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ScienceDirect

Hearing Research 239 (2008) 107–125

Hearing Research

www.elsevier.com/locate/heares

Research paper

Coding of FM sweep trains and twitter calls in area CM of marmoset auditory cortex

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Received 18 May 2006; received in revised form 28 January 2008; accepted 31 January 2008
Available online 8 February 2008

Abstract

The primate auditory cortex contains three interconnected regions (core, belt, parabelt), which are further subdivided into discrete areas. The caudomedial area (CM) is one of about seven areas in the belt region that has been the subject of recent anatomical and physiological studies conducted to define the functional organization of auditory cortex. The main goal of the present study was to examine temporal coding in area CM of marmoset monkeys using two related classes of acoustic stimuli: (1) marmoset twitter calls; and (2) frequency-modulated (FM) sweep trains modeled after the twitter call. The FM sweep trains were presented at repetition rates between 1 and 24 Hz, overlapping the natural phrase frequency of the twitter call (6–8 Hz). Multiunit recordings in CM revealed robust phase-locked responses to twitter calls and FM sweep trains. For the latter, phase-locking quantified by vector strength (VS) was best at repetition rates between 2 and 8 Hz, with a mean of about 5 Hz. Temporal response patterns were not strictly phase-locked, but exhibited dynamic features that varied with the repetition rate. To examine these properties, classification of the repetition rate from the temporal response pattern evoked by twitter calls and FM sweep trains was examined by Fisher's linear discrimination analysis (LDA). Response classification by LDA revealed that information was encoded not only by phase-locking, but also other components of the temporal response pattern. For FM sweep trains, classification was best for repetition rates from 2 to 8 Hz. Thus, the majority of neurons in CM can accurately encode the envelopes of temporally complex stimuli over the behaviorally-relevant range of the twitter call. This suggests that CM could be engaged in processing that requires relatively precise temporal envelope discrimination, and supports the hypothesis that CM is positioned at an early stage of processing in the auditory cortex of primates.

Keywords: Temporal; Synchrony; Vocalization; Primate; Auditory

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Abbreviations: A1, primary (core) auditory area 1; AII, auditory area II; AAF, anterior auditory field; AM, amplitude modulated; BCF, best classification frequency; BMF, best modulation frequency; BW, bandwidth; CF, characteristic frequency; CL, caudolateral belt area; CM, caudomedial belt area; FM, frequency-modulated; FRA, frequency response area; IM, intramuscular; LDA, linear discriminant analysis; LS, lateral sulcus; maxF, maximum frequency of synchronization; MER, mean error rate; MGC, medial geniculate complex; MGv, ventral division of the MGC; MGd, dorsal division of the MGC; MI, mutual information; MU, multiunit; MTF, modulation transfer function; PCA, principal component analysis; rBMF, rate best modulation frequency; rMTF, rate modulation transfer function; SAMt, sinusoidally amplitude-modulated tones; tEMF, temporal envelope modulated frequency; tw, twitter call; VS, vector strength; vsBMF, vector strength best modulated frequency; vsMTF, vector strength modulation transfer function

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doi:10.1016/j.heares.2008.01.015

1. Introduction

Our working model of the primate auditory cortex includes approximately 12 areas distributed among three regions: core, belt, and parabelt (Kaas and Hackett, 2000; Kaas et al., 1999). These areas are topographically interconnected, and each receives a unique blend of inputs from the medial geniculate complex (MGC) and several multisensory nuclei in the posterior thalamus (Hackett et al., 2007a,b; Jones, 2007). The patterns of connections between areas suggest that auditory cortical processing involves serial and parallel elements (Kaas and Hackett, 1998; Rauschecker et al., 1997). According to the model, information ascends a regional core–belt–parabelt hierarchy, representing three stages of processing. Within each region, areas work in parallel on inputs from several cortical and thalamic sources. Based on the hierarchical relationships between regions, neurons in later stages of processing (i.e., belt, parabelt) are expected to exhibit response properties distinct from that of earlier stages (e.g., core), including: (i) longer response latency; (ii) wider spectro-temporal integration, and (iii) greater stimulus selectivity (Rauschecker, 1998).

Recordings in core and belt areas of various primate species have produced a variety of evidence in support of the first two predictions. Neurons in the lateral belt areas generally have longer response latencies and wider spectro-temporal tuning compared to neurons in area A1 of the core region (Bieser and Muller-Preuss, 1996; Kajikawa et al., 2005; Kosaki et al., 1997; Lakatos et al., 2005; Merzenich and Brugge, 1973; Rauschecker and Tian, 2004; Rauschecker et al., 1995; Rauschecker et al., 1997; Recanzone et al., 2000a; Recanzone et al., 2000b; Tian et al., 2001; Woods et al., 2006). In addition, selectivity for the spatial and non-spatial features of sounds is greater in the belt region, and varies topographically between areas (Recanzone, 2000; Tian et al., 2001; Woods et al., 2006).

Given that neurons in the lateral belt tend to exhibit longer response latencies and increased spectro-temporal integration, a fourth prediction is that synchronization to repetitive or cyclic sounds would be degraded in the belt areas. In general, it has been observed that periodicity or temporal envelope coding degrades along the ascending auditory pathway (Joris et al., 2004), presumably due to the intervening synaptic relay (Berry and Pentreath, 1976; Miles, 1986; Sutor and Hablitz, 1989). If those principles also apply to auditory cortex, temporal resolution should be greater in the core than the belt areas. At present, almost nothing is known about temporal fidelity of neurons in the belt areas, as most studies have focused on neurons in A1 (Cheung et al., 2001; Liang et al., 2002; Luczak et al., 2004; Malone et al., 2007; Nagarajan et al., 2002; Wang and Kadia, 2001; Wang et al., 1995). In a study of several areas in the awake squirrel monkey, Bieser and Muller-Preuss (1996) found that the average best modulation frequency (BMF) for sinusoidally amplitude-modulated tones (SAMt) in the lateral belt areas was lower than in A1, consistent with results obtained in A1 and AII of cats (Eggermont, 1998; Schreiner and Urbas, 1986).

Although these results support predictions about areas in the core–belt–parabelt hierarchy, several studies suggest that at least one of the belt areas, the caudomedial belt area (CM), does not fully conform to the generic profile of a belt area. In ketamine-anesthetized marmosets, we reported that the distributions of minimum response latencies in A1 and CM were highly overlapping, but significantly shorter overall in CM for tones and noise bursts (Kajikawa et al., 2005). Tuning bandwidth was relatively broad in CM. In awake macaques, Lakatos et al. (2005) found that response latencies in A1 for tones were shorter compared to CM, whereas latencies for noise were longer in A1. Finally, in the peri-insular belt area (Pi), which partly corresponds to CM, Bieser and Muller-Preuss (1996) reported shorter mean latencies for tones compared to A1, while BMFs for sinusoidal amplitude-modulated tones were comparable among neurons in A1 and Pi (CM). These findings indicate that neurons in CM have broad spectral tuning typical of lateral belt areas, but also suggest that their temporal fidelity may be typical of neurons in A1.

In the present study, we set out to test this latter prediction in area CM of marmoset monkeys. Temporal coding was studied using two related classes of repetitive acoustic stimuli: (1) marmoset twitter call; and (2) frequency-modulated (FM) sweep trains. The marmoset twitter call is a multi-syllabic vocalization, consisting of 6–8 upward FM phrases repeated at about 7–8 Hz. This call is frequently uttered during social interactions (Epple, 1968), and has been the subject of several studies in A1 of marmosets (Cheung et al., 2005; Luczak et al., 2004; Nagarajan et al., 2002; Wang and Kadia, 2001; Wang et al., 1995). Generally, neuron response profiles in A1 faithfully represent the twitter call's temporal envelope, with a preference for its natural form over temporally modulated or degraded versions of the call. The FM sweep trains were modeled after the phrases of the marmoset twitter call, but modified to estimate temporal fidelity across a range of repetition rates. The number of sweeps in a train was limited to 7, which approximates the average number of phrases in the twitter call. The temporal envelope was modulated by changing the repetition rate of successive sweeps within the train from 1 to 24 Hz, widely overlapping the typical envelope modulation frequency of the twitter call. The spectro-temporal structure of individual sweeps was held constant. Given the short response latency and broad spectral tuning observed in CM, we predicted that the temporal precision for twitter calls and FM sweeps would remain high across the 6–8 Hz range (natural phrase frequency), but would be degraded at higher rates.

The results of the present study confirmed this prediction, demonstrating that neurons in CM appear to contribute to the processing of vocalizations in a manner that preserves temporal details. This adds new insight into the functional significance of this auditory field and its place in the hierarchy. In addition, since auditory cortex is required for the discrimination of species-specific calls