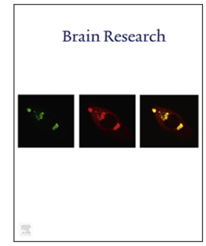
Available online at www.sciencedirect.com
ScienceDirect
www.elsevier.com/locate/brainres




Research Report

# A temporal predictive code for voice motor control: Evidence from ERP and behavioral responses to pitch-shifted auditory feedback

*Roozbeh Behroozmand*[a,*], *Stacey Sangtian*[a], *Oleg Korzyukov*[b], *Charles R. Larson*[b]

[a]*Speech Neuroscience Lab, Department of Communication Sciences and Disorders, University of South Carolina, United States*
[b]*Speech Physiology Lab, Department of Communication Sciences and Disorders, Northwestern University, United States*

ARTICLE INFO

*Article history:*
Accepted 25 January 2016
Available online 2 February 2016

*Keywords:*
Voice motor control
Auditory feedback
Internal forward model
Predictive code
Pitch-shift stimulus
Event-related potential

ABSTRACT

The predictive coding model suggests that voice motor control is regulated by a process in which the mismatch (error) between feedforward predictions and sensory feedback is detected and used to correct vocal motor behavior. In this study, we investigated how predictions about timing of pitch perturbations in voice auditory feedback would modulate ERP and behavioral responses during vocal production. We designed six counterbalanced blocks in which a +100 cents pitch-shift stimulus perturbed voice auditory feedback during vowel sound vocalizations. In three blocks, there was a fixed delay (500, 750 or 1000 ms) between voice and pitch-shift stimulus onset (predictable), whereas in the other three blocks, stimulus onset delay was randomized between 500, 750 and 1000 ms (unpredictable). We found that subjects produced compensatory (opposing) vocal responses that started at 80 ms after the onset of the unpredictable stimuli. However, for predictable stimuli, subjects initiated vocal responses at 20 ms before and followed the direction of pitch shifts in voice feedback. Analysis of ERPs showed that the amplitudes of the N1 and P2 components were significantly reduced in response to predictable compared with unpredictable stimuli. These findings indicate that predictions about temporal features of sensory feedback can modulate vocal motor behavior. In the context of the predictive coding model, temporally-predictable stimuli are learned and reinforced by the internal feedforward system, and as indexed by the ERP suppression, the sensory feedback contribution is reduced for their processing. These findings provide new insights into the neural mechanisms of vocal production and motor control.



*Correspondence to: University of South Carolina, Department of Communication Sciences and Disorders, Keenan Building, Rm 356, 1224 Sumter St., Columbia, SC 29208, United States. Fax: +1 803 777 3081.
E-mail address: r-behroozmand@sc.edu (R. Behroozmand).

http://dx.doi.org/10.1016/j.brainres.2016.01.040
0006-8993/

## 1. Introduction

Skilled motor behavior is driven by the effective integration of feedforward and sensory feedback mechanisms to achieve the optimal goals of performed actions (Wolpert and Ghahramani, 2000). This effectiveness is determined by the relative contribution and weighting of feedforward and feedback mechanisms to generate, monitor and control our movements (Wolpert et al., 2011, 1995). Among all actions, speaking is one of the most complex goal-directed motor behaviors developed to facilitate human communication. A widely-accepted idea hypothesizes that during speech production, a copy of the motor commands known as the efference copy (Wolpert and Flanagan, 2001) is translated by an internal forward model to provide predictions about sensory consequences of self-produced speech sounds (Hickok and Poeppel, 2007; Houde and Nagarajan, 2011). This process is part of a predictive coding model in which speech errors resulting from a mismatch between the internally-predicted and actual sensory feedback are used to monitor and correct subsequent motor behavior during speech production and control (Guenther et al., 2006; Hickok, 2012; Houde and Nagarajan, 2011; Tourville et al., 2008).

In recent years, a growing number of studies have been conducted to better understand the predictive coding mechanism as it relates to vocal production and motor control. An effect associated with the predictive coding has been consistently reported by showing that the N1 component of the auditory-evoked event-related potentials (ERPs) was suppressed during vocal production of speech sounds compared with passive listening to the playback of the same self-produced speech (Curio et al., 2000; Heinks-Maldonado et al., 2006, 2005; Houde et al., 2002). It has been proposed that this motor-induced suppression effect results from the cancellation of sensory neural responses to self-produced speech by the internal feedforward predictions during vocal production. This notion was further supported by a study showing that the suppression was maximum for normal voice auditory feedback and was reduced or almost completely eliminated when a pitch-shift stimulus created mismatch between the internal predictions and the auditory feedback during vocalization (Behroozmand and Larson, 2011; Heinks-Maldonado et al., 2006). In addition, a study by Wang et al. (2014) showed that the activation of inferior frontal gyrus (IFG) at about 300 ms before speaking is associated with the suppression of N1 responses in auditory cortex at about 100 ms following speech onset. Thus, it was concluded that the transmission of predictive codes from motor-related areas such as IFG is responsible for the suppression of neural activity in the auditory cortex during speaking. These findings suggest that the motor-driven feedforward internal predictions play a key role in achieving the communication goals during vocal production and motor control.

Converging evidence from more recent studies has suggested that predictions about different aspects of sensory feedback stimuli subsequently affect behavioral and neural responses during vocal production and motor control. In a study by Scheerer and Jones (2014), behavioral vocal responses to predictable and unpredictable pitch-shift stimulus magnitude were examined and they reported that the magnitude of vocal responses was significantly reduced for predictable vs. unpredictable stimuli. Behroozmand et al. (2012) and Korzyukov et al. (2012) examined the effect of pitch-shift stimulus direction predictability and found that the magnitude of opposing (compensatory) vocal responses to unpredictable stimulus direction was significantly larger than following responses (Behroozmand et al., 2012), and there was a significantly larger number of opposing responses for unpredictable vs. predictable stimulus direction (Korzyukov et al., 2012). Korzyukov et al. (2012) and Scheerer and Jones (2014) also reported that the amplitude of the N1 component of ERPs was significantly reduced for predictable vs. unpredictable stimulus direction and magnitude, respectively. Moreover, Scheerer and Jones (2014) found that the latency of the P1 and N1 components was significantly shorter for predictable stimulus magnitude. Although behavioral vocal responses were not measured in Chen et al.'s (2012) study, they reported that the amplitude of the P2 ERP responses was reduced for manually-triggered temporally-predictable vs. unpredictable pitch-shift stimuli. Findings of these studies have suggested that the expectancy of the predictable stimulus eventually develops into recognition of the perturbation as being an external stimulus thereby leading to reduced vocal compensation (i.e., opposing responses) and a change in the underlying sensory-motor neural processes as indexed by modulation of the P1/N1/P2 components (Behroozmand et al., 2012; Chen et al., 2012; Korzyukov et al., 2012; Scheerer and Jones, 2014). In addition, these findings suggest that exposure to repeated presentations of predictable stimuli results in the increased contribution of feedforward mechanisms during vocal motor control. This reasoning supports the framework for predictions by the internal forward model: learned predictions result in more accurate efference copies and, consequently, a decreased mismatch in sensory feedback (Chen et al., 2012; Korzyukov et al., 2012; Scheerer and Jones, 2014; Wang et al., 2014; Wolpert and Flanagan, 2001).

Although the behavioral and neural correlates of vocalization have been examined for predictable pitch-shift stimulus magnitude and direction (Behroozmand et al., 2012; Korzyukov et al., 2012; Scheerer and Jones, 2014), research on temporal predictability effects on voice motor control is limited. Previous studies have shown that the suppression of neural responses in the auditory cortex in response to pure tones (Aliu et al., 2009) and speech (Behroozmand et al., 2011; Chen et al., 2012) develops for zero time delays but does not generalize to non-zero delays between feedforward predictions and sensory feedback perturbation. These findings indicate that the neural mechanisms of auditory feedback processing are sensitive to timing between the vocal motor commands and the incoming auditory feedback, and therefore, the observed suppression effect is not merely a movement-related non-specific effect. Further support for this notion is provided by studies showing that the degree of auditory suppression can be modulated by variations in vocal production (Sitek et al., 2013), speech targets (Ventura et al., 2009) and categorical boundaries of a spoken vowel sound (Niziolek and Guenther, 2013; Niziolek et al., 2013).