Structural, Functional, and Perceptual Differences in Heschl's Gyrus and Musical Instrument Preference

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ABSTRACT: The musical pitch of harmonic complex sounds, such as instrumental sounds, is perceived primarily by decoding either the fundamental pitch (keynote) or spectral aspects of the stimuli, for example, single harmonics. We divided 334 professional musicians, including symphony orchestra musicians, 75 amateur musicians, and 54 nonmusicians, into either fundamental pitch listeners or spectral pitch listeners. We observed a strong correlation between pitch perception preference and asymmetry of brain structure and function in the pitch-sensitive lateral areas of Heschl's gyrus (HG), irrespective of musical ability. In particular, fundamental pitch listeners exhibited both larger gray matter volume measured using magnetic resonance imaging (MRI) and enhanced P50m activity measured using magnetoencephalography (MEG) in the left lateral HG, which is sensitive to rapid temporal processing. Their chosen instruments were percussive or high-pitched instruments that produce short, sharp, or impulsive tones (e.g., drums, guitar, piano, trumpet, or flute). By contrast, spectral pitch listeners exhibited a dominant right lateral HG, which is known to be sensitive to slower temporal and spectral processing. Their chosen instruments were lower-pitched melodic instruments that produce rather sustained tones with characteristic changes in timbre (e.g., bassoon, saxophone, french horn, violoncello, or organ). Singers also belonged to the spectral pitch listeners. Furthermore, the absolute size of the neural HG substrate depended strongly on musical ability. Overall, it is likely that both magnitude and asymmetry of lateral HG, and the related perceptual mode, may have an impact on preference for particular musical instruments and on musical performance.

KEYWORDS: pitch perception; Heschl's gyrus; asymmetry; musical instrument preference; harmonic complex tones; orchestra

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Harmonic complex tones, such as instrumental sounds, may be described by objective aspects as the time period of the sound pressure curve or the envelope of the frequency spectrum. However, the perceived musical pitch differs largely by up to three or four octaves, when the same sound is presented to different individuals, even for professional musicians. For example, if the 5th, 6th, and 7th harmonic of 500 Hz is played, the perceived pitch ranged between one-line octave B and four-line octave F sharp. Some subjects recognized predominantly the fundamental pitch, that is, the keynote of a sound. Others predominantly perceived single harmonics of the complex sounds.[1–4] Such subjective aspects have been described earlier by Hermann von Helmholtz[5,6] who introduced a "synthetical mode," based on fundamental pitch perception, and an "analytical mode," based on the perception of single harmonics of the complex sounds. To psychoacoustically quantify the large perceptual differences, we performed a new pitch test[4] using tone pairs of complex tones. Participants were asked to identify the dominant direction of pitch shift in a large sample of 144 tone pairs. For each subject, an index of pitch perception preference ($\delta_p = (f_{sp} - f_0)/(f_{sp} + f_0)$) was measured by identifying the percentage of fundamental (f_0) versus spectral (f_{sp}) pitch perception. We measured 334 professional musicians, including symphony orchestra musicians from the Royal Liverpool Philharmonic Orchestra (RLPO),[7] 75 amateurs, and 54 nonmusicians and observed a large bimodal distribution that enabled the classification in fundamental and spectral pitch listeners.

How are these perceptual differences related to structural and functional attributes of the human auditory cortex (AC)? In a subgroup of 87 subjects, magnetic resonance imaging (MRI) and magnetoencephalography (MEG) studies demonstrated a strong neural basis for both types of pitch perception irrespective of musical ability.[4] The fundamental pitch listeners exhibited a pronounced leftward asymmetry of gray matter volume and functional P50m activity in the pitch-sensitive[8,9] areas of lateral Heschl's gyrus (lHG) whereas, in contrast, spectral pitch listeners exhibited a corresponding pronounced rightward asymmetry.[4]

The relative hemispheric lateralization was observed to correlate with pitch preference irrespective of musical ability. In FIGURE 1 we depict the strong correlation between pitch perception asymmetry (δ_p) and either gray matter aymmetry of lHG structurally (δ_s) on the left panel (A) or pitch asymmetry and auditory-evoked P50m asymmetry functionally (δ_f) on the right panel (B). The correlation is equally strong for nonmusicians and musicians. Furthermore, there is a link to musical instrument preference. The left AC is known to be sensitive to rapid temporal processing.[10–12] Therefore, fundamental pitch listeners may make use of short, sharp, and impulsive tones. Indeed, as shown in FIGURE 1, they play mainly percussive instruments (drums or guitar) or higher-pitched solo instruments (trumpet, flute, or piccolo). By contrast, the right AC is sensitive to slower temporal and spectral processing.[10,12] Therefore, spectral pitch listeners may make use of sustained tones with characteristic formants in their frequency spectrum. Consistently, we observed that the musical instruments of their choice were melodic instruments producing sustained tones (strings, woodwind, or brass, without trumpet, organ, or the singing voice). However, most professional musicians simultaneously perceive both the keynote and single harmonics from an ambiguous tone, and the subjective differences are relative rather than absolute.

To quantify in more detail the relationship between pitch perception and musical instrument preference, all 463 psychometrically tested musicians were subdivided

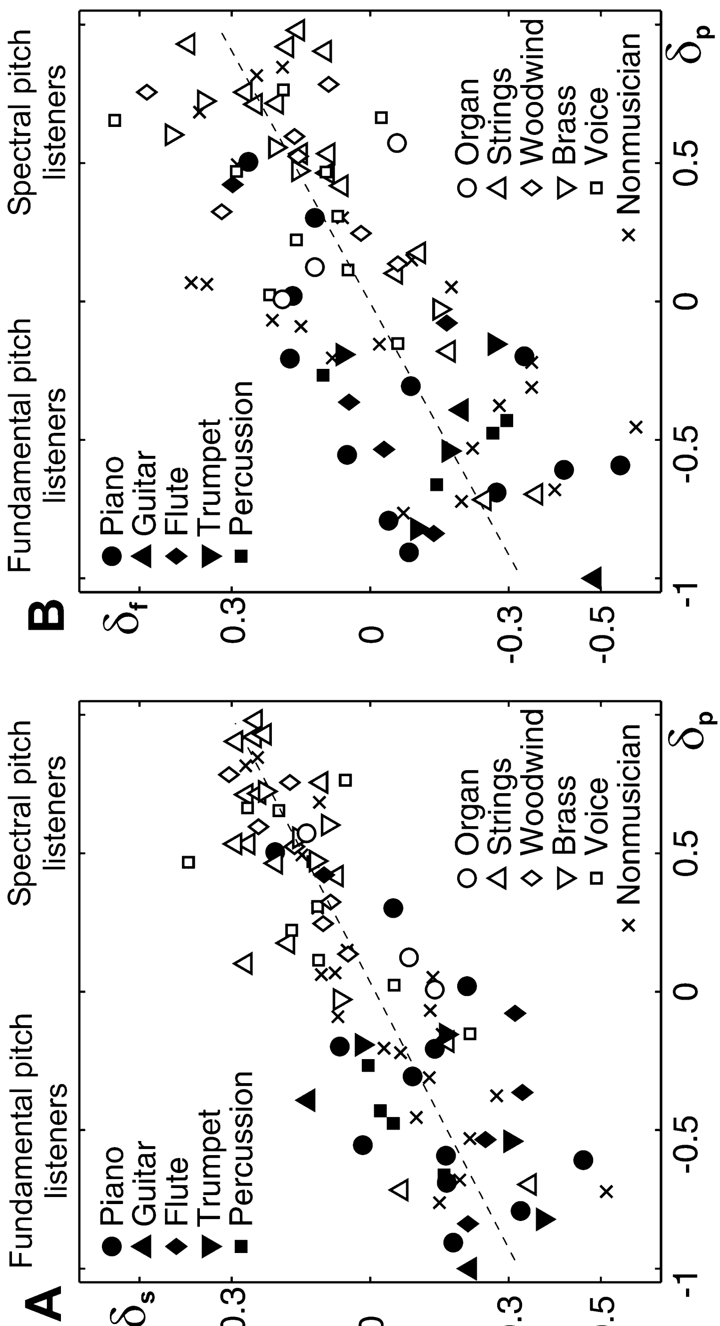

FIGURE 1. Correlation of pitch perception preference (δ_p) versus (**A**) structural asymmetry (δ_s) and (**B**) functional asymmetry (δ_f) of the neural substrate in lateral HG. The correlation is strong for both nonmusicians (*x* symbols) and musicians (symbols indicate their main instrument).

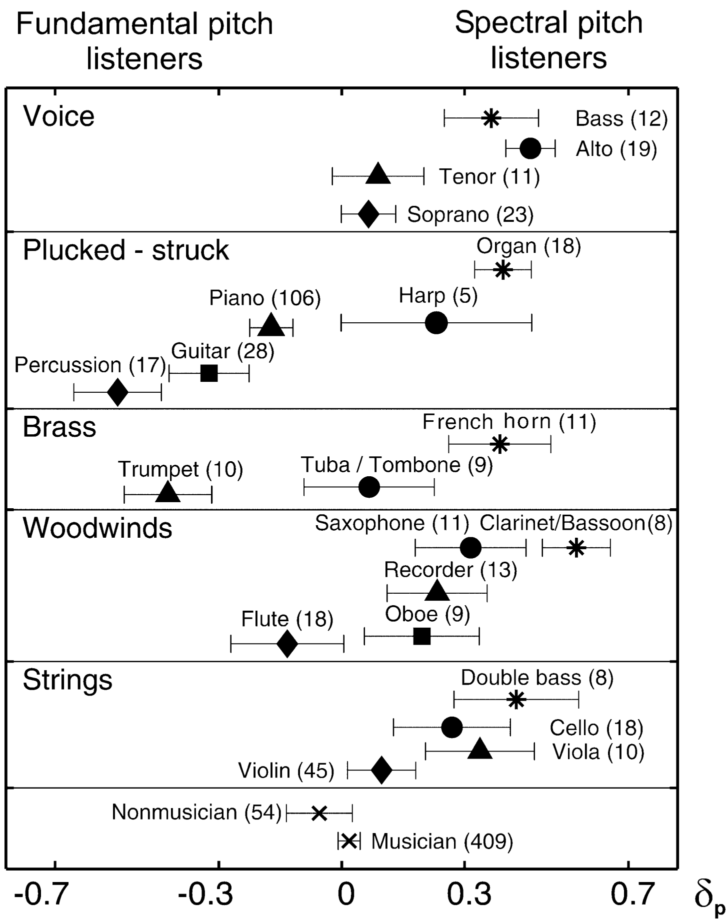

FIGURE 2. The index of pitch perception preference (δ_p) was classified for musical instrument families (mean ± SEM), nonmusicians, and all musicians (*bottom*). Fundamental pitch listeners played predominantly percussive or high-pitched instruments, whereas spectral pitch listeners prefered lower-pitched melodic instruments and singing.

according to their main instrument (FIG. 2). The index of pitch perception preference (δ_p) was averaged over instrumental groups, and the psychometric results were analyzed for different instrument families. Percussionists showed the most pronounced fundamental pitch percept, followed by trumpeters, guitarists, and flutists. On the other hand, players of lower-pitched melody instruments (bassoon, double bass, organ, or basses and altos in a choir) were found to show the most pronounced spectral pitch percept. Regarding the distribution of one single group, 65% of the pianists were fundamental pitch listeners, and 35% were spectral pitch listeners. We believe that this pronounced variation may be explained by an additional influence of the perceptual and neuronal asymmetry on musical performance style. For example, a pianist predominantly perceiving the fundamental pitch may prefer to perform with virtuosity and enjoy playing complex rhythmic patterns, whereas a pianist predominantly perceiving harmonics may prefer slower music and may concentrate more on timbral or melodic aspects of the music.

Within singers, sopranos showed enhanced fundamental pitch perception as compared to altos, women in the female bass register ($F_{1,41} = 12.2$, $P < .0001$), and male basses ($F_{1,34} = 3.7$, $P < .05$). Pianists exhibited strongly enhanced fundamental pitch perception as compared to organists ($F_{1,123} = 13.5$, $P < .0001$). Within the brass family, trumpet players demonstrated an almost opposite perception mode as compared to french horn and tuba players ($F_{1,29} = 21.3$, $P < .0001$). Within the woodwinds, flute and piccolo players were completely separated from the saxophonists ($F_{1,28} = 5.7$, $P < .01$). Last, but not least, percussionists frequently perceived the missing fundamental pitch, but string players did only relatively rarely ($F_{1,97} = 39.2$, $P < .0001$). Consistently, the players of higher pitched descant instruments of each instrument family (trumpet, flute, or violin) demonstrated enhanced fundamental pitch perception as compared to the lower-pitched instruments. However, the pitch perception preference was not significantly different between musicians and nonmusicians ($F_{1,462} = 2.6$, n.s.).

Musical sounds from percussive and high-pitched instruments all exhibit a short attack time[13,14] (i.e., raise time of the amplitude envelope) in the time range of 20–50 ms, whereas lower-pitched instruments typically show attack times of 100–300 milliseconds. These time ranges fit excellently with the timescales of temporal sensitivity in lHG and may also be reflected in the separation of transient and sustained AC activity.[15] As a consequence, the pronounced left lHG of percussionists and guitarists may lead to the predilection of impulsive short tones with rapid decay. By contrast, the large right lHG of singers or string players may facilitate the processing of slower sustained tones, including characteristic spectral information in the form of natural resonances like formants or vowels in the singing voice.[16] Accordingly, the rightward lateralization of voice processing has been demonstrated by functional imaging.[17]

In FIGURE 3 we show a large collection of individual 3D-reconstructed auditory cortices[4] of both musicians and nonmusicians (bottom). Fundamental pitch listeners were grouped left of the dashed line and spectral pitch listeners right of the dashed line. This grouping is already consistent with the standard seating arrangement of a modern symphony orchestra. In an orchestra, the first violins are positioned to the conductor's left, the lower strings to the right. The woodwinds form a center square directly behind the strings, followed by brass and percussion. Historically, trumpets and timpani have been placed together to play fanfares, even before the time of Beethoven.[18] Conductors were predominantly fundamental pitch listeners. Special arrangements may include a choir or solo instruments (e.g., piano, harp, or organ). Overall, percussive or higher-pitched solo instruments are placed more to the left in the orchestra and lower-pitched melody instruments more to the right.

Detailed interviews regarding musical qualifications and the intensity of musical practice revealed that musical performance depends on pitch perception preference. Thus, listeners with a different type of pitch perception who prefer the same instrument may differ in musical performance style.

Our data demonstrated, furthermore, that the absolute size of the neural HG substrate depended strongly on musical ability.[4,19] First, individual segmentation and

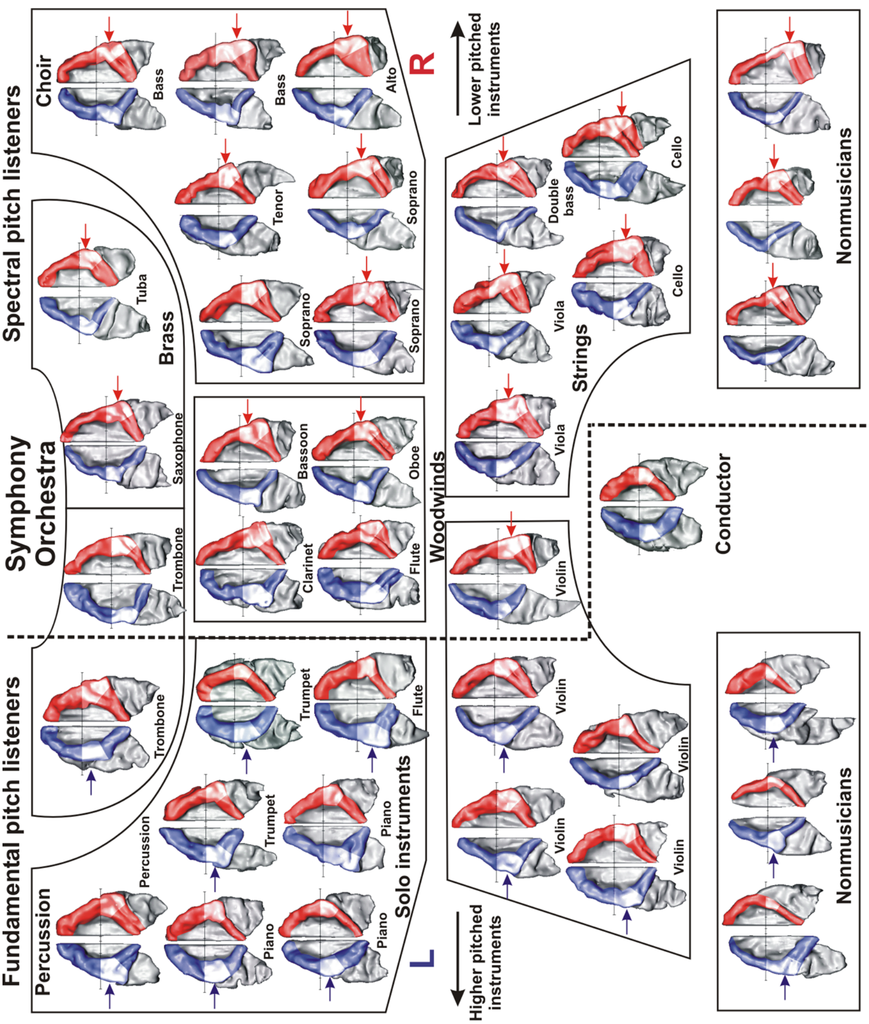

FIGURE 3. *See opposite page for legend.*

3D-reconstruction of the AC revealed that the gray matter volume of HG and anterior supratemporal gyrus was twofold larger in professional musicians as compared to nonmusicians.[4,19] Second, the magnitude of the auditory-evoked P50m activity in response to harmonic complex tones as measured by MEG was, on average, fivefold larger in professional musicians as compared to nonmusicians. However, this effect vanished completely for the subsequent prominent N100m activation. To understand these large group–specific differences in relation to musical ability, we collected in detail from all 463 subjects the individual histories of musical training, and performed the Advanced Measure of Music Audiation (AMMA) test of Edwin E. Gordon.[20] According to Gordon, musical aptitude represents the potential to learn music and stabilizes prior to the outset of intensive musical education at the age of about nine years. Furthermore, musical aptitude was related to *audiation*, a term coined by Gordon, which means "to hear and comprehend music for which the sound is not physically present." Thus, the result of the AMMA test may be linked to auditory imagery.

The volume of gray matter in both the HG and supratemporal gyrus correlated strongly with the tonal score of the AMMA test. Thus, the neural substrate subserving musical aptitude and audiation may reside in the HG and may not be largely modified by long-term musical performance throughout life. By contrast, the auditory-evoked P50m magnitude in lHG only correlated strongly with long-term musical practice. Therefore, our data suggest a functional–structural dissociation between long-term musical training and musical aptitude in the AC of musicians and nonmusicians.

In conclusion, our psychoacoustic data provide evidence that the perceptual mode of listening may have an impact on preference of timbre, tone, and size of particular musical instruments and in particular on musical performance. Interestingly, the perceptual mode may be predicted by MRI and MEG studies of the asymmetry and absolute magnitude of structure and function of the auditory cortex.

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FIGURE 3. Individual HG morphometry of orchestra musicians. The classification in fundamental pitch and spectral pitch listeners (left/right to the *dashed line*) is consistent with a typical symphony orchestra seating arrangement. Fundamental pitch listeners exhibit a larger left lHG and spectral pitch listeners a larger right lateral Heschl's gyrus in most cases (*highlighted, arrows*). Percussive and high-pitched instruments are placed more to the left and low-pitched instruments more to the right. Furthermore, professional musicians showed significantly increased gray matter volume within the anterior part of the auditory cortex (*gray shaded part, top–bottom*) irrespective of asymmetry (*left–right*).

[Competing interests: The authors declare that they have no competing financial interests.]

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