Dissection of a Nonlinear Cascade Model for Sensory Encoding

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Action potential encoding in the cockroach tactile spine neuron may be treated as a single-input, single-output dynamic nonlinear process, where the input is the electric current flowing across the neuronal membrane and the output is the resultant train of action potentials. The nonlinear behavior of the system may be characterized by a functional expansion method which efficiently and accurately yields similar kernels to the Wiener method. A simple nonlinear cascade consisting of sequential dynamic linear, static nonlinear, and dynamic linear components was identified and gives a good approximation to the response of the neuron to random stimulation. Next, we attempted to study the components of the cascade by the use of a drug, phentolamine, which selectively modifies the dynamic behavior of the encoder. Application of phentolamine to the neuron caused a significant change in the first dynamic linear component of the cascade without affecting the other components. The change was much larger than the variability between results obtained from individual animals. This finding has implications for the biophysical processes which are involved in the components of the cascade.

Keywords—Nonlinear analysis, Sensory encoding, Wiener kernels, Action potential, Mechanoreceptor, Pseudorandom noise, Cascades.

INTRODUCTION

White-noise analysis techniques have been used in a number of attempts to model nonlinear information coding by sensory systems (12,20,21). These experiments used the cross-correlation method of Lee and Schetzen (19) or a related frequency domain
approach developed by French and Butz (7) to obtain the Wiener kernels of the system (25). However, these methods are not only very time consuming, but often give inaccurate system identification because of the impossibility of providing stimuli with infinite bandwidths, amplitude ranges, and durations.

An alternative fast orthogonal method for estimating nonlinear system kernels has been developed by Korenberg (16). This method does not require the input signal to be white, Gaussian, or of infinite duration. It implicitly creates a set of functionals which are orthogonal for the given input signal. Using this method, accurate kernel estimates can be obtained efficiently from shorter data records. The kernel estimates depend on the form of the input signal because the method minimizes the mean square error between the output of the unknown system and the output of the functional series for the particular input sequence used in the experiment. However, if this input is approximately Gaussian white noise, the kernels obtained are good approximations to the Wiener kernels.

The femoral tactile spine of the cockroach is a mechanoreceptor organ that contains a single sensory neuron (11). Afferent activity in the neuron can be observed by extracellular recording from the main sensory nerve in the femur. The neuron is silent in the resting condition but responds to movements of the spine with rapidly adapting bursts of action potentials. It is incapable of producing a steady discharge in response to a constant stimulus. With continuous sinusoidal or random stimulation a high-pass frequency response is seen, which can be well characterized as a non-integer power law or fractional differentiator (2,8). However, the behavior of the neuron is strongly nonlinear in several respects. The output is not a continuous function of time, but a series of brief action potentials; the response is unidirectional and rectifies any input. Similar dynamic behavior has been observed in a range of other arthropod and vertebrate mechanoreceptors (6).

There is evidence that the dynamic behavior of the tactile spine neuron is dominated by the encoding of the receptor current into action potentials. Direct recordings of the receptor current in response to movements of the spine gave a linear and frequency-independent relationship (3) while direct electrical stimulation of the neuron in the axosomatic region gave rapid adaptation to step increases in current and the familiar power law relationship between randomly varying current and the resulting action potentials (4). This latter, reduced preparation allows system identification to be performed on the portion of the neuron that is crucial in producing the dynamic nonlinear response.

In previous experiments we used the fast orthogonal procedure to identify system kernels for action potential encoding in the tactile spine neuron (9,17). To simulate the behavior of the neuron, we used a nonlinear LNL cascade model consisting of a static nonlinear component sandwiched between two dynamic linear components. This model satisfied the requirement of predicting the form of the second-order kernel from the two dynamic linear components (13) and produced a system output with spike components that matched the actual system action potentials with an accuracy of about 80% (9).

In our previous work we attempted to relate the components of the cascade to known biological processes in the neuron. However, to test these hypotheses it is necessary to be able to modify parts of the neural encoder while performing system identification. In the present work, we describe the first such analysis. We show that the system kernels for encoding behavior in the neuron are highly reliable and reproduc-