Contributions of sensory tuning to auditory-vocal interactions in marmoset auditory cortex

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ABSTRACT

During speech, humans continuously listen to their own vocal output to ensure accurate communication. Such self-monitoring is thought to require the integration of information about the feedback of vocal acoustics with internal motor control signals. The neural mechanism of this auditory-vocal interaction remains largely unknown at the cellular level. Previous studies in naturally vocalizing marmosets have demonstrated diverse neural activities in auditory cortex during vocalization, dominated by a vocalization-induced suppression of neural firing. How underlying auditory tuning properties of these neurons might contribute to this sensory-motor processing is unknown. In the present study, we quantitatively compared marmoset auditory cortex neural activities during vocal production with those during passive listening. We found that neurons excited during vocalization were readily driven by passive playback of vocalizations and other acoustic stimuli. In contrast, neurons suppressed during vocalization exhibited more diverse playback responses, including responses that were not predictable by auditory tuning properties. These results suggest that vocalization-related excitation in auditory cortex is largely a sensory-driven response. In contrast, vocalization-induced suppression is not well predicted by a neuron’s auditory responses, supporting the prevailing theory that internal motor-related signals contribute to the auditory-vocal interaction observed in auditory cortex.

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1. Introduction

Recent investigations in both humans and non-human primates have begun to reveal the role of the central auditory system, and in particular the auditory cortex, in representing the sound of an animal’s own vocalizations during vocal production. During vocal communication, vocalized sounds are heard by both the intended recipients and the individual producing them (Bekesy, 1949). Neural encoding of this vocal feedback is thought to be crucial for monitoring one’s own voice (Hickok et al., 2011; Houde and Nagarajan 2011; Levelt, 1983), and may play a role in feedback-dependent control of vocalization in both animals (Brumm et al., 2004; Leonardo and Konishi, 1999; Schuller et al., 1974; Sinnott et al., 1975) and humans (Burnett et al., 1998; Houde and Jordan, 1998; Lane and Tranel, 1971; Lee, 1950).

Single neuron recordings in the auditory cortex of the marmoset (Callithrix jacchus), a highly vocal New World primate, have demonstrated the presence of two types of responses during vocal production, vocalization-induced suppression and vocalization-related excitation (Eliades and Wang, 2003). Vocalization-induced suppression affects approximately 70% of neurons in marmoset auditory cortex (Eliades and Wang, 2013), is observed across different types of vocalizations, and is thought to be caused by inhibitory signals originating from brain regions that initiate and control vocal production. Moreover, neurons showing vocalization-induced suppression exhibit an increased sensitivity to alterations in auditory feedback during vocalization and may play a role in self-monitoring (Eliades and Wang, 2008a, 2012). In contrast, neurons showing vocalization-related excitation, representing a small proportion of auditory cortex neurons, tend to respond during a more limited set of vocalization types (Eliades and Wang, 2013) and are less sensitive to altered auditory feedback (Eliades and Wang, 2008a). The origin of the differences between these two groups of neurons is not clear.

Several recent parallel human investigations have addressed the
suppression of human auditory cortex during speech (Crone et al., 2001; Curio et al., 2000; Christoffels et al., 2007; Flinker et al., 2010; Greenlee et al., 2011; Heinks-Moldonado et al., 2005; Houde et al., 2002). These studies demonstrated that auditory cortex is activated during both speech production and perception, with reduced responses during speaking, termed speech-induced suppression. Human studies have also demonstrated vocal feedback sensitivity similar to that observed in marmosets (Behroozmand and Larson, 2011; 2016; Chang et al., 2013). However, a lack of spatial resolution has prevented a more accurate characterization of the auditory component of speech production-related activity in human auditory cortex.

More recent work in rodents has begun to reveal possible neural circuits underlying such suppression. These experiments have revealed a direct suppression of auditory cortex from connections originating in M2, a putative equivalent of pre-motor cortex (Nelson et al., 2013; Schneider et al., 2014; Schneider and Mooney, 2015a). When paired with a predictable motor-triggered tone, there is a suppression of the tone-evoked sensory response in auditory cortex (Schneider and Mooney, 2015b), similar to what has been described in human subjects (Martikainen et al., 2005; Agnew et al., 2013). Although this suppression of self-generated sensory responses is thought to have a generally similar mechanism to vocalization- and speech-induced suppression, the extent of the mechanistic overlap remains an open question.

A better understanding of these auditory-vocal interactions and their underlying mechanisms requires a more thorough characterization of the contributions of sensory inputs. However, our previous efforts to examine these integration mechanisms has not revealed meaningful differences in auditory tuning between vocalization suppressed and excited auditory cortex neurons (Eliades and Wang, 2003, 2008a). Here we conducted further analyses of single neuron recordings obtained from auditory cortex of two naturally vocalizing marmosets (Eliades and Wang, 2013) in order to more specifically compare auditory and vocal responses of each neuron. We expand on our previous results by examining responses to previously un-analyzed auditory control stimuli. In contrast to our previous findings in which auditory tuning of suppressed and excited neurons were found to be similar, this new analysis demonstrates that vocalization-related excitation is highly predictable based on a neuron’s passive auditory responses, whereas neurons exhibiting vocalization-induced suppression exhibit more diverse auditory tuning properties, including vocal responses that could not be predicted based upon auditory responses. Given the scarcity of single neuron data obtained from naturally vocalizing monkeys, these results add valuable contributions to our understanding of auditory-vocal interaction mechanisms in the primate brain.

2. Materials methods

All experiments were conducted under the guidelines and protocols approved by the Johns Hopkins University Animal Care and Use Committee. The neural data analyzed in this report were obtained from the same animals studied in our previous work (Eliades and Wang, 2013). In these chronic recording experiments, we typically collected a large amount of data under multiple experimental conditions from each neuron. In the Eliades and Wang (2013) study, we focused on comparing vocal responses in auditory cortex of marmosets between different classes of marmoset vocalization. This previous publication, however, only included responses from a limited subset of the auditory control stimuli tested. The present study includes analyses of previously unpublished neural responses to auditory control stimuli and additional analyses including modeling of vocal responses, described further below. Details of the neural recording experiments can be found in our previous publication (Eliades and Wang, 2013) and are only briefly described below.

2.1. Electrophysiological recordings

Two marmoset monkeys (Callithrix jacchus) were each implanted bilaterally with Warp-16 multielectrode arrays (Neuralynx, Bozeman, MT). Each array contained 16 individually moveable microelectrodes (2–4 MΩm impedances). Details on the electrode arrays and recordings, as well as spike sorting procedures, have been previously described (Eliades and Wang, 2008a,b). Auditory cortex was located with standard single-electrode methods prior to array placement (Lu et al., 2001). Both hemispheres were recorded for each animal, starting first in the left hemisphere and subsequently in both simultaneously. Histological examination showed arrays spanning primary auditory cortex, lateral belt and possibly a portion of parabelt fields (Eliades and Wang, 2008b).

2.2. Auditory response characterization

Auditory responses were measured within a soundproof chamber (Industrial Acoustics, Bronx, NY), with the animal seated and head restrained in a custom primate chair. Auditory stimuli were presented free-field by a speaker (B&W DM601) located 1 m in front of the animal. Stimuli included both tone- and noise-based sounds to assess frequency tuning and rate-level responses. Tone-based stimuli consisted of randomly ordered 100 ms pips at 500 ms inter-stimulus intervals, with frequencies spanning 1–32 kHz (5 octaves) at 1/10th octave steps. During most sessions, frequency tuning was measured at 3 sound pressure levels (30, 50, 80 dB SPL); a subset of sessions used a more extensive SPL range (–10 to 90 dB in 10 or 20 dB intervals) to measure the full frequency response area (FRA) map. Band-pass noise stimuli were presented similarly to tones, but were 200 ms in duration, 0.5 octave in bandwidth, and the center frequency varied at 1/5th octave steps. Selected tone and bandpass frequencies were tested more extensively at multiple SPLs (–10 to 90 dB in 10 dB intervals) to assess rate-level tuning. Rate-level functions using wideband (white) noise stimuli were also collected from all units.

In addition, multiple examples of recorded vocalizations were played at different sound levels (“playback”). These include samples of the animal’s own vocalizations (previously recorded from that animal) and conspecific vocalization samples (from other animals living in the marmoset colony). These included multiple exemplars (6–10) from each of the four major marmoset vocalization classes: phee, trillphee, trill, and twitter (Agamaite et al., 2015; Eppl, 1968). Based upon the responses to these vocalization stimuli, one or two samples of each call type were selected and presented at multiple SPLs (0–90 dB in 10 dB steps) to assess vocal rate-level tuning. All vocalization samples were previously recorded at 50 kHz sampling rate, filtered to exclude low-frequency (<1 kHz) background noise, and normalized to have equal stimulus power. A subset of vocalization stimuli were also presented with a parametrically varying mean frequency, computed using a hetro-dynique technique (Schuller et al., 1974). This technique involves serial convolution of a vocal signal with cosines of different frequencies and results in a linear frequency shift of a desired magnitude. Samples were first up-sampled (3×), scaled in frequency by convolution with a 25 kHz cosine, high-pass filtered to remove the aliased signal, convolved with a second cosine of 25-f kHz (where f is the desired frequency shift), low-pass filtered, and finally down-sampled back to the original sample rate. The responses from these additional vocalization stimuli, including parametric changes in loudness and mean frequency, were not
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