Characterizing neural gain control using spike-triggered covariance

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Abstract

Spike-triggered averaging techniques are effective for linear characterization of neural responses. But neurons exhibit important nonlinear behaviors, such as gain control, that are not captured by such analyses. We describe a spike-triggered covariance method for retrieving suppressive components of the gain control signal in a neuron. We demonstrate the method in simulation and on retinal ganglion cell data. Analysis of physiological data reveals significant suppressive axes and explains neural nonlinearities. This method should be applicable to other sensory areas and modalities.

White noise analysis has emerged as a powerful technique for characterizing response properties of spiking neurons. A sequence of stimuli are drawn randomly from an ensemble and presented in rapid succession, and one examines the subset that elicit action potentials. This “spike-triggered” stimulus ensemble can provide information about the neuron’s response characteristics. In the most widely used form of this analysis, one estimates an excitatory linear kernel by computing the spike-triggered average (STA); that is, the mean stimulus that elicited a spike [e.g., 1, 2]. Under the assumption that spikes are generated by a Poisson process with instantaneous rate determined by linear projection onto a kernel followed by a static nonlinearity, the STA provides an unbiased estimate of this kernel [3]. Recently, a number of authors have developed interesting extensions of white noise analysis. Some have examined spike-triggered averages in a reduced linear subspace of input stimuli [e.g., 4]. Others have recovered excitatory subspaces, by computing the spike-triggered covariance (STC), followed by an eigenvector analysis to determine the subspace axes [e.g., 5, 6].

Sensory neurons exhibit striking nonlinear behaviors that are not explained by fundamentally linear mechanisms. For example, the response of a neuron typically saturates for large amplitude stimuli; the response to the optimal stimulus is often suppressed by the presence of a non-optimal mask [e.g., 7]; and the kernel recovered from STA analysis may change shape as a function of stimulus amplitude [e.g., 8, 9]. A variety of these nonlinear behaviors can be attributed to gain control [e.g., 8, 10, 11, 12, 13, 14], in which neural responses are suppressively modulated by a gain signal derived from the stimulus. Although the underlying mechanisms and time scales associated with such gain control are current topics of research, the basic functional properties appear to be ubiquitous, occurring throughout the nervous system.