

FUNCTIONAL CONGRUITY IN LOCAL AUDITORY CORTICAL MICROCIRCUITS

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Abstract—Functional columns of primary auditory cortex (AI) are arranged in layers, each composed of highly connected fine-scale networks. The basic response properties and interactions within these local subnetworks have only begun to be assessed. We examined the functional diversity of neurons within the laminar microarchitecture of cat AI to determine the relationship of spectrotemporal processing between neighboring neurons. Neuronal activity was recorded across the cortical layers while presenting a dynamically modulated broadband noise. Spectrotemporal receptive fields (STRFs) and their nonlinear input/output functions (nonlinearities) were constructed for each neuron and compared for pairs of neurons simultaneously recorded at the same contact site. Properties of these local neuron pairs showed greater similarity than non-paired neurons within the same column for all considered parameters including firing rate, envelope-phase precision, preferred spectral and temporal modulation frequency, as well as for the threshold and transition of the response nonlinearity. This higher functional similarity of paired versus non-paired neurons was most apparent in infragranular neuron pairs, and less for local supragranular and granular pairs. The functional similarity of local paired neurons for firing rate, best temporal modulation frequency and two nonlinearity aspects was laminar dependent, with infragranular local pair-wise differences larger than for granular or supragranular layers. Synchronous spiking events between pairs of neurons revealed that simultaneous ‘Bicellular’ spikes, in addition to carrying higher stimulus information than non-synchronized spikes, encoded faster modulation frequencies. Bicellular functional differences to the best matched of the paired neurons could be substantial. Bicellular nonlinearities showed that synchronous spikes act to transmit stimulus information with higher fidelity and

precision than non-synchronous spikes of the individual neurons, thus, likely enhancing stimulus feature selectivity in their target neurons. Overall, the well-correlated and temporally precise processing within local subnetworks of cat AI showed laminar-dependent functional diversity in spectrotemporal processing, despite high intra-columnar congruity in frequency preference. © 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: local circuits, subnetworks, microarchitecture, microcircuits, fine-scale networks.

INTRODUCTION

The primary auditory cortex (AI) is composed of circuits at multiple scales, such as inter-areal, inter-columnar, interlaminar, and intralaminar (Mitani and Shimokouchi, 1985; Barbour and Callaway, 2008; Lee and Winer, 2011; Winer, 2011). At the finest scales, local circuits are formed between nearby neurons, resulting in a tapestry of precisely connected subnetworks (Thomson et al., 2002; Holmgren et al., 2003; Oswald and Reyes, 2008; Otsuka and Kawaguchi, 2009). The connections between adjacent cells may be considered a stereotypical cortical circuit (Defelipe, 1997), and the accompanying activation rules can be complex (Krause et al., 2014). This stereotypy produces a microstructure that is anatomically well-organized, and where the connection strength and cell type are precisely regulated (Defelipe, 1997; Silberberg et al., 2002; Douglas and Martin, 2004). Despite the breadth of these small-circuit descriptions, we know little about the functional processing at these fine scales. Consequently, while functional processing varies with layer (Atencio et al., 2009; Atencio and Schreiner, 2010a,b), few studies have examined the layer-dependent functional micro-organization of auditory cortical processing (Bandyopadhyay et al., 2010; Rothschild et al., 2010; Winkowski and Kanold, 2013). This leaves the question: do neurons at the finest scales of spatial relationship within the tonotopic construct have similar or dissimilar spectrotemporal response preferences?

Two lines of evidence suggest that fine-scale networks within a cortical column can display considerable variability within AI layers. First, nearby neurons in the ventral portion of cat AI appear to have a larger scatter of characteristic frequencies (CFs) than in other regions of AI (Schreiner and Sutter, 1992). Multi-unit data, comprised of multiple single units, revealed

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Abbreviations: AI, primary auditory cortex; ASI, Asymmetry Index; BMFs, best modulation frequencies; bSMF, best spectral modulation frequency; bTMF, best temporal modulation frequency; CF, characteristic frequency; CL, confidence limit; DMR, dynamic moving ripple; FFT, fast Fourier transform; HW, half-width; MTF, modulation transfer function; RMS, root-mean-squared; RN, Ripple Noise; RPI, response precision index; RTF, ripple transfer function; SD, standard deviation; sMTF, spectral modulation transfer function; STRF, spectrotemporal receptive field; tMTF, temporal modulation transfer function.

broad, pure-tone tuning curves in ventral AI, while contributing single-units often had narrower tuning and disparate CFs. This indicated that multi-unit data can mask the tuning variability in local neuron populations.

The second line of evidence comes from recent imaging work in mouse AI, which revealed a fractured micro-tonotopy, at least in the upper cortical layers (Bandyopadhyay et al., 2010; Rothschild et al., 2010). Previously, single-unit recordings in mice at large spatial scales showed consistent, and largely continuous, tonotopy (Stiebler et al., 1997; Guo et al., 2012). Two-photon imaging revealed that in supragranular layers, neurons within 50–100 μm of each other may differ in CF by up to four octaves (Rothschild et al., 2010). CFs were more similar in granular layers (Winkowski and Kanold, 2013; Kanold et al., 2014). Functional heterogeneity was also observed by imaging the synaptic preference of pyramidal neuron spines. Each synaptic contact appeared to be tuned to relatively different frequencies, implying that nearby neurons provide varying receptive field information (Chen et al., 2011).

Therefore, to examine the functional variability within cortical columns we recorded from pairs of nearby neurons across the laminar extent of cat AI and constructed spectrotemporal receptive fields (STRFs) and nonlinear input/output functions for each neuron to assess the characteristics of functional processing of cat AI at the finest spatial scales.

Our previous study on local circuit processing established in the cat a precise temporal relationship between the activity of neighboring neurons (Atencio and Schreiner, 2013). We also have demonstrated a high similarity of frequency-preference between neurons in local networks and in the same column (Atencio and Schreiner, 2010a, 2013). Here, we significantly extend this work by addressing (1) whether spectrotemporal processing characteristics, including nonlinear input/output functions, show local diversity, (2) whether local functional variability is similar across different cortical layers, and (3) whether synchronous spiking of local pairs of neurons transmits the same spectrotemporal information as the constituent neurons.

EXPERIMENTAL PROCEDURES

Surgical procedures, stimulation, and recording

The University of California, San Francisco Committee for Animal Research approved all experimental procedures under protocol AN086113. We previously described the experimental procedures that were used in this study (Atencio and Schreiner, 2010a,b). Briefly, young adult cats ($N = 10$) were given an initial dose of ketamine (22 mg/kg) and acepromazine (0.11 mg/kg), and then anesthetized with pentobarbital sodium (Nembutal, 15–30 mg/kg) during the surgical procedure. The animal's temperature was maintained with a thermostatic heating pad. Bupivacaine was applied to incisions and pressure points. Surgery consisted of a tracheotomy, reflection of the soft tissues of the scalp, craniotomy over AI, and durotomy. After surgery pentobarbital sodium was discontinued and, to maintain an areflexive state, the animal

received a continuous infusion of ketamine/diazepam (2–5 mg/kg/h ketamine, 0.2–0.5 mg/kg/h diazepam in lactated Ringer solution).

With the animal inside a sound-shielded anechoic chamber (IAC, Bronx, NY, USA), we delivered stimuli via a closed speaker system to the ear contralateral to the exposed cortex (diaphragms from Stax, Japan). We made extracellular recordings with multi-channel silicon recording probes, which were provided by the University of Michigan Center for Neural Communication Technology. The probes contained 16 linearly spaced recording channels, with each channel separated by 150 μm . We used probes with channel impedances between 2 and 3 $\text{M}\Omega$, since these impedances allowed us to resolve single units. Probes were carefully positioned orthogonally to the cortical surface and lowered to depths between 2300 and 2400 μm using a microdrive (David Kopf Instruments, Tujunga, CA, USA).

Stimulus

For each recording site, pure tones were presented in a random sequence. The amplitudes and frequencies of the tones spanned 0–70 dB (5 dB steps) and 2.5–40 kHz (0.1 octave steps), respectively. All neurons were also probed with a broadband (0.5–40 kHz) dynamic moving ripple (DMR) stimulus (Escabi and Schreiner, 2002; Atencio et al., 2008). The maximum spectral modulation frequency of the DMR was 4 cyc/oct, and the maximum temporal modulation frequency was 40 cyc/s (Escabi and Schreiner, 2002). The maximum modulation depth of the spectrotemporal envelope was 40 dB. Mean intensity was set at 30–50 dB above the average pure tone threshold. For a small subset of sites, we also presented a Ripple Noise (RN) stimulus. The RN is the sum of 16 independently created DMR stimuli. The spectrotemporal envelopes of the DMR and RN stimuli are dissimilar: the DMR contains local correlations while the RN does not (see Fig. 2A, G).

Recording

We followed the recording and spike-sorting procedure outlined in Atencio and Schreiner (2013). Neural traces were bandpass filtered between 0.6 and 6 kHz and recorded with a Neuralynx Cheetah A/D system at sampling rates between 18 and 27 kHz. After each experiment the traces were sorted off-line with a Bayesian spike sorting algorithm that is conceptually and mathematically described in Lewicki (1994, 1998). Only events in the traces that exceeded the DC baseline by five RMS noise levels were used in the spike sorting procedure (termed spike events). Most channels of the probe yielded 1–2 well-isolated single units (similar to (Peyrache et al., 2012)). The Bayesian spike sorting allows the proper classification of spikes so long as the peak in one spike waveform does not overlap with the trough of another spike waveform; when spike waveforms overlap, the combined waveform must exceed the five root-mean-squared (RMS) threshold to be detected. If an event is detected, and cannot be assigned to a single unit, an overlap decomposition procedure is performed. To resolve a

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