Harmonic relationships influence auditory brainstem encoding of chords

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The cortical processing of musical sounds is influenced by listeners' sensitivity to the structural regularities of music, and particularly by sensitivity to harmonic relationships. As subcortical and cortical processing dynamically interact to shape auditory perception in an experience-dependent manner, we asked whether subcortical processing of musical sounds would be sensitive to harmonic relationships. We examined auditory brainstem responses to a chord that was preceded either by a harmonically related chord, by an unrelated chord, or was repeated. We observed higher spectral response magnitudes in the related than in the unrelated or repeated conditions, for both musician and nonmusician listeners. Our results suggest that listeners' implicit knowledge of musical regularities influences subcortical auditory processing. *NeuroReport* 22:504–508 © 2011 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

Music is a complex, highly structured, auditory stimulus. Western music sequences follow organizational principles often considered analogous to linguistic syntax [1,2]. These musical structures shape perception even in listeners without musical training [3]. Listeners are thought to acquire an implicit knowledge of musical structures by learning the statistical regularities underlying them [4,5]. Consistent with this idea, sensitivity to musical structures emerges in children at approximately 5 years of age [6]. Taken together, these results imply that music processing can provide a window into the neural mechanisms underlying the learning of and sensitivity to the structural regularities of our auditory environment.

One principle that is paramount to musical structures is the harmonic relationship between events. Two chords are said to be harmonically related if they share parent keys (e.g., C-major and G-major chords both belong to the parent key of F). The influence of harmonic relationships on behavioral and neurophysiological processes has been studied extensively. The perceptual processing of a chord is facilitated if it is preceded by a harmonically related chord [7,8] or, in longer sequences, if it is related to the key of its presentation context [5–9]. Harmonic relationships also modulate event-related potentials (e.g., right anterior negativities [10,11], N5 components [12], and P3-like components [13]) and neural activity in several cortical areas (e.g., superior temporal gyrus and rostromedial prefrontal cortex [14]). Given that harmonic relationships influence perceptual and cortical processes, we asked whether they also modulate neural processing subcortically.

There is a growing evidence that subcortical auditory processing interacts dynamically with cortical processes via the corticofugal pathway to shape auditory perception in an experience-dependent manner [15,16]. Human subcortical function is thought to be shaped by top–down processes on multiple time scales ranging from the immediate context [17], a short-time scale (90 min) [18], short-term training (weeks) [19], and lifelong linguistic [20] and musical experience [21]. Given that the sensitivity to harmonic structure is considered to originate predominately from top–down effects reflecting listeners' lifelong exposure to musical structures [2,4,5], our subcortical testing approach offers a unique opportunity to investigate whether this lifelong exposure to music modulates this aspect of auditory processing.

One potential confound, however, when studying the processing of harmonic relationships is that two harmonically related chords share more spectral components than two unrelated chords. Consequently, if a chord's subcortical processing was influenced by its immediate predecessor, this influence could be interpreted as a bottom–up (signal-based) effect reflecting processing of acoustic similarity rather than a top–down (cognitive) effect reflecting listeners' implicit knowledge of musical structure. For example, a heightened neural response to a

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C chord preceded by a G chord (harmonically related) compared with the same C chord preceded by an F-sharp chord (harmonically unrelated) could be explained more parsimoniously by acoustic similarity (G and C chords have a note in common, whereas the F-sharp and C do not) than by listeners' implicit knowledge. In this study, we investigated whether the brainstem encoding of a musical chord is influenced by its immediate presentation context when the harmonic relationship between the target chord and its predecessor was varied. The target chord, always the same, was preceded either by a harmonically related chord or by an unrelated chord. Our primary hypothesis was that brainstem encoding of the target chord would be enhanced when preceded by a harmonically related chord compared with when preceded by an unrelated chord. To examine whether the effect was driven by processes linked to listeners' implicit knowledge or by processes linked to the greater acoustic similarity between harmonically related than between unrelated chords, we included a third condition in which the target chord was repeated. If acoustic similarity were driving the subcortical modulation, then it would be the largest in the repeated condition in which both chords are identical relative to the related and unrelated conditions. If, on the other hand, the modulation was the largest in the related condition, then this would support a top–down explanation, in line with previous studies that have shown facilitated processing for harmonically related chords [7,8,22].

Finally, we investigated the effect of musical expertise by including musician and nonmusician groups. Although behavioral studies of musical structures have consistently found the same effects for musicians and nonmusicians [3], the effects of harmonic structure on event-related potentials are inconsistent in that they have either: only been observed in musicians [12], been found to be larger in musicians than in nonmusicians [10], or have been found to be the same in musicians and nonmusicians [13]. On this basis, we expected musicians and nonmusicians to show the same patterns of results, but with potentially more pronounced effects for musicians than for nonmusicians.

Materials and methods

Participants

Nineteen adults participated in this study. All participants had audiometric thresholds at or below 20 dB hearing level for octaves from 0.125 to 8 kHz. Ten participants were categorized as musicians (mean age, 23.2 ± 4.2 years; mean instrumental practice, 14.9 ± 5.5 years; at least 11 years of continuous contemporary instrumental practice; starting age of practice, 5.7 ± 2.0 years), and nine participants were categorized as nonmusicians (mean age, 24.4 ± 3.9 years; mean instrumental practice, 0.8 ± 0.8 years; no more than 2 years of instrumental practice at any time in their lives; ending age of practice when applicable, 11.8 ± 1.9 years). The research protocol was approved by the Institutional Review Board of Northwestern University.

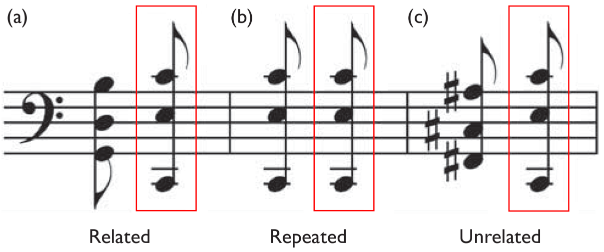
Stimuli

A C chord (hereafter referred to as the target chord) was presented in three conditions: preceded by a G chord (related condition), by an F-sharp chord (unrelated condition), or by the same C chord (repeated condition; Fig. 1). The G and C chords are harmonically related because they share parent keys. In addition, the G–C progression forms the core of a perfect cadence, one of the most important musical structures in Western music. Conversely, the F-sharp and C chords are unrelated because they do not share a parent key, and this progression is virtually unused in Western music. Finally, the repeated condition (repeated C chord) does not form a harmonic progression and was used as a control for the effect of acoustic similarity. The chords, played by a virtual tuba, were created with Finale 2008 (MakeMusic, Inc., MakeMusic, Eden Prairie, Minnesota, USA). Each chord was 150 ms long, separated by 30 ms of silence.

Procedure

The three conditions were presented in three separate testing blocks, with block order counterbalanced across participants. The chord pairs were presented binaurally with Neuroscan Stim2 (Compumedics, Charlotte, North Carolina, USA) through electromagnetically shielded insert earphones (ER3; Etymotic Research, Elk Grove Village, Illinois, USA) at an intensity of 70 dB sound pressure level, in alternating polarities. The interval between chord pairs was randomized between 203 and 223 ms. Each chord pair was presented approximately 4000 times, with approximately 2000 of each stimulus polarity. Responses were differentially recorded using Scan 4.3 (Compumedics) with Ag/AgCl scalp electrodes placed at Cz (active), earlobes (linked reference), and forehead (ground).

Fig. 1



Chord pairs used. The second chord (target chord, in red box) was always the same C chord (component notes, from low to high: C2, E3, C4). The first chord was either: a G chord (component notes: G2, D3, B3) in the related condition (a), a C chord in the repeated condition (b), or an F-sharp chord (component notes: F2-sharp, C3-sharp, A3-sharp) in the unrelated condition (c).

Contact impedance was lower than 5 kΩ. The experiment lasted for approximately 2 h per participant. To facilitate a wakeful yet restful state, participants watched a muted movie of their choice with subtitles during testing.

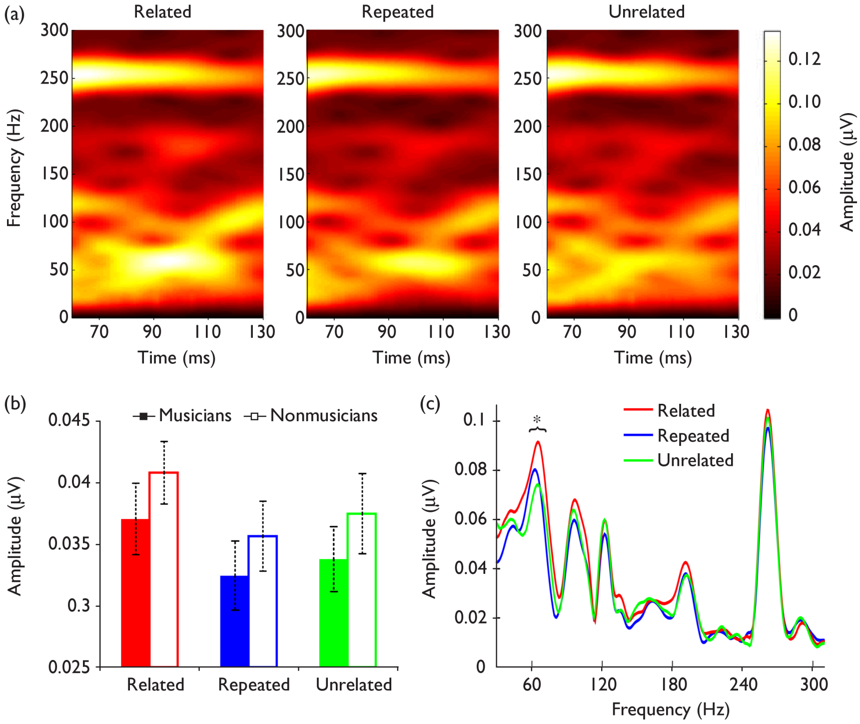
Data analysis

Filtering, artifact rejection, and averaging were performed offline using Scan 4.3. Responses were bandpass filtered from 30 to 2000 Hz (24 dB/octave roll off), and sweeps with activity greater than ± 35 μV were considered artifacts and rejected. The remaining sweeps were averaged with a time window spanning 40 ms before the onset of the first chord in the pair and 10 ms after the offset of the second chord in the pair. Responses to each stimulus polarity were added together to minimize the stimulus artifact and cochlear microphonic.

Neural responses to the target chord were analyzed in the frequency domain. On account of the confound of the nonperiodic attack information that relates to stimulus timbre [23] the initial 30 ms of the responses were excluded from the analyses. Short-time Fourier transforms on overlapping 60 ms windows (overlap, 59 ms) were calculated over the 30–160 ms portion of the response and regions of interest were visually identified. As the responses' spectral components were predominantly found below 300 Hz (reflecting the low-pass characteristic of the brainstem response), we restricted our frequency analyses to focus on the 30–300 Hz range. Fast Fourier transforms over the 30–300 Hz frequency range, as well as specific frequency bands of interest (55–75, 87–107, 112–132, 181–201, and 251–271 Hz) that related to the frequency components of the stimulus, were calculated for each participant in each condition. All spectrograms and spectra were computed in MATLAB (The Mathworks, Natick, Massachusetts, USA) using custom routines.

Statistical differences were assessed by 3 × 2 analyses of variance with harmonic relationship (related/repeated/unrelated) as a within-participant factor and expertise (musicians/nonmusicians) as a between-participants factor. The Greenhouse-Geisser correction was used for the harmonic relationship factor. Two-tailed paired *t*-tests were used for pairwise comparisons.

Fig. 2



Spectral analysis of the brainstem responses to the target chord. (a) Spectrograms calculated on the steady-state part of the brainstem responses (between 30 and 160 ms). The spectrograms were calculated on overlapping sliding windows of 60 ms each. The first window encompassed 30 to 90 ms and the last encompassed 100 to 160 ms. Windows are plotted as a function of the center of the sliding windows. Spectral components were concentrated below 300 Hz, hence the plotting between 0 and 300 Hz. (b) Average spectral magnitude over 30–300 Hz in the three conditions and for musicians and nonmusicians. A main effect of harmonic relationship was found but no effect of expertise was observed. Error bars represent one standard error. (c) Spectra computed over the steady-state part of the brainstem response, showing the individual frequency components present in the response between 30 and 300 Hz. Harmonic relationship modulated the amplitude of the lowest component; *65 Hz, which corresponds to the fundamental frequency of the lowest note of the target chord.

Results

Subcortical responses to the target chord depended on the harmonic relationship between the target chord and the preceding sound. Spectral magnitudes averaged over the 30–300 Hz range were modulated by harmonic relationship [$F(2,34) = 10.26$; $P < 0.001$; $\eta_p^2 = 0.38$] (Fig. 2a and b), with the averaged spectral magnitude being higher in the related condition relative to either the unrelated [$t(18) = 2.99$; $P < 0.01$] or the repeated condition [$t(18) = 4.08$; $P < 0.001$]. The repeated and unrelated conditions were not statistically different [$t(18) = 1.77$; $P = 0.09$]. No effect (neither main nor interaction) was found for expertise (Fig. 2b; all Fs < 1).

Analyzing each frequency component individually (Fig. 2c) showed that the observed modulation of spectral magnitudes was driven by the F_0 of the lowest note of the target chord ($F_0 = 65$ Hz, fundamental frequency of the C2 note), given that the 55–75 Hz region was the only band showing significant differences [$F(2,34) = 4.64$; $P < 0.05$; $\eta_p^2 = 0.22$]. Consistent with the effects reported above, the spectral magnitude of the 55–75 Hz band was larger in the related than in the unrelated [$t(18) = 2.82$; $P < 0.05$] and in the repeated condition [$t(18) = 2.35$; $P < 0.05$], but the repeated and unrelated conditions were not statistically different [$t(18) = 0.38$; $P = 0.71$].

Discussion

Summary

Here, we provide evidence that brainstem encoding of musical sounds is sensitive to harmonic relationships between chords, one of the main structural principles of Western music. The harmonic relationship between the target and the preceding chord modulated the spectral magnitude of the brainstem response to the target chord, with both musicians and nonmusicians showing higher spectral magnitudes in response to the target chord in the related condition than in the repeated and unrelated conditions. These results suggest that listeners' subcortical encoding of musical sounds is influenced by the structural regularities of music and that this influence does not depend on listeners' musical expertise. Previous studies have shown that the brainstem is sensitive to acoustic features relevant to music perception (i.e., consonance/dissonance) [23,24] as well as to the auditory presentation context [17,18]. Our data extend these findings by showing that subcortical responses are sensitive to the contextual cues relevant for music perception.

Top–down versus bottom–up effects

This study used a repeated-chord paradigm to examine whether the effect of harmonic relationships was driven by top–down (cognitive) processes linked to listeners' implicit knowledge of musical structures or by bottom–up (signal-based) processes linked to acoustic similarity between chords. As the two chords of the related condition are acoustically more similar than the two chords of the unrelated condition, our finding of larger spectral magnitudes in the related, relative to the unrelated, condition could be explained by acoustic similarity. In this scenario, enhanced encoding would be driven by the physical similarity between the chord pairs. However, if acoustic similarity were implicated, then spectral magnitudes should have been the greatest in the repeated condition, in which the two chords are identical. This is not the case; the smaller spectral magnitudes in the repeated relative to the related condition thus speaks against an acoustic similarity account of our effect and favours a top–down interpretation linked to listeners' implicit knowledge of harmonic relationships. Additional support for a top–down interpretation is that the observed effect was evident primarily for the target chord's fundamental frequency. This frequency was not part of the preceding chord in the either related or unrelated conditions and thus its modulation cannot be accounted for by acoustic overlap between the chords. In conclusion, we posit that our effect was driven by cognitive top–down processes and not by acoustic similarity, consistent with previous investigations of music structures' processing in behavioral [5,9,22] and cortical studies [10,13].

No physiological differences were observed between the musician and nonmusician listeners, despite previous research documenting a musician advantage for the subcortical encoding of speech and music sounds [21]. However, we did not focus on the strength of brainstem encoding of music sounds, but rather on how the encoding of a musical sound is influenced by the harmonic relationships between the sound and its immediate context. It is well known that nonmusicians are sensitive to the structural regularities of music, and particularly to harmonic relationships [3]. Previous electrophysiological research on listeners' sensitivity to harmonic relationships has found that unrelated chords often elicit the same event-related potentials in nonmusicians and musicians [10,13]. This does not preclude the possibility that musically trained individuals could exhibit distinctive enhancements to more harmonically complex sound sequences. Nevertheless, based on the findings presented here, it would appear that listeners acquire sensitivity to basic structural regularities of music implicitly, through passive, lifelong exposure to music, independently of formal music training [4,5]. Our present finding strengthens the view that daily life exposure shapes auditory perception independently of listeners' formal musical expertise.

Previous investigations of music structural regularities have drawn comparisons with the processing of linguistic syntax [1,14], by presenting evidence of shared cortical resources for processing linguistic syntax and the structural regularities of music. In addition, statistical learning studies have suggested that similar learning processes may be at play when acquiring knowledge of musical and linguistic structures [25]. Although we used simple musical structures in this study (i.e., pairs of chords), manipulating the harmonic relationship between chords could be compared with a syntactic manipulation as syntax refers to the principles governing the combination of discrete structural elements into sequences [2]. This study suggests that the investigation of shared processing mechanisms between music and linguistic syntax manipulation can be fruitfully pursued at the subcortical level.

Conclusion

Our results show that brainstem responses are modulated by harmonic relationships. This effect occurs irrespective of music expertise suggesting that listeners' implicit knowledge of music structures shapes subcortical neurobiological processing of sound.

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