarly distributed across hemispheres, with no obvious lateralization (Norman-Haignere et al., 2015). The repeated-measures ANOVA described above showed no evidence of lateralization in either musicians or non-musicians (**Figure 6B**; musicians: $F(1, 9) = 1.55$, $p = 0.24$, $\eta_p^2 = 0.15$; non-musicians: $F(1, 9)$

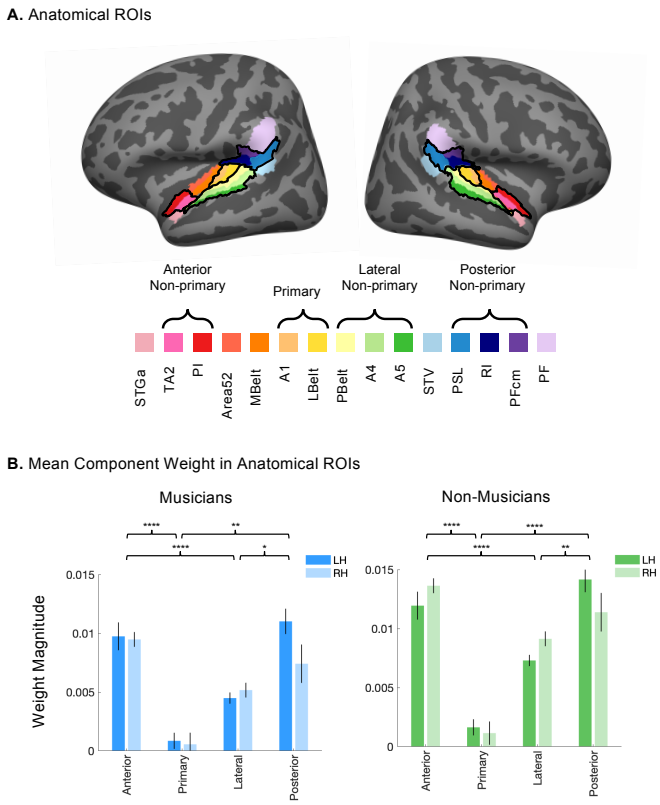



**Figure 6. Quantification of bilateral anterior/posterior concentration of voxel weights for the music-selective components inferred in musicians and non-musicians separately.** (A) Fifteen standardized anatomical parcels were selected from Glasser et al. (2016), chosen to fully encompass the superior temporal plane and superior temporal gyrus (STG). To come up with a small set of ROIs to use to evaluate the music component weights in our current study, we superimposed these anatomical parcels onto the weights of the music component from our previously published study (Norman-Haignere et al., 2015), and then defined ROIs by selecting sets of the anatomically-defined parcels that correspond to regions of high (anterior non-primary, posterior non-primary) vs. low (primary, lateral non-primary) music component weights. The anatomical parcels that comprise these four ROIs are indicated by the brackets, and outlined in black on the cortical surface. (B) Mean music component weight across all voxels in each of the four anatomical ROIs, separately for each hemisphere, and separately for musicians (left, blue shading) and non-musicians (right, green shading). A repeated-measures ROI x hemisphere ANOVA was conducted for each group separately. Error bars plot one standard error of the mean across participants. Brackets represent pairwise comparisons that were conducted between ROIs with expected high vs. low component weights, averaged over hemisphere. See Table 3 for full results; * = significant at $p < 0.05$ two-tailed, ** = significant at $p < 0.01$ two-tailed, *** = significant at $p < 0.001$ two-tailed, **** = significant at $p < 0.0001$ two-tailed. Note that because our prior hypotheses required that all four of these pairwise contrasts be significant, there is no need to correct for multiple comparisons.

= 0.02, p = 0.91, $\eta_p^2$ = 0.001). Furthermore, for both groups, the effect size of ROI within a hemisphere was significantly larger than the effect size of hemisphere (measured by bootstrapping across participants to get 95% CIs around the difference in the effect size for the two main effects, i.e. $\eta_{pROI}^2$ - $\eta_{pHemi}^2$; the significance of the difference in main effects was evaluated by determining whether or not each group's 95% CI for the difference overlapped with zero: musicians' CI = [0.05 0.81], non-musicians' CI = [0.38 0.90]).

We note that both groups showed a significant ROI x hemisphere interaction (musicians: F(3, 27) = 4.45, p = 0.01, $\eta_p^2$ = 0.15; non-musicians: F(3, 27) = 4.04, p = 0.02, $\eta_p^2$ = 0.31). However, a Bayesian repeated-measures ANOVA provided no evidence for an ROI x hemisphere interaction. We used JASP (JASP Team, 2020), using its default prior (Cauchy distribution, r = 0.5), and computed the Bayes Factor for inclusion of each main effect and/or interaction (the ratio between the likelihood of the data given the model including the effect in question vs. the likelihood of the next simpler model without the effect in question). The Bayes Factor for the interaction between ROI and hemisphere were close to 1 ($BF_{incl}$ for musicians = 0.51, $BF_{incl}$ for non-musicians = 1.65). There was also either no evidence for a main effect of hemisphere ($BF_{incl}$ for musicians = 0.45) or evidence against it ($BF_{incl}$ for non-musicians = 0.23). By contrast, the main effect of ROI was well supported (Bayes factor of inclusion, $BF_{incl}$, for ROI for musicians = 1.62e10, and for non-musicians = 1.39e17). So while we cannot exclude the possibility of some differences between music selectivity in the two hemispheres, or that such differences might interact with musical training, any such hemispheric differences appear modest relative to the pronounced ROI differences within hemisphere, as these were by far the dominant effect for both groups.

| | | ROI | t-Value | Cohen's d | p-value |
|---|---|---|---|---|---|
| MUSICIANS | 1 | Anterior non-primary<br>Primary | 11.45 | 3.61 | 1.12e-06 |
| | 2 | Anterior non-primary<br>Lateral non-primary | 7.72 | 2.42 | 2.94e-05 |
| | 3 | Posterior non-primary<br>Primary | 4.54 | 1.42 | 0.0014 |
| | 4 | Posterior non-primary<br>Lateral non-primary | 2.77 | 0.86 | 0.0217 |
| NON-MUSICIANS | 1 | Anterior non-primary<br>Primary | 15.70 | 5.03 | 5.60e-08 |
| | 2 | Anterior non-primary<br>Lateral non-primary | 8.74 | 2.84 | 1.08e-05 |
| | 3 | Posterior non-primary<br>Primary | 7.34 | 2.29 | 4.38e-05 |
| | 4 | Posterior non-primary<br>Lateral non-primary | 3.95 | 1.21 | 0.0034 |

**Table 3.** Results of pairwise comparisons between mean weights in ROIs shown in **Figure 5B**. Component weights were first averaged over hemispheres, and significance between ROI pairs was evaluated using paired t-tests. Note that because our strict criteria required that all four of these pairwise contrasts be significant, there is no need to correct for multiple comparisons.

The fact that the music component inferred from non-musicians exhibits all of the previously described features of music selectivity (Norman-Haignere et al., 2015) suggests that explicit musical training is not necessary for a music-selective neural population to arise in the human brain. In addition, the results from musicians suggest that that the signature properties of music selectivity are not drastically altered by extensive musical experience. Both groups exhibited a single response component selective for music. And in both groups, this selectivity was present for both instrumental and vocal music, was localized to anterior and posterior non-primary auditory cortex, and was present bilaterally.

### *Contrasting music selectivity in musicians vs. non-musicians*

The results presented thus far answer the main questions of this study: music-selective brain responses are present in people with little or no musical training, and have similar coarse characteristics in trained musicians. Next, we conducted a series of exploratory analyses asking whether musicians differ from non-musicians in the magnitude, anatomical location, or selectivity of their music responses. We note that despite the large amount of data included in the current study (6

hours of fMRI scanning per participant, for a total of 120 hours of fMRI data), our statistical power to answer these questions is limited to detecting large group differences. However, *a priori* we thought it possible that such large group differences might indeed exist, and so we show here the results of these exploratory investigations.

So that individual participants' component weight magnitudes could be compared, we ran the voxel decomposition analysis on the data from all 20 participants, and compared the weights of musicians vs. non-musicians for the resulting components (see **Supplemental Information** and **Supplemental Figure 4** for more details about the components inferred from all 20 participants, which were similar overall to those inferred separately for each group).

Music component weight magnitude is comparable for musicians and non-musicians

We first compared the magnitude of the weights of the music-selective component between expert musicians and non-musicians. Although there are many ways to summarize a participant's component magnitude, we used the median weight over their voxels with the top 10% of component weights (using independent data to select the voxels vs. quantify selectivity), though results were robust to the fraction of voxels selected (see Methods for details). Participants' median component weights measured in this way had high split-half reliability (r-values ranging from 0.49 to 0.90, r = 0.72 for the music component). The decision to select a subset of voxels was made because music selectivity is typically sparse and limited to a small fraction of voxels. Selecting voxels individually for each participant is analogous to identifying a functional ROI (Saxe et al., 2006; Nieto-Castañón and Fedorenko, 2012).

To get a sense for how large a group difference we would be able to detect using this measure, we conducted a power analysis using the data from Norman-Haignere et al. (2015). We compared the music component weights for the participants in that study (n = 10) with a second population of 10 participants created by sampling participants with replacement and then shifting their component weights by various amounts, representing various models for how the music component weights might change in musicians (see Methods). The results of this analysis suggested that we could expect to detect a significant group difference with 80% power for n = 10 if the groups' music component weights differed by 47% (**Figure 7A**). This difference is comparable to the variability that exists between individual participants' median music component weights, which differ by approximately 49.4% as measured by the coefficient of variation (the ratio of the standard deviation to the mean, (Allison, 1978).

Using this measure, the strength of the music component was slightly higher in musicians compared with non-musicians, but this difference did not reach significance (p = 0.1144, component 6 **Figure 7B**; two-tailed nonparametric test permuting subject groupings 10,000 times; not corrected for the six components tested). A Bayesian independent-sample t-test was inconclusive (t(18) = 1.68, p = 0.11, $BF_{10}$ = 1.03; prior on the effect size following a Cauchy distribution with r = $\sqrt{2}/2$), which suggests that the data are equally likely under the null hypothesis that groups do not differ in their music component weight magnitude vs. the alternative hypothesis that they do. There was also no significant group difference for the other five components (components 1-5, **Figure 7B**, all p's > 0.1, two-tailed tests, not corrected for the six components tested), and Bayesian independent-samples t-tests provided only weak evidence of a lack of difference between musicians and non-musicians ($BF_{10}$ for components 1-5 ranging from 0.51 to 0.83; Cauchy prior distribution with r = $\sqrt{2}/2$). Results were also non-significant if we instead used participants' median weight over all voxels as a measure of the strength of the music component, rather than the median over the top 10% of voxels. Together, these results do not rule out differences between the strength of music selectivity in individuals at the two extremes of musical training, but they suggest that any such differences are not large.

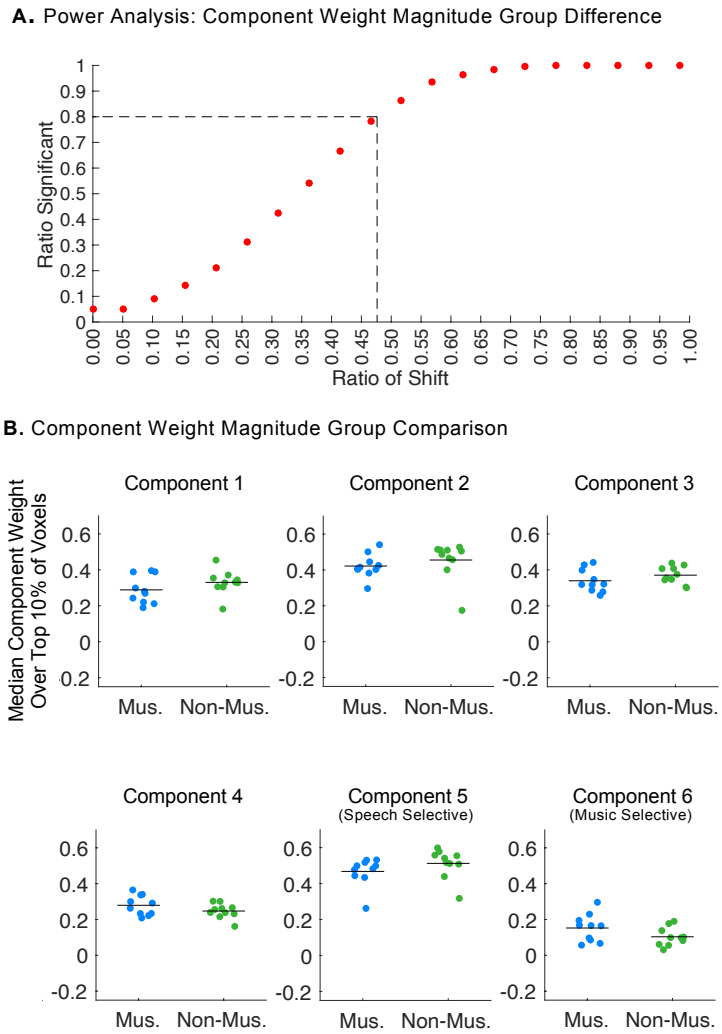



**Figure 7. Direct comparison of music component weight magnitudes in musicians vs. non-musicians, using the music component inferred from all 20 participants.** (**A**) Power analysis for music component weight magnitude comparison, using the data from Norman-Haignere et al. (2015). We computed a measure of the strength of the music component in those 10 participants and then compared them to second population of 10 participants created by sampling participants with replacement and shifting their component weights by various amounts, representing various models for how the music component weights might change in musicians. We quantified the strength of the music component by selecting the 10% of voxels with the largest music component weights, separately for each participant, and then using left-out data to measure the median music component weight in those voxels. The median weights were averaged across participants, separately for each group, and the difference between these group averages was computed. The significance of this group difference was assessed by permuting participant groupings 1,000 times. For each shift amount (x-axis), we repeated this entire resampling procedure 1,000 times, and plotted the proportion of resamplings in which we detected a significant difference (y-axis). The dashed line represents the shift amount at which we were able to detect a significant difference in the two groups' median weights 80% of the time. (**B**) Comparison of musicians' (blue) and non-musicians' (green) component weights for all six components (using components inferred from the full set of 20 participants, calculated as described in A). Black horizontal line indicates the mean across participants within each group. Mus. = musicians, Non-Mus. = non-musicians.

Similar anatomical distribution of music component weights in musicians and non-musicians

To address the possibility that musicians and non-musicians might show different anatomical distributions of the music component weights, we conducted a random effects analysis on individual participants' music component weight matrices after projecting them to the cortical surface (using the music component derived together from all 20 participants so that weights could be directly compared). First, we performed a random effects analysis separately for musicians and non-musicians, in order to visualize which voxels showed significant music component weights in each group separately (**Figure 8A**). The resulting weight maps show similar anatomical distributions of high music component weights for musicians and nonmusicians. A random effects analysis directly comparing the two groups supported this impression, showing very little difference between the weight magnitudes of musicians and non-musicians, with not a single voxel surviving FDR correction (q = 0.05, **Figure 8B**). By contrast, analogous comparisons between mismatching components (e.g. non-musicians' music component and musicians' other components) resulted in significant differences over large swaths of auditory cortex (with anywhere from 10% to 45% of voxels showing a significant difference from music component weights), indicating that group differences in the music component weight maps would be detectable if they were on par with the differences between different components. This can also be seen in **Figure 3D**, which shows low correlations between the anatomical weight distributions of mismatching components.

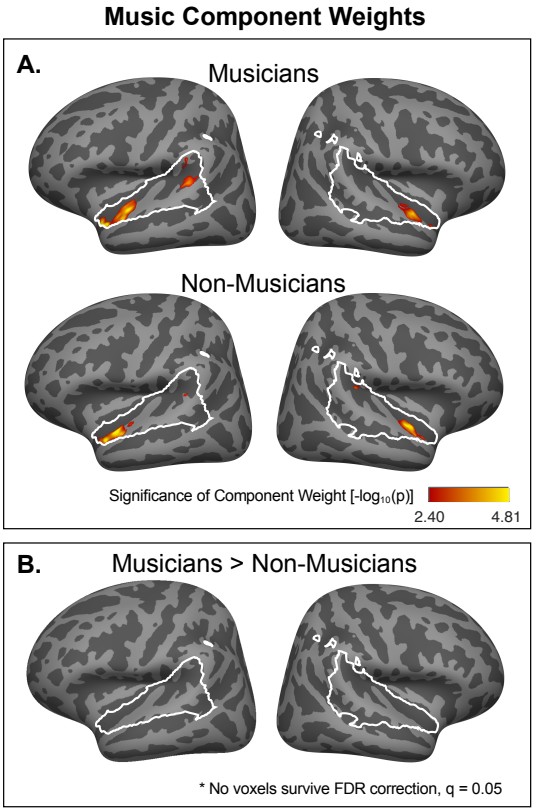



**Figure 8. Direct comparison of the anatomical distribution of music component weights in musicians vs. non-musicians, using the music component inferred from all 20 participants.** (**A**) Voxel weights for the music component inferred from the full set of 20 participants, shown separately for musicians and non-musicians. First, individual participant component weights were inferred using the component response profiles (inferred from all 20 participants) and individual participant voxel responses to the 192-sound stimulus set. Then, to visualize group data, a random effects analysis tested whether component weights were significantly greater than zero across participants at each voxel. This analysis was performed separately for the 10 musicians (top) and 10 non-musicians (bottom), in both cases using participants' weights for the component inferred from all 20 participants. Note that this differs from **Figure 3**, which concerns the components inferred from each group separately. Component weights were compared against 0; p values are logarithmically transformed ($-\log_{10}[p]$). The white outline indicates the voxels that were included in the analysis (reliably sound-responsive at the group level). The color scale represents voxels that are significant at FDR q = 0.05. (**B**) Results of the direct comparison of the two groups' music component weights, in which not a single voxel survived FDR correction (q = 0.05).

Taken together, these exploratory contrasts between musicians and nonmusicians find no significant differences in the magnitude or anatomical distribution of the music component. We emphasize that these contrasts are only powered to detect large differences between groups, and do not exclude the possibility that modest differences could be detectable with substantially larger sample sizes. However, they are consistent with the overall conclusions of the earlier analyses that the main properties of music-selectivity in the auditory cortex are present at both extremes of musical experience in Westerners.

***New insights into music selectivity: Music-selective regions of auditory cortex show high responses to drum rhythms and unfamiliar musical genres***

Because our experiment utilized a broader stimulus set than the original study (Norman-Haignere et al., 2015), we were able to use the inferred components to ask additional questions about the effect of experience on music selectivity, as well as gain new insights into the nature of cortical music selectivity. The set of natural sounds used in this study included a total of 62 music stimuli, spanning a variety of instruments, genres, and cultures. Using this diverse set of music stimuli, we can begin to address the questions of (1) whether music selectivity is specific to the music of one's own culture, and (2) whether music selectivity is driven solely by features related to pitch, like the presence of a melody. Here we analyze the music component inferred from all 20 participants since similar music components were inferred separately from musicians and non-musicians.

To expand beyond the original stimulus set from Norman-Haignere et al. (2015), which contained music exclusively from traditionally Western genres and artists, we selected additional music clips from several non-Western musical cultures that varied in tonality and rhythmic complexity (e.g. Indian raga, Balinese gamelan, Chinese opera, Mongolian throat singing, Jewish klezmer, Ugandan lamellophone music) (**Figure 9A**). We expected that our American participants would have less exposure to these musical genres, allowing us to see whether the music component makes a distinction between familiar and less familiar music. The non-Western music stimuli were rated by American Mechanical Turk participants as being similarly musical (mean rating on 1-100 scale for Western music = 86.28, sd = 7.06; Non-Western music mean = 79.63, sd = 9.01; $p = 0.37$, 10,000 permutations) but less familiar (mean rating on 1-100 scale for Western music = 66.50, sd = 8.23; Non-Western music mean = 45.50, sd = 15.83; $p < 1.0e-5$, 10,000 permutations) than typical Western music. Despite this difference in familiarity, the magnitude of non-Western music stimuli within the music component was only slightly smaller than the magnitude of Western music stimuli (Cohen's $d = 0.64$), a difference that was only marginally significant (**Figure 9B**; $p = 0.052$, nonparametric test permuting music stimulus labels 10,000 times). Moreover, the magnitudes of both Western and non-Western music stimuli were both much higher than non-music stimuli (Western music stimuli vs. non-music stimuli: Cohen's $d = 3.79$, $p < 0.0001$, 10,000 permutations; non-Western music vs. non-music: Cohen's $d = 2.85$; $p < 0.0001$, 10,000 permutations). Taken together, these results suggest that music-selective responses in auditory cortex occur even for relatively unfamiliar musical systems and genres.

Which stimulus features drive music selectivity? One of the most obvious distinctions is between melody and rhythm. While music typically involves both melody and rhythm, when assembling our music stimuli we made an attempt to pick clips that varied in the prominence and complexity of their melodic and rhythmic content. In particular, we included 13 stimuli consisting of drumming from a variety of genres and cultures, because drum music mostly isolates the rhythmic features of music while minimizing (though not eliminating) melodic features. Whether music-selective auditory cortex would respond highly to these drum stimuli was largely unknown, partially because the Norman-Haignere et al. (2015) study only included two drum stimuli, one of which was just a stationary snare drum roll that produced a low response in the music component, likely because it lacks both musical rhythm and pitch structure. However, the drum stimuli in our study ranked relatively high in the music component response profile, averaging only slightly below the other instrumental and vocal music category responses (Cohen's $d = 1.42$, $p < 8.76e-07$), and considerably higher than the other non-music stimulus categories (Cohen's $d = 1.75$, $p < 9.60e-11$) (**Figure 9C**). This finding suggests that the music component is not simply tuned to melodic information, but is also sensitive to rhythm.

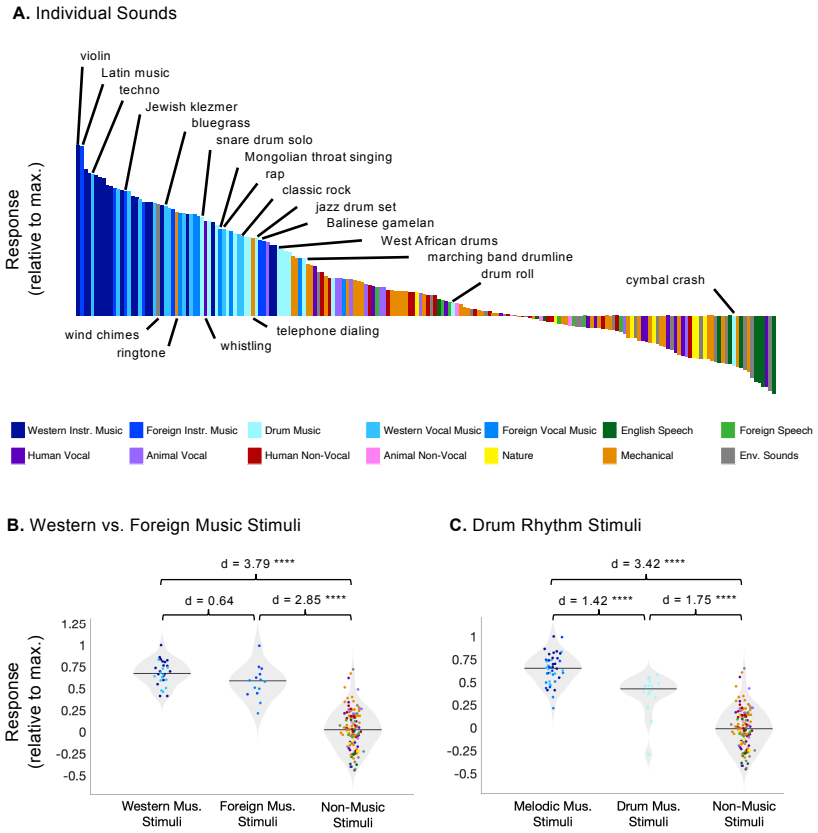



**Figure 9.** (**A**) Close-up of the response profile (192 sounds) for the music component inferred from all participants (n = 20), with example stimuli labeled. Note that there are a few "non-music" stimuli (categorized as such by Amazon Mechanical Turk raters) with high component rankings, but that these are all arguably musical in nature (e.g. wind chimes, ringtone). Conversely, "music" stimuli with low component rankings (e.g. "drumroll" and "cymbal crash") do not contain salient melody or rhythm, despite being classified as "music" by human listeners. (**B**) Distributions of Western music stimuli (left), non-Western music stimuli (middle), and non-music stimuli (right) within the music component response profile inferred from all 20 participants, with the mean for each stimulus group indicated by the horizontal black line. The separability between categories of stimuli (as measured using Cohen's d) is shown above the plot. Note that drum stimuli were left out of this analysis. (**C**) Distributions of melodic music stimuli (left), drum rhythm stimuli (middle), and non-music stimuli (right) within the music component response profile inferred from all 20 participants, with the mean for each stimulus group indicated by the horizontal black line. The separability between categories of stimuli (as measured using Cohen's d) is shown above the plot. Sounds are colored according to their semantic category. **** = significant at $p < 0.0001$ two-tailed.

## DISCUSSION

Our results show that cortical music selectivity does not require explicit musical training. Indeed, the same six response components that characterize human auditory cortical responses to natural sounds were present in both musicians and non-musicians. In both groups, voxel decomposition produced a single music-selective component, which was selective for both instrumental and vocal music, and was concentrated bilaterally in anterior and posterior superior temporal gyrus (STG). While it remains plausible that some differences exist in properties of music selectivity or its anatomical location between musicians and non-musicians, the results presented here suggest that any effect of explicit training is modest. We also observed that the music-selective component responds strongly to both

drums and less familiar non-Western music. Together, these results show that passive exposure to music is sufficient for the development of music selectivity in non-primary auditory cortex, and that extensive explicit musical training does not qualitatively alter the most salient characteristics of this selectivity.

***Origins of music selectivity***

Our study suggests that music-selective responses in the auditory cortex are either present from birth or result from passive exposure to music. If present from birth, music selectivity could in principle represent an evolutionary adaptation for music, definitive evidence for which has long been elusive (Darwin, 1871). But it is also plausible that music-specific representations emerge over development from the common presence of music in human environments. For example, optimizing a neural network model to solve ecological speech and music tasks yields separate processing streams for the two tasks (Kell et al., 2018), suggesting that musical tasks sometimes require music-specific features. Music-specific features might also emerge in humans or machines without tasks per se. Music is acoustically distinct from other natural sounds, and generic unsupervised learning, for instance for producing efficient representations of sound (Lewicki, 2002; Carlson et al., 2012; Młynarski and McDermott, 2019), might produce a set of features that are activated primarily by musical sounds.

Nearly all of our participants reported listening to music on a daily basis, and in other contexts this everyday musical experience has clear effects (Bigand, 1983; Bigand and Pineau, 1997; Koelsch et al., 2000; Tillmann et al., 2000; Tillmann, 2005; Bigand and Poulin-Charronnat, 2006), providing an example of how unsupervised learning from music might alter representations in the brain. For instance, behavioral studies of non-industrialized societies who lack much contact with Western culture show pronounced differences from Westerners in many aspects of music perception (McDermott et al., 2016; Jacoby and McDermott, 2017; Jacoby et al., 2019; McPherson et al., 2020). Thus, our data do not show that music selectivity in the brain is independent of experience. Indeed, it is possible that the brains of people who grow up with less extensive musical exposure than our participants would not display such pronounced music selectivity. Rather, these results show that typical exposure to music in Western culture is sufficient for cortical music selectivity to emerge.

***What does cortical music selectivity represent?***

The music-selective component responds strongly to a wide range of music and weakly to virtually all other sounds, demonstrating that it is driven by a set of features that are relatively specific to music. One possibility is that there are simple acoustic features that differentiate music from other types of stimuli. Speech and music are known to differ in their temporal modulation spectra, peaking at 5 Hz and 2 Hz, respectively (Ding et al., 2017). However, standard auditory models based on spectrotemporal modulation do not capture perception of speech and music (McDermott and Simoncelli, 2011) or neural responses selective for speech and music (Overath et al., 2015; Kell et al., 2018; Norman-Haignere and McDermott, 2018; Zuk et al., 2020). In particular, the music-selective component responds substantially less to sounds that have been synthesized to have the same spectrotemporal modulation statistics as natural music, suggesting that the music component does not simply represent the audio or modulation frequencies that are prevalent in music (Norman-Haignere and McDermott, 2018).

Our finding that the music-selective component shows high responses to less familiar musical genres places some constraints on what these properties might be, as does the short duration of the stimuli used to characterize music selectivity. For instance, the music-specific features that drive the response are unlikely to be specific to Western music, and must unfold over relatively short timeframes. Features that are common to nearly all music, but not other types of sounds, include stable and sustained pitch organized into discrete note-like elements, and temporal patterning with regular time intervals. Because the music component anatomically overlaps with more general responses to pitch (Norman-Haignere et

al., 2015), it is natural to wonder if it represents higher-order aspects of pitch, such as the above-mentioned stability, or discrete jumps from one note to another. However, the high response to drum rhythms in the music component that we observed here indicates that the component is not only sensitive to pitch structure. Instead, this result suggests that melody and rhythm might be jointly analyzed, rather than dissociated, at least at the level of auditory cortex. One possibility is that the underlying neural circuits extract temporally local representations of melody and rhythm motifs that are assembled elsewhere into the representations of contour, key, meter, groove etc. that are the basis of music cognition (Janata et al., 2002; Brett and Grahn, 2007; Lee et al., 2011; Fedorenko et al., 2012; Matthews et al., 2020).

***Limitations***

Our musician participants had substantial explicit musical training, and our non-musicians virtually none, thus maximizing our chance of detecting a difference if one was present. However, it remains possible (and perhaps likely) that a real difference between music selectivity in musicians and non-musicians exists, but was too small to be detected in our study. We note that our study required collecting 60 scan sessions across 20 participants, each 2 hours in duration, so collecting substantially more data would be a non-trivial enterprise. But the study is nonetheless underpowered for detecting moderate, let alone small, difference between groups in the responses that we measured. We emphasize that the detection of such differences was not the goal of the study, but this is nonetheless a limitation.

Our paradigm used relatively brief stimuli since music-selective regions are present just outside of primary auditory cortex, where integration periods appear to be short (Overath et al., 2015). And we used an intentionally simple task (intensity discrimination) in order to encourage subjects to generically attend to all stimuli. It is thus possible that more complex stimuli or tasks would reveal additional aspects of music-selective responses, and potentially larger differences in music selectivity between musicians and nonmusicians. One relevant point of comparison is the finding that amusic participants with striking pitch perception deficits show pitch-selective auditory cortical responses that are indistinguishable from those of control participants with univariate analyses (Norman-Haignere et al., 2016). Recent evidence suggests it is nonetheless possible to discriminate amusic participants from controls, and to predict participants' behavioral performance, using fMRI data collected in the context of a pitch task (Albouy et al., 2019). Utilizing a music-related task might produce larger differences between musicians and non-musicians, as might longer music stimuli (compared to the 2-second clips used in this experiment), which could be argued to contain richer melodic, harmonic, and/or rhythmic information.

Finally, our study is limited by resolution of fMRI. Voxel decomposition is intended to help overcome the spatial limitations of fMRI, and indeed appears to reveal responses that are not evident in raw voxel responses but can be seen with finer-grained measurement substrates such as electrocorticography (Norman-Haignere et al., 2019). But the spatial and temporal resolution of the BOLD signal inevitably constrain what is detectable, which likely explains why we have only been able to detect six reliable response components across all of auditory cortex. Music-selective brain responses might well exhibit additional characteristics that would only be evident in fine-grained spatial and temporal patterns that cannot be resolved with fMRI.

***Effects of musical expertise***

Although our results do not exclude the possibility that musical training alters music-selective neural populations within non-primary auditory cortex, it is natural to wonder whether the brain basis of musical expertise might take some other form. For instance, it is possible musical training could exert larger effects on neural responses outside of auditory cortex in areas that are not reliably sound-

responsive and so would not have been detected in this study (see **Supplemental Figure 6**), such as frontal or parietal regions involved in decision making or attention (Strait and Kraus, 2011; Harris and De Jong, 2015; Puschmann et al., 2018), or in motor or limbic regions (Janata and Grafton, 2003; Baumann et al., 2007; Chen et al., 2008; Grahn and Rowe, 2009; Luo et al., 2012; Alluri et al., 2015; Saari et al., 2018; de Aquino et al., 2019). When we run voxel decomposition on all voxels with reliable responses to sound across the entire brain, the resulting components are very similar to what we reported here for the analysis restricted to the superior temporal and posterior parietal cortices (**Supplemental Figure 7A**) and music component weights are mostly confined to anterior and posterior STG (**Supplemental Figure 7B**, right column). However, small regions within frontal motor areas have significant music component weights, and within these frontal regions, musicians do show stronger music component weights than non-musicians, perhaps reflecting covert motor rehearsal. Another possibility is that musical training primarily alters not functional but anatomical properties of auditory (Schneider et al., 2002, 2005; Bermudez et al., 2009; Foster and Zatorre, 2010), motor (Elbert et al., 1995; Gaser and Schlaug, 2003; Bermudez et al., 2009; Bashwiner et al., 2016), or limbic regions like the hippocampus (Teki et al., 2012), or their connections (Imfeld et al., 2009; Halwani et al., 2011; de Manzano and Ullén, 2017).

***Future directions***

One of the most interesting open questions raised by our findings is whether cortical music selectivity reflects implicit knowledge gained through typical exposure to music, or whether it is present from birth. These hypotheses could be addressed by testing people with very different musical experiences from non-Western cultures or other populations whose lifetime perceptual experience with music is limited in some way (e.g., people with musical anhedonia, children of deaf adults). It would also be informative to test whether music selectivity is present in infants or young children. Finally, much remains much to be learned about the nature of cortical music selectivity, such as what acoustic or structural features might be driving it. The voxel decomposition approach provides one way of answering these questions and exploring the quintessentially human ability for music.

## MATERIALS & METHODS

### *Participants*

Norman-Haignere et al. (2015) inferred a music-selective component from an analysis of ten participants. Although these participants were described as "non-musicians" (defined as no formal training in the five years preceding the study) many of the participants had substantial musical training earlier in life. We therefore used stricter inclusion criteria to recruit 10 musicians and 10 non-musicians for the current study, in order to have statistical power within each group comparable to that of our previous study.

Twenty young adults (14 female, mean = 24.7 years, sd = 3.8 years) participated in the experiment: 10 musicians (8 female, median = 23.5 years, sd = 3.3 years) and 10 non-musicians (6 female, median = 25.8 years, sd = 4.1 years). Inclusion criteria for musicians were beginning formal training before the age of seven (Penhune, 2011), and continuing training until the current day. Our sample of ten musicians had an average of 16.30 years of training (ranging from 11-23 years, sd = 2.52). To be classified as a non-musician, participants were required to have less than two years of total music training, which could not have occurred either before the age of seven or within the last five years. Out of the ten non-musicians in our sample, eight had zero years of musical training, one had a single year of musical training (at the age of 20), and one had two years of training (starting at age 10). These training measures do not include any informal "music classes" included in participants' required elementary school curriculum, because (at least in the United States) these classes are typically compulsory, are only for a small amount of time per week (e.g. 1 hour), and primarily consist of simple sing-a-longs. Details of participants' musical experience can be found in **Table 1**.

Non-parametric Wilcoxon rank sum tests indicated that there were no significant group differences in median age (musician median = 24.0 years, sd = 3.3, non-musician median = 25.0 years, sd = 4.1, $z = -1.03$, $p = 0.30$, effect size $r = -0.23$), education (musician median = 6.0 years, sd = 8.2 years, non-musician median = 6.5 years, sd = 7.5 years, $z = -0.08$, $p = 0.94$, effect size $r = -0.02$), or socioeconomic status as measured by the Barrett Simplified Measure of Social Status questionnaire (BSMSS; (Barratt, 2006) (musician median = 54.8, sd = 7.1, non-musician median = 53.6, sd = 15.4, $z = 0.30$, $p = 0.76$, effect size $r = 0.07$). All participants were native English speakers and had normal hearing (audiometric thresholds <25 dB HL for octave frequencies 250Hz to 8kHz). The study was approved by MIT's human participants review committee (COUHES), and written informed consent was obtained from all participants.

To validate participants' self-reported musicianship, we measured participants' abilities on a variety of psychoacoustical tasks for which prior evidence suggested that musicians would outperform non-musicians, including frequency discrimination, sensorimotor synchronization, melody discrimination, and "sour note" detection. As predicted, musician participants outperformed non-musician participants on all behavioral psychoacoustic tasks. See **Supplemental Information** for more details.

### *Study design*

Each participant underwent a 2-hour behavioral testing session as well as three 2-hour fMRI scanning sessions. During the behavioral session, participants completed an audiogram, filled out questionnaires about their musical experience, and completed a series of basic psychoacoustic tasks described in **Supplemental Information**.

### *Natural sound stimuli for fMRI experiment*

Stimuli consisted of 2-second clips of 192 natural sounds. These sounds included the 165-sound stimulus set used in Norman-Haignere et al. (2015), which broadly sample frequently heard and

recognizable sounds from everyday life. Examples can be seen in **Figure 1A**. This stimulus set was supplemented with 27 additional music and drumming clips from a variety of musical cultures, so that we could examine responses to rhythmic features of music, as well as comparing responses to more versus less familiar musical genres. Stimuli were normalized in root mean square level (RMS = 0.1) and ramped on and off with a 25ms linear ramp. During scanning, auditory stimuli were presented over MR-compatible earphones (Sensimetrics S14) at 75 dB SPL.

An online experiment (via Amazon's Mechanical Turk) was used to assign a semantic category to each stimulus, in which 180 participants (95 females; mean age = 38.8 years, sd = 11.9 years) categorized each stimulus into one of fourteen different categories. The categories were taken from Norman-Haignere et al. (2015), with three additional categories ("non-Western instrumental music," "non-Western vocal music," "drums") added to accommodate the additional music stimuli used in this experiment.

A second Amazon Mechanical Turk experiment was run to ensure that American listeners were indeed less familiar with the non-Western music stimuli chosen for this experiment, but that they still perceived the stimuli as "music." In this experiment, 188 participants (75 females; mean age = 36.6 years, sd = 10.5 years) listened to each of the 62 music stimuli and rated them based on (1) how "musical" they sounded, (2) how "familiar" they sounded, (3) how much they "liked" the stimulus, and (4) how "foreign" they sounded.

***fMRI data acquisition and preprocessing***

Similar to the design of Norman-Haignere et al (2015), sounds were presented during scanning in a "mini-block design," in which each 2-second natural sound was repeated three times in a row. Sounds were repeated because we have found this makes it easier to detect reliable hemodynamic signals. We used fewer repetitions than in our prior study (3 vs. 5), because we wanted to test a larger number of sounds and because we observed similarly reliable responses using fewer repetitions in pilot experiments. Each stimulus was presented in silence, with a single fMRI volume collected between each repetition (i.e. "sparse scanning," (Hall et al., 1999)). To encourage participants to pay attention to the sounds, either the second or third repetition in each "mini-block" was 12dB quieter (presented at 67 dB SPL), and participants were instructed to press a button when they heard this quieter sound (**Figure 1B**). Overall, participants performed well on this task (musicians: mean = 92.06%, sd = 5.47%; non-musicians: mean = 91.47%, sd = 5.83%; no participant's average performance across runs fell below 80%). Each of the three scanning sessions consisted of sixteen 5.5-minute runs, for a total of 48 functional runs per participant. Each run consisted of 24 stimulus mini-blocks and five silent blocks during which no sounds were presented. These silent blocks were the same duration as the stimulus mini-blocks, and were distributed evenly throughout each run, providing a baseline. Each specific stimulus was presented in two mini-blocks per scanning session, for a total of six mini-block repetitions per stimulus over the three scanning sessions. Stimulus order was randomly permuted across runs and across participants.

MRI data were collected at the Athinoula A. Martinos Imaging Center of the McGovern Institute for Brain Research at MIT, on a 3T Siemens Prisma with a 32-channel head coil. Each volume acquisition lasted 1 second, and the 2-second stimuli were presented during periods of silence between each acquisition, with a 200ms buffer of silence before and after stimulus presentation. As a consequence, one brain volume was collected every 3.4 seconds (1 second + 2 seconds + 0.2*2 seconds) (TR = 3.4s, TA = 1.02s, TE = 33ms, 90 degree flip angle, 4 discarded initial acquisitions). Each functional acquisition consisted of 48 roughly axial slices (oriented parallel to the anterior-posterior commissure line) covering the whole brain, each slice being 3mm thick and having an in-plane resolution of 2.1 x 2.1mm (96 x 96 matrix, 0.3mm slice gap). An SMS acceleration factor of 4 was used in order to

minimize acquisition time (TA = 1.02s). To localize functional activity, a high-resolution anatomical T1-weighted image was obtained for every participant (TR = 2.53 seconds, voxel size: 1mm$^3$, 176 slices, 256 x 256 matrix).

Preprocessing and data analysis were performed using FSL software and custom Matlab scripts. Functional volumes were motion-corrected, slice-time-corrected, skull-stripped, linearly detrended, and aligned to each participant's anatomical image (using FLIRT and BBRegister; (Jenkinson and Smith, 2001; Greve and Fischl, 2009). Motion correction and function-to-anatomical registration was done separately for each run. Preprocessed data were then resampled to the cortical surface reconstruction computed by FreeSurfer (Dale et al., 1999), and smoothed on the surface using a 3mm FWHM kernel to improve SNR. The data were then downsampled to a 2mm isotropic grid on the FreeSurfer-flattened cortical surface.

Next, we estimated the response to each of the 192 stimuli using a general linear model (GLM). Each stimulus mini-block was modeled as a boxcar function convolved with a canonical hemodynamic response function (HRF). The model also included six motion regressors and a first-order polynomial noise regressor to account for linear drift in the baseline signal. Note that this analysis differs from our prior paper (Norman-Haignere et al., 2015), in which signal averaging was used in place of a GLM. We made this change because BOLD responses were estimated more reliably using an HRF-based GLM, potentially due to the use of shorter stimulus blocks causing more overlap between BOLD responses to different stimuli.

***Voxel selection***

The first step of this analysis method is to determine which voxels serve as input to the decomposition algorithm. All analyses were carried out on voxels within a large anatomical constraint region encompassing bilateral superior temporal and posterior parietal cortex, as in Norman-Haignere et al. (2015). In practice, the vast majority of voxels with a robust and reliable response to sound fell within this region (**Supplemental Figure 6**), which explains why our results were very similar with and without this anatomical constraint (**Supplemental Figure 7**). Within this large anatomical region, we selected voxels that displayed a significant ($p < 0.001$, uncorrected) response to sound (pooling over all sounds compared to silence). This consisted of 51.45% of the total number of voxels within our large constraint region. We also selected only voxels that produced a reliable response pattern to the stimuli across scanning sessions. Note that rather than using a simple correlation to determine reliability, we used the equation from Norman-Haignere et al. (2015) to measure the reliability across split halves of our data. This reliability measure differs from a Pearson correlation in that it assigns high values to voxels that respond consistently to sounds and does not penalize them even if their response does not vary much between sounds, which is the case for many voxels within primary auditory cortex:

$$r = 1 - \frac{\| \boldsymbol{v}_1 - proj_{\boldsymbol{v}_2}\boldsymbol{v}_1 \|^2}{\| \boldsymbol{v}_1 \|^2}$$

$$proj_{\boldsymbol{v}_2}\boldsymbol{v}_1 = \boldsymbol{v}_2 \left( \frac{\boldsymbol{v}_2{}^T}{\| \boldsymbol{v}_2 \|^2} \boldsymbol{v}_1 \right)$$

where $\boldsymbol{v}_1$ and $\boldsymbol{v}_2$ indicate the vector of beta weights from a single voxel for the 192 sounds, estimated separately for the two halves of the data ($\boldsymbol{v}_1$ = first three repetitions from runs 1-24, $\boldsymbol{v}_2$ = last three repetitions from runs 25-48), and $\| \ \|$ is the L2 norm. Note that these equations differ from Equations 1 and 2 in Norman-Haignere et al. (2015), because the equations reported previously contained an error: the L2-norm terms were not squared. We used the same reliability cutoff as in our prior study ($r > 0.3$).

Of the sound-responsive voxels, 54.47% of them also met the reliability criteria. Using these two selection criteria, the median number of voxels per participant = 1,286, sd = 254 (**Supplemental Figure 5A**). The number of selected voxels did not differ significantly between musicians (median = 1,216, sd = 200) and non-musicians (medians = 1,341, sd = 284; z = -1.40, p = 0.16, effect size r = -0.31, two-tailed Wilcoxon rank sum test), and the anatomical location of the selected voxels was largely similar across groups (**Supplemental Figure 5B**).

Unlike our prior study, we collected whole-brain data in this experiment and thus were able to repeat our analyses without any anatomical constraint. While a few additional voxels outside of the mask do meet our selection criteria (**Supplemental Figure 6**), the resulting components are very similar to those obtained using the anatomical mask, both in response profiles (**Supplemental Figure 7A**; correlations ranging from r = 0.91 to r > 0.99, sd = 0.03) and voxel weights (**Supplemental Figure 7B**).

***Decomposition algorithm***

The decomposition algorithm approximates the response of each voxel ($\boldsymbol{v}_i$) as the weighted sum of a small number of component response profiles that are shared across voxels (**Figure 1B**):

$$\boldsymbol{v}_i \approx \sum_{k=1}^{K} \boldsymbol{r}_k w_{k,i}$$

where $\boldsymbol{r}_k$ represents the $k^{\text{th}}$ component response profile that is shared across all voxels, $w_{k,i}$ represents the weight of component $k$ in voxel $i$, and $K$ is the total number of components.

We concatenated the selected voxel responses from all participants into a single data matrix $\boldsymbol{D}$ ($S$ sounds × $V$ voxels). We then approximated the data matrix as the product of two smaller matrices: (1) a response matrix $\boldsymbol{R}$ ($S$ sounds x $K$ components) containing the response profile of all inferred components to the sound set, and (2) a weight matrix $\boldsymbol{W}$ ($K$ components × $V$ voxels) containing the contribution of each component response profile to each voxel. Using matrix notation this yields:

$$\boldsymbol{D} \approx \boldsymbol{RW}$$

The method used to infer components was described in detail in our prior paper (Norman-Haignere et al., 2015) and code is available online (https://github.com/snormanhaignere/nonparametric-ica). The method is similar to standard algorithms for independent components analysis (ICA) in that it searches amongst the many possible solutions to the factorization problem for components that have a maximally non-Gaussian distribution of weights across voxels (the non-Gaussianity of the components inferred in this study can be seen in **Supplemental Figure 1**). The method differs from most standard ICA algorithms in that it does so by directly minimizing the entropy of the component weight distributions across voxels as measured by a histogram, which is feasible due to the large number of voxels. Entropy is a natural measure to minimize because the Gaussian distribution has maximal entropy. The algorithm achieves this goal in two steps. First, PCA is used to whiten and reduce the dimensionality of the data matrix. This was implemented using the singular value decomposition:

$$\boldsymbol{D} \approx \boldsymbol{U}^k \boldsymbol{S}^k \boldsymbol{V}^k$$

where $\boldsymbol{U}^k$ contains the response profiles of the top $K$ principal components (192 sounds × $K$ components), $\boldsymbol{V}^k$ contains the whitened voxel weights for these components ($K$ components × 26,792 voxels), and $\boldsymbol{S}^k$ is a diagonal matrix of singular values ($K \times K$). The number of components ($K$) was chosen by measuring the amount of voxel response variance explained by different numbers of components and the accuracy of the components in predicting voxel responses in left-out data.

Specifically, we chose a value of $K$ that balanced these two measures such that the set of components explained a large fraction of the voxel response variance (which increases monotonically with additional components), but still maintained good prediction accuracy (which decreases once additional components begin to cause overfitting). In practice, the plateau in the amount of explained variance coincided with the peak of the prediction accuracy.

The principal component weight matrix is then rotated to maximize the negentropy (*J*) summed across components:

$$\widehat{\boldsymbol{T}} = \underset{\boldsymbol{T}}{\operatorname{argmax}} \sum_{c=1}^{N} J(\boldsymbol{W}[c,:]), \quad \text{where } \boldsymbol{W} = \boldsymbol{T}\boldsymbol{V}^{k}$$

where $\boldsymbol{W}$ is the rotated weight matrix ($K \times 26{,}792$), $\boldsymbol{T}$ is an orthonormal rotation matrix ($K \times K$), and $\boldsymbol{W}[c,:]$ is the c$^{\text{th}}$ row of $\boldsymbol{W}$. We estimated entropy using a histogram-based method (Moddemeijer, 1989) applied to the voxel weight vector for each component ($\boldsymbol{W}[c,:]$), and defined negentropy as the difference in entropy between the empirical weight distribution and a Gaussian distribution of the same mean and variance:

$$J(\boldsymbol{y}) = H(\boldsymbol{y}_{gauss}) - H(\boldsymbol{y})$$

The optimization is performed by iteratively rotating pairs of components to maximize negentropy, which is a simple algorithm that does not require the computation of gradients, and is feasible for small numbers of components (the number of component pairs grows as $\binom{K}{2}$).

We carried out this voxel decomposition analysis on three different data sets: i) on voxels from the 10 musicians only, ii) on voxels from the 10 non-musicians only, and iii) on voxels from all twenty participants.

***Matching components using the Hungarian algorithm***

Because the inferred components have no order, we reordered them to match those from Norman-Haignere et al. (2015) using the Hungarian algorithm (Kuhn, 1955). To ensure independence between this component matching procedure and further analyses on those components (e.g. measuring the correlation between response profiles as shown in **Figure 2B** or **Figure 3B**, or the correlation between voxel weights as shown in **Figure 3D**), the Hungarian algorithm was always run with the component voxel weight matrices before analyses focused on component response profiles, and vice versa. In practice, this was of no significance because the optimal component ordering was the same, regardless of whether the Hungarian algorithm was run on response profile matrices or voxel weight matrices (which was true even for the bootstrapped participant samples described in the next section).

***Correlations between musicians' and non-musicians' response profiles & voxel weights***

The re-ordered components of musicians and non-musicians (inferred and re-ordered separately) were highly correlated in both their response profiles and voxel weights (**Figure 3B** & **3D**, r-values on the diagonals). However, there were also relatively high correlations between "mis-matching" pairs of components, which is inevitable because the components from a single group exhibit substantial correlations. To determine whether the matched-component correlations were significantly higher than the correlations between mis-matched components (**Figure 3B** & **3D**, r-values on the off-diagonals), we calculated bootstrapped 95% CIs around the r-values for corresponding pairs of components. We bootstrapped across participants within each group and inferred a set of components for each sample. However, we found that when bootstrapped samples contained fewer than 9 unique participants, the resulting components occasionally deviated substantially from those of the full group in ways that were idiosyncratic to the particular sample. For this reason, we used only bootstrapped samples that

included 9 unique participants (somewhat akin to a leave-one-out analysis, but maintaining a total of 10 participants per sample), resulting in a total of 90 bootstrapped samples for each group. A set of components was inferred from each of these bootstrapped participant samples, and re-ordered to match the components from Norman-Haignere et al. (2015) using the Hungarian algorithm. Then, we correlated all pairwise combinations of the 90 resulting sets of components from bootstrapped musician and non-musician samples, and computed the 95% CIs of the distribution of r-values for each component. We then determined whether the observed r-values for mismatched components (**Figure 3B** & **3D**, off-diagonals) fell outside of these bootstrapped CIs (e.g. do all r-values in row 1 and column 1 of the correlation matrix fall outside of the CI around the r-value for component 1). This analysis was done for both response profiles (**Figure 3B**) and voxel weights (**Figure 3D**), and in all cases the bootstrapped CIs around the r-values on the diagonal did not include any of the off-diagonal values.

The strength of the correlations between musicians' and non-musicians' components is limited by the reliability of the components themselves. To quantify whether the observed correlations were lower than would be expected given the component reliabilities, we permuted participant groupings 10,000 times, each time inferring a new set of components for each group and measuring the correlation between the two music-selective components. The observed musician-non-musician correlation was compared to this null distribution by fitting the null distribution with a Gaussian and calculating the probability of the observed correlation. This was done for both the response profiles and voxel weights.

***Measuring component selectivity***

To quantify the selectivity of the music component, we measured the difference in mean response profile magnitude between music and non-music sounds, divided by their pooled standard deviation (Cohen's d). This measure provides a measure of the separability of the two sound categories within the response profile. We measured Cohen's d for several different pairwise comparisons of sound categories. In each case, the significance of the separation of the two stimulus categories was determined using a permutation test (permuting stimulus labels between the two categories 10,000 times). This null distribution was then fit with a Gaussian, a p-value from which was assigned to the observed value of Cohen's d.

***Anatomical component weight maps***

To visualize the anatomical distribution of component weights, individual participants' component weights were projected onto the cortical surface of the standard Freesurfer FsAverage template, and a random effects analysis (t-test) was performed to determine whether component weights were significantly greater than zero across participants at each voxel. To visualize the component weight maps separately for musicians and non-musicians, a separate random effects analysis was run for the participants in each group. To correct for multiple comparisons, we adjusted the false discovery rate (FDR, $c(V) = 1$, $q = 0.05$) using the method from Genovese, Lazar, and Nichols (Genovese et al., 2002).

To directly compare the music component weights between musicians and non-musicians, we conducted a group contrast (t-test) for each voxel using individual participants' weights for the component derived from all 20 participants (**Figure 8**).

***Component voxel weights within anatomical ROIs***

In addition to projecting the weight distributions on the cortical surface, we summarized their anatomical distribution by measuring the mean component voxel weight within a set of standardized anatomical parcels (Glasser et al., 2016). These mean weights were computed separately for each participant, and then averaged across participants for visualization purposes (e.g. **Figure 3G**). We then ran a 4 (ROI) x

2 (hemisphere) repeated-measures ANOVA on these weights. A separate ANOVA was run for musicians and non-musicians, to evaluate each group separately.

To compare the magnitude of the main effect of ROI with the main effect of hemisphere, we bootstrapped across participants, resampling participants 1,000 times. We re-ran the repeated-measures ANOVA on each sample, each time measuring the difference in the effect size for the two main effects, i.e. $\eta_{pROI}^2$ - $\eta_{pHemi}^2$. We then calculated the 95% CI of this distribution of effect size differences. The significance of the difference in main effects was evaluated by determining whether or not each group's 95% CI for the difference overlapped with zero.

In addition, we ran a Bayesian repeated-measures ANOVA on these same data, implemented in JASP v.0.13.1, using the default prior (Cauchy distribution, r = 0.5). Effects are reported as the Bayes Factor for inclusion ($BF_{inc}$) of each main effect and/or interaction, which is the ratio between the likelihood of the data given the model including the effect in question vs. the likelihood of the next simpler model without the effect in question.

***Comparisons of component weight magnitude***

When inferring components, we selected voxels primarily based on functional criteria (sound-responsive, with a reliable response across scanning sessions), within a large anatomical constraint region encompassing superior temporal and posterior parietal cortices (shown in **Figure 3F** and **Supplemental Figures 4** & **5**). As a consequence, the selected voxels could vary substantially in their anatomical location from participant to participant. To ensure that any group differences could not be explained by this variation, we compared weights between musicians and non-musicians across all voxels within a fixed anatomical region that was much narrower than the original constraint region. This more restricted anatomical region was computed by averaging voxel responses in standardized anatomical coordinates across participants and applying the same functional selection criteria described above to these group-averaged responses. The anatomical constraint regions resulting from applying this method to the data from musicians and non-musicians separately can be seen in **Figures 3** and **4**, and for all 20 participants in both groups in **Figure 8** and **Supplemental Figure 4**). The constraint region was very similar if we instead averaged across musicians or non-musicians only.

We compared voxel weights between groups within this more restricted anatomical region. For each participant, we measured the strength of the music component. Since music-selectivity is typically limited to a small fraction of voxels, we defined component strength as the median weight over the voxels with the top 10% of component weights. Similar results were obtained using other thresholds, as noted below. Weights were measured in a cross-validated fashion to avoid double-dipping. Specifically, for a given participant, we (1) inferred components using data from the other 19 participants, (2) determined the anatomical constraint region from which voxels were selected based on the group-averaged data from these 19 participants (using the criteria and process outlined above), (3) inferred voxel weights in the left-out participant by applying the pseudoinverse of the response profile matrix to the response of each individual voxel (separately for each half of the left-out participant's data), (4) selected the top 10% of voxels for each component using half of the data from the left out participant, (5) measured the median weight over those voxels using the other half of the left-out participant's data. The significance of the musician vs. non-musician difference for each component was assessed by permuting participant groupings 10,000 times and recalculating the group difference in component medians to build up a null distribution against which to compare the observed group difference. We also conducted Bayesian independent-samples t-tests on participants' median component weights, implemented in JASP v.0.13.1 using default effect size priors on the effect size (Cauchy distribution with r = $\sqrt{2}/2$). Results are reported using the two-tailed Bayes factor that represents $p$(data | $H_1$: musicians = non-musicians / $p$(data | $H_0$: musicians = non-musicians).

Results of this cross-validation procedure were robust to the threshold chosen for selecting left-out participants' voxels (we repeated the analyses selecting the top 1%, 5%, 10%, 25%, and 50% of voxels). The same is true regardless of whether we use individual participants' mean component weight as a measure of component strength, rather than their median component weight. Similarly, results remain unchanged if we simply use individual participants' mean or median component weight over all voxels within the anatomical constraint region determined using the data from the entire group of 20 participants (as described above).

***Weight magnitude comparison power analysis***

We ran a power analysis using the data from Norman-Haignere et al. (2015) to determine the magnitude of difference between the music component weights of musicians and non-musicians that we would be able to reliably detect given our sample size. We computed a measure of the strength of the music component (the median of the top 10% of the weights) in those 10 participants using the same cross-validated approach described above. Because the data from Norman-Haignere et al. (2015) included three repetitions of each stimulus (not two as in the current study), we used two thirds of each participants' data to select the 10% of voxels with the largest music component weights, and then measured the median weight of these voxels in the left-out data.

We then compared the music component strength in these participants to a second population of 10 participants created by sampling participants with replacement and then increasing their component weights by various amounts (ranging from 0% to 100%, in increments of 5%), with each shift amount representing a model for how the music component weights might change in musicians. The difference between the groups' median weights was computed, and the significance of this group difference was assessed by permuting participant groupings 1,000 times.

For each shift amount, we repeated this entire procedure 1,000 times, each time sampling a new set of 10 participants for each group. The probability of detecting a significant group difference for each shift amount was recorded, and the results showed that we were able to detect a significant group difference 80% of the time if the two groups' median weights differed by 47% (**Figure 7A**).

We repeated this power analysis using multiple different percentage thresholds for selecting voxels (i.e. measuring participants' median weight over the top 5%, 7.5%, 10%, 15%, and 20% of voxels), and note that the results were relatively robust to the setting of this parameter, with detectable group differences occurring 80% of the time by the point at which the groups' median weights differed by 45-53% (**Supplemental Figure 8**).

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## SUPPLEMENTAL INFORMATION

***Behavioral data acquisition & analysis***

To validate participants' self-reported musicianship, we measured participants' abilities on a variety of psychoacoustical tasks for which prior evidence suggested that musicians would outperform non-musicians. For all psychoacoustic tasks, stimuli were presented using Psychtoolbox for Matlab (Brainard, 1997). Sounds were presented to participants at 70dB SPL over circumaural Sennheiser HD280 headphones in a soundproof booth (Industrial Acoustics) (SPL level was computed without any weighting across time or frequency). After each trial, participants were given feedback about whether or not they had answered correctly. Group differences for each task were measured using non-parametric Wilcoxon rank sum tests.

Pure tone frequency discrimination. Because musicians have superior frequency discrimination abilities when compared to non-musicians (Spiegel and Watson, 1984; Kishon-Rabin et al., 2001; Micheyl et al., 2006), we first measured participants' pure tone frequency discrimination thresholds using an adaptive two-alternative forced choice (2AFC) task. In each trial, participants heard two pairs of tones. One of the tone pairs consisted of two identical 1 kHz tones, while the other tone pair contained a 1 kHz tone and a second tone of a different frequency. Participants determined which tone interval contained the frequency change. The magnitude of the frequency difference was varied adaptively using a 1-up 3-down procedure (Levitt, 1971), which targets participants' 79.4% threshold. The frequency difference was changed initially by a factor of two, which was reduced to a factor of $\sqrt{2}$ after the fourth reversal. Once 10 reversals had been measured, participants' thresholds were estimated as the average of these 10 values. Multiple threshold estimations were obtained per participant (3 threshold estimations for the first seven participants, and 5 for the remaining 13 participants), and then averaged.

Synchronized tapping to an isochronous beat. Sensorimotor abilities are crucial to musicianship, and finger tapping tasks show some of the most reliable effects of musicianship (Repp, 2005, 2010; Bailey and Penhune, 2010). Participants were asked to tap along with an isochronous click track. They heard ten 30-second click blocks, separated by 5 seconds of silence. The blocks varied widely in tempo, with interstimulus intervals ranging from 200ms to 1 second (tempos of 60 to 300 bpm). Each tempo was presented twice, and the order of tempi was permuted across participants. We recorded the timing of participants' responses using a tapping sensor we constructed and have used in previous studies (Jacoby and McDermott, 2017; Polak et al., 2018). We then calculated the difference between participants' response onsets and the actual stimulus onsets. The standard deviation of these asynchronies between corresponding stimulus and response onsets was used as a measure of sensorimotor synchronization ability (Polak et al., 2018).

Melody discrimination. Musicians have also been reported to outperform non-musicians on measures of melodic contour and interval discrimination (Fujioka et al., 2004; McDermott et al., 2010; McPherson and McDermott, 2018). In each trial, participants heard two five-note melodies, and were asked to judge whether the two melodies were the same or different. Melodies were composed of notes that were randomly drawn from a log uniform distribution of semitone steps from 150Hz to 270Hz. The second melody was transposed up by half an octave and was either identical to the first melody or contained a single note had that had been altered either up or down by 1 or 2 semitones. Half of the trials contained a second melody that was the same as the first melody, while 25% contained a pitch change that preserved the melodic contour and the remaining 25% contained a pitch change that violated the melodic contour. There were 20 trials per condition (same/different melody x same/different contour x 1/2 semitone change), for a total of 160 trials. This task was modified from (McPherson and McDermott, 2018).

"Sour note" detection. To measure participants' knowledge of Western music, we also measured participants' ability to determine whether a melody conforms to the rules of Western music theory. The melodies used in this experiment were randomly generated from a probabilistic generative model of Western tonal melodies that creates a melody on a note-by-note basis according to the principles that (1) melodies tend to be limited to a narrow pitch range, (2) note-to-note intervals tend to be small, and (3) the notes within the melody conform to a single key (Temperley, 2008). In each trial of this task, participants heard a 16-note melody and were asked to determine whether the melody contained an out-of-key ("sour") note. In half of the trials, one of the notes in the melody was modified so that it was rendered out of key. The modified notes were always scale degrees 1, 3, or 5 and they were modified by either 1 or 2 semitones accordingly so that they were out of key (i.e. scale degrees 1 and 5 were modified by 1 semitone, and scale degree 3 was modified by 2 semitones). Participants judged whether the melody contained a sour note (explained as a "mistake in the melody"). There were 20 trials per condition (modified or not x 3 scale degrees), for a total of 120 trials. This task was modified from (McPherson and McDermott, 2018).

***Psychoacoustic results***

As predicted, musicians outperformed non-musicians on all behavioral psychoacoustic tasks, replicating prior findings (**Supplemental Figure 9**). Consistent with previous reports (Spiegel and Watson, 1984; Kishon-Rabin et al., 2001; Micheyl et al., 2006), musicians performed slightly better on the frequency discrimination task (median discrimination threshold = 0.51%, sd = 0.12%) than non-musicians (median discrimination threshold = 0.57%, sd = 0.23%); this difference was marginally significant ($z = -1.32$, $p = 0.09$, effect size $r = -0.30$, one-tailed Wilcoxon rank sum test, **Supplemental Figure 9A**). Musicians were also better able to synchronize their finger tapping with an isochronous beat, showing significantly less variability than non-musicians in their response (sd = 22.4ms) than non-musicians (sd = 37.7ms, $z = -2.68$, $p < 0.01$, effect size $r = -0.60$, one-tailed Wilcoxon rank sum test, **Supplemental Figure 9B**). When presented with musical melodies, musicians were better able to discriminate between two similar melodies (musician median ROC area = 0.82, sd = 0.08, non-musician mean ROC area = 0.66, sd = 0.09, $z = 3.21$, $p < 0.001$, effect size $r = 0.72$, one-tailed Wilcoxon rank sum test, **Supplemental Figure 9C**), and to detect scale violations within melodies (musician mean ROC area = 0.89, sd = 0.06, non-musicians mean ROC area = 0.70, sd = 0.10, $z = 3.44$, $p < 0.001$, effect size $r = 0.77$, one-tailed Wilcoxon rank sum test, **Supplemental Figure 9D**). These behavioral effects validate our participants' self-reported status as trained musicians or non-musicians.

***Replication of Norman-Haignere et al. (2015) using data from all 20 participants***

In addition to conducting the voxel decomposition analysis separately for musicians and non-musicians, we were able replicate the full results from Norman-Haignere et al. (2015) using data from all 20 participants from both groups. The components from this combined analysis were used when directly comparing component weights between groups (described in Results sections titled "Music component weight magnitude differs only slightly between musicians and non-musicians" and "Similar anatomical distribution of music component weights in musicians and non-musicians"). Here, we describe that analysis in more detail, and explain more about the four components that are selective for acoustic stimulus features.

In our previous study (Norman-Haignere et al., 2015), prior to applying the voxel decomposition algorithm, each participant's responses were de-meaned across voxels, such that each participant had the same mean response (across voxels) for a given sound. This normalization was included to prevent the voxel decomposition algorithm from discovering additional components that were driven by a single participant (e.g. due to non-replicable sources of noise, such as motion during a scan). However, this

analysis step would also remove any group difference in the average response to certain sounds (e.g. music stimuli). To prevent this effect from influencing the comparison of the two groups, we ran the voxel decomposition algorithm without demeaning by individual participants. As expected, this resulted in a larger number of components, with 8 components being needed to optimally model the data from all 20 participants, explaining 89.83% of the voxel response variance, after which the amount of explained variance for each additional component plateaued.

Of the 8 components derived from the non-demeaned data, six of them were each very similar to one of the 6 components from Norman-Haignere et al. (2015) and accounted for 87.54% of voxel response variance. Because the components inferred using ICA have no order, we first used the Hungarian algorithm (Kuhn, 1955) to optimally reorder the components, maximizing their correlation with the components from our previous study. As expected, the reordered components were highly correlated, with r-values ranging from 0.76 to 0.98 (**Supplemental Figure 4A**; see **Supplemental Figure 4B** for the response profiles of the components, and **Supplemental Figure 4C** for the profiles averaged within sound categories). To confirm that these strong correlations are not simply an artifact of the Hungarian algorithm matching procedure, we ran a permutation test in which we re-ordered the sounds within each component 1,000 times, each time using the Hungarian algorithm to match these permuted components with those from our previous study. The resulting correlations between the original components their corresponding permuted components were very low (mean r-values ranging from 0.086 to 0.098), with the maximum correlation over all 1,000 permutations not exceeding r = 0.3 for any component.

The additional two components were much less correlated with any of the six original components, with the strongest correlation being r = 0.28. As expected, the weights of these additional two components were concentrated in a small number of participants (one almost entirely loading onto a single non-musician participant, and the other onto a small group comprised of both musicians and non-musicians). For this reason, we omitted these two components from further analyses and focused on the set of six components that closely match those discussed previously (**Supplemental Figure 4B-H**). The non-Gaussianity of these 6 components can be seen in **Supplemental Figure 1A** (skewness ranging from 1.06 to 2.96, log-kurtosis ranging from 1.70 to 2.79).

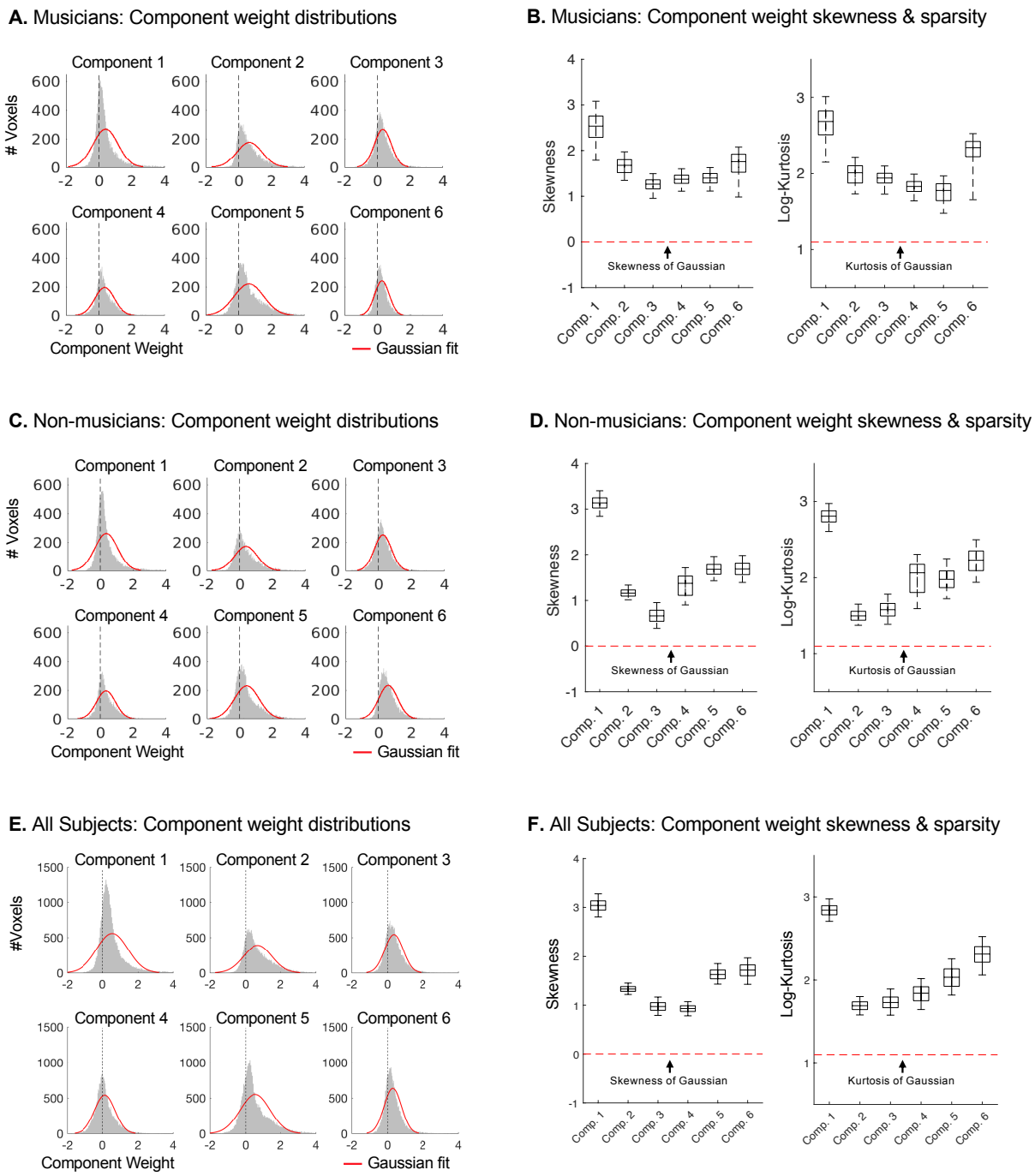
As in Norman-Haignere et al. (2015), four of the components were selective for different acoustic properties of sound (**Supplemental Figure 4D** & **E**), while two components were selective for speech (component 5) and music respectively (component 6) (**Supplemental Figure 4B** & **C)**. The components replicated all of the functional and anatomical properties from our prior study, which we briefly describe here.

Components 1 and 2 exhibited high correlations between their response profiles and measures of stimulus energy in either low (component 1) or high frequency bands (component 2) (**Supplemental Figure 4D**). The group anatomical weights for components 1 and 2 concentrated in the low and high-frequency regions of primary auditory cortex (**Supplemental Figure 4F** & **H**) (Rauschecker et al., 1995; Humphries et al., 2010; Da Costa et al., 2011; Baumann et al., 2013). We did not measure tonotopy in the individual participants from this study, but our previous study did so, and found a close correspondence between individual participant tonotopic maps and the weights for these two components. Components also showed tuning to spectrotemporal modulations (**Supplemental Figure 4E**), with a tradeoff between selectivity for fine spectral and slow temporal modulation (components 1 and 4) verses coarse spectral and fast temporal modulation (components 2 and 3) (Singh and Theunissen, 2003; Rodríguez et al., 2010). Component 4, which exhibited selectivity for fine spectral modulation, was concentrated anterior to Heschl's gyrus (component 4, **Supplemental Figure 4F** & **H**), similar to prior work that has identified tone-selective regions in anterolateral auditory cortex in humans

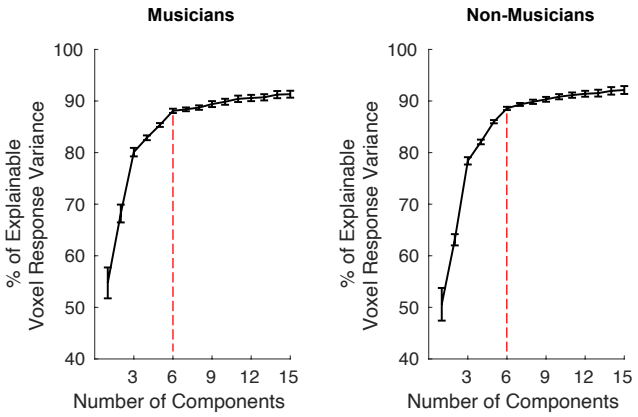
(Patterson et al., 2002; Penagos et al., 2004; Norman-Haignere et al., 2013). Conversely, selectivity for coarse spectral modulation and fast temporal modulation was concentrated in posterior regions of auditory cortex (component 3, **Supplemental Figure 4F** & **H**) (Santoro et al., 2014), consistent with previous studies reporting selectivity for sound onsets in caudal areas of human auditory cortex (Hamilton et al., 2018).

The two remaining components responded selectively to speech and music, respectively (component 5 and 6, **Supplemental Figure 4C**), and were not well accounted for using acoustic properties alone (**Supplemental Figure 3B**). The weights for the speech-selective component (component 5) were concentrated in the middle portion of the superior temporal gyrus (midSTG, **Supplemental Figure 4F** & **H**), as expected (Scott et al., 2000; Hickok and Poeppel, 2007; Overath et al., 2015). In contrast, the weights for the music-selective component (component 6) were most prominent anterior to PAC in the planum polare, with a secondary cluster posterior to PAC in the planum temporale (**Supplemental Figure 4F** & **H**) (Ohnishi et al., 2001; Margulis et al., 2009; Dick et al., 2011; Fedorenko et al., 2012; Angulo-Perkins et al., 2014; Armony et al., 2015; Norman-Haignere et al., 2015).

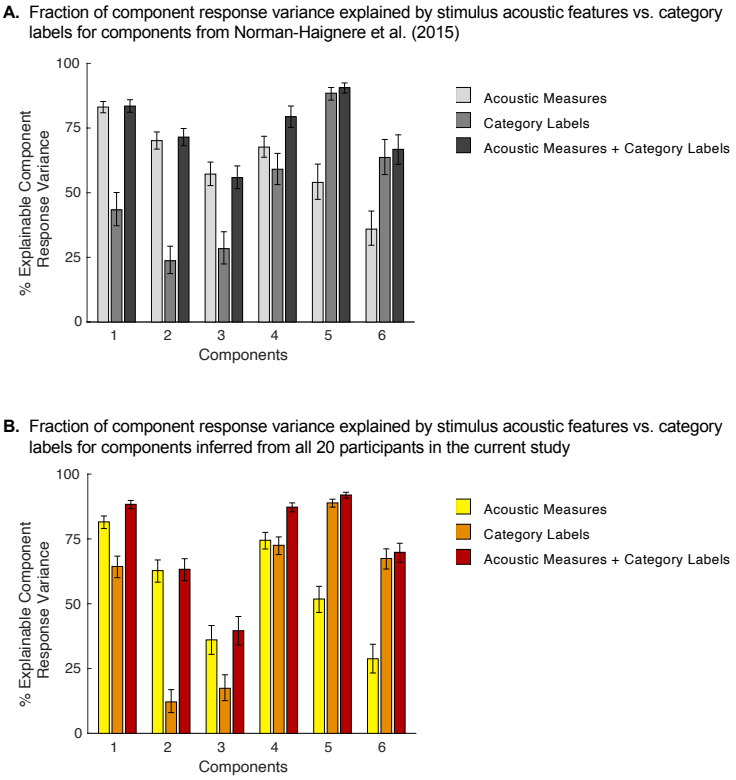
These results closely replicate the functional organization of human auditory cortex reported by Norman-Haignere et al. (2015), including the existence and anatomical location of inferred music-selective neural populations.




**Supplemental Figure 1.** Like ICA, the voxel decomposition method searches amongst the many possible solutions to the factorization problem for components that have a maximally non-Gaussian distribution of weights across voxels. (**A**) Histograms showing the weight distributions for each component inferred from musicians (n = 10) can be seen here, along with their Gaussian fits (red). (**B**) Skewness and log-kurtosis (a measure of sparsity) for each component inferred from musicians (n = 10), illustrating that the inferred components are skewed and sparse compared to a Gaussian (red dotted lines). Box-and-whisker plots show central 50% (boxes) and central 95% (whiskers) of the distribution for each statistic (via bootstrapping across subjects). For both the weight distribution histograms and analyses of non-Gaussianity, we used independent data to infer components (runs 1-24) and to measure the statistical properties of the component weights (runs 25-48). (**C, D**) Same as **A&B**, but for the components inferred from non-musicians (n = 10). (**E, F**) Same as **A&B**, but for the components inferred from all 20 participants



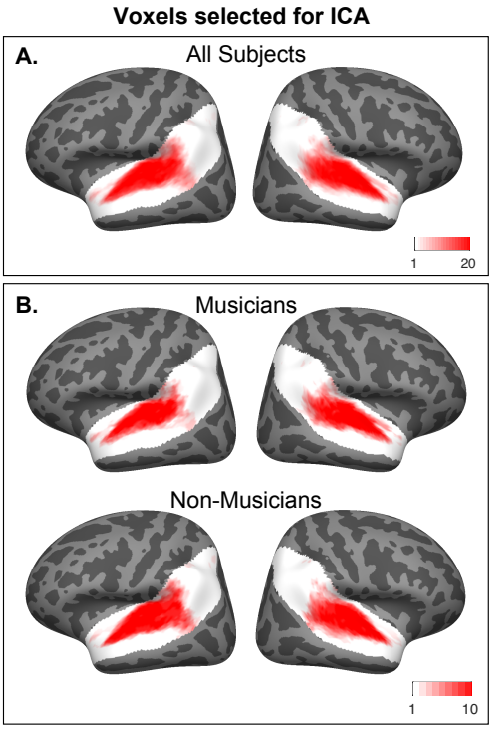

**Supplemental Figure 2.** The proportion of voxel response variance explained by different numbers of components, for both musicians (left) and non-musicians (right). The figure plots the median variance explained across voxels (noise corrected by split-half reliability), calculated separately for each subject and then averaged across the ten subjects in each group. Error bars plot one standard error of the mean across subjects. For both groups, 6 components were sufficient to explain over 88% of the noise-corrected variance.



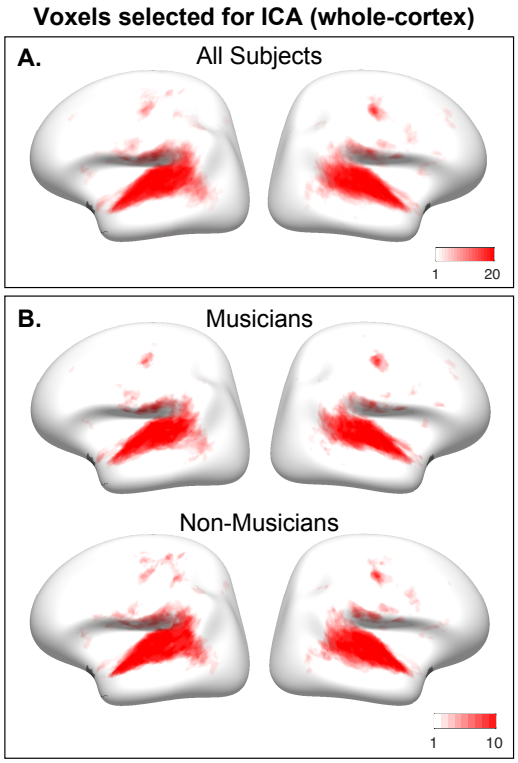

**Supplemental Figure 3**. Total amount of component response variation explained by (1) all acoustic measures (frequency content and spectrotemporal modulation energy), (2) all category labels (as assigned by Amazon Mechanical Turk workers), and (3) the combination of acoustic measures and category labels. (**A**) Results for components from previous study (Norman-Haignere et al., 2015). For components 1–4, category labels explained little additional variance beyond that explained by acoustic features. For Components 5 (speech-selective) and 6 (music-selective), category labels explained most of the response variance, and acoustic features accounted for little additional variance. (**B**) Same as **A** but for the components inferred from all 20 participants in the current study.

A. Replication of Previous Study
Component 1
Component 2
Component 3
Component 4
Component 5
Component 6
Previous Study
Current Study
Corr. (r) = - 1
1
B. Response Profiles for All 192 Sounds
Response (relative to max).
Individual Sounds
C. Average Response to Each Sound Category
Sound Category
Western Instr. Music
Foreign Instr. Music
Drum Music
Western Vocal Music
Foreign Vocal Music
English Speech
Foreign Speech
Human Vocal
Animal Vocal
Human Non-Vocal
Animal Non-Vocal
Nature
Mechanical
Env. Sounds
D. Correlations Between Response Profiles and Sound Frequency
Normalized Corr.
Center Frequency (kHz)
E. Correlations Between Response Profiles and Sound Spectrotemporal Modulation Energy
Spectral Mod. (cycles/octave)
Temporal Modulation (Hz)
Normalized Corr. (r) = -1
1
F. Anatomical Distribution of Component Weights
G. Voxels Selected for ICA
LH
RH (flipped)
Significance of Component Weight
-log10(p)
1.88
10.05
-3.49
12.54
1.55
9.85
-3.35
7.83
1.62
11.33
-3.56
7.94
1
20
H. Mean Component Weights in Anatomical ROIs
Mean Comp. Weight (AU)
RH
LH
STGa
TA2
PI
Area52
MBelt
A1
LBelt
PBelt
A4
A5
STV
PSL
RI
PFcm
PF

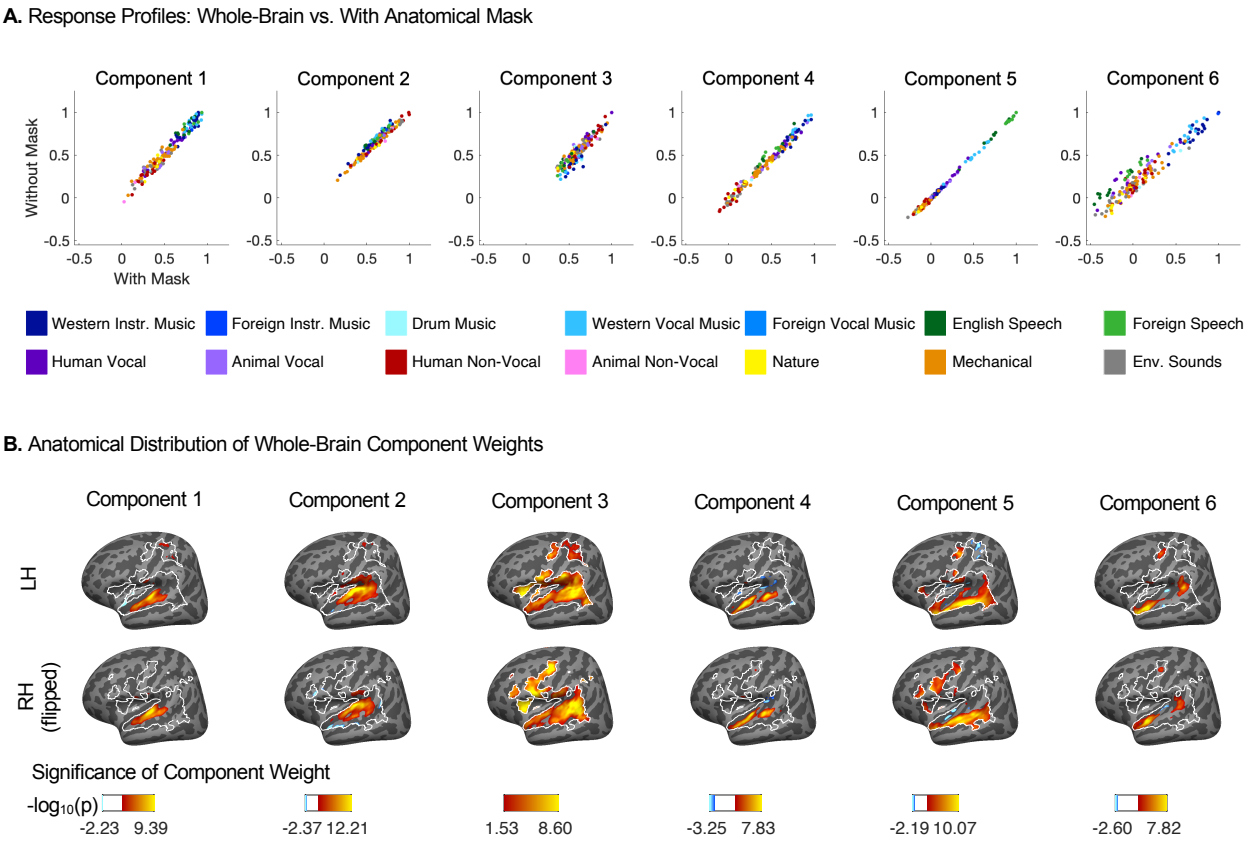
**Supplemental Figure 4.** Independent components inferred from voxel decomposition of auditory cortex of all 20 participants (as compared to the components in **Figure 3**, which were inferred from musicians and non-musicians separately). Additional plots are included here to show the extent of the replication of the results of Norman-Haignere et al. (2015). (**A**) Scatterplots showing the correspondence between the components from our previous study (y-axis) and those from the current study (x-axis). Only the 165 sounds that were common between the two studies are plotted. Sounds are colored according to their semantic category, as determined by raters on Amazon Mechanical Turk. (**B**) Response profiles of components inferred from all participants (n = 20), showing the full distribution of all 192 sounds. Sounds are colored according to their category. Note that "Western Vocal Music" stimuli were sung in English. (**C**) The same response profiles as above, but showing the average response to each sound category. Error bars plot one standard error of the mean across sounds from a category, computed using bootstrapping (10,000 samples). (**D**) Correlation of component response profiles with stimulus energy in different frequency bands. (**E**) Correlation of component response profiles with spectrotemporal modulation energy in the cochleograms for each sound. (**F**) Spatial distribution of component voxel weights, computed using a random effects analysis of participants' individual component weights. Weights are compared against 0; p values are logarithmically transformed ($-\log_{10}[p]$). The white outline indicates the 2,249 voxels that were both sound-responsive (sound vs. silence, $p < 0.001$ uncorrected) and split-half reliable ($r > 0.3$) at the group level. The color scale represents voxels that are significant at FDR $q = 0.05$, with this threshold being computed for each component separately. Voxels that do not survive FDR correction are not colored, and these values appear as white on the color bar. The right hemisphere (bottom row) is flipped to make it easier to visually compare weight distributions across hemispheres. (**G**) Subject overlap maps showing which voxels were selected in individual subjects to serve as input to the voxel decomposition algorithm (same as **Supplemental Figure 5A**). To be selected, a voxel must display a significant ($p < 0.001$, uncorrected) response to sound (pooling over all sounds compared to silence), and produce a reliable response pattern to the stimuli across scanning sessions (see equations in Methods section). The white area shows the anatomical constraint regions from which voxels were selected. (**H**) Mean component voxel weights within standardized anatomical parcels from Glasser et al. (2016), chosen to fully encompass the superior temporal plane and superior temporal gyrus (STG). Error bars plot one standard error of the mean across participants.



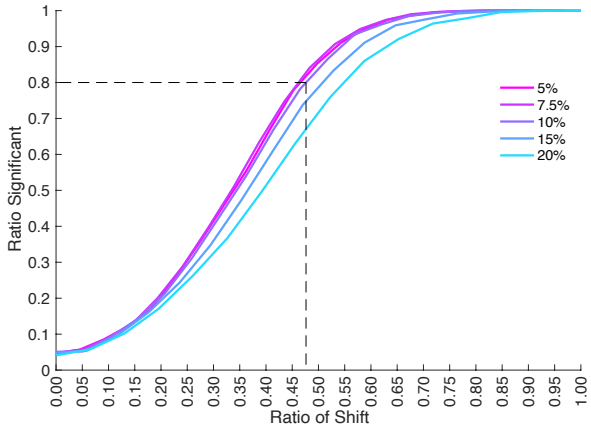

**Supplemental Figure 5**. Subject overlap maps showing which voxels were selected in individual subjects to serve as input to the voxel decomposition algorithm. To be selected, a voxel must display a significant ($p < 0.001$, uncorrected) response to sound (pooling over all sounds compared to silence), and produce a reliable response pattern to the stimuli across scanning sessions (see equations in Methods section). The white area shows the anatomical constraint regions from which voxels were selected. (**A**) Overlap map for all twenty subjects. (**B**) Overlap maps for musicians and non-musicians separately, illustrating that the anatomical location of the selected voxels was largely similar across groups. Also shown in **Figure 3F**.



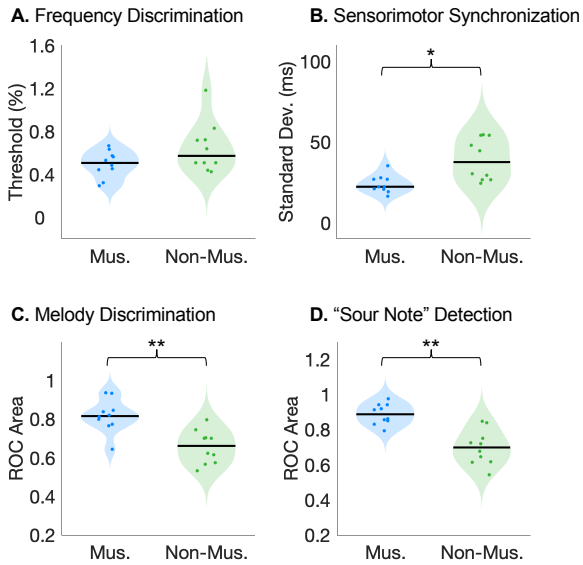

**Supplemental Figure 6**. Subject overlap maps showing which voxels pass the selection criteria as described in **Supplemental Figure 5**, but without any anatomical mask applied before selecting voxels.




**Supplemental Figure 7**. **Similarity between components with anatomical mask vs. whole-brain.** (**A**) Scatter plots showing the components inferred from all 20 participants, using the voxel decomposition algorithm both with and without the anatomical mask shown in **Supplemental Figure 5**. Individual sounds are colored according to their semantic category. (**B**) Spatial distribution of whole-brain component voxel weights, computed using a random effects analysis of participants' individual component weights. Weights are compared against 0; p values are logarithmically transformed ($-\log_{10}[p]$). The white outline indicates the voxels that were both sound-responsive (sound vs. silence, $p < 0.001$ uncorrected) and split-half reliable ($r > 0.3$) at the group level. The color scale represents voxels that are significant at FDR $q = 0.05$, with this threshold being computed for each component separately. Voxels that do not survive FDR correction are not colored, and these values appear as white on the color bar. The right hemisphere (bottom row) is flipped to make it easier to visually compare weight distributions across hemispheres.




**Supplemental Figure 8**. The same as **Figure 7A**, but showing the results of the power analysis repeated using various thresholds to select voxels over which to measure participants' median music component weights. Note that the results are relatively robust to the setting of this parameter, with detectable group differences occurring 80% of the time by the time the groups' median weights differed by 47%. The dashed line represents the shift amount in which we were able to detect a significant difference in the two groups' median weights 80% of the time with a selection threshold of 10% (the value used in the paper).




**Supplemental Figure 9.** Musicians outperform non-musicians on psychoacoustic tasks. (**A**) Participants' pure tone frequency discrimination thresholds were measured using a 1-up 3-down adaptive two-alternative forced choice (2AFC) task, in which participants indicated which of two pairs of tones were different in frequency. Note that lower thresholds correspond to better performance. (**B**) Sensorimotor synchronization abilities were measured by instructing participants to tap along with an isochronous beat at various tempos, and comparing the standard deviation of the difference between participants' response onsets and the actual stimulus onsets. (**C**) Melody discrimination was measured using a 2AFC task, in which participants heard two five-note melodies (with the second one transposed up by a tritone) and were asked to judge whether the two melodies were the same or different. (**D**) We measured participants' ability to determine whether a melody conforms to the rules of Western music theory by creating 16-note melodies using a probabilistic generative model of Western tonal melodies (Temperley, 2008), and instructing participants to determine whether or not the melody contained an out-of-key ("sour") note. Mus. = musicians, Non-Mus. = non-musicians. * = significant at $p < 0.01$ one-tailed, ** = significant at $p < 0.001$ one-tailed.