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Short communication

Differential sensitivity to changes in pitch acceleration in the auditory brainstem and cortex

Ananthanarayan Krishnan, Chandan H. Suresh, Jackson T. Gandour *

Department of Speech Language Hearing Sciences, Purdue University, USA

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A B S T R A C T

The cortical pitch-specific response (CPR) is differentially sensitive to pitch contours varying in rate of acceleration—time-variant Mandarin Tone 2 (T2) versus constant, linear rising ramp (Linear)—as a function of language experience (Krishnan, Gandour, & Suresh, 2014). CPR and brainstem frequency following response (FFR) data were recorded concurrently from native Mandarin listeners using the same stimuli. Results showed that T2 elicited larger responses than Linear at both cortical and brainstem levels (CPR: Na–Pb, Pb–Nb; FFR). However, Pb–Nb exhibited a larger *difference* in magnitude between T2 and Linear than either Na–Pb or FFR. This finding highlights differential weighting of brain responses elicited by a specific temporal attribute of pitch. Consistent with the notion of a distributed, integrated hierarchical pitch processing network, temporal attributes of pitch are differentially weighted by subcortical and cortical level processing.

1. Introduction

There is now increasing recognition that the effects of language experience can occur at many levels of sensory, perceptual and cognitive processing that implicate pre-categorical representations (Iverson, Wagner, & Rosen, 2016, and references therein). We also have a better understanding of the effects of language experience on pre-categorical representations at the level of the brainstem and auditory cortex (for reviews, Chandrasekaran & Kraus, 2010; Chandrasekaran, Skoe, & Kraus, 2014; Kraus & Banai, 2007; Kraus & White-Schwoch, 2015; Krishnan & Gandour, 2009, 2014; Krishnan, Gandour, & Bidelman, 2012). Indeed, the brainstem has generally been accepted to be part of a distributed, integrated circuit in language processing that involves both subcortical as well as cortical structures.

Pitch is an auditory perceptual attribute that plays an important role in the perception of speech, language and music. The scalp-recorded brainstem frequency following response (FFR) and the cortical pitch response (CPR) represent pitch-relevant neural activity at brainstem and cortical levels, respectively. The scalp-recorded FFR reflects sustained phase-locked activity in a population of neural elements within the rostral brainstem (Chandrasekaran & Kraus, 2010; Krishnan, 2007) that has been shown to preserve pitch relevant information (Krishnan, 2007; Krishnan & Gandour, 2014). The CPR, similar to the MEG-derived pitch onset response (POR), reflects pitch-specific synchronized neural activity in the auditory cortex. Source analysis (Gutschalk, Patterson, Rupp, Uppenkamp, & Scherg, 2002; Krumbholz, Patterson, Seither-Preisler, Lammertmann, & Lutkenhoner, 2003)—corroborated by human depth electrode recordings (Griffiths et al., 2010; Schonwiesner & Zatorre, 2008)—indicates that the POR is localized to the anterolateral portion of Heschl's gyrus, the putative site of pitch processing (Johnsrude, Penhune, & Zatorre, 2000; Penagos, Melcher, & Oxenham, 2004). The CPR, in addition, is characterized by multiple transient components that may index different temporal attributes of pitch contours (Krishnan, Gandour, Ananthakrishnan, & Vijayaraghavan, 2014; Krishnan, Gandour, & Suresh, 2014). Simultaneous recording of brainstem FFR and cortical CPR responses affords us a window to make a direct comparison of changes in magnitude of pitch relevant neural activity for each cortical and subcortical component. Such comparisons make it possible to draw inferences about their respective roles in the encoding of temporal pitch attributes.

* Corresponding author at: Purdue University, Department of Speech Language Hearing Sciences, Lyles-Porter Hall, 715 Clinic Drive, West Lafayette, IN 47907, USA.
E-mail addresses: rkrish@purdue.edu (A. Krishnan), hs0@purdue.edu (C.H. Suresh), gandour@purdue.edu (J.T. Gandour).

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An important temporal attribute of dynamic, curvilinear pitch contours is acceleration rate. Using stimuli that differ in acceleration rate, time-variant vs. constant, language experience effects are not evident in FFR responses to linear rising and falling ramps (Xu, Krishnan, & Gandour, 2006) or even trilinear rising ramps (Krishnan, Gandour, Bidelman, & Swaminathan, 2009). A language-dependent effect, however, is observed in FFR responses when Mandarin listeners, relative to English, are presented with a native lexical tone (Tone 2, T2), a curvilinear pitch contour with changing rate of acceleration. As reflected by CPR components Na–Pb and Pb–Nb (Krishnan et al., 2014), Mandarin listeners show greater peak-to-peak amplitude than English in response to T2 only. Other CPR experiments consisted of stimuli varying in acceleration rate that were not designed to address specifically the question of changing vs. constant acceleration rates. In Krishnan, Gandour, Ananthakrishnan, and Vijayaraghavan (2015), acceleration rates covaried with stimulus duration; with pitch direction and location of peak acceleration (Krishnan, Gandour, & Suresh, 2015b); and with stimuli that fell inside and outside the normal voice range (Krishnan, Gandour, & Suresh, 2015a). In those experiments, amplitude of neural responses recorded at a frontocentral scalp location (Fz) is larger in Mandarin than English listeners as reflected by both Na–Pb and Pb–Nb. Thus, pitch encoding at both subcortical and cortical levels is acutely sensitive to changes in acceleration rate throughout the duration of native lexical tones.

CPR components have been shown to be differentially-weighted in their sensitivity to particular temporal attributes of pitch. Another well-known attribute of pitch is its *salience*, which is closely related to the strength of temporal periodicity in the stimulus waveform. Using a nonspeech homolog of T2, parametric variation of pitch salience from weak to strong pitch was manipulated by holding acceleration constant (Krishnan, Gandour, & Suresh, 2016). A language-dependent advantage for Mandarin listeners is restricted to the Na–Pb component only. This restriction to Na-Pb suggests that the relative weighting of CPR components vary depending on the sensitivity of neural activity within a particular temporal window to a specific attribute of pitch. In the same study, regardless of language experience, a direct comparison of cortical and brainstem responses further reveal different patterns of relative changes in magnitude along the pitch salience continuum (FFR, monotonic; CPR, non-monotonic). Such patterns suggest that certain attributes of pitch are processed differentially at separate levels along the auditory pathway. In Krishnan et al. (2014), T2 is opposed to a linear high rising ramp (Linear). They differ in acceleration rate only, whereas pitch salience and pitch height are fixed. The question remains whether CPR components show differential sensitivity to a time-variant pitch contour relative to one with a fixed rate of acceleration, all else being equal.

Accordingly, the specific aim of this study is to compare the concurrently-recorded cortical CPR data, presented in Krishnan et al. (2014), with brainstem data (FFR). A novel approach enables us to view pitch-relevant neural activity at the cortical and brainstem level concurrently and to draw inferences about nature of their coordination. We chose to restrict this follow-up study to Chinese listeners only because CPR effects elicited by T2 and Linear were larger in Chinese listeners than English (Krishnan et al., 2014). In addition, a direct comparison between corresponding sections of T2 and Linear pitch contours (Krishnan et al., 2009), FFR-derived pitch strength of Chinese listeners—but not English—was larger in just those sections of T2 exhibiting higher degrees of acceleration. Importantly, T2 and Linear share the same pitch onset and offset as well as average pitch acceleration rate. Their shared acoustic properties provide an opportunity to isolate the effects of another temporal attribute of pitch: acceleration rate, time-variant vs. constant. Though changes in pitch salience show that the Na–Pb component separates Chinese from English listeners (Krishnan et al., 2016), we hypothesize that the Pb–Nb component of the CPR shows a relatively greater sensitivity to changes from a constant to a time-variant acceleration when compared to Na–Pb and brainstem FFR. If pitch processing at brainstem and cortical levels is differentially sensitive to acceleration rate, we further expect to see differences in the pattern of relative changes in magnitude among CPR and FFR components.

2. Results

2.1. Response morphology of CPR and FFR components

Grand averaged CPR and FFR response waveforms, elicited by T2 (red) and Linear (blue) pitch contours, are displayed in Fig. 1A and 1B, respectively. CPR components are clearly identifiable. The amplitude of the cortical pitch-relevant components (Na, Pb, Nb) are more robust in response to T2 as compared to Linear. FFR time waveforms show more robust periodicity encoding relative to Linear.

2.2. Response magnitude per component and stimulus

Fig. 1C displays the normalized mean response magnitude of T2 and Linear for each component. Results of a two-way (component × stimulus) ANOVA conducted on normalized amplitude yielded a significant stimulus main effect ($F_{1,18} = 68.78$, $p < 0.0001$, $\eta_p^2 = 0.793$) and a marginally significant interaction effect between component and stimulus ($F_{2,72} = 3.43$, $p = 0.0377$, $\eta_p^2 = 0.087$). The stimulus main effect showed that T2 was larger in amplitude than Linear. By component, simple effects revealed that response magnitude of T2 was larger than Linear irrespective of component. By stimulus, pairwise comparisons of components failed to reach significance. The fact that T2 elicits more robust responses than Linear in both cortical and brainstem structures underscores the ecological relevance of dynamic, curvilinear pitch contours in natural speech.

2.3. Magnitude of difference between T2 and Linear

Fig. 1D shows the normalized magnitude of the difference between T2 and Linear for each component (Na–Pb, Pb–Nb, FFR). A one-way ANOVA yielded a significant component effect ($F_{2,36} = 6.52$, $p = 0.0038$, $\eta_p^2 = 0.266$). Post hoc multiple comparisons showed that Pb–Nb exhibited a larger difference in magnitude than either Na–Pb or FFR. This means that Pb–Nb has heightened sensitivity to changes in rate of acceleration relative to other transient cortical pitch-specific markers as well as to the sustained frequency following response at the level of the brainstem.

3. Discussion

3.1. Transient components of CPR are differentially sensitive to specific temporal attributes of pitch

A comparison with data obtained from an earlier CPR experiment allows us to demonstrate that Na–Pb and Pb–Nb are modulated by differential weighting of particular pitch attributes. These differences in weighting have revealed a relationship between acceleration rate (time-variant, constant) and CPR component (Na–Pb, Pb–Nb). In Krishnan et al. (2016), acceleration rate was uniform across stimuli, whereas pitch salience was varied parametrically from weak to strong. Peak-to-peak amplitude of both Na–Pb and Pb–Nb in the Chinese group gets larger with increasing pitch salience. However, experience-dependent sensitivity to changes in pitch salience is limited to Na–Pb (Chi-