



Research paper

Cross-correlations between three units in cat primary auditory cortex

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ABSTRACT

Here we use a modification of the Joint-Peri-Stimulus-Time histogram (JPSTH) to investigate triple correlations between cat auditory cortex neurons. The modified procedure allowed the decomposition of the xy -pair correlation into a part that is due to the correlation of the x and y units with the trigger unit, and a remaining 'pair correlation'. We analyzed 16 sets of 15-minute duration stationary spontaneous recordings in primary auditory cortex (AI) with between 11 and 14 electrodes from 2 arrays of 8 electrodes each that provided spontaneous firing rates above 0.22 sp/s and for which reliable frequency-tuning curves could be obtained and the characteristic frequency (CF) was estimated. Thus we evaluated 11,282 conditional cross-correlation functions.

The predictor for the conditional cross-correlation, calculated on the assumption that the trigger unit had no effect on the xy -pair correlation but using the same fraction of xy spikes, was equal to the conventional pair-wise correlation function between units xy . The conditional correlation of the xy -pair due to correlation of the x and/or y unit with the trigger unit decreased with the geometric mean distance of the xy pair to the trigger unit, but was independent of the pair cross-correlation coefficient. The conditional pair correlation coefficient was estimated at 78% of the measured pair correlation coefficient. Assuming a geometric decreasing effect of activities of units on other electrodes on the conditional correlation, we estimated the potential contribution of a large number of contributing units on the measured pair correlation at 35–50 of that correlation. This suggests that conventionally measured pair correlations in auditory cortex under ketamine anesthesia overestimate the 'true pair correlation', likely resulting from massive common input, by potentially up to a factor 2.

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1. Introduction

Pair correlations in auditory cortex have been studied extensively (Brosch and Schreiner, 1999; Dickson and Gerstein, 1974; Eggermont, 1992, 1994) especially with relation to receptive field overlap. The results indicate that these correlations are mostly of the common-input type, extend over large distance, and have significant but relatively small (mostly <0.1) cross-correlation coefficients. Pair correlation coefficients have been used in a cluster analysis for recordings with micro-electrode arrays (Eggermont, 2006), and

resulted in relatively small groups of neurons up to a few mm in distance that had higher within-cluster correlation than with any other neurons outside the cluster. The resulting neuron clusters reflected patches of correlated neurons in cortex, of several mm^2 in size that expand and contract in response to different stimuli. Clusters crossed area boundaries only in 5% of the cases where simultaneous recording were made in AI and posterior auditory field. Questions that emerged from this study were related to the sufficiency of pair correlations to describe local cortical processing.

We recently showed (Gourévitch and Eggermont, 2010) that most of the information about click-repetition rate or amplitude modulation of stimuli in cortical neurons is contained in single-unit spike bursts, or in the firings of at most two or three synchronized units, suggesting that multiple-spike train analysis methods should mainly focus on pairs or triplets of neurons. We also found that the information carried by synchronized multi-channel activity or single-neuron spike bursts is additional to information carried by single-channel single-spike firings.

The problem of multiple-unit correlations can be explored in several ways. Techniques such as gravitational clustering (Gerstein

Abbreviations: AI, primary auditory cortex; CF, characteristic frequency; JPSTH, Joint-Peri-Stimulus-Time Histogram, Joint-Peri-Spike-Time Histogram; MSU, multiple single unit; PST, post stimulus time, post spike time; SD, standard deviation

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et al., 1985) and unitary-event analysis (Grün et al., 2002) are capable of showing multiple simultaneous interactions between neurons in an ensemble. In addition, a modification of the joint peri stimulus time histogram (JPSTH; Aertsen et al., 1989; Eggermont, 1991, 1994) can give some insight in interactions between three simultaneously recorded neurons. Here, instead of using stimulus onset as a trigger, spikes from a third neuron are used. This method has been used as a tool to detect synchrony among 3 neurons in a synfire chain pattern (Prut et al., 1998; Abeles and Gat, 2001) and is related to the snowflake analysis (Perkel et al., 1975; Abeles, 1983; Czanner et al., 2005). The JPSTH procedure using spikes as trigger can decompose the cross-correlation into a part that is due to the correlation of each of the two units with the trigger unit and a remaining 'pair correlation'. Here we present a JPSTH-like analysis of common input to triplets of neurons recorded with multi-electrode arrays from AI in cat. As we will demonstrate, an estimate of the combined effect of all potential conditional cross-correlations on the raw pair correlation can amount up to 50%.

2. Methods

The experimental methods are the same as in Noreña and Eggermont (2005) and Eggermont (2006), and part of the data collected in those two studies have been analyzed here. The care and the use of animals reported in this study was approved (BI10R-04) by the Life and Environmental Sciences Animal Care Committee of the University of Calgary. All animals were maintained and handled according to the guidelines set by the Canadian Council of Animal Care. The stimulus types used, the recording procedure, and the data analysis procedures are reviewed here. Note that all correlation data analyzed here are from 15-minute duration spontaneous activity recordings.

2.1. Recording and spike separation procedure

Two arrays of eight electrodes (Frederic Haer) with electrode impedances between 1 and 2 MΩ were used. The electrodes were arranged in a 4 × 2 configuration with inter-electrode distance within rows and columns equal to 0.5 mm (see inset in Fig. 7). Each electrode array was oriented such that all electrodes were touching the cortical surface and then were manually and independently advanced using a Narishige M101 hydraulic microdrive (1 drive for each array). The depth of recording was between 700 and 1200 μm, and thus the electrodes were likely in deep layer III or layer IV. The signals were amplified 10,000 times using a Frederic Haer HiZx8 set of amplifiers with filter cut-off frequencies set at 300 Hz and 5 kHz. The signals were processed by a TDT-Pentusa multi-channel data-acquisition system (filter bandwidth: 300 Hz–10 kHz). Spike sorting was done off-line using a semi-automated procedure based on principal component analysis and K-means clustering implemented in MATLAB. The spike times and waveforms were stored. The multiple single-unit (MSU) data presented in this paper represent only well-separated single units that, because of their regular spike waveform likely are from pyramidal cells. For statistical purposes, the separated single-unit spike trains were added again to form a MSU spike train, thereby eliminating potential contributions from thalamocortical afferents or fast spikes from interneurons. For inclusion in the data set, the spontaneous MSU record (after spike sorting and recombining) required more spikes than 200 in 900 s, i.e., a rate >0.22 spikes/s.

2.2. Cortical frequency tuning

Frequency-tuning curves were measured by randomly presenting 27 gamma-tone pips with frequencies covering five octaves (e.g., 1.25–40 kHz) in equal logarithmic steps and presented at eight

different stimulus levels in 10-dB steps (e.g., 5–75 dB SPL) at a rate of 4/s such that each intensity–frequency combination was repeated five times. The duration of the gamma-tone pips at half-peak amplitude was 15 ms, and the envelope was truncated at 50 ms, where the amplitude is down by 64 dB compared with its peak value.

2.3. Cross-correlation of spontaneous activity

Cross-correlograms were calculated using custom made Matlab programs (Eggermont, 1992; Tomita and Eggermont, 2005; Eggermont, 2006). Quantification of neural correlation in those studies was done on the basis of the cross-correlation coefficient:

$$R_{xy}(\tau) = \frac{C_{xy}(\tau) - E_{xy}}{\sqrt{(N_x - N_x^2/N)(N_y - N_y^2/N)}} \quad (1)$$

which for relatively low spike counts (N_x, N_y) compared to the number of bins in the record (N) reduces to:

$$R_{xy}(\tau) = \frac{C_{xy}(\tau) - E_{xy}}{\sqrt{N_x N_y}} \quad (2)$$

where $C_{xy}(\tau)$ is the number of coincidences in the bin corresponding to lag time τ , E_{xy} is the expected value for coincidences under the assumption of independent spike trains, $E_{xy} = (N_x N_y)/N$, with $N = T/\Delta$, where N_x and N_y are the number of x and y spikes in the recording, Δ is the bin size, and T the duration of the recording. $|R_{xy}(\tau)| \leq 1$. Stationarity estimates of the recordings were based on the S-test described in Gourévitch and Eggermont (2007).

The cross-correlation coefficients were considered significantly different from zero at a level of 5 SD (i.e., >0.005 for 2 ms bins in a 900 s recording; Eggermont, 1992).

2.4. The Joint Peri Stimulus Time Histogram

The Joint Peri Stimulus Time Histogram, JPSTH ($k\Delta, m\Delta$) is defined (Aertsen et al., 1989) as the number of coincidences from neurons x and y in bin ($k\Delta, m\Delta$) given the occurrence of stimulus z onset in bin (0,0), where Δ is again the bin size and $k = 0, \dots, K - 1, m = 0, \dots, M - 1$. Usually the number of bins is the same for both axes, $K = M$. We will use the symbol τ to indicate the time lag, $\tau = k\Delta$ and symbol v to indicate the time lag $v = m\Delta$. The expected value of the JPSTH under the assumption of independence of the two spike trains is given by the outer product (*) of the zx and zy PST histograms:

$$\text{PSTprod}(\tau, v) = \text{PST}_{zx}(\tau) * \text{PST}_{zy}(v) \quad (3)$$

The standard deviation for the PST-predictor under the assumption of independence and the additional assumption of Poisson distributed numbers of coincidences per bin (Abeles and Gat, 2001) is given by the square root of PSTprod(τ, v). Thus:

$$\rho_{\text{JPSTH}}(\tau, v) = \frac{\text{JPSTH}(\tau, v) - \text{PSTprod}(\tau, v)}{\sqrt{\text{PSTprod}(\tau, v)}} \quad (4)$$

The JPSTH(τ, v) and PSTprod(τ, v) are calculated per stimulus sweep and per bin. When $\rho_{\text{JPSTH}}(\tau, v)$ is integrated across bins along and parallel with the main diagonal the result is a cross-correlation coefficient function (Aertsen et al., 1989).

We apply a variant of the JPSTH by substituting a spike train of a third neuron (instead of stimulus onsets) as the trigger sequence z , and resulting in the joint peri spike time histogram (JPSTH). The trigger is now located at the center of the JPSTH, and $k = -(K - 1), -(K - 2), \dots, 0, \dots, (K - 2), (K - 1)$; $m = -(M - 1), -(M - 2), \dots, 0, \dots, (M - 2), (M - 1)$. The cross-

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