



## Neural networks involved in voluntary and involuntary vocal pitch regulation in experienced singers

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### ABSTRACT

In an fMRI experiment, we tested experienced singers with singing tasks to investigate neural correlates of voluntary and involuntary vocal pitch regulation. We shifted the pitch of auditory feedback ( $\pm 25$  or 200 cents), and singers either: (1) ignored the shift and maintained their vocal pitch or (2) changed their vocal pitch to compensate for the shift. In our previous study, singers successfully ignored and compensated for 200-cent shifts; in the present experiment, we hypothesized that singers would be less able to ignore 25-cent shifts, due to a prepotent, corrective pitch-shift response. We expected that voluntary vocal regulation during compensate tasks would recruit the anterior portion of the rostral cingulate zone (RCZa) and posterior superior temporal sulcus (pSTS), as our earlier study reported; however, we predicted that a different network may be engaged during involuntary responses to 25-cent shifts. Singers were less able to ignore 25-cent shifts than 200-cent shifts, suggesting that pitch-shift responses to small shifts are under less voluntary control than responses to larger shifts. While we did not find neural activity specifically associated with involuntary pitch-shift responses, compensate tasks recruited a functionally connected network consisting of RCZa, pSTS, and anterior insula. Analyses of stimulus-modulated functional connectivity suggest that pSTS and intraparietal sulcus may monitor auditory feedback to extract pitch-shift direction in 200-cent tasks, but not in 25-cent tasks, which suggests that larger vocal corrections are under cortical control. During the compensate tasks, the pSTS may interact with the RCZa and anterior insula before voluntary vocal pitch correction occurs.

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### 1. Introduction

Electrophysiological, tracer, and lesion studies in animals have demonstrated that vocalization recruits a constellation of neural structures, ranging from motor/premotor cortical areas [i.e., primary motor cortex, supplementary motor area, anterior cingulate cortex] and subcortical regions (basal ganglia, thalamus) to an array of brainstem structures, including periaqueductal gray, substantia

nigra, reticular formation, and motoneuron pools (Jurgens, 2002). Neuroimaging studies have confirmed that many of these regions are also involved in human vocalization, including speech and various singing tasks (Brown, Martinez, Hodges, Fox, & Parsons, 2004; Brown, Martinez, & Parsons, 2006; Jeffries, Braun, & Fritz, 2003; Kleber, Birbaumer, Veit, Trevorrow, & Lotze, 2007; Ozdemir, Norton, & Schlaug, 2006; Paus, Petrides, Evans, & Meyer, 1993; Perry et al., 1999; Riecker, Ackermann, Wildgruber, Dogil, & Grodd, 2000; Schulz, Varga, Jeffries, Ludlow, & Braun, 2005). Sensory feedback during vocalization not only stems from proprioception from the vocal apparatus but also from auditory feedback processed by temporal lobe regions [e.g., superior temporal gyrus (STG), superior temporal sulcus (STS)], which process vocal sounds, speech, and other auditory stimuli (Belin, Zatorre, & Ahad, 2002; Scott & Johnsrude, 2003). At times, vocal adjustments are necessary if there is a mismatch between the intended and actual vocal output or if the environmental tasks change (e.g., noisy background); this vocal regulation requires the integration of vocal motor control and auditory processes (also known as “audio-vocal integration”), but the neural substrates involved in this process are not well-understood.

*Abbreviations:* ACC, anterior cingulate cortex; aINS, anterior insula; aSTG, anterior superior temporal gyrus; BA, Brodmann area; IPL, inferior parietal lobule; IPS, intraparietal sulcus; M1, primary motor cortex; mid-PMC, mid-premotor cortex; PAC, primary auditory cortex; PostC, postcentral gyrus; pre-SMA, pre-supplementary motor area; pSTG, posterior superior temporal gyrus; pSTS, posterior superior temporal sulcus; PT, planum temporale; RCZa, anterior portion of rostral cingulate zone; SMA, supplementary motor area; SMG, supramarginal gyrus; STG, superior temporal gyrus; STS, superior temporal sulcus; vPMC, ventral premotor cortex.

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Previous behavioral studies have investigated audio–vocal integration underlying vocal pitch regulation by manipulating auditory feedback, either by adjusting the feedback amplitude (Lombard, 1911; Siegel & Pick, 1974) or by altering the fundamental frequency (i.e., perceived pitch) of the auditory feedback (Burnett, Freedland, Larson, & Hain, 1998; Burnett & Larson, 2002; Burnett, McCurdy, & Bright, 2008; Donath, Natke, & Kalveram, 2002; Hafke, 2008; Hain et al., 2000; Jones & Keough, 2008; Jones & Munhall, 2000, 2005; Larson, 1998; Larson, Burnett, & Kiran, 2000; Natke, Donath, & Kalveram, 2003; Natke & Kalveram, 2001). Such auditory feedback perturbations often elicit fast, compensatory adjustments in either vocal amplitude or pitch, such as the Lombard reflex [an increase in vocal amplitude in response to decreased feedback amplitude (Lombard, 1911; Siegel & Pick, 1974)] or the pitch-shift response, in which the vocal pitch is quickly adjusted, often in the opposite direction of the feedback shift (Burnett et al., 1998; Burnett & Larson, 2002). In a previous neuroimaging experiment (Zarate & Zatorre, 2008), we modified the pitch-shift paradigms used by Larson and Burnett to target cortical substrates of audio–vocal integration. Rather than delivering pitch-shifted feedback for less than 1 s as in the Larson/Burnett studies, we maintained a  $\pm 200$ -cent shift in feedback (one whole tone, in musical terminology) for approximately 3 s to increase the likelihood of capturing neural activity associated with audio–vocal integration. Subjects were instructed either to: (1) ignore the pitch-shifted feedback and keep their vocal output steady, or (2) compensate for the pitch shift, so that the shifted feedback would sound like the original target note (i.e., cancel out the pitch shift in the feedback). We believed the latter task would recruit the brain regions involved in audio–vocal integration, since subjects needed to monitor auditory feedback while regulating their vocal output to cancel out the feedback shift. We tested non-musicians and experienced singers to determine if vocal training would modify neural activity associated with these singing tasks. During our “compensate” task, we found two possible substrates for audio–vocal integration, each of which was dependent on vocal experience: (1) non-musicians showed increased activity in the dorsal premotor cortex (dPMC), and (2) experienced singers showed increased activity in the anterior portion of the rostral cingulate zone (RCZa) and posterior STS (pSTS). The dPMC has been implicated in selecting movements associated with particular sensory cues (Chouinard & Paus, 2006; Petrides, 1986), including auditory–motor interactions (Chen, Penhune, & Zatorre, 2008; Chen, Zatorre, & Penhune, 2006; Zatorre, Chen, & Penhune, 2007), and thus may serve as a basic sensorimotor interface as people, regardless of vocal experience, adjust their vocal output after hearing feedback perturbation. In general, the RCZa is implicated in conflict monitoring (Botvinick, Cohen, & Carter, 2004; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter et al., 1998; Durston et al., 2003; MacDonald, Cohen, Stenger, & Carter, 2000; Picard & Strick, 1996, 2001), while the pSTS processes vocal stimuli (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Kriegstein & Giraud, 2004) and may be involved in extracting specific sound features (Celsis et al., 1999; Warren, Scott, Price, & Griffiths, 2006; Warren, Uppenkamp, Patterson, & Griffiths, 2003). We proposed that as people undergo more vocal training or experience, the interface between the RCZa and pSTS may be increasingly recruited for audio–vocal integration (Zarate & Zatorre, 2008).

Although we outlined possible substrates for voluntary vocal regulation in this prior study, we did not systematically study the neural correlates of the pitch-shift response itself, which is also a form of vocal regulation that relies on audio–vocal integration. Since the pitch-shift response may be more involuntary, it may be governed by different substrates than those outlined above for voluntary vocal regulation. In fact, Burnett et al. (1998) suggested that the midbrain periaqueductal gray (PAG) may be a possible candidate for audio–vocal integration during the pitch-shift response,

due to its connections and its role in vocalization. Electrical and pharmacological stimulation of the squirrel monkey PAG elicits vocalization (Dujardin & Jurgens, 2005; Suga & Yajima, 1988), and the human PAG is active during voiced speech when compared to whispered speech, suggesting that the PAG is involved in motor networks that produce vocal fold activity (Schulz et al., 2005). The PAG receives input from a huge array of sensory cortical and sub-cortical regions, including higher order auditory areas (e.g., STS), superior and inferior colliculi, lateral lemniscus, and the nucleus gracilis, which suggests that the PAG may be involved in vocal responses to external stimuli (Dujardin & Jurgens, 2005). The PAG may receive information about auditory feedback via the inferior colliculus (Huffman & Henson, 1990) or the lateral lemniscus and initiate a quick, compensatory vocal response to any changes in feedback, such as the Lombard reflex (Nonaka, Takahashi, Enomoto, Katada, & Unno, 1997) or the pitch-shift response.

In our earlier study (Zarate & Zatorre, 2008), we made an interesting observation—during the ignore task, we saw pitch-shift responses only in the non-musicians; we therefore concluded that vocal training must have helped singers suppress pitch-shift responses when asked to ignore a large, 200-cent shift. Given that only singers suppressed pitch-shift responses when ignoring large pitch perturbations and generally produced more uniform behavioral results than non-musicians in our previous experiment, in the current study, we investigated the neural correlates of audio–vocal integration during both small pitch-shift responses and larger, intended vocal adjustments only in experienced singers. In the present experiment, singers performed the same ignore and compensate tasks from our first experiment, but we utilized two different shift magnitudes: 200-cent and 25-cent pitch shifts. Since our previous experiment has already shown that singers can successfully ignore and compensate for a 200-cent shift, we expected that the response magnitudes between these tasks would be significantly different. In contrast, given that pitch-shift responses are better suited to fully correct for smaller pitch perturbations than larger ones (Liu & Larson, 2007), and hence are thought to be under more automatic control, we hypothesized that singers would be less able to suppress pitch-shift responses to 25-cent shifts than to 200-cent shifts; thus, we did not expect significant differences in response magnitudes for ignoring and compensating for this smaller shift. We predicted that the brain regions that singers recruited for ignoring and compensating for the large shift would be similar to those reported in our prior experiment (Zarate & Zatorre, 2008). However, during the 25-cent tasks, we hypothesized that not only similar regions would be recruited as in the large-shift tasks, but that the PAG would also be specifically recruited during elicited pitch-shift responses in the ignore task.

## 2. Materials and methods

### 2.1. Subjects

A total of 13 healthy subjects were recruited from the McGill University community and surroundings areas. All subjects (mean age =  $23 \pm 3.93$  years old) were right-handed, had normal hearing, and were devoid of neurological or psychological disorders and contraindications for functional magnetic resonance imaging (fMRI) techniques. All subjects gave informed consent to participate in this study, in accordance with procedures approved by the Research Ethics Committees of the McConnell Brain Imaging Centre and the Montréal Neurological Institute. Three subjects were withdrawn from the study due to problems performing the tasks, and another subject was excluded for moving excessively during the scanning session. The remaining nine subjects (three male), all categorized as experienced singers, had an average of 11 years ( $\pm 4.28$  years) of formal vocal training and/or experience, were currently practicing or performing at the time of the study, and did not participate in our previous experiment (Zarate & Zatorre, 2008). According to self-report, none of the subjects possessed absolute pitch.

### 2.2. Equipment

During familiarization sessions, subjects sat in front of a lab computer screen and were given a microphone (Røde NT5, Silverwater, Australia) and a pair of

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