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Research report

Language-experience plasticity in neural representation of changes in pitch salience

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ABSTRACT

Neural representation of pitch-relevant information at the brainstem and cortical levels of processing is influenced by language experience. A well-known attribute of pitch is its *salience*. Brainstem frequency following responses and cortical pitch specific responses, recorded concurrently, were elicited by a pitch salience continuum spanning weak to strong pitch of a dynamic, iterated rippled noise pitch contour—homolog of a Mandarin tone. Our aims were to assess how language experience (Chinese, English) affects i) enhancement of neural activity associated with pitch salience at brainstem and cortical levels, ii) the presence of asymmetry in cortical pitch representation, and iii) patterns of relative changes in magnitude along the pitch salience continuum. Peak latency (Fz: Na, Pb, and Nb) was shorter in the Chinese than the English group across the continuum. Peak-to-peak amplitude (Fz: Na–Pb, Pb–Nb) of the Chinese group grew larger with increasing pitch salience, but an experience-dependent advantage was limited to the Na–Pb component. At temporal sites (T7/T8), the larger amplitude of the Chinese group across the continuum was both limited to the Na–Pb component and the right temporal site. At the brainstem level, F0 magnitude gets larger as you increase pitch salience, and it too reveals Chinese superiority. A direct comparison of cortical and brainstem responses for the Chinese group reveals different patterns of relative changes in magnitude along the pitch salience continuum. Such differences may point to a transformation in pitch processing at the cortical level presumably mediated by local sensory and/or extrasensory influence overlaid on the brainstem output.

1. Introduction

Pitch is a perceptual attribute that plays an important role in the perception of speech, language and music. For many types of complex sounds, including speech and music, pitch and its *salience* is closely related to the temporal periodicity strength in the stimulus waveform fine structure (Shofner, 2002; Yost, 1996a). Iterated rippled noise (IRN) is a complex sound that permits systematic manipulation of the temporal fine structure, and therefore the magnitude of pitch salience. IRN is produced by

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adding a delayed copy of random noise to the original noise and then repeating this delay-and-add process *n* times (Yost, 1996b). Increasing the number of iterations produces an increase in temporal regularity of the noise and a spectral ripple in its long-term power spectrum. Perceptually, IRN yields a pitch corresponding to the reciprocal of the delay (Patterson et al., 1996). Its corresponding pitch salience grows with increasing number of iterations. The increase in pitch salience with increasing temporal regularity of the IRN stimulus is correlated with an increase in pitch-relevant neural activity in both cortical and subcortical auditory neurons as evidenced by data from physiological (Griffiths et al., 1998; Sayles and Winter, 2007); electrophysiological (Krishnan et al., 2010a; Krumbholz et al., 2003; Soeta et al., 2005); functional brain imaging (Griffiths et al., 2001); and intracranial electrode recordings (Schonwiesner and Zatorre, 2008).

Pitch provides an excellent window for studying experience-dependent effects on both brainstem and cortical components of a well-coordinated, hierarchical processing network. There is growing empirical evidence to support the notion that the neural representation of pitch relevant information at both brainstem and cortical levels of processing is influenced by one's long-term experience or short-term training with language and music (see Chandrasekaran and Kraus, 2010; Gandour and Krishnan, 2014; Krishnan and Gandour, 2014; Patel, 2008; Zatorre and Baum, 2012, for reviews). There is neuroanatomical evidence of ascending and descending pathways (Saldana et al., 1996) and physiological evidence of improved signal representation in subcortical structures mediated by the corticofugal system (Suga et al., 2003). These findings suggest that neural processes mediating experience-dependent plasticity for pitch at the brainstem and cortical levels may be well-coordinated. The effects of musical training, for example, yield a correlation between brainstem and cortical responses (Musacchia et al., 2008), implying that neural representations of pitch, timing and timbre cues at the two levels are shaped in a coordinated manner through corticofugal modulation of subcortical afferent circuitry. However, little is known about how language experience shapes specific attributes of pitch at each level of the processing hierarchy or how it modulates the nature of the interplay between them. The scalp-recorded brainstem frequency following response (FFR) and the cortical pitch response (CPR) represent neural activity relevant to pitch at brainstem and cortical levels, respectively. As such, they provide physiologic windows to evaluate the hierarchical organization of pitch processing along the auditory pathway.

The short latency (7–12 ms) FFR reflects sustained phase-locked neural activity in a population of neural elements primarily within the rostral brainstem (Chandrasekaran and Kraus, 2010; Krishnan, 2007) with appreciable cortical contribution of phase-locked FFR-like activity with longer latencies limited to frequencies below 100 Hz (Herdman et al., 2002; Steinschneider et al., 1999). Pitch-relevant information preserved in the FFR is strongly correlated with perceptual pitch measures (Bidelman and Krishnan, 2011; Krishnan and Plack, 2009; Krishnan et al., 2010a; Parbery-Clark et al., 2009), suggesting that acoustic features relevant to pitch are already emerging in representations at the level of the brainstem. Of special relevance to this study, FFR neural periodicity strength increases with increasing pitch salience and accurately predicts the perceptual salience of IRN pitch (Krishnan et al., 2010a). FFRs further reveal that experience-dependent brainstem mechanisms for pitch are especially sensitive to those attributes of pitch contours that provide cues of high perceptual saliency in degraded as well as normal listening conditions (Krishnan et al., 2010b).

The Na component of the CPR, an EEG correlate of the MEG-derived pitch onset response (POR), reflects pitch-specific synchronized neural activity in the auditory cortex. Source analysis of MEG derived pitch onset response (Gutschalk et al., 2002; Krumbholz et al., 2003)—corroborated by human depth electrode recordings (Griffiths et al., 2010; Schonwiesner and Zatorre, 2008) and source analysis of the EEG derived Na (Bidelman and Grall, 2014) indicates that the POR is localized to the anterolateral portion of Heschl's gyrus, the putative site of pitch processing (Johnsrude et al., 2000; Penagos et al., 2004). The CPR, in addition, is characterized by multiple transient components (Na: 125–150 ms, Pb: 200–220, Nb: 270–285 ms) that may index different temporal attributes of pitch contours (Krishnan et al., 2014a, 2014b). We have adopted the Krumbholz et al. experimental paradigm to EEG recordings in order to extract the CPR and FFR concurrently (Krishnan et al., 2012a). In response to IRN *steady-state* pitch stimuli, English monolinguals exhibit larger magnitude in response to strong as compared to weak pitch at both brainstem and cortical levels, i.e., more robust encoding for salient pitch. This change in response magnitude is strongly correlated with behavioral measures of change in perceptual pitch salience. As far as we know, no one has yet to carry out a systematic parametric evaluation of the nature of the interplay underlying processing of *dynamic* pitch stimuli between these two levels of pitch processing along the auditory pathway.

The aim of this study is to determine how systematic changes in pitch salience along a continuum going from weak to strong pitch of a dynamic, IRN high-rising pitch contour—a homolog of Mandarin Chinese Tone 2 (T2)—may alter the strength of the representation of pitch-relevant information preserved in the simultaneously recorded brainstem FFR and cortical CPR as a function of language experience (Chinese, English) (cf. Krishnan et al., 2012a, steady-state pitch). This gives us a unique window to examine the coordination between different stages of pitch processing in real time, which may otherwise be obscured by inferences drawn from separate evaluation of neural responses evoked by different stimulation/acquisition paradigms or comparisons across studies. We hypothesize that language experience enhances sensitivity to changes in pitch salience at the auditory brainstem and cortex, and preferentially recruits the right hemisphere for pitch processing.

A direct comparison of cortical and brainstem responses is expected to reveal different patterns of relative changes in magnitude along the pitch salience continuum. Such findings would implicate a transformation in the nature of processing between the two levels with respect to pitch salience.

2. Results

2.1. Cortical pitch response components

2.1.1. Response morphology

Fig. 1 (top) illustrates that Fz-linked(T7/T8)-derived CPR components (Na, Pb, and Nb) of the pitch-eliciting segment (color)