

Coding of naturalistic stimuli by neurons in rat somatosensory cortex: A spike-triggered covariance analysis

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What sensory features do cortical neurons extract and encode? We addressed this issue by recording neuronal spike trains in the somatosensory cortex of the rat in response to deflection of the whiskers with a complex, dynamic stimulus. By applying spike-triggered covariance analysis, we found that two stimulus features dominated neuronal response. To a first approximation, the firing of these neurons is determined by the velocity and acceleration on a time-scale of ~ 30 ms. The firing rate is proportional to the stimulus “energy”.

Introduction

Understanding the neural code in a given system requires the answer to two fundamental questions: (1) What is basic information-bearing unit of the spike trains; (2) What message is conveyed to the rest of the brain by the occurrence of such a unit? Our previous work (Panzeri et al, 2001; Petersen et al, 2001) addressed the first question, using the rat somatosensory system as a model. We found that most of the total information available in the spike trains of simultaneously recorded neuron pairs could be accounted for by the precise timing of individual spikes. Since spike time correlations played a minor role, these results support the hypothesis that the basic information-bearing unit in this neural system is the precisely timed, individual spike.

In the light of these findings, we now consider the second question. We would like to understand what features of a natural stimulus a cortical neuron extracts and signals to its downstream targets. The standard procedure for addressing this question is reverse correlation (spike-triggered averaging). This method has led to considerable insight into neurons that perform essentially linear filtering of their input, but fails for non-linear neurons. For example, reverse correlation fails to capture non-linear properties like the invariance of complex cells to the location of an oriented bar within their receptive fields.

Although such non-linear effects cannot be extracted from the spike-triggered average stimulus, they impose structure on higher order spike-triggered statistics. Provided that the stimulus is gaussian (not necessarily white), the spike-triggered covariance provides sufficient information for determining the feature space to which a non-linear neuron is sensitive (Brenner et al, 2000). In principle, by recording the responses of a neuron to a gaussian stimulus, it is possible to recover a complete, nonlinear description of what stimulus features cause a neuron to spike and what information its spike train conveys to its downstream targets. We have applied this method to

study what cortical neurons signal about a naturalistic, dynamic sensory signals. Our model is the rat whisker system.

Physiological Methods

Rats were anaesthetised with urethane and the right somatosensory “barrel” cortex exposed. Whiskers on the left side of the snout were fed through a fine plastic grid mounted on a piezoelectric ceramic wafer. This stimulator was moved in the vertical plane by applying a time-varying voltage in the range -160 to 160 Volts, controlled by computer. Neuronal activity was recorded using quartz-insulated Platinum-Iridium electrodes (Uwe Thomas), filtered (bandpass 300 - 6000 Hz), amplified and digitised at 30 kHz (Neuralynx), then stored for off-line analysis. Custom spike sorting software was used to isolate stable single units.

Stimulus Statistics

Barrel cortical neurons are known to respond to changes in position rather than to position per se, we therefore generated a 30-minute, band-limited gaussian white noise in the velocity domain (0 - 50 Hz) at 1 kHz sampling rate.

Data Analysis

Without loss of generality, the dependence of a neuron’s instantaneous firing rate at time t $r(t)$ on an arbitrary, time-varying stimulus can be written as a nonlinear function $g[\cdot]$ of the convolution of N linearly independent features f_j with the stimulus $s(t)$ (Brenner et al, 2000):

$$r(t) = \bar{r} g[k_1(t), k_2(t), \dots, k_N(t)]$$

$$k_j(t) = \int_0^\infty s(t-\tau) f_j(\tau) d\tau$$

Where \bar{r} is the firing rate averaged over stimuli. For stimuli with zero auto-covariance, the space spanned by the set of features $\{f_1, f_2, \dots, f_N\}$ is equal to that spanned by the columns (or rows) or the spike-triggered covariance matrix C_s . For correlated stimuli, with auto-covariance C , it is the column space of the difference matrix $\Delta C = C_s - C$ that is relevant. Since $\{f_j\}$ can be expressed in any basis, this formalism does not uniquely specify each individual feature vectors f_j . It is only the space spanned by the features that is unique.

The first step in the analysis was to estimate the matrices C and C_s . We resampled the stimulus at 2 ms intervals and considered stimulus histories of up to 100 ms. These matrices were therefore 50×50 . We determined the rank of ΔC , and hence the number of significant filters N , by counting the number of eigenvectors of ΔC that had eigenvalues significantly different to zero. The filters $\{f_j\}$ were obtained by deconvolving the eigenvectors of ΔC by C .

Next, we determined the nonlinearity $g[\cdot]$. By Bayes theorem:

$$\frac{r_t}{\bar{r}} = \frac{\Pr[s | \text{spike}]}{\Pr[s]} = \frac{\Pr[k_1, k_2, \dots | \text{spike}]}{\Pr[k_1, k_2, \dots]}$$

Using the estimated features $\{f_j\}$, we evaluated the projection of each filter $\{k_j\}$ onto the stimulus preceding each spike and, from these data, estimated the probability density $\text{Pr}[k_1, k_2, \dots | \text{spike}]$ by a kernel-smoothing method. Similarly, $\text{Pr}[k_1, k_2, \dots]$ was estimated by picking stimulus segments at random times.

Results

All analyses were conducted in terms of stimulus velocity. Figure 1 shows a typical example of how the spike-triggered covariance differs from the auto-covariance of the stimulus itself. Within a time period roughly 50 ms preceding the spike, stimuli at nearby times were significantly positively correlated; stimuli at more distant times were significantly negatively correlated. We analysed this correlation structure as follows.

In order to find the number of filters necessary to describe the neuron, we estimated the eigenvalue spectrum of ΔC . The result, shown in Figure 2, was that, there were two eigenvalues much greater than the others. To a first approximation, therefore, the operation that this neuron conducts on the stimulus can be described in terms of two filters. These filters are shown in Figure 3. They measure the average velocity and acceleration over a time-scale of 20-30 ms preceding a spike. Taking the Fourier transform of these features shows directly that they are band-pass filters centred at about 30Hz. It is also important to note that the second feature is approximately the first one, phase-shifted by 90° .

The next step was to estimate the firing rate produced by each possible velocity-acceleration combination. This function $g[\cdot]$ is plotted in Figure 4. The neuron has a high probability of emitting a spike both for large absolute velocities and large absolute accelerations. Although this neuron had a slight preference for negative over positive velocities, the nonlinearity had striking radial symmetry. Putting this result together with the finding that the two features constitute a quadrature pair, this means that, to a first approximation, the neuron can be described as detecting the “energy” in a frequency band centred around $\sim 30\text{Hz}$. Other neurons were also sensitive to energy, but the precise frequency band differed across cells (see also Arabzadeh, this meeting).

Conclusion

Our results suggest that the firing of individual spikes by neurons in somatosensory cortex in response to a complex dynamic stimulus is mainly determined by the “energy” in a neuron-dependent frequency band. This energy therefore seems to be an important part of the message that these spikes convey to the rest of the brain.

References

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- Panzeri S, Petersen RS, Schultz S, Lebedev M, Diamond ME (2001) *Neuron* 29: 769.
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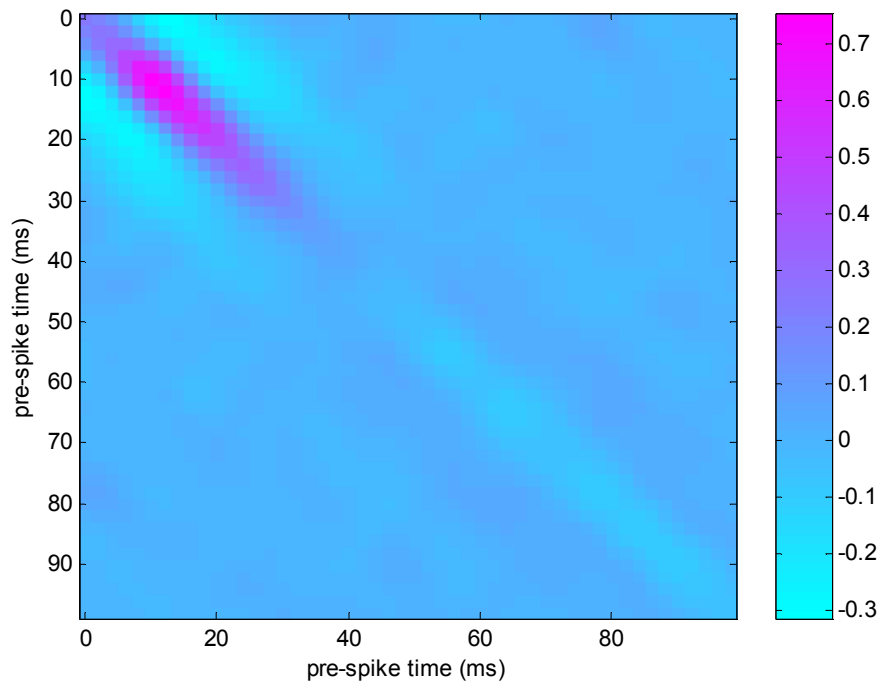


Figure 1. Example of the ΔC matrix. Stimulus normalised to unity variance.

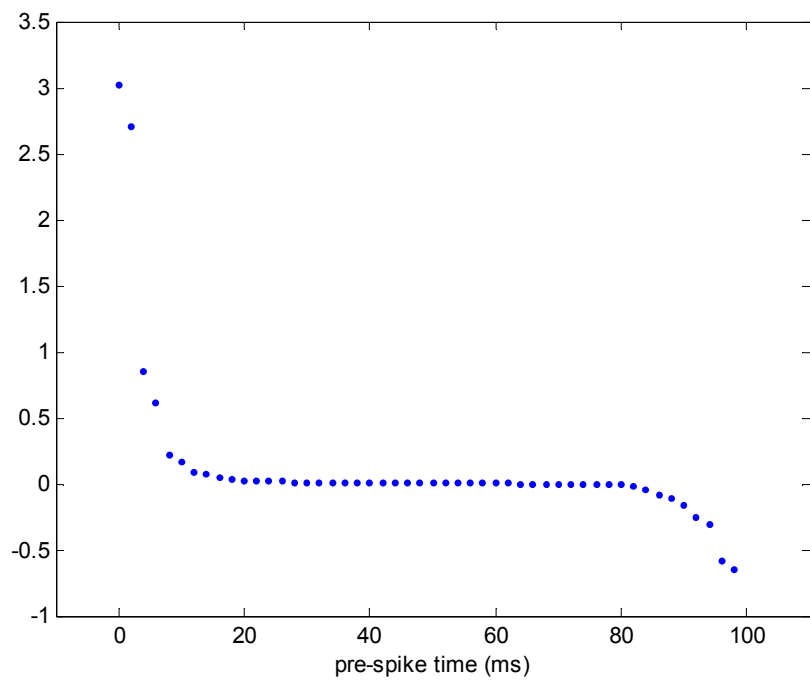


Figure 2. Eigenvalue spectrum of ΔC for the data shown in Figure 1.

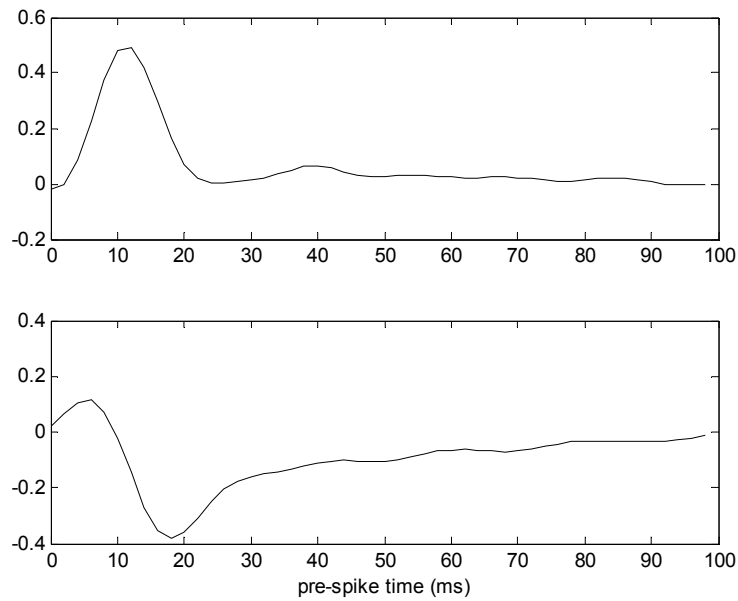


Figure 3. Features corresponding to the two largest eigenvalues of ΔC shown in Figure 2. Vertical scale is stimulus velocity.

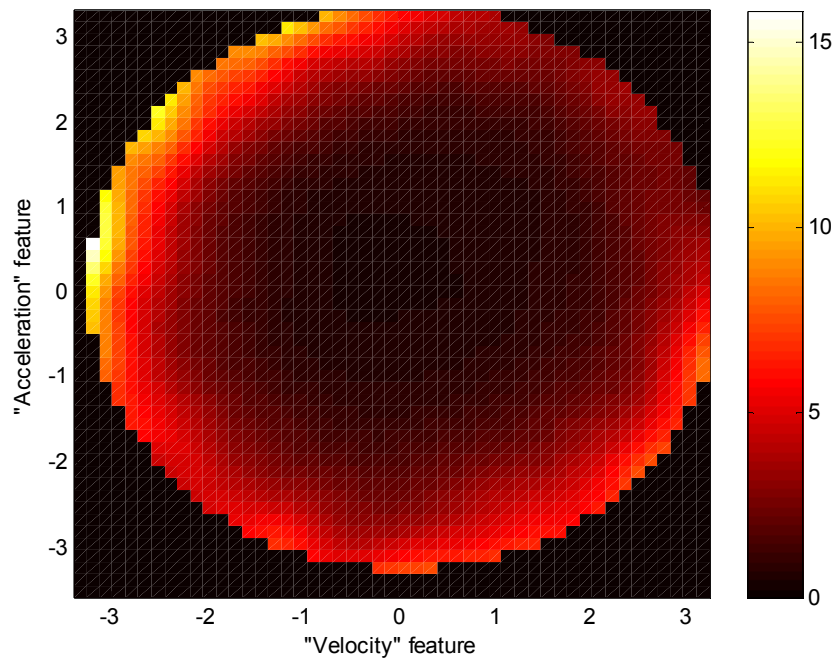


Figure 4. The relative probability of a spike given the projection of the stimulus onto the “velocity” and “acceleration” features shown in Figure 3. Units on the horizontal and vertical axes are standard deviations of the stimulus. The colour scale is the firing rate given each velocity, acceleration combination to average firing rate.