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Hearing Research 210 (2005) 63–79
HEARING RESEARCH
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On the prediction of sweep rate and directional selectivity for FM sounds from two-tone interactions in the inferior colliculus

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Received 10 June 2005; accepted 8 July 2005
Available online 2 November 2005

Abstract

Two-tone stimuli have traditionally been used to reveal regions of inhibition in auditory spectral receptive fields, particularly for neurons with low spontaneous rates. These techniques reveal how different frequencies excite or suppress the response to an excitatory frequency of a cell, but have often been assessed at a fixed masker–probe time interval. We used a variation of this methodology to determine whether two-tone spectrotemporal interactions can account for rate-dependent directional selectivity for frequency modulations (FM) in the mustached bat inferior colliculus (IC). First, we quantified the response to upward and downward sweeping, linear, fixed-bandwidth FM tones centered at a unit's characteristic frequency (CF) at 6 sweep durations ranging from 2 to 64 ms. Then, to examine how responses to instantaneous frequencies contained within the sweeps might interact in time, we varied the frequency and relative onset of a brief (4 ms) "conditioner" tone paired with a fixed 4-ms CF probe tone. We constructed "conditioned response areas" (CRA) depicting regions of suppression and facilitation of the probe tone caused by the conditioning tone. We classified the CRAs as predominantly excitatory (40.9%), inhibitory (22.7%), or mixed (36.4%). To generate FM response predictions, the CRAs were multiplied with spectrograms of the same sweeps used to assess response to FM. The predictions of FM rate and directionality were accurate by our criteria in approximately 20% of units. Conversely, the CRAs from the remaining units failed to predict FM responses as accurately, suggesting that most IC units respond differently to FM sweeps than they do to tone-pairs matched to the instantaneous frequencies contained in those sweeps. The implications of these results for models of FM directionality are discussed.

Keywords: Auditory midbrain; Frequency modulation; Spectrotemporal receptive field; Mustached bat; Neural delay lines; FM models; Temporal processing

1. Introduction

Frequency modulations (FM) are dynamic acoustic features found in most mammalian utterances, including human speech. The FM components in such sounds vary in dimensions such as modulation rate (rate of change of frequency over time), sweep direction (low to high, high to low), and depth (sweep bandwidth), and these salient acoustic features often differentiate

Abbreviations: CF, characteristic frequency; CRA, conditioned response area; DS, directional selectivity; DSI, directional selectivity index; EFi, instantaneous effective frequency; FM, frequency modulation; FSL, first spike latency; IC, inferior colliculus; ICc, central nucleus of the inferior colliculus; ICXv, ventral division of the external nucleus of the inferior colliculus; NB, narrow band; SEM, standard error of the mean; STRF, spectrotemporal receptive field

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doi:10.1016/j.heares.2005.07.005

between communication sounds. Studies in a variety of species have found neurons selective for FM direction and rate. Numerous conceptual models for FM rate and directional selectivity have been proposed, but few have been tested for their ability to predict responses to FM sounds quantitatively. More specifically, the temporal and spectral dependence of inhibitory and excitatory interactions thought to underlie preference for rate and direction of FM are not clearly understood.

Classical models propose that directionality arises from either suppression of responses to sweeps in the non-preferred (*null*) direction, facilitation of responses to sweeps in the preferred direction, or both. Suppression of null-direction sweeps has been attributed to asymmetrical inhibitory sidebands in the spectral receptive field in a number of studies (Fuzessery, 1994; Fuzessery and Hall, 1996; Heil et al., 1992b; Shannon-Hartman et al., 1992; Suga, 1965b; Suga et al., 1974; Gordon and O'Neill, 1998). Facilitation in the preferred sweep direction is less well documented, but has been modeled by some as temporally dependent dendritic spatial summation (Erulkar et al., 1968; Fuzessery and Hall, 1996; Heil et al., 1992b; Poon et al., 1992).

Directional preferences for FM sweeps arise in the cochlear nucleus (Britt and Starr, 1976; Erulkar et al., 1968), and are well documented in studies in the auditory midbrain. In previous work in the mustached bat inferior colliculus (IC), we demonstrated that directionality was mainly attributable to suppression by null-direction sweeps, and that the "maximally rejected" rate and direction were significantly correlated with a "best inhibitory delay" revealed by two-tone interactions modeling the tonal components of the FM sweep (Gordon and O'Neill, 1998). The results showed that the timing, and not simply the presence, of sideband inhibition is a critical determinant of FM directionality, and that this could account for the fact that directional preferences are often evident only over a certain range of modulation rates. In a subsequent study of directional preferences in the suprageniculate nucleus of the medial geniculate body, we showed that directionality involved not only suppression by sweeps in the null-direction, but also facilitation by sweeps in the preferred direction (O'Neill and Brimijoin, 2002).

Although many studies have correlated directional selectivity with spectral response areas obtained with two-tone-stimuli (Fuzessery, 1994; Gordon and O'Neill, 1998; Shannon-Hartman et al., 1992; Suga, 1965a), these earlier studies varied the conditioning stimulus (masker) along only one dimension (frequency or time) while holding the other dimension constant, and made no attempt to predict FM responses quantitatively. In the current study, we recorded single units in a portion of the central nucleus of the IC that is tuned to the second harmonic (~59 kHz) of the bat's FM-containing biosonar call, as well as in a similarly tuned region in the ventral division of the external nucleus of the IC (ICXv) where units were shown to be directionally selective (Gordon and O'Neill, 2000). To better our understanding of the spectrotemporal interactions underlying directional selectivity, we expanded the aforementioned two-tone forward masking procedure by extending the analysis in the spectral as well as the temporal domain. By varying one tone (the *conditioner*) along two dimensions, viz. interstimulus onset time interval and frequency, relative to a pure-tone *probe* fixed at the CF, we constructed a *conditioned response area* (CRA) that elucidates the local spectral and temporal interactions that may be relevant for the coding of FM sweeps. This method shares much in common with that used by Brosch et al. (1999), but is measured with higher resolution over a narrower range of frequencies and relative onset times than has been previously attempted. To test the possibility that the CRA measures response properties related to selectivity for FM sweep dimensions, we used the CRA obtained for each unit to predict responses to a set of biologically relevant linear FM sweeps, and compared the predictions to that unit's actual responses to those same sweeps.

2. Methods

2.1. Preparation

Recordings were made from 4 wild-caught male Trinidadian mustached bats (*Pteronotus parnelli rubiginosus*). All husbandry, surgery, and experimental procedures were approved by the University Committee on Animal Resources. Bats were housed in a temperature (24 °C) and relative humidity (80%) controlled flight room and fed fortified mealworms. Surgery to mount a head-restraining post, implant an indifferent electrode, and expose the IC was performed under methoxyflurane anesthesia (Metofane, Pittman-Moore) using techniques described previously (O'Neill, 1985). For the experiments, awake bats were administered a low dose of an opioid agonist (butorphanol tartrate, 0.7 mg/kg i.p.; Abbot Laboratories, North Chicago, IL), and restrained painlessly in a stereotactic frame (Schuller et al., 1986). Single unit recordings were made in the IC on the left side exclusively, using sharpened 1 M Na^+ acetate-filled glass micropipettes with tip impedances ranging from 9 to 12 MΩ. The recorded potentials were referenced to a tungsten indifferent electrode embedded in the skull in contact with the dura, contralateral to the recording site. Recordings in each bat were made over a 4–6-week period, 2–3 days/week, in 4–6 h sessions.