

Bifurcations of neural transient responses

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This paper presents an investigation into the responses of neurons to errors in presynaptic spike trains. Errors are viewed as brief-duration changes in stationary presynaptic spike trains that induce large-magnitude transient responses. A permeability-based model of the crayfish slowly-adapting stretch receptor organ (SAO) and associated inhibitory synapse [1] was presented with pacemaker presynaptic spike trains that contained *errors*, or missing spikes. Simulations were performed using custom C code and the ODEPACK ODE integration library; analysis was done in Matlab.

The SAO and model are pacemakers, producing spikes separated by an invariant *natural* interval N . Simulations involved almost identical presynaptic spike trains: **1.** $\mathcal{H} = \{s_1, s_2, \dots, s_n\}$, $I = I_k = s_k - s_{k-1}$, pacemaker *reference* trains with spikes at times $\{s_k\}$ and interspike interval I , and **2.** $\mathcal{H}_e = \mathcal{H} - \mathcal{H}_{\mathcal{X}}$, *erroneous* trains identical to \mathcal{H} except for the removal of selected spikes at times $\mathcal{H}_{\mathcal{X}}$ at least 15s apart (the *errors*).

For each \mathcal{H} , the model settled to a stationary discharge. Stationarity, dynamical behavior, and error aftereffects were judged by assimilating the postsynaptic train to the point process of spike times $\mathcal{T} = \{\dots, t_{i-1}, t_i, \dots\}$ and reconstructing its attractor via the *phase return map*. *Phases* are the cross intervals from postsynaptic spikes to preceding presynaptic ones, $\phi_i = t_i - s_k$, $s_k = \max_{\forall j} s_j < t_i$. The first-order phase return map is the plot of (ϕ_i, ϕ_{i+1}) . This was constructed for each \mathcal{H} train after startup transients settled. For the corresponding \mathcal{H}_e , return map points for 10 postsynaptic spikes before and 20 after each error were also computed. The distance between each of these points and the nearest point on the reference phase return map was computed using the Matlab `deLaunay` and `dsearch` functions.

The plot of distances versus time from the error was termed a *recovery plot* and showed the time course of the neuron's error recovery. The global bifurcation behavior of the model's transient response was determined by constructing an Arnol'd map, or two dimensional bifurcation diagram [2]. Presynaptic rate $1/I$ (normalized as N/I) and the synaptic strength (the maximum synaptic permeability, \bar{P}_{syn}) were the bifurcation parameters used. A total of 27,500 simulations were run on a cluster of 15 1.5GHz Pentium 4 machines running Linux, such that the space $(N/I, \log \bar{P}_{syn})$ in the range $0.2 \leq N/I \leq 2.0$, $1.0 \times 10^{-9} \leq \bar{P}_{syn} \leq 1.0 \times 10^{-6}$ was covered evenly. Half of the simulations were reference and half erroneous, producing 13,750 recovery plots. Each recovery plot was then reduced to a single number by taking the maximum perturbation. A conventional Arnol'd map of the model's stationary behavior was also constructed using the reference simulations only by determining, for each simulation, the minimum variance of differences of coordinates in the first through fifth order phase return plots, $\phi_i - \phi_{i+q}$, $q = 1, 2, 3, 4, 5$.

The Arnol'd map for reference, non-erroneous input trains is presented in Figure 1(A), and shows characteristic vertical phase locking "tongues". The Arnol'd map for error response transients is presented in Figures 1(B) and (C). Comparison of (B) with the stationary Arnol'd map in (A) shows that the maximum perturbation has peaks and undergoes sudden changes at the boundaries of locking regions. Figure 1(C) illustrates that within locking regions, and excepting the neighborhood of bifurcations, maximum perturbations vary smoothly. Outside the broad locking regions, there is significant variation of maximum perturbation.

These results demonstrate that the large-scale transient behavior of a nonlinear dynamical system can be analyzed in terms of its global bifurcation structure. This analysis is based on spike timing information alone, which is observable by other neurons. Previous work on error correction coding in this model demonstrated

that both bifurcations and stationary behaviors are influential [3]. This can be explained by considering the system's *response space*, composed of all of its state spaces containing all of its attractors [4].

When a transient is induced, the model's state moves within this response space, possibly crossing the locations of stationary bifurcation points into basins of qualitatively different attractors. After the error, the re-established stationary input draws the state back to the corresponding stationary attractor. If the displacement in the response space lies entirely within the basins of qualitatively similar attractors, such as in the central part of the 1:1 locking region, the return to stationarity is monotonic and rapid, a result of the smoothly-varying attractors and basin gradients. If the pre-error behavior is near a bifurcation, then one or more bifurcations may be crossed. After the error, the state is drawn through the basins of multiple attractors and a longer-duration, possibly nonmonotonic recovery may result.

The influence of stationary behavior is also important in other respects: **1.** Periodic attractors are more strongly attractive than non-locked behaviors, and thus recovery is faster there. **2.** Aperiodic attractors can occupy a larger volume of the state space than periodic ones. Thus, the model's state may not be perturbed as far away from the attractor. **3.** Low ratio locking regions are much broader than nonlocked ones; therefore the density of bifurcations within the response space is lower near lockings. So, locked regions correspond to "simpler," more homogeneous transients. This is readily apparent in the differing surface smoothness or roughness in Figure 1(C).

In living neurons, dynamical behaviors are assumed to be contaminated by "noise". It therefore is relevant to consider the effects of spike timing precision on error responses, as, intuitively, lower precision timing should perturb stationary behaviors away from their attractors. Some basic effects of timing precision on transient responses have been investigated [3] already; extensions of the current work to include varying spike timing precision are ongoing.

References

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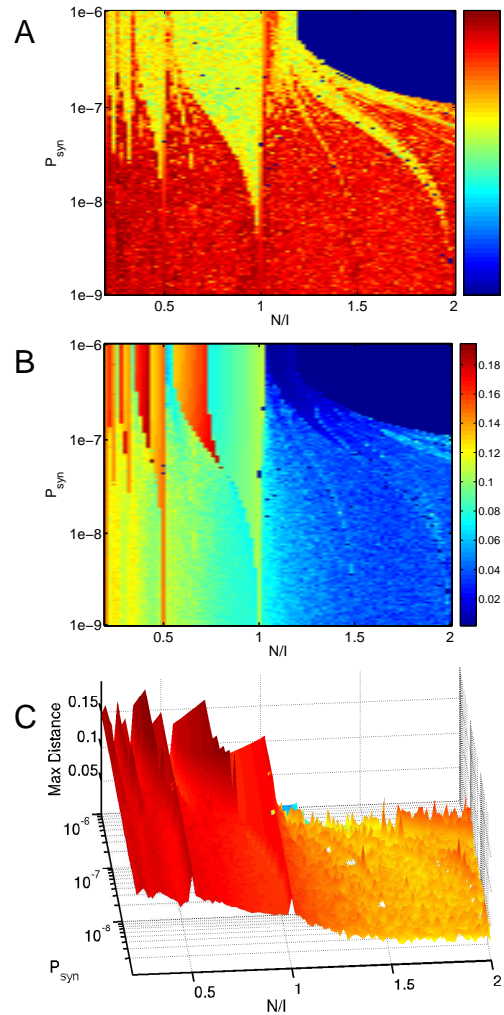


Figure 1: Arnol'd maps of error free responses (A), and maximum distance to attractor normalized by N/I (B, C).