



Functional organization for musical consonance and tonal pitch hierarchy in human auditory cortex



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ARTICLE INFO

Article history:

Accepted 5 July 2014

Available online 12 July 2014

Keywords:

Auditory event-related potentials (ERPs)

Musical tonality

Pitch-onset response (POR)

Pitch perception

Neural organization

ABSTRACT

Pitch relationships in music are characterized by their degree of consonance, a hierarchical perceptual quality that distinguishes how pleasant musical chords/intervals sound to the ear. The origins of consonance have been debated since the ancient Greeks. To elucidate the neurobiological mechanisms underlying these musical fundamentals, we recorded neuroelectric brain activity while participants listened passively to various chromatic musical intervals (simultaneously sounding pitches) varying in their perceptual pleasantness (i.e., consonance/dissonance). Dichotic presentation eliminated acoustic and peripheral contributions that often confound explanations of consonance. We found that neural representations for pitch in early human auditory cortex code perceptual features of musical consonance and follow a hierarchical organization according to music-theoretic principles. These neural correlates emerge pre-attentively within ~150 ms after the onset of pitch, are segregated topographically in superior temporal gyrus with a rightward hemispheric bias, and closely mirror listeners' behavioral valence preferences for the chromatic tone combinations inherent to music. A perceptual-based organization implies that parallel to the phonetic code for speech, elements of music are mapped within early cerebral structures according to higher-order, perceptual principles and the rules of Western harmony rather than simple acoustic attributes.

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Introduction

Western music practice stipulates that constituent tones which form its scales and tonal structure carry different weight, or importance, within a musical framework (Aldwell and Schachter, 2003; Rameau, 1722/1971). Consequently, different pitch combinations (e.g., intervals, chords) follow a hierarchical organization in accordance with their functional role in musical composition (Krumhansl, 1990). Tonal pairs associated with stability and finality are regarded as consonant while those associated with instability (i.e., requiring resolution) are deemed dissonant. Given their anchor-like function in musical contexts, consonant relationships tend to occur more frequently in tonal music (Budge, 1943; Vos and Troost, 1989), are preferred by listeners relative to their dissonant counterparts (Bidelman and Krishnan, 2009; Kameoka and Kuriyagawa, 1969b; McDermott et al., 2010; Plomp and Levelt, 1965; Schwartz et al., 2003), and consequently carry higher status in both music-theoretic and perceptual-cognitive ranking (Aldwell and Schachter, 2003; Itoh et al., 2010; Krumhansl, 1990; Malmberg, 1918; Rameau, 1722/1971). It is the hierarchical organization and ebb

and flow between these perceptual-cognitive attributes which produce the sense of musical key and pitch structure intrinsic to Western tonal music (Rameau, 1722/1971).

Given its fundamental role in music, the origins of musical consonance have enjoyed a rich history of explanations developed over many centuries. These accounts have ranged from the purely mathematical and acoustical factors noted by ancient Greek scholars (e.g., frequency ratios of two vibrating bodies) (Galilei, 1638/1963; Gill and Purves, 2009) to psycho-physiological properties of the peripheral auditory system (e.g., cochlear filtering and auditory masking) (Helmholtz, 1877/1954; Plomp and Levelt, 1965) [for review, see Bidelman (2013)]. Modern neuroimaging studies have challenged many of these long-held beliefs by demonstrating that when acoustic or peripheral factors are controlled (which typically covary with perceived consonance), brain activity provides a sufficient basis to account for the fundamental organizational principles of tonal music (Bidelman, 2013; Bidelman and Krishnan, 2009; Itoh et al., 2010). Both human (scalp-recorded potentials) and animal (intracellular) electrophysiological recordings reveal preferential encoding of consonant relative to dissonant pitch relationships (Bidelman and Heinz, 2011; Bidelman and Krishnan, 2009, 2011; Tramo et al., 2001). Moreover, listeners' behavioral preferences for intervallic and chordal harmonies (i.e., simultaneously sounding pitches) are well predicted based on underlying

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sensory pitch representations along the early auditory pathway (rostral brainstem and auditory nerve) (Bidelman and Heinz, 2011; Bidelman and Krishnan, 2009). These studies demonstrate that nascent features of tonal structure and musical pitch hierarchy are present in the earliest (pre-attentive) stages of the auditory system in neurocomputations operating below conscious awareness.

Multichannel event related potentials (ERPs) provide direct assays of neuronal activity and thus, the potential to further clarify the nature of cerebral mechanisms engaged in processing musical pitch relations. Prominent ERP components elicited by auditory stimuli emerge within a few hundred milliseconds following stimulus onset (e.g., the classic P1–N1–P2–N2) and are thought to reflect initial sound processing in early auditory cortical fields within the supratemporal plane (Picton et al., 1999; Scherg et al., 1989). Employing these obligatory responses, neural correlates of musical consonance/dissonance have been identified in the latency of the P2–N2 complex, ~200–300 ms after the onset of sound (Habibi et al., 2013; Itoh et al., 2010). However, these components are both generated and modulated by a wide range of stimuli and largely reflect the encoding of energy onset (Näätänen and Picton, 1987) in addition to any one specific acoustic feature (e.g., musical pitch).

To disentangle overlapping obligatory onset responses from those specific to pitch, Krumbholz et al. (2003) designed a novel stimulus paradigm in which a continuous sound is constructed from a segment of noise followed by a segment of iterated rippled noise (IRN). IRN is created by delaying broadband noise and adding it back onto itself matched in intensity and overall spectral profile. This delay-and-add process yields a noisy pitch percept corresponding to the reciprocal of the time delay (d), whose perceptual salience scales with the number of iterations (n) (Yost, 1996).¹ The recursion process produces temporal regularity in the noise and a sinusoidal ripple in its long-term power spectrum yielding a harmonically rich sound. Yet, IRN lacks a prominent temporal envelope and does not produce typical cochlear place cues (e.g., prominent peaks in the excitation pattern) associated with most pitch bearing signals (see Fig. 1 in Krumbholz et al., 2003). Concatenating IRN with a preceding noise yields a salient perceptual change at the transition; the percept smoothly changes from a “hiss” (noise segment) to a musical note with distinct pitch (IRN segment).

This stimulus design offers two important advantages for studying musical pitch: (1) the segments differ only in a single acoustic parameter (periodicity) and thus isolate the percept of interest, i.e., pitch; (2) the segmentation (i.e., noise → IRN) allows for the temporal separation of the onset of pitch from the onset of the stimulus energy as a whole thereby disentangling the response to these two events. Neuromagnetic (MEG) responses to these stimuli show clear onset components, reflecting an obligatory response to the initial noise segment and further response deflections following the initiation of pitch (Gutschalk et al., 2002, 2004; Krumbholz et al., 2003). This so-called pitch onset response (POR) is thought to reflect cortical activity to pitch-bearing information.² This is suggested by its response properties and neuroanatomical generators. Studies demonstrate a strong dependence of POR latency and magnitude on specific features of pitch (e.g., salience, fundamental

frequency). An earlier, more robust POR is generated by salient pitch percepts whereas a smaller, delayed response is evoked by weaker pitch percepts (Krumbholz et al., 2003; Seither-Preisler et al., 2006). Strikingly similar responses are produced by either monaurally or binaurally (e.g., Huggins pitch) generated pitch, suggesting that even disparate pitch percepts converge into a common cortical representation reflected by the POR (Chait et al., 2006; Hertrich et al., 2005). Finally, source analyses (Gutschalk et al., 2002, 2004; Krumbholz et al., 2003) corroborated by human depth electrode recordings (Schonwiesner and Zatorre, 2008) indicate that POR generators are localized to the anterolateral portion of Heschl's gyrus (HG), the putative site of pitch processing and pitch sensitive neurons (Bendor and Wang, 2005; Griffiths et al., 1998; Johnsrude et al., 2000; Penagos et al., 2004; Zatorre, 1988). Given both its sensitivity and consistency across a number of studies, the POR offers an ideal window for studying early cortical representations of musical pitch relationships. To our knowledge, this is the first study to systematically examine the effects of musical pitch attributes (consonance/dissonance) on the neuroelectric POR response.

To this end, we recorded cortical POR responses while participants listened passively to dyadic (two-note) musical intervals varying in their degree of consonance/dissonance. In previous attempts to decipher their neural basis, it is often unclear whether the alleged brain correlates reflect an underlying percept or merely changes in neural activity that covary with stimulus acoustics or byproducts of phenomena propagated from the auditory periphery [e.g., cochlear beating, roughness] (Bidelman, 2013). Our stimulus paradigm included two controls to safeguard against such confounds. First, intervals were presented to listeners dichotically (one note to each ear). While dichotic presentation does not alter musical consonance percepts, critically, it removes acoustic and peripheral factors (e.g., beating/roughness) that often cloud interpretation of its origins (Bidelman, 2013; McDermott et al., 2010). Additionally, we adopted the novel noise → pitch stimulus paradigm introduced above to temporally offset musical pitch intervals from the overall onset of acoustic stimulus energy. These stimuli repress obligatory neural activity that dominates auditory evoked responses and isolates a pitch-specific cortical activity (Krumbholz et al., 2003). Under the hypothesis that chromatic intervals are represented in the brain according to music-theoretic and/or perceptual principles, we expected the magnitude of early cortical activity to follow hierarchical relations of musical pitch structure and predict listeners' subsequent behavioral consonance judgments. Source reconstruction of neural responses probed whether the spatial encoding of music is based on feature based scheme following the perceptual construct of consonance. The latter would indicate that musical pitch intervals are mapped according to their perceptual rather than rudimentary acoustic features, paralleling the abstract phonetic organization observed for speech (Gutschalk and Uppenkamp, 2011; Scharinger et al., 2011; Shestakova et al., 2004).

Methods

Participants

Nine, normal-hearing adults participated in the experiment (3 females). All participants were strongly right-handed as measured by the Edinburgh Handedness Inventory (laterality: $97.2 \pm 6.2\%$) (Oldfield, 1971), had a similar level of education ($\mu \pm \sigma$: 20.7 ± 1.95 years), and were monolingual speakers of American English. We recruited listeners with musical training (18.9 ± 7.1 years) given their larger auditory evoked potentials (Bidelman et al., 2011b,c; Itoh et al., 2010; Zendel and Alain, 2014), and hence, better response signal-to-noise ratio necessary for accurate source localization. It should be noted, however, that consonance ratings are largely independent of musical training; both musicians and nonmusicians show similar behavioral preferences (Bidelman and Krishnan, 2009, 2011; McDermott et al., 2010) and cortical ERPs to musical pitch intervals (Itoh et al.,

¹ The manipulation of pitch via IRN periodicity is fundamentally different than the effects of simply adding noise to a pitched signal (e.g., complex tone). The former alters the internal representation of the pitch itself while the latter primarily alters detectability (Gockel et al., 2006).

² Recent debate in the neuroimaging literature questions the use of IRN in studying the neural correlates of pitch. fMRI studies argue that the cortical response to IRN may not be driven to pitch *per se*, but rather other complex acoustic features inherent to IRN (e.g., spectrotemporal flux; Barker et al., 2011; Hall and Plack, 2009). Yet, our recent EEG study confirms that the cortical POR response to IRN indexes changes in pitch rather than other latent acoustic features of IRN, e.g., slow spectrotemporal flux (Krishnan et al., 2012). The ability of neuroelectric (EEG) but not hemodynamic (fMRI) responses to reflect the perceptual dimension of pitch was also confirmed in a recent study directly comparing the two techniques using the same pitch stimuli; BOLD signals (an indirect measure of neural activity) were shown to reflect only slow, non-pitch-specific stimulus fluctuations whereas EEG/MEG coded stimulus features specific to pitch operating at a millisecond resolution (Steinmann and Gutschalk, 2012).

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