



Left-hemisphere activation is associated with enhanced vocal pitch error detection in musicians with absolute pitch



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ABSTRACT

The ability to process auditory feedback for vocal pitch control is crucial during speaking and singing. Previous studies have suggested that musicians with absolute pitch (AP) develop specialized left-hemisphere mechanisms for pitch processing. The present study adopted an auditory feedback pitch perturbation paradigm combined with ERP recordings to test the hypothesis whether the neural mechanisms of the left-hemisphere enhance vocal pitch error detection and control in AP musicians compared with relative pitch (RP) musicians and non-musicians (NM). Results showed a stronger N1 response to pitch-shifted voice feedback in the right-hemisphere for both AP and RP musicians compared with the NM group. However, the left-hemisphere P2 component activation was greater in AP and RP musicians compared with NMs and also for the AP compared with RP musicians. The NM group was slower in generating compensatory vocal reactions to feedback pitch perturbation compared with musicians, and they failed to re-adjust their vocal pitch after the feedback perturbation was removed. These findings suggest that in the earlier stages of cortical neural processing, the right hemisphere is more active in musicians for detecting pitch changes in voice feedback. In the later stages, the left-hemisphere is more active during the processing of auditory feedback for vocal motor control and seems to involve specialized mechanisms that facilitate pitch processing in the AP compared with RP musicians. These findings indicate that the left hemisphere mechanisms of AP ability are associated with improved auditory feedback pitch processing during vocal pitch control in tasks such as speaking or singing.

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1. Introduction

Acquiring musical skills strongly relies on accurate pitch processing for the control of musical instruments or the voice. In recent years, there has been considerable interest in understanding the neural mechanisms that underlie vocal pitch control during speaking and singing (Behroozmand, Karvelis, Liu, & Larson, 2009; Burnett, Freedland, Larson, & Hain, 1998; Chang, Niziolek, Knight, Nagarajan, & Houde, 2013; Eliades & Wang, 2008; Greenlee et al., 2013; Guenther, Ghosh, & Tourville, 2006; Hawco, Jones, Ferretti, & Keough, 2009; Zarate, Wood, & Zatorre, 2010b; Zarate & Zatorre, 2005, 2008). These studies have generally relied on electrophysiological and neuroimaging techniques to unravel information regarding the role of auditory feedback in vocal pitch error detection and correction. The findings of these studies have suggested that vocal pitch control involves interactions between sensory-motor processing networks including but not limited to pre-motor, motor, auditory, parietal and inferior frontal cortices (Chang et al., 2013; Greenlee et al., 2013; Guenther, 2006; Guen-

ther et al., 2006; Parkinson et al., 2012; Tourville, Reilly, & Guenther, 2008; Zarate & Zatorre, 2005).

Although it has been established that the functional role of these areas are potentially related to sensory feedback-based control of vocal production, it is not well understood how the specific localization of functions may vary within such complex sensory-motor loops as a result of extensive vocal or musical training or the development of absolute pitch (AP) ability. While many musicians, as a result of years of professional training, can tune instruments relatively accurately to a note, AP musicians have the ability to assign verbal labels to absolute pitches and to identify notes without first determining the note's tonal relationship with another known note (Takeuchi & Hulse, 1993). This unique ability in AP musicians significantly differentiates them from relative pitch (RP) musicians, who control vocal or instrumental pitches using tonal relationships between a target and an external referent note. More interestingly, the duration of musical training is by and large ineffective in differentiating AP and RP musicians, while the early-learning theory suggests that individuals who received musical training before a certain critical age (3–6 years) may develop AP ability. Data also suggest that AP ability may only develop if said early musical training includes affirming the relation between

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pitch names and their respective absolute pitches. Takeuchi and Hulse (1993) argue that if training focuses on the relational aspects of pitch, then the child may not develop AP ability despite receiving musical training within the early-learning period. Adults are therefore unable to learn AP because they are no longer able to perceive a single, absolute tone outside of its relationship to other tones. Regardless, after the critical age, AP ability may not be achieved, meaning that the RP musicians cannot acquire AP ability with increased musical experience (Takeuchi & Hulse, 1993). Such differences in pitch processing between AP and RP musicians suggest that the neural mechanisms of auditory feedback processing for vocal pitch control may differ between these two groups and also between musicians and non-musicians (NM) during speech production and singing.

A study by Schlaug, Jancke, Huang, and Steinmetz (1995) has reported that AP ability is associated with a larger planum temporale of the left-hemisphere in AP compared with RP musicians. More recently, Jancke, Langer, and Hanggi (2012) provided evidence that AP processing ability may be associated with fewer distant projections and a higher density of peri-sylvian connectivity between different anatomical areas of the brain, including the planum temporale, Heschl's gyrus and lateral superior temporal gyrus. A study by Loui, Zamm, and Schlaug (2012) has also found evidence of hyper-connectivity in the left hemisphere areas of the superior temporal gyrus in AP possessors compared with non-AP possessors. Taken together, these reports provide strong support for different neural mechanisms and anatomical connectivity in the left-hemisphere language areas of the brain in AP musicians. As part of the functional significance of these findings, it should be noted that categorization of musical notes involving mechanisms in the planum temporale is a hallmark of AP ability (Jancke et al., 2012; Loui et al., 2012; Schlaug et al., 1995). However, the question remains if there are other functions of musical or vocal control ability that are associated with AP possessors.

It is well known that the left hemisphere is dominant for speech and language processing and it has been suggested that the AP musicians may utilize these mechanisms in order to gain a higher level of functional expertise for pitch processing during speaking or singing (Jancke et al., 2012; Loui et al., 2012; Zatorre & Belin, 2001). These functions include fine temporal resolution of acoustical stimuli and the ability to make absolute categorization of acoustical stimuli, such as the ability to perceive the acoustical difference between two vowels. Other than these possibilities, it is still unclear how left hemisphere processing provides some musicians with AP ability. By the same token, it is not known if there are differences in the left and right hemispheres for the control of voice, regardless of its relevance to AP processing in trained musicians.

One potentially useful tool for studying the behavioral and neurophysiological aspects of vocal pitch control is the auditory feedback pitch perturbation paradigm. From the behavioral perspective, it has been shown that delivering pitch-shifts to voice auditory feedback during steady vowel phonations elicit short latency (~100 ms) compensatory vocal responses that stabilize voice fundamental frequency (F0) (Burnett et al., 1998; Chen, Liu, Xu, & Larson, 2007; Donath, Natke, & Kalveram, 2002; Jones & Munhall, 2000; Kawahara & Aikawa, 1996). Such reflexive vocal reactions to feedback pitch perturbation were suggested to be driven by negative feedback controller mechanisms that correct for pitch errors by comparing the voice F0 feedback with an internal representation established by pitch memory or motor-driven mechanisms such as efference copy (Sperry, 1950; von Helmholtz, 1867; Wolpert, Ghahramani, & Jordan, 1995). A disparity between the feedback and predicted output leads to a response that returns F0 to the desired level (Behroozmand et al., 2009; Burnett et al., 1998; Chang et al., 2013; Greenlee et al., 2013; Heinks-Maldonado,

Mathalon, Gray, & Ford, 2005; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Larson, Altman, Liu, & Hain, 2008).

Evidence for such predictive mechanisms has been found in the audio-vocal modalities by showing that the N1 responses to self-generated sounds or vocalizations are suppressed compared with passive listening to the playback of the same auditory stimuli (Eliades & Wang, 2003, 2005; Heinks-Maldonado, Nagarajan, & Houde, 2006; Heinks-Maldonado et al., 2005; Houde et al., 2002; Müller-Preuss & Ploog, 1981). Although the nature of this phenomenon is not well-understood, it has been proposed that the suppression effect may be driven by motor-induced cancellation of predicted sensory feedback that does not carry new information for the brain (Bendixen, SanMiguel, & Schroger, 2012). This mechanism has also been suggested to be involved in identifying the source of incoming sounds and differentiating self- from externally-generated auditory stimuli (Behroozmand & Larson, 2011; Heinks-Maldonado et al., 2005). However, when the auditory feedback is altered during speaking, the mismatch between predicted and actual sensory input is proposed to enhance neural sensitivity for the detection and correction of vocal motor errors (Behroozmand et al., 2009; Chang et al., 2013; Eliades & Wang, 2008; Greenlee et al., 2013).

In this context, since the auditory feedback signal is hypothetically compared with an internal referent note, it can be expected that trained musicians would utilize different neural mechanisms for voice motor control, and in turn, would show different reactions to pitch perturbations in their voice auditory feedback compared with NMs. It has been demonstrated that well-trained singers can vocalize and almost completely suppress their vocal responses to perturbations in their voice auditory feedback whereas NMs by contrast produce much larger reflexive responses to such perturbations (Zarate & Zatorre, 2008; Zarate et al., 2010b).

From the neurophysiological perspective, the pitch-shift stimulus serves as a precise temporal marker for a change in the auditory feedback and can be used to study the electrophysiological correlates of vocal pitch error detection and compensation. Several studies have recorded event-related potentials (ERPs) in response to pitch-shifted auditory feedback during vocalization (Behroozmand et al., 2009; Hawco et al., 2009; Heinks-Maldonado et al., 2005). Results of these studies have indicated that different ERP components (e.g. N1 or P2) are sensitive to specific features of pitch-perturbation stimuli while a person is controlling voice F0. For example, the amplitude of the P2 responses was shown to be modulated by the magnitude of pitch-shifts in voice auditory feedback (Behroozmand et al., 2009). In addition, the N1 responses were reported to be sensitive to predictability of the stimulus and whether or not the feedback signal is self- or externally-generated (Bass, Jacobsen, & Schroger, 2008; Behroozmand & Larson, 2011; Heinks-Maldonado et al., 2005; Knolle, Schroger, & Kotz, 2013).

In the present study, we adopted the auditory feedback pitch perturbation paradigm combined with ERP recordings in order to investigate the behavioral and neurophysiological aspects of vocal pitch control in three subject groups of AP and RP musicians as well as NMs. Subjects were asked to repeatedly maintain a steady vocalization of the vowel sound /a/ while they randomly received brief (200 ms) upward (+100 cents) and downward (−100 cents) pitch-shifts in their voice auditory feedback. The recording of the ERPs in response to feedback pitch perturbations allowed us to specify the spatio-temporal characteristics of the ERP responses during vocal pitch control, specifically in terms of modulation of individual ERP components by stimulus features across different subject groups. Furthermore, the electrophysiological correlates of lateralized functions during vocal production and control were studied by comparing the ERP responses in the left and right hemispheres. We hypothesized that the AP musicians would show greater left-hemisphere activation, as evidenced by larger

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