Synaptic Coding of Time-Varying Spike Trains[‡]

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Abstract

Spike-producing neurons produce complex responses to stationary input trains. These responses have been described using techniques from the field of nonlinear dynamics, and are typical of those from periodically perturbed nonlinear oscillators.

Here we are concerned with the effects of nonstationary input trains. We present recent simulation results, largely in agreement with experimental results on a living preparation, emphasizing the relationships between stationary and nonstationary behaviors. The implications for synaptic coding are considered. We suggest that the viewpoint of a neuron as a nonlinear dynamical system has important contributions to make to our understanding of neural computation.

1 Introduction

Spike-producing neurons produce complex responses to stationary input trains [1, 2, 3]. These responses, previously obscure, have been described using techniques from the field of nonlinear dynamics [4, 5, 6, 7]. They are typical of those from periodically perturbed nonlinear oscillators [8, 9, 10, 11, 12, 13, 14, 15, 16].

Here we are concerned with the effects of *nonstationary* input trains. We present recent simulation results, largely in agreement with experimental results on a living preparation, and emphasize the relationships between stationary and nonstationary behaviors. Its implications for *synaptic coding*, the relationship between presynaptic and postsynaptic trains of a neuron [17], are considered. As the synapse is the functional unit of neural networks, its code is the computational unit, modified by connectivity and other factors [18, 19].

2 Methods

The simulation results were produced using a physiological model of the crayfish slowly adapting stretch receptor organ (SAO), which includes a prototypical inhibitory synapse [20, 6, 21]. This model, like the living preparation, produces periodic, pacemaker outputs when unperturbed, with all interspike intervals equal to N , the *natural* interval.

We sought to duplicate experiments conducted on the SAO, which used frequency-modulated input trains [22, 23, 24]. Presynaptic trains were produced by starting with a *modulation*, or *rate control*, waveform $r(t)$, here a triangle wave. This described the instantaneous rate of the presynaptic train, with minimum $1/I_m$, maximum $1/I_M$, and period P . Given a presynaptic spike

at time s_0 , subsequent spike times can be computed from $s_{k+1} = s_k + 1/r(s_k)$. The spike train was applied to the simulated neuron as natural IPSPs, and the resultant postsynaptic spikes were assimilated to a *point process* [25]. Three sets of event times were recorded: the presynaptic times $\langle \dots, s_{k-1}, s_k, s_{k+1}, \dots \rangle$, the postsynaptic times $\langle \dots, t_{i-1}, t_i, t_{i+1}, \dots \rangle$, and the start time of each cycle of $r(t)$, $\langle \dots, c_{j-1}, c_j, c_{j+1}, \dots \rangle$.

Analysis was based on intervals and cross intervals computed from these event times. Intervals were computed for presynaptic and postsynaptic events; $I_k = s_k - s_{k-1}$ and $T_i = t_i - t_{i-1}$, respectively. The presynaptic interval was often normalized by the natural interval as N/I_k . Cross intervals were computed from a postsynaptic event back to the most recent preceding event of another type. One type was $\phi_i = t_i - s_k$, or the *phase*, and the other was $\psi_i = t_i - c_j$, the *modulation phase*.

For brevity's sake, only one type of graph is shown for each of the stationary and nonstationary cases; both based on the *return map*. A return map displays the relationship between an interval or cross interval and a subsequent one, plotted as T_i versus T_{i+1} , for instance (in this case, termed a *first-order interval return map*).

For stationary input, each choice of N/I will produce a characteristic set of return maps; we draw a three-dimensional plot of those maps as functions of normalized input rate. For modulated input, ψ_i is used as the third dimension to produce the 3-D return maps (T_i, T_{i+1}, ψ_i) and $(\phi_i, \phi_{i+1}, \psi_i)$. As $r(t)$ is periodic, ψ_i uniquely determines input rate, so the ψ axis can also be considered a rate axis. This is the basis of our comparison of parametrized stationary return maps (*bifurcation diagrams* [12]) with 3-D modulation return maps.

3 Results

Figure 1 compares a stationary response (A, B) with two different modulation simulations (C through F); intervals left (A, C, E) and phases right (B, D, F). In all cases, the range of rates was $0.3 \leq N/I_k \leq 1.3$, with $\psi_i = P/2$ corresponding to $N/I_k = 1.3$ and $\psi_i = \{0, P\}$, $N/I_k = 0.3$.

The stationary plots show the division of the rate scale into periodic, *locked* responses (where 1-D curves occur) and aperiodic, nonlocked responses (where there are dense bands, mostly representing *walkthroughs*). These features were duplicated faithfully by slow modulation periods (C, D), where the 1-D curves indicate *alternation*, the more general, nonstationary counterpart of locking. Faster modulation produced more distorted responses (E, F); however, the basic features of the stationary bifurcation diagrams are still evident. The points also form sharp features with little scatter, indicating that each cycle of the modulation produced identical behaviors, validating the unstated assumption underlying this graph.

4 Discussion

The implications of these results for neural computation are potentially far-reaching; we shall only touch upon major points, leaving detailed discussion to ongoing work [26]. Nonstationary, changing neural inputs are the rule rather than the exception in animals, reflecting changes in their environment and their reactions [19]. We therefore view these experiments as critical for elucidating the computations implemented by synaptic coding, modeling for instance repetitive motor activities such as swimming or breathing [22].

These results are in agreement with those found for the SAO, demonstrating the profound

Figure 1: Comparison of stationary and nonstationary responses. Stationary interval (A) and phase (B) return maps, parametrized by normalized input interval N/I . Nonstationary 3-D return maps for $P = 60s$ (C, D) and $P = 7s$ (E, F).

influence stationary behaviors have on neurons' responses to nonstationary input. Additionally, the differences between Figure 1(C, D) and (E, F) suggest the significance of parameters P , I_m , and I_M , as well as average rate slope $\Delta I_k/\Delta t$ and range $(I_M - I_m)$ [22, 23].

Additionally, the synapse's inhibitory nature only shows itself in terms of overall average input and output rates and in the paradoxical *accelerating* trends during alternating responses. This fact is often ignored in neural network models. We suggest that the viewpoint of a neuron as a nonlinear dynamical system, capable of complex responses to smooth changes in inputs and characterized by dynamical behaviors, bifurcations, spike timing pattern, etc., has important contributions to make to our understanding of neural computation.

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