Effect of noise on the coding properties of two fundamental types of neurons

J. Benda,[*] M. St-Hilaire[*], A.V.M. Herz[†] and A. Longtin[*]

Abstract

It is known that from a dynamics-systems point of view there are two fundamental classes of spiking neurons: type-I and II. Here we analyse the effect of noise on basic properties of these two classes (f-I-curves, latencies, phase-resetting curves). We also contrast the relative information coding capabilities of each type for band-limited Gaussian signals. With increasing noise, the f-I-curves of both classes become similar. However, the two classes are still distinguishable based on latency, phase resetting and spike clustering measurements. The unexpected result of the information study is that the "resonator" type-II neuron encodes at least as well as the type-I neuron.

Introduction

In information theoretical analysis the coder, like a spiking neuron, is treated as a black box. However, triggered by the work of Hodgkin and Huxley (1952) numerous results have been achieved about the properties of the spike generator as a dynamical system. Here we want to open the black box and link information processing with basic properties of the spike generator.

Based on spiking behavior evoked by current injections two different types of repetitive spiking neurons can be distinguished. Hodgkin (1948) already recognized this dichotomy in his recordings from crustacean axons. He classified neurons which are capable to fire with arbitrary low frequencies to constant stimulation as class-I neurons (also referred to here as type-I neurons). In contrast, above threshold class-II neurons fire always with non-zero frequencies. Their f-I-curve (firing frequency versus input current) has a discontinuity. The reason for these two different qualitative behaviors of neurons is the type of bifurcation between the rest state and periodic firing as shown by Rinzel and Ermentrout (1998). Type-I neurons have a saddle-node bifurcation, while type-II neurons undergo a subcritical Hopf bifurcation.

This classification is important for theoretical as well as for experimental studies on spiking neurons. The type of bifurcation determines the dynamics of spiking, which manifests itself in various measurable properties. The type of neuron chosen for a theoretical

[*]Department of Physics, University of Ottawa, K1N 6N5 Canada
[†]Innovationskolleg Theoretische Biologie, Humboldt-University, 10115 Berlin, Germany

study may strongly influence the results (see for example Hansel et al., 1995; Ermentrout, 1996; Gutkin and Ermentrout, 1998), while different aspects measured in a real neuron can be explained by the underlying bifurcation (e.g. subthreshold oscillations and spike clustering observed in Alonso and Klink, 1993, originate from a Hopf bifurcation).

While many results have been obtained about the properties of deterministic type-I and type-II neurons (Hansel et al., 1995; Ermentrout, 1996; Izhikevich, 2000), the effect of noise, which may originate from channels, synapses, etc., on these two types of neurons has only partially been examined (Schneidman et al., 1998).

Here we summarize these effects on basic properties of these two classes of neurons, such as f-I-curves, latencies, and phase resetting curves. We especially focus on how these measures can be used to distinguish between the two types of neurons experimentally. Then we analyse the coding of information in both types of neurons. For the investigations we use the Morris-Lecar model (Morris and Lecar, 1981) in its two different parameterizations as a type-I and a type-II neuron (Rinzel and Ermentrout, 1998).

Characteristics

In type-I neurons the threshold current where the saddle-node bifurcation occurs separates the neural dynamics between subthreshold and superthreshold regimes. In type-II neurons below the Hopf bifurcation, there is a region of bistability where a stable fixed point coexists with a stable limit cycle, so that there are in fact three different regimes of dynamics (see Fig. 1).

Additive noise to the input current has only a small linearizing effect on the f-I-curve of a type-I neuron. In contrast, in type-II neurons noise smears out the discontinuity of its f-I-curve in the region of bistability, making it more similar to a type-I f-I-curve. In this region, the variability of interspike intervals is very large, since repetitive spiking on the limit cycle is interrupted by periods of silence (where the system stays close to the fixed point) of different durations (see Schneidman et al., 1998, for a detailed discussion of this phenomenon). The corresponding interspike interval histogram shows a long tail. Above the region of bistability, repetitive firing in type-II neurons is very similar to that of type-I neurons, in that noise just jitters the spikes, which results in a narrow interspike interval histogram.

The dependence on stimulus intensity of the latency of the first spike following the onset of a constant stimulus is nearly unaffected by noise. The mean latency is on the order of the corresponding interspike interval in the type-I neuron, while it is much shorter in the type-II neuron. However, the variance of the latency is very small in the type-II neuron, while in the type-I neuron it increases with decreasing distance to the bifurcation.

Phase resetting curves describe the shift of a spike induced by a small perturbation during repetitive firing. An advance of a spike results in positive phase shifts, while a delay results in negative phase shifts. Type-I neurons have a positive phase resetting curve as derived from the properties of a saddle-node bifurcation by Ermentrout (1996). Numerical studies show that in type-II neurons there is a region of negative phase shifts followed by a region of positive phase shifts (Hansel et al., 1995). Our study reveals that these properties are preserved in the presence of noise (Fig. 2).
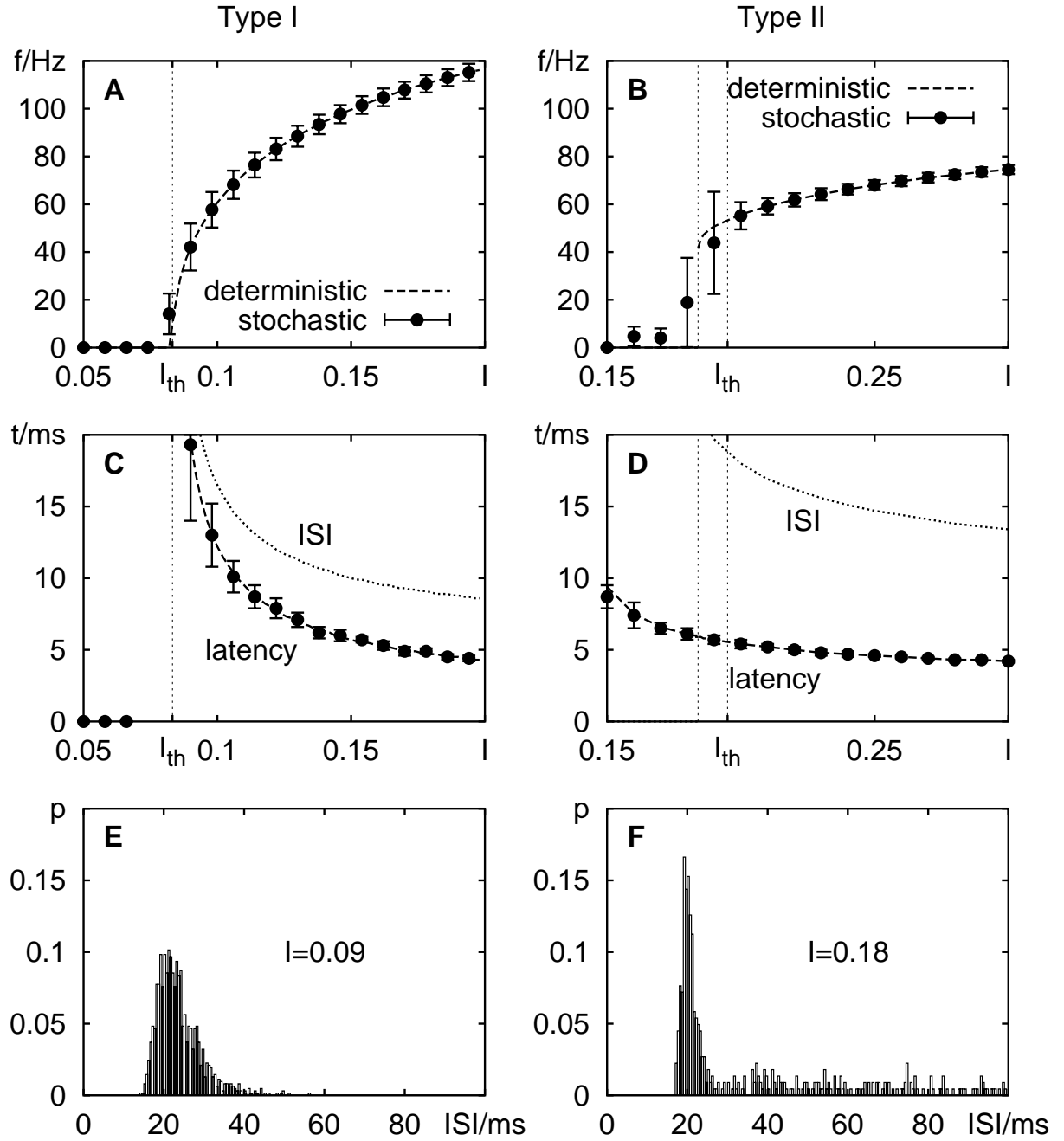
Figure 1: Influence of noise (gaussian white noise with standard deviation 0.02, cut-off frequency 1000Hz) on basic properties of type-I and type-II neurons. Vertical dotted lines mark the bifurcations. In type-II neurons below the Hopf bifurcation (right line) there is a bifurcation where the stable limit cycle emerges (left line). Between those two bifurcations is a region of bistability. A, B: f-I-curves. C, D: Latencies in comparison with the corresponding interspike interval (ISI). E, F: Interspike interval histogram for a current I as indicated. The currents where choosen to illustrate that in a type-II neuron one can get a histogram with a sharp peak and a very long tail due to the bistability, while such a tail cannot be observed in a type-I neuron. Increasing the current makes the histograms of both types of neurons more narrow.
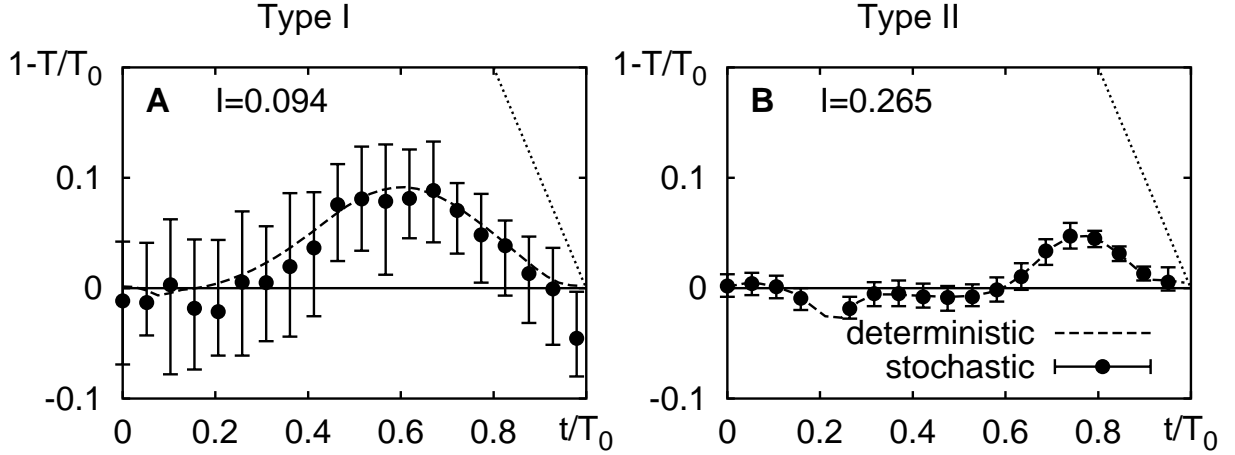
Figure 2: Phase resetting curves measured in the noisy type-I and type-II neuron for a baseline current as indicated. Shown are medians of the noisy data with their second and third quartile in comparison with the deterministic case. T_0: unperturbed ISI, T: perturbed ISI, t: time of perturbation. Due to causality no data can ly above the dotted line.

Coding

Since the type-I neuron does not have a characteristic time scale for deterministic firing, due to the saddle-node bifurcation, one might expect that it can better track time-varying stimuli than a type-II neuron, which tends to fire preferentially around its characteristic frequency (associated with the Hopf bifurcation). We now present a computational analysis of the capabilities of type-I and type-II neurons to encode time-varying stimuli. We wish to contrast these capabilities using two models that are in most respects identical, except for the bifurcation. Since for the Morris-Lecar model the globally attracting steady states are well characterized in both cases, one can hope that the comparison using that model can be made quite fairly. By this we mean that any differences between the coding capability could be ascribed mainly to the bifurcation, which determines among other things the f-I-curve, latency and phase-resetting properties of the model neurons.

We focused on time-varying band-limited continuous input signals that are either presented on their own, or are applied as modulations of a carrier wave. The latter case applies to a number of sensory modalities, namely the processing of certain acoustic or electrosensory stimuli. For example, weakly electric fish perform active electrolocation using amplitude modulations of their electric organ discharge, which is a quasi-sinusoidal carrier of frequency that is four or five times higher than the signals to be encoded. Here we present results on this case of amplitude modulated carriers.

For simplicity the amplitude modulated sine waves are added to the voltage equation in the Morris-Lecar system, rather than as genuine synaptic inputs with reversal potentials. We include background additive noise to cover synaptic and conductance fluctuations. Here we present numerical computations of the coding fraction, which is a measure of the quality of encoding basedon the linear stimulus reconstruction technique (Wessel et al., 1996). It is an indirect method of information rate estimation. Also, our comparison is
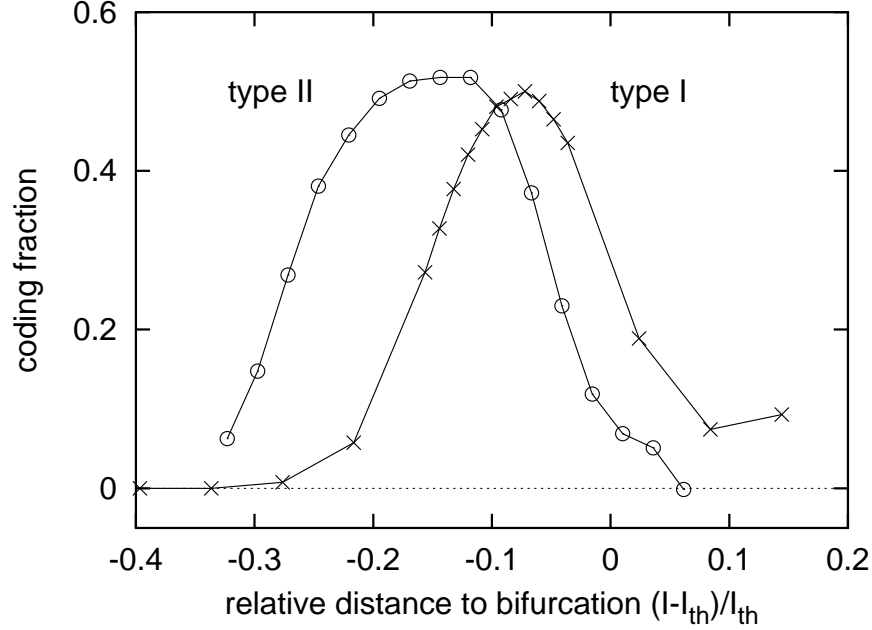
Figure 3: The coding fraction of the type-I and the type-II neuron in dependence on the relative distance to the bifurcation $(I - I_{th})/I_{th}$.

done for parameter sets for which the mean firing rates are approximately the same for both models.

We have found that for very low internal noise, the type-I model codes slightly better than the type-II model. However, as soon as there is some of internal noise, the type-II performs slightly better. But there are no strong differences from this perspective, as noise simply linearizes the f-I curves for both models, and both models code relatively well. What is more striking is the fact that the type-II model codes well over a relatively larger range of bias currents than the type-I does. This bias current sets the baseline about which the modulated carrier fluctuates. Further, this range is also shifted to more subthreshold bias values for the type-II, as shown in Fig. 3. This figure was obtained with a small amount of background noise. The characteristics of these two curves, and in particular their relation to the phase-resetting results discussed above, will be explained in more detail in our talk. The interesting conclusion here is that the "resonator" type-II neuron can encode as well as if not slightly better than the type-I neuron under a variety of conditions.

Conclusion

In the first part of our work, we summarized how f-I-curves, latencies, and phase reset-ting curves of a spiking neuron are affected by additive internal noise. Based solely on f-I-curves it is not possible to distinguish between type-I and type-II neurons. However, latencies and phase resetting curves still allow this distinction. In addition, spike cluster-ing can only be observed in the region of bistability of type-II neurons. Also, the very low variability of latencies is unique in type-II neurons. This was for example found by

Fricker and Miles (2000) in hippocampal neurons. The second part of our study contrasts the information transfer capabilities of type-I and type II neurons, in the context of sinusoidal carriers whose amplitude is modulated by the stimulus. We find that both models are comparable with respect to their best coding, but that the type-II neuron can encode over a broader range of bias currents.

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