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Identification of neural feature space from spike triggered covariance expressed as a function of PRC

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For the purpose of elucidating the neural coding process based on the neural excitability mechanism, some researchers have investigated the relationship between the neural dynamics and the spike triggered stimulus ensemble (STE), which indicates what stimuli are more likely or less likely to induce neural spikes. Ermentrout et al. have analytically derived the relational equation between the phase response curve (PRC) and the spike triggered average (STA), which is the average of the STE, when regular spikes with a period T are disturbed by sufficiently small white noise, as $STA(\tau)=-\sigma^2 Z'(T-\tau)$ (1). Here, τ is the time relative to a spike, σ is the noise intensity, and Z is PRC [1]. Furthermore, they showed that Eq. (1) holds true for real neurons. Their study has made meaningful progress in relating the neural dynamics to the neural coding for real neurons. However, the STA is the first cumulant of the STE. In order to approximately identify the distribution of STE as a Gaussian, we should determine its second cumulant, called spike triggered covariance (STC).

We derive the relational equation between STC and PRC on the basis of the formulation introduced in [2] and analytically solve it by the expansion used in [3]. The result is

$$\begin{aligned} STC(\tau_1,\tau_2) &= \sigma^2\delta(\tau_1-\tau_2)+\frac{1}{2}\sigma^4 Z'(T)Z(T)\delta(\tau_1-\tau_2) \\ &\quad +\sigma^4 H_{1/2}(\tau_2-\tau_1)Z''(T-\tau_2)Z(T-\tau_1)+\sigma^4 H_{1/2}(\tau_1-\tau_2)Z''(T-\tau_1)Z(T-\tau_2), \end{aligned} \tag{2}$$

where $H_{1/2}(x)$ represents the Heaviside function which takes 1/2 at $x=0$. Moreover, we analyze the eigenfunctions of $\Delta C(\tau_1-\tau_2)=STC(\tau_1-\tau_2)-\sigma^2\delta(\tau_1-\tau_2)$ in order to extract the neural feature space, which is a low dimensional subspace of the full stimulus space characterizing the stimulus encoded by neurons. The eigenfunctions associated with the positive and negative eigenvalues of ΔC are called the excitatory and suppressive eigenfunction, respectively. In this case, the stimuli in the subspace spanned by excitatory eigenfunctions cause shorter interspike intervals (ISIs) than T, while the stimuli in the subspace spanned by suppressive eigenfunctions cause longer ISIs.

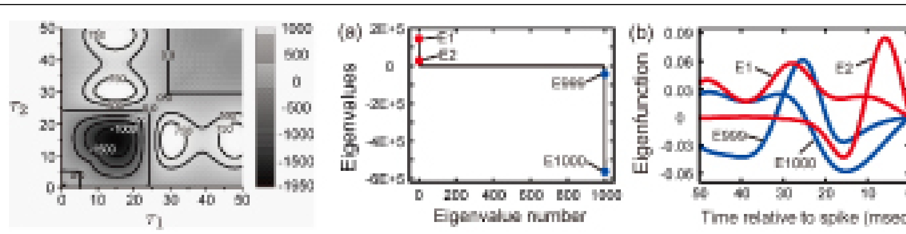

Figure. 1 left: STC of the rat hippocampal CA1 pyramidal neuron. (a) Eigenvalue spectrum of ΔC for the same neuron as illustrated in the left panel. (b) Excitatory (red) and suppressive (blue) eigenfunctions corresponding to the eigenvalues in (a).

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Figure 1 shows the STC of a rat hippocampal CA1 pyramidal neuron as calculated by Eq. (2), where the PRC could be estimated by our algorithm [4]. Note that it is difficult to measure the STC for real neurons directly, because the number of neural spikes required for a stable calculation of STC is nearly square of the number required for the STA. Figure 1 suggests that the neural feature space of this rat hippocampal CA1 pyramidal neuron can be described by the four eigenfunctions in Fig. 1b.

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