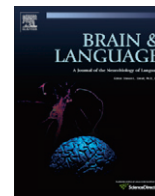




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Short Communication

Functional ear (a)symmetry in brainstem neural activity relevant to encoding of voice pitch: A precursor for hemispheric specialization?

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ABSTRACT

Pitch processing is lateralized to the right hemisphere; linguistic pitch is further mediated by left cortical areas. This experiment investigates whether ear asymmetries vary in brainstem representation of pitch depending on linguistic status. Brainstem frequency-following responses (FFRs) were elicited by monaural stimulation of the left and right ear of 15 native speakers of Mandarin Chinese using two synthetic speech stimuli that differ in linguistic status of tone. One represented a native lexical tone (Tone 2: T2); the other, T2', a nonnative variant in which the pitch contour was a mirror image of T2 with the same starting and ending frequencies. Two 40-ms portions of f_0 contours were selected in order to compare two regions (R1, early; R2 late) differing in pitch acceleration rate and perceptual saliency. In R2, linguistic status effects revealed that T2 exhibited a larger degree of FFR rightward ear asymmetry as reflected in f_0 amplitude relative to T2'. Relative to midline (ear asymmetry = 0), the only ear asymmetry reaching significance was that favoring left ear stimulation elicited by T2'. By left- and right-ear stimulation separately, FFRs elicited by T2 were larger than T2' in the right ear only. Within T2', FFRs elicited by the earlier region were larger than the later in both ears. Within T2, no significant differences in FFRs were observed between regions in either ear. Collectively, these findings support the idea that origins of cortical processing preferences for perceptually-salient portions of pitch are rooted in early, preattentive stages of processing in the brainstem.

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1. Introduction

Hemispheric laterality for neural processing in the cerebral cortex is predictable based on low-level, spectral-temporal features of stimuli, but also can be modulated by their linguistic function (Meyer, 2008; Poeppel, Idsardi, & van Wassenhove, 2008; Zatorre & Gandour, 2008). The left hemisphere (LH) has been demonstrated to be recruited in the processing of linguistic pitch in attention-modulated, tasks; the right hemisphere (RH), in the processing of pitch regardless of functional status. Early processing of linguistic pitch may be implemented at the level of the auditory brainstem by an experience-dependent encoding scheme (Krishnan & Gandour, 2009). The question herein is whether ear asymmetries at the level of the rostral brainstem (inferior colliculus) can be modulated by functional changes in pitch based on

linguistic status rather than the fixed, structural asymmetries in the auditory pathway.

Tone languages allow us to investigate the functional ear asymmetry of linguistic pitch given that pitch variations are meaningful at the lexical level of representation (Yip, 2003). Besides consonants and vowels, Mandarin Chinese has four lexical tones: *ma*¹ 'mother', *ma*² 'hemp', *ma*³ 'horse', *ma*⁴ 'scold'. Tones 1 to 4 can be described phonetically as high level, high rising (hereafter referred to as T2), low falling rising, and high falling, respectively (Howie, 1976). Voice fundamental frequency (f_0) contours provide the dominant cue for tone recognition (Xu, 1997).

The mismatch negativity (MMN) is a cortical event-related potential that provides us with a window on linguistic pitch discrimination at early, preattentive stages of cortical processing (Naatanen, 2001). The MMN is modulated by long-term experience with Mandarin lexical tones (Chandrasekaran, Krishnan, & Gandour, 2007). Looking at hemispheric differences, lexical tones elicit a stronger MMN over the RH than the LH from Mandarin speakers (Luo et al., 2006). RH dominance is also observed in MMNs evoked by intonation as well as lexical tone (Ren, Yang, & Li, 2009). In an experiment examining categorical perception of lexical tones, both acoustic and phonological information is

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processed within the MMN time window (cf. Maess, Jacobsen, Schroger, & Friederici, 2007; Xi, Zhang, Shu, Zhang, & Li, 2010). MMN responses over the RH and LH, respectively, are presumed to reflect their roles in acoustic and phonological processing. Indeed, using an MMN passive oddball paradigm to explore categorical perception of lexical tone, brain areas activated by acoustic variation *within* tonal categories were located in the dorsal and posterior-lateral superior temporal gyrus (STG) bilaterally, with the strongest activation in the *right* mid STG (Zhang et al., *in press*). In contrast, brain areas activated by phonological variation *across* tonal categories, as compared to within-category acoustic variation, were located in the *left* mid middle temporal gyrus. Collectively, these MMN findings suggest an early, preattentive interaction between the two hemispheres in the processing of linguistic pitch.

As a window into early, preattentive stages of *subcortical* linguistic pitch encoding in Mandarin, we measure electrophysiological activity at the level of the brainstem using the human frequency-following response (FFR). The FFR reflects phase-locked activity in a population of neural elements in the rostral brainstem that preserves information relevant to pitch of the stimulus (Krishnan, 2007). It is a preattentive, sustained response characterized by a periodic waveform which follows the individual cycles of the stimulus. Using monaural right ear stimulation, the FFR has revealed that neural representation of pitch-relevant information is enhanced in tone language speakers when presented with linguistically-relevant stimuli (Krishnan & Gandour, 2009). Language-dependent enhancement of pitch-relevant periodicities is especially sensitive to dynamic, rapid changes in pitch that span subparts (e.g., Fig. 1: T2, 130–200 ms) rather than the whole of pitch contours (Krishnan, Gandour, & Bidelman, 2010; Krishnan, Gandour, Bidelman, & Swaminathan, 2009; Krishnan, Gandour, Smalt, & Bidelman, 2010; Krishnan, Swaminathan, & Gandour, 2009). This heightened sensitivity to the degree of acceleration of pitch trajectories is evident in both speech and nonspeech contexts (Krishnan, Swaminathan, et al., 2009; Swaminathan, Krishnan, & Gandour, 2008).

As far as we know, there are no previously published reports on ear asymmetries in representation of FFRs elicited by linguistic pitch for monaural stimulation of both the right and the left ear. This is necessary if we are to consider possible interactions between cortical and brainstem levels of processing. Using nonspeech signals (e.g., clicks, tone bursts), ear asymmetry in FFRs has been shown to mimic hemispheric specialization for sound

processing (Ballachanda, Rupert, & Moushegian, 1994; Sininger & Cone-Wesson, 2004, 2006). Using a speech signal (/da/), a right ear advantage was observed in the FFRs derived from the segmental, but not the suprasegmental (f_0) component of the signal (Hornickel, Skoe, & Kraus, 2009). Their f_0 , however, had a linear trajectory that is not ecologically representative of pitch contours in natural speech. Moreover, language-dependent, pitch encoding in the brainstem is sensitive to linearity. Using tri-linear and linear approximations to a natural, curvilinear pitch contour (T2), no language-dependent effects were observed at the level of the brainstem regardless of how close a linear pitch pattern approximates a native lexical tone (Krishnan, Gandour, et al., 2009; Xu, Krishnan, & Gandour, 2006). Thus, we choose to compare functional ear asymmetry in the brainstem using *curvilinear* pitch contours, one native to the Mandarin tonal space, and one that is not.

FFRs are elicited by monaural stimulation of both the left ear (LE) and right ear (RE) of native speakers of Mandarin using two speech stimuli that differ in their linguistic status (Fig. 1). One exhibits a pitch contour that is exemplary of a native lexical tone (T2); the other does not (T2'). In fact, its pitch contour, a mirror image of T2, does not occur in the Mandarin tonal space or, for that matter, that of any tone language. Both pitch contours are superimposed on a low front rounded vowel [æ] that does not occur in Mandarin in order to minimize interactions between native vowels and tone (Tong, Francis, & Gandour, 2008). Using this stimulus pair, we are able to assess whether ear asymmetries in the brainstem FFR may be modulated by linguistic status of pitch.

We choose to measure the magnitude of the f_0 component in the FFR spectra of two portions, or regions, of the pitch contours (Fig. 1). One region, R2, was chosen because it coincides with brief, perceptually-salient portions of T2 that exhibit rapidly-changing pitch, and that contribute importantly to tonal recognition (Whalen & Xu, 1992). In the brainstem, pitch encoding of T2 has been shown to be enhanced primarily in those same portions of T2 that exhibit a higher rate of acceleration, i.e., rate of change in pitch per unit time (Bidelman, Gandour, & Krishnan, 2011; Krishnan, Gandour, Smalt, et al., 2010; Krishnan, Swaminathan, et al., 2009; Swaminathan et al., 2008). In contrast, the other region (R1) of T2 exhibits slowly-changing pitch that is less perceptually-salient than that of R2 (Whalen & Xu, 1992).

In terms of fixed, *structural* asymmetries in the auditory pathway, the FFR is presumably generated in the inferior colliculus (IC) contralateral to the ear of stimulation due to dominant contralateral projections (Krishnan, 2007). The IC's primary output projects to the medial geniculate body (MGB) and auditory cortex on the same side. Thus, monaural stimulation of either ear primarily drives the IC and auditory cortex on the contralateral side. We can then evaluate *functional* ear asymmetries in the IC related to pitch encoding. On the basis of linguistic status, we hypothesize a left ear advantage for non-linguistic pitch (T2'), a bisymmetric or right ear advantage for linguistic pitch (T2).

2. Results

Fig. 2A displays FFR ear asymmetry in f_0 amplitude for T2 and T2' in two regions of interest. T2 exhibited a larger degree of asymmetry in the FFR favoring the right ear in f_0 encoding amplitude *relative* to T2' in the late region (R2) [$\alpha_{\text{individual}} = 0.025_{\text{Bonferroni}}$; $F_{1,14} = 2.70$, $p = 0.0172$]. No linguistic-dependent effects were observed in the early region (R1). Per stimulus (T2, T2'), as measured on an *absolute* scale ($-1.0 \dots +1.0$), one-sample t -tests revealed that a left ear advantage elicited by T2' in the late region (R2) reached significance [$t_{14} = -3.13$, $p = 0.0073$]; cf. T2 [$t = 0.76$, $p = 0.4605$]. The absence of absolute ear dominance for T2 indicates

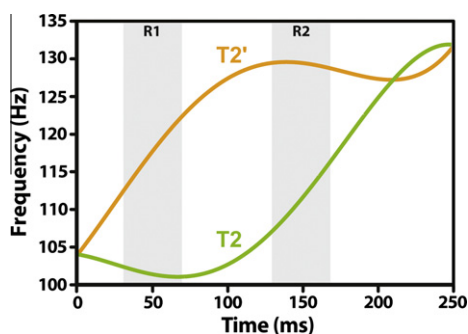


Fig. 1. Synthetic speech stimuli used to evoke brainstem responses from the left and right ears. (A) Time-normalized (250 ms) voice fundamental frequency (f_0) contours modeled after Mandarin Tone 2 (T2) using a 4th-order polynomial equation (Xu, 1997) and its mirror image, an inverted polynomial variant (T2'). In terms of Mandarin, f_0 contour of T2 is native; that of T2' nonnative. Gray-shaded time intervals demarcate two 40 ms regions (R1, R2) that contrast rapidly- with slowly-changing pitch. R2 was chosen because language experience is observed to have an influence primarily in those portions of T2 exhibiting higher degrees of pitch acceleration. R1 and R2, regions of interest.

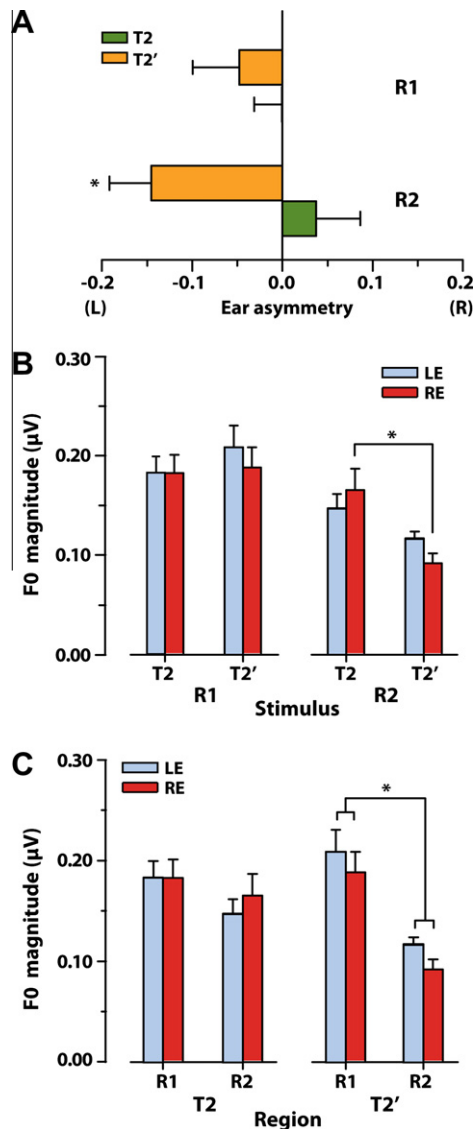


Fig. 2. (A) Ear asymmetry of brainstem responses depends on the functional status of pitch in a listener's native language. An asymmetry favoring left ear stimulation is observed in response to a nonnative pitch contour (T2') in R2. No ear asymmetry is observed in response to a native pitch contour. (B) By region, mean f_0 encoding magnitude derived from FFRs obtained from each stimulus presented to the LE and RE separately. FFRs were larger in T2 (native) than T2' (nonnative) in the RE only. (C) By stimulus, mean f_0 encoding magnitude derived from FFRs obtained from each region presented to the LE and RE separately. FFRs show an acoustic effect (R1 > R2) in response to T2' in both ears. FFR, frequency-following response; LE, left ear; RE, right ear; Error bars represent ± 1 SE. See also caption to Fig. 1.

that the two ears are balanced, irrespective of region, when processing pitch contours exemplary of those native to Mandarin. Per stimulus (T2, T2'), no psychophysical-dependent effects between regions were observed on ear asymmetry for either T2 [$F_{1,14} = -0.66$, $p = 0.5225$] or T2' [$F = 1.40$, $p = 0.1825$].

Fig. 2B displays mean f_0 magnitude plotted by stimulus (T2, T2') for each region (R1, R2). By ear, the FFR elicited by T2 in the late region (R2) was larger than T2' in the right ear only [$F_{1,14} = 3.11$, $p = 0.0077$; cf. left ear: $F = 1.93$, $p = 0.0739$], meaning encoding of linguistic pitch, relative to non-linguistic, is preferentially processed in the left IC and left cortex (i.e., a right ear advantage). In Fig. 2C, mean f_0 magnitude is plotted by region (R1, R2) for each stimulus (T2, T2'). The f_0 amplitude in response to T2' was larger in the early region (R1) as compared to the late (R2) in both ears [left ear: $F_{1,14} = 3.99$, $p = 0.0013$; right ear: $F = 4.26$, $p = 0.0008$].

No FFR effects between regions were observed within T2 in either ear [left ear: $F_{1,14} = 1.66$, $p = 0.1192$; right ear: $F = 0.37$, $p = 0.5515$].

3. Discussion

Our results demonstrate a functional ear asymmetry in the human brainstem that varies depending upon the linguistic status of pitch contours in response to left and right monaural stimulation. In the late region of interest, the lexical tone (T2) exhibited a comparatively larger degree of rightward ear asymmetry in pitch encoding than the nonnative pitch contour (T2'). On an absolute scale, however, an asymmetry favoring left ear stimulation was evoked by nonnative pitch contour only; no ear asymmetry was detected in response to the lexical tone. In response to left- and right-ear stimulation, the FFR evoked by the lexical tone was larger than its flipped variant with right ear stimulation only. Acoustic effects between regions were observed within the nonnative pitch contour only. FFRs in the early region were larger than in the late in both ears. For the lexical tone, no acoustic effects between regions were observed regardless of ear of stimulation. Taken together, these functional ear (a)symmetries do not simply reflect structural asymmetries in the auditory pathway, but instead show that encoding of voice pitch in the rostral brainstem is sensitive to rapid changes in pitch that are perceptually-relevant features of lexical tones.

3.1. Functional ear asymmetry in the brainstem: Acoustic, perceptual and/or linguistic features?

One possible explanation for the leftward asymmetry in response to the nonnative T2' is based on acoustic features exclusively. T2', in addition to being unfamiliar to native listeners, can be distinguished from T2 simply on the basis of acceleration rates. Within the late region (R2), pitch is rapidly-changing in T2, slowly-changing in T2'. This explanation emerges from differences in the speed with which dynamically-changing spectral and temporal information is processed (Abrams, Nicol, Zecker, & Kraus, 2008; Hutsler & Galuske, 2003; Poeppel, 2003; Poeppel et al., 2008; Zaehle, Jancke, Herrmann, & Meyer, 2009; Zatorre, Belin, & Penhune, 2002). Prima facie, our data are compatible with this idea of a relative trade-off in temporal and spectral resolution in the left and right hemispheres, respectively. No ear is dominant in response to T2. Not only does pitch require fine frequency resolution (RH), but it is also rapidly-changing within a short temporal integration window (LH), and thus engages processing from both hemispheres.

The ear asymmetry in our brainstem response favoring left ear stimulation using T2', attributed to a more slowly-modulated pitch contour, is consistent with the observation of cortical RH dominance in response to slow-varying temporal features of speech (Abrams et al., 2008; Poeppel, 2003). FFRs are also larger in T2 than T2' in the right ear only. This right ear preference elicited by rapidly-changing, perceptually-salient portion of a pitch contour may be projected to engage left auditory cortical areas preferentially. It is plausible that the observed asymmetries favoring right ear stimulation for T2, and left ear stimulation for T2', respectively, reflects an emerging, functional separation of periodicity and spectral representations, respectively, at the midbrain level. Indeed, the influence of brainstem processing on cortical hemispheric preferences is suggested by the diminished LH dominance to speech sounds in children who show timing deficits in the onset and offset brainstem responses (Abrams, Nicol, Zecker, & Kraus, 2006).

Our findings on ear (a)symmetry for T2 and T2', however, cannot be solely due to differences in acceleration rates. If that were the case, we would have expected psychophysical-dependent

effects to show a larger FFR in the late region (R2) as compared to the early (R1) in the lexical tone, and just the opposite in the non-native pitch contour. Instead, we find no differences in FFRs between regions within T2 in response to either left- or right-ear stimulation. Within T2', however, the early region was larger than the late in response to either ear. Based on acoustic features alone (i.e., acceleration rates), we are left to explain why the effect occurs in one stimulus (T2') but not the other (T2), especially in view of the fact that acceleration rates for corresponding slow/fast regions across stimuli were virtually identical.

Consequently, we argue in favor of an alternative account of ear (a)symmetry based on the linguistic status of T2 and T2'. T2 represents a prototypical pitch contour of a lexical tone; T2' does not. Its strong, asymmetry in the FFR favoring left ear stimulation may reflect the well-established role of the RH in mediating lower-level processing of pitch features. Because its pitch contour falls outside the boundaries of the Mandarin tonal space, we observe negligible contribution from the right ear at the level of the IC. T2, on the other hand, exhibits a rightward asymmetry relative to T2', and importantly, a right ear, but not left ear, advantage over T2' in response to monaural stimulation. The fact that the IC responded about equally well to T2 from both ears may be attributed to the increased contribution from the right ear. Taken together, these findings lead us to hypothesize that the response symmetry observed for T2 may originate in the brainstem, and be reflected at the level of higher processing structures in the cerebral hemispheres. The involvement of both hemispheres in processing lexical tones is consistent with neuroimaging studies showing hemodynamic responses to pitch information varies between left and right perisylvian areas as a function of language experience (Zatorre & Gandour, 2008).

Another observation of interest is the significant reduction in f_0 magnitude for the late region (R2) of the response compared to the early (R1) for both ears for T2'. A similar trend is observed for T2. This reduction in the magnitude of f_0 in the later region is consistent with neural adaptation to a sustained stimulus observed at different levels along the auditory pathway (Ingham & McAlpine, 2004; Yates, Robertson, & Johnstone, 1985). One possible role for adaptation could be in determining the sensitivity of auditory neurons in context-dependent signal selection (Malone & Semple, 2001). Their sensitivity could be mediated by invoking stimulus property-dependent neural mechanisms that influence either the magnitude and time course of neural adaptation and/or the balance of interaction between excitatory and inhibitory neurons generating the FFR. Enhanced representation of T2 could be maintained if the adaptive properties of the excitatory and inhibitory neurons are different. For example, excitatory components could recover much more rapidly than inhibitory in response to T2, but much more slowly in response to T2' (cf. Ananthanarayan & Gerken, 1987).

A question may arise as to the relationship of neural data at the brainstem level to behavioral data relevant to perceptual salience of pitch features. The absence of behavioral data in this experiment notwithstanding, a strong correlation has been reported between FFR pitch strength and behavioral measures (f_0 difference limens) related to pitch salience (Krishnan, Bidelman, & Gandour, 2010). Their finding suggests that information relevant to perceptually-salient properties of pitch may be extracted and preserved early along the auditory pathway at preattentive, sensory-level stages of processing.

3.2. The role of corticofugal projections along the auditory pathway

Crosslanguage differences in brainstem pitch representation reflect long-term experience-dependent sensitivity of the neural mechanism underlying pitch encoding in native speakers of tone

languages (Krishnan & Gandour, 2009). While we believe that the corticofugal system is triggered during learning to enhance sensory encoding of specific dimensions that are behaviorally relevant, it is not necessarily dedicated to maintenance of long-term, permanent on-line subcortical processing (Gao & Suga, 1998; Yan, Zhang, & Ehret, 2005).

Our finding of differences in ear asymmetries in pitch representation for T2 and T2' suggests that language experience also influences stimulus-driven functional organization in the inferior colliculus. First, the lateralized response in each hemisphere directly reflects subcortical activity in the MGB and IC on the same side with a dominant drive from contralateral ear stimulation (Langgers, van Dijk, & Backes, 2005; Schonwiesner, Krumbholz, Rubsamen, Fink, & von Cramon, 2007). Second, corticofugal projections are dominant ipsilaterally. Linguistic pitch (e.g., T2) is likely to be initially reinforced by corticofugal input from the left auditory cortex to promote reorganization in the left IC during language development to enhance stimulus features that are linguistically relevant. Non-linguistic pitch (e.g., T2'), on the other hand, is expected to preferentially engage the RH, thus triggering a more robust corticofugal input with left ear stimulation as compared to right ear. This functional reorganization of the IC incorporates the differential sensitivity to temporal and spectral properties of the stimulus that is driving the hemispheric lateralization.

3.3. Conclusion

Linguistic-dependent ear (a)symmetries related to processing perceptually-salient features of pitch are present at the level of the brainstem before they are evident in the cerebral cortex. Pitch encoding is enhanced in response to stimuli that will also be preferentially processed in the contralateral hemisphere, or both, depending on their linguistic status. This early shaping of the auditory signal at a preattentive, sensory stage of processing is compatible with the idea that nascent representations of acoustic-phonetic features emerge early along the auditory pathway.

4. Methods

4.1. Participants

Fifteen adult native speakers of Mandarin Chinese (C: 6 male, 9 female) were recruited from the Purdue University student body to participate in the experiment (Supplementary material: text; methods.doc).

4.2. Stimuli

A pair of synthetic speech stimuli related to Mandarin Chinese were constructed that varied in f_0 only (Fig. 1). T2 represents an exemplary lexical tone of Mandarin; T2', in contrast, represents a pitch contour that does not occur in the Mandarin tonal space (Supplementary material: audio; T2_nativetone+nonnativevowel.mp3; T2'_nonnativetone+nonnativevowel.mp3). To minimize perceptual interactions from native formant structure (Tong et al., 2008), f_0 contours were superimposed on a nonnative vowel quality (low front rounded, [œ]). Both T2 and T2' are nonwords, effectively ruling out a lexical effect. This stimulus pair permitted us to compare FFR f_0 amplitude in which the tone is changed but vowel quality is not.

Two 40 ms analysis regions, R1 (30–70) and R2 (130–170), centered at 50 and 150 ms, respectively, were selected (Fig. 1). These two analysis windows offer a contrast in degree of f_0 acceleration (average/maximum in Hz per ms) between T2 (R1: $-0.0331/-0.0614$; R2: $0.2454/0.2748$) and T2' (R1: $0.2551/0.2831$; R2:

–0.0202/–0.0492). Based on perceptual data, R2 was chosen because it coincides with those brief portions of T2, characterized by larger upward changes in f_0 , that contribute most importantly to its tonal recognition (Whalen & Xu, 1992). Based on FFRs, our previous work has demonstrated that pitch encoding of T2 is enhanced primarily in those same portions of T2, i.e. those exhibiting higher degrees of acceleration (Bidelman et al., 2011; Krishnan, Swaminathan, et al., 2009; Swaminathan et al., 2008). Within T2, R2 is characterized by rapidly-changing pitch; R1, by slowly-changing pitch. Just the opposite is the case within T2'. The rapidly- and slowly-changing acceleration rates are virtually identical between corresponding regions of T2 and T2': $T2/R2 = T2'/R1$; $T2/R1 = T2'/R2$. Within stimuli, the two regions allow us to test whether acceleration rates alone are sufficient to drive ear (a)symmetry in the brainstem.

Synthetic versions of the low front rounded vowel [œ] were generated using the Klatt cascade formant synthesizer (Klatt & Klatt, 1990) as implemented in Praat (Boersma & Weenink, 2009). Its formant frequencies were modeled after productions of International Phonetic Association (IPA) cardinal vowel 12 (= [œ]) as produced by a professional phonetician (Ladefoged & Johnson, 2011). Their values expressed in frequency and bandwidths (within parentheses) were: F1, 465 (42) Hz; F2, 1186 (120); F3, 2281 (65); F4, 3153 (150). (Supplementary material: text; methods.doc).

4.3. Data acquisition

The FFR recording protocol was similar to that used in previous reports from our laboratory (Krishnan, Gandour, Smalt, et al., 2010; Krishnan et al., 2010) (Supplementary material: text; methods.doc).

4.4. Data analysis

FFR pitch encoding was quantified by measuring the magnitude of the f_0 component (amplitude of the spectral component at a frequency corresponding to f_0) from each response waveform for each stimulus per ear. Two 40 ms sections (30–70, 130–170) of the FFR were extracted corresponding to the sustained portion of the response to rapidly- (T2/R2, T2'/R1) and slowly-changing (T2/R1, T2'/R2) pitch. The spectrum of each response segment was computed by taking the FFT of a time-windowed version of its temporal waveform (Gaussian window, 1 Hz resolution). For each subject per stimulus-ear condition, the magnitude of f_0 was measured as the peak in the FFT, relative to the noise floor, which fell in the same frequency range as the f_0 of the input stimulus (T2: 100.9–131.8 Hz; T2': 103.9–131.7; see stimulus f_0 tracks, Fig. 1A). All FFR data analyses were performed using customized routines coded in MATLAB® 7.9 (The MathWorks, Inc., Natick, MA, USA).

We computed the degree of ear asymmetry for each stimulus by subtracting the left FFR f_0 amplitude from the right FFR f_0 amplitude and dividing by the sum of those two values $[(Rf_0 - Lf_0)/(Rf_0 + Lf_0)]$ (cf. King, Nicol, McGee, & Kraus, 1999). Responses eliciting symmetric brainstem activity produce a value of zero; asymmetric responses, a positive or negative value for right or left ear dominance, respectively. All t -tests against 0 (laterality) were corrected with a Bonferroni adjustment at a significance level of 0.05.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bandl.2011.05.001.

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