SURVIVAL OF SUBTHRESHOLD OSCILLATIONS: THE INTERPLAY OF NOISE, BIFURCATION STRUCTURE, AND RETURN MECHANISM

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Abstract. Mixed mode oscillations (MMO’s) composed of subthreshold oscillations (STO’s) and spikes appear via a variety of mechanisms in models of neural dynamics. Two key elements that can influence the prominence of the STO’s are multiple time scales and time varying parameters near critical points. These features can lead to dynamics associated with bifurcation delay, and we consider three systems with this behavior. While it is well known that bifurcation delay related to a slow time scale is sensitive to noise, we compare other aspects of the noise-sensitivity in the context of MMO’s, where not only bifurcation delay, but also coherence resonance and dynamics in the interspike interval play a role. Noise can play a role in amplifying the STO’s but it can also drive the system into repetitive spiking without STO’s. In particular we compare integrate and fire models with models that capture both spike and STO dynamics. The interplay of the underlying bifurcation structure and the modeling of the return mechanism following the spike are major factors in the robustness and noise sensitivity of the STO’s in the context of multiple time scales.

1. Introduction. Computational models of neural dynamics often rely on reduced systems that capture the essential features rather than all details, particularly in network models that become computationally expensive with increasing network size. For example, integrate and fire (IF) neurons have been used extensively to model a variety of individual and network behaviors (for example, see [8, 10, 13, 25] and many references therein). IF models typically include modeling dynamics in the subthreshold phase of the neuron, to capture the interspike interval (ISI) and the approach to a threshold. Once the threshold is crossed, the complex dynamical equations are replaced in the (faster) spiking phase by simple spiking dynamics, and a reset mechanism is used to return to the subsequent refractory period and the ISI. Intermediate levels of complexity include replacing all or part of the reset mechanism by modeling the control variable with slow dynamics in the ISI and fast
relaxation during the spike (e.g. see [14] and [19]). While convenient for simplicity of the simulation, the choice of model reduction and reset or return mechanism coupled with the nonlinearities may change the noise sensitivity of the model.

The goal of this paper is to highlight the sources of noise sensitivity in reduced systems exhibiting periods of subthreshold oscillations (STO’s) interspersed with regular spiking, one type of mixed mode oscillations (MMO’s). In particular we consider both a FitzHugh Nagumo (FHN)-type model [22] in contexts where the control or bifurcation parameter is fixed and where it varies slowly, and a more complex model for stellate cells first proposed in [1] and a reduced IF version of this model studied in [26] and [27]. These models exhibit dynamics typical of slow-fast systems with an underlying bifurcation delay structure; that is, in the ISI there is a period of damped oscillations followed by a period where the STO’s are prominent.

We compare the STO-spike transition in these systems with STO-bursts in an elliptic bursting model to highlight different sources of noise sensitivity that influence the robustness of the STO’s, directly related to the appearance of MMO’s and clustering/bursting dynamics. Here and in the rest of the paper clustering is defined as the succession of two spikes with no period of STO’s in the ISI, referring to the specific dynamics where there is potential for STO’s in the ISI but instead one spike follows another. In contrast, bursting refers to the transition to an active state of tonic spiking for a significant period without the possibility for STO’s between the spikes in this phase. These active bursts are interspersed with periods of subthreshold behavior (small oscillations or quiescence, depending on the setting).

In experimental single-cell measurements on stellate cells from the entorhinal cortex [2, 32], increasing depolarization of the cells typically induces STO’s, MMO’s with rare spiking, clustering and sometimes bursting (i.e. sequences of 3–5 spikes followed by a period of a few STO’s). The term clustering is used regularly in [2, 32], and clustering and bursting are used somewhat interchangeably in [9]. Clustering is also used in [23] to describe intermittent small groups of spikes in the context of a noisy van der Pol oscillator.

Since clustering corresponds to omitting STO’s between spikes, it usually corresponds to a decrease in the proportion of STO’s in the time series. We consider the relationship of noise and cluster fraction, the ratio of the number of clusters (pairs of spikes without STO’s in between) to the total number spikes over a long time interval, as a measure of the robustness of the STO’s and corresponding MMO’s to noise. The common theme that emerges from comparing these different systems is that a combination of features influences the noise sensitivity of the STO’s/ISI’s and spike onset: the multiple time scales, the bifurcation structure, and the return mechanism that restarts the ISI.

In this paper we consider three three-dimensional systems, a FHN-type model, a reduced model for stellate cells, and a model for elliptic bursting. Each of these systems has one fast variable, a slow variable with a corresponding intermediate slow time scale, and a second slow variable with the slowest time scale. The second intermediate slow variable typically corresponds to the relaxation oscillation, that is, following a spike there is a sharp relaxation to a quiescent state. As also described in the literature on the canard phenomenon, for example [16], this slow variable plays a critical role for the sharp transition from small amplitude oscillations to large amplitude oscillations in oscillators exhibiting the canard phenomenon. The third and slowest variable plays the role of a slowly varying bifurcation or control parameter in the ISI, often termed a ramp in the context of delay bifurcations.
In the models analyzed here we consider cases where the third variable is indeed slower than the second, although this is not strictly necessary. A second similarity among the systems compared here is that the slow variation of this bifurcation or control parameter is in close proximity to a Hopf bifurcation, so that the STO-spike transition exhibits behavior associated with the dynamics of bifurcation delay. We consider models with parameter values such that for smaller noise levels, the slowest time scale allows well-defined periods of STO’s. Then we consider the survival of these STO’s for different modeling choices and different noise levels. The time scales are discussed in more detail in the context of each model. In addition to the three systems described above, we also consider a seven variable stellate cell model that has one of the three variable systems as a subsystem.

Connections with delay bifurcations:

The term delay bifurcation is motivated by a comparison of the full dynamics with the dynamics of a subsystem where the slowest variable is treated as a fixed parameter, yielding a 2D subsystem in the examples we consider here. As the slowest variable in the full system slowly ramps through the value corresponding to a bifurcation in the 2D subsystem, the full system does not immediately make the transition to the behavior corresponding to the bifurcation of the 2D system. Figure 1 gives a schematic for two types of the classical behavior one expects to see in the context of a delay bifurcation or a slowly varying ramp. There the control parameter varies slowly through a critical value (marked in Figure 1 with a * at the time when it is reached) corresponding to a bifurcation in the 2D system. The dependent variable is attracted to the steady state or fixed point for values below this critical point, followed by a delayed transition to the different behavior of the bifurcation as the parameter slowly crosses it, as shown in Figure 1. We show the behavior of the slow variable passing through a Hopf bifurcation, where the transition is from a fixed point to oscillations as in (1),(2). The slow passage through a pitchfork bifurcation is shown for a model of the form \( x_t = \epsilon x - x^3 \), where there is a transition from one fixed point to another fixed point. In either case the slow variation of the ramp allows attraction to the fixed point in the subthreshold values of the ramp and plays a key role in the memory-like effect that delays the transition to the bifurcation behavior. The delay behavior indicated here is reduced or eliminated with additive perturbations, consistent with the sensitivity of these models to noise discussed below. For example, as discussed in [17], there is no delay if there is an \( O(\epsilon) \) perturbation to the pitchfork bifurcation case.

It is well known from previous studies that for delay bifurcations, or more generally for certain systems with alternating slow/fast dynamics, the sensitivity of the slow dynamics is exponentially sensitive to noise. That is, for noise levels above those exponentially small in terms of the slow time scale, the behavior of the slow dynamics is qualitatively changed by the noise, as discussed for examples of delay bifurcations and resonance in [4, 5, 7, 23, 29] and in other slow systems [12, 20, 21]. In these different systems the common effect of noise is the disruption of an otherwise close approach to a slow manifold, resulting in a change of behavior. For the model with pitchfork bifurcation shown above, and for FHN and FitzHugh-Rinzel models with a slow ramp, small additive noise dramatically reduced the delay period on average (see [4, 18, 19] and references therein).

The exponential noise sensitivity demonstrated in models of delay bifurcation motivates this study to concentrate on relatively low levels of noise, as it is known
that in this range the qualitative behavior of MMO’s and STO’s survives, in the absence of other model variations. Within this context we focus on the influence of underlying bifurcation structure and modeling of the return mechanism on the noise sensitivity of the STO’s.

In the following sections we highlight similarities of the ISI (or interburst period) behavior for the models considered in this paper to the delay bifurcation dynamics illustrated above. The refractory period after the spike is analogous to the period where the control parameter is below the critical point, with sufficient dissipation to damp the influence of the noise so that in the ISI the system decays or “winds in” to a fixed point of the (sub)system. Once the control parameter crosses a critical point, there is a gradual “winding out” exhibiting STO’s on the transition to the spiking state. Within the ISI there can also be a type of coherence resonance (CR) where noise amplifies the STO’s in the presence of weak damping (see references in [15, 34]), so that they are a prominent and prolonged feature in the ISI. But stronger amplification can drive the system out of the STO behavior into spiking, thus shortening the ISI. For instances of heightened noise sensitivity, noise can drive the system off of the winding in/out trajectory onto a direct approach to the threshold, resulting in clusters of spikes without periods of STO’s in between. Then the survival of the STO’s depends on a balance of the two effects of the noise: CR and the shortening of the period of STO’s. Relatively small variations in model parameters can increase this noise sensitivity by limiting the dissipation in the refractory period, or by changing the interaction of the return mechanism in IF models with the slow time scales.
Noise sensitivity connected to modeling

The exponential noise sensitivity related to the slow variation of the bifurcation or control parameter has been demonstrated in models of delay bifurcation, so we focus here on relatively low levels of noise. We consider aspects of model choice that can reduce or eliminate the periods of STO’s in the presence of noise, similar to previous studies of bifurcation delay that considered the reduction of the delay by noise [4, 18, 19]. Then the noise sensitivity is measured in terms of the clustering rate that increases with noise when the model is more susceptible to the removal of STO’s, that is, to the transition from MMO’s to clusters of spikes or repetitive spiking.

The return mechanism is modeled both with a functional form describing feedback between the voltage-type variable and the control variable, and with a reset mechanism similar to IF models, where the spike is not calculated and the return mechanism is given by resetting values of the dependent variables in the refractory period. Even though there is similar dynamical behavior for these different models, the overall bifurcation structure and choice of return mechanisms can change the fractions of clusters and removal of STO’s for increased noise levels. Different return mechanisms and parameters can be combined and tuned to reproduce the same cluster fraction in the MMO’s for any given noise level, making it difficult to distinguish the mechanism for a transition from MMO’s to clustering by looking at a single noise level. However, it is possible to extract differences between different models and different parameter choices by comparing the noise sensitivities indicated by changes in the clustering fraction. As we observe in this paper, the change in clustering fraction as a function of noise can vary with different model mechanisms as well as different control parameter choices. For example, for smaller noise levels the clustering fractions may be similar for different return mechanisms, but for larger noise levels the clustering is more frequent in IF models, unless the reset mechanism is chosen carefully to introduce more dissipation. Similarly, STO’s driven by delay bifurcation rather than by CR are more likely to be eliminated by larger noise levels. These differences also influence the spike-ISI transitions as well as the character of the STO’s as studied in more detail in [6].

Understanding the noise sensitivity then has implications for choices of models and parameter values corresponding to different return mechanisms. For example, as speculated in [11] based on the large compartmental model of the stellate cell, modeling accurately the feedback from the spike to the ISI dynamics is important since small changes are enough to induce or discourage clustering in the model. Comparing noise sensitivities in terms of transitions from MMO’s to clusters is a first step in identifying and comparing collections of different mechanisms for STO’s, and developing mathematical and computational approaches to quantify these mechanisms in order to compare to experimental measurements. Such comparisons also identify experimental measurements that could contribute to verifying the models, naturally comparing a number of different aspects to narrow it down [28].

In Section 2 we consider the MMO-clustering transition for a FitzHugh Nagumo-type model and compare different return mechanisms in the context of a slowly varying bifurcation parameter. In Section 3 we look at the noise sensitivity of the clustering fraction for different choices of underlying bifurcation structure and return mechanisms in a reduced model for stellate cells. In Section 4 we review results for a noisy elliptic burster, and in Section 5 we compare its STO-bursting
transition with the STO spike transition of the other models. We see similar effects of the reset mechanism for IF models, and also illustrate how more complex spike to ISI transitions and underlying bifurcation structure can contribute either to STO’s or to spike clustering.

2. FitzHugh-Nagumo-type model. Makarov et al. [22] proposed a simple FitzHugh-Nagumo-type model for relaxation oscillations,

\[\begin{align*}
edu &= \left[u(u - a)(1 - u) - v\right] dt \\
dv &= g(u - b) dt + \sqrt{2D} dw \\
g(x) &= k_1 x^2 + k_2(1 - e^{-x/k_2})
\end{align*}\]

with \(u\) a voltage-like variable, \(v\) a recovery-type variable, and \(w\) a standard Brownian motion. Here we use the same parameters as in [22] \(a = .9, k_1 = 7, k_2 = .08, \epsilon = .005\). Near the fixed point of the deterministic system \(u = b, v = b(b - a)(1 - b)\) the dynamics are similar to that of a van der Pol (VDP) oscillator; indeed for \(g(u - b)\) replaced by \(u - b\) and \(a = -1\) (1) is a noisy van der Pol oscillator. However, away from the fixed point the nonlinearities of \(g\) support spikes that are fast relative to the usual VDP. Note that \(\epsilon = .005\) yields a slow time scale, resulting in relaxation oscillations as described in the introduction.

We first review the results for the bifurcation parameter \(b\) constant, before considering the cases with a slowly varying bifurcation parameter. The focus in [22] is to demonstrate alternating quasi-harmonic STO’s with noise-activated spiking. In that study a constant value of \(b\) was chosen in the interval with stable small amplitude oscillations, that is, between the Hopf bifurcation at \(b = b_H\) and the canard transition to stable large oscillations at \(b = b_c > b_H\). A sketch of the bifurcation structure for this model is given in Figure 10. It was further noted that a similar type of noise-driven behavior could be achieved if \(b < b_H\), and this was indeed the case studied in detail in [24], demonstrating CR of the type where optimal noise drives coherent spiking events for an FHN model, and in [23] for the VDP oscillator with noise. In [23] an asymptotic analysis gives different parameter ranges corresponding to CR in the spike dynamics, intermittency, and single spike dynamics.

Sample trajectories of (1) are shown in Figure 2, in both the phase plane and the time domain. For \(b < b_H\), but \(|b - b_H|\) relatively small, values of \((u, v)\) near the fixed point are also near sensitive regions of the phase plane leading to a fast transition to the right branch of the \(u\) nullcline. Then small noise can amplify unstable trajectories for small oscillations or drive the system to spike. For \(b_H < b < b_c\), the deterministic system has stable small periodic oscillations, and again the noise can perturb these small periodic oscillations or drive the system to spike. Note that the noise can be responsible for amplifying the STO’s but it can also be responsible for rapid transitions to spiking that avoid the STO’s altogether.

A detailed comparison of the VDP model with (1) [6] illustrates that there is increased occurrence of spikes and spike clusters for the noisy VDP oscillator as compared with (1), where STO’s and MMO’s are a prevalent feature of the dynamics even for a range of \(b_H < b < b_c\). A simple explanation for the increased robustness of the STO’s in (1) is the larger interval of \(b\) values for stable small oscillations in the underlying deterministic system. The choice of parameters \(a = .9\), as compared with \(a = -1\) in VDP, increases \(|b_c - b_H|\) giving a larger interval of stable small
amplitude oscillations and limiting clustering for $b$ near $b_H$. For the parameters used here, $b_H \approx .3154$ and $b_c \approx .3185$.

For $b = .316$ the spiking rate for (1) is roughly 50% larger than if the noise is instead in the voltage equation only (appropriately scaled as in [23]), and the clustering rate is also roughly 7-10% higher. In contrast for the VDP model, there was no quantitative difference observed between the clustering driven by either noise source. This suggests that the nonlinearities in (1) play a higher order role in the small amplitude oscillations, which can be viewed as providing additional strength of attraction to the small amplitude oscillations. We pursue this comparison elsewhere [6], noting that the source of the noise can play a role in the transition to clustering, in addition to the features discussed below.

Motivated by the bifurcation delay dynamics of the stellate cell model in Section 3 and the bursting model in Section 4, we consider the noise-driven transition to clustering in a three dimensional model given by (1) augmented with a time varying control parameter $b = b(u, t)$. We consider several versions of this model motivated by the structure of the stellate cell model and the elliptic burster. One version is an IF-type model with the ISI dynamics for $b$ given by

$$db = \epsilon_2 \, dt, \quad \epsilon_2 = .0005. \quad (2)$$

The parameter $\epsilon_2$ is chosen so that a clearly defined period of STO’s in the ISI survives in a range of noise levels comparable to levels used in [22]. Then $\epsilon_2 t$ is the slowest time scale in the problem, corresponding to the slow variation of the control parameter $b$. When $u$ crosses a threshold characterizing the spike transition, reset
values for $u$ and $v$ are chosen in the refractory period near the left branch of the $u$ nullcline, and $b$ is set to $b < b_H$. Then (1) with control parameter $b$ described by (2) is essentially an IF model with a simple ramp for the control parameter. We also consider a second model for variability of $b$ as an explicit function of $u$ for all $t$, with behavior similar to the control variable $r_s$ in the stellate cell model of the next section,

$$db = \left[ \frac{2}{1 + e^{{u-2}/1}} - c_b b \right] \tau_b^{-1} dt, \quad \tau_b = 5e^{-(u-8)/15} + 1. \quad (3)$$

Here the control parameter $b$ increases slowly in the ISI and during a spike it relaxes quickly to a value below $b_H$ for $c_b = 1$ and $D = 0$, yielding stable MMO’s. For larger values of $c_b$ and $D = 0$ these MMO’s lose stability to small amplitude oscillations for $u$.

We compare the time series for (1) augmented with (2) or (3) in Figure 3 for several cases:

(i) $b$ as in (2) with a reset: $(u, v, b) = (-0.025, 0.045, 0.31)$;
(ii) $b$ as in (3) with $c_b = 1$ and the same reset as in (i);
(iii) $b$ as in (3) with $c_b = 1$ for all $t$;
(iv) $b$ as in (3) with $c_b = 1.2$ for all $t$.

We first discuss the time series for these cases shown in Figure 3 before comparing the noise-sensitivity of the models due to the different return mechanisms. Cases (i) and (ii) are both IF models, with a linear ramp for the control parameter $b$ in case (i) and with a nonlinear dependence of $b$ on $u$ in the ISI for case (ii). Cases (iii) and (iv) both have the same functional dependence (3) of $b$ on $u$, used for all time. The different parameter values used in these cases allows an examination of the influence of different underlying attracting states on the transition to clustering in the presence of noise.

In (i) and (ii) the reset value for $b$ is well below the Hopf point $b_H$ of the 2D system, and the reset values of $u$ and $v$ are chosen to be near the left branch of the $u$ nullcline shown in Figure 2. Then even with noise the time series has dynamics in the ISI analogous to delay bifurcation-type behavior discussed in the Introduction, with decay towards the steady state followed by increased oscillations as $b$ increases. In (iii) for $D = 0$ the control variable $b$ relaxes to $b \approx 0.313$ following a spike, and it increases in the ISI more rapidly than in the case of (i) using (2), thus yielding an ISI for (iii) with limited damping of the STO’s. For (iv) with $D = 0$, the stronger damping in (3) results in an attracting oscillatory state, with small oscillations for $u$, $v$ and $b$ oscillating near $b = 0.318$. As shown in Figure 3 $D \neq 0$ causes transitions to the spiking state in (iv). Then following a spike, $b$ relaxes to reduced values below the Hopf point. For all of the cases above, $b$ can increase to levels above $b_c$ for low noise levels, so that the delay effect can be observed also for the canard point. However, for increasing noise this delay does not occur, and the system typically spikes before $b$ reaches the canard point. A detailed comparison of the different characteristics of the STO’s is pursued in [6].

Figure 4 compares the clustering fraction of the spiking events for cases (i)-(iv), indicating the combined influence of the noise, slow variation of $b$, and the reset mechanism on the robustness of the STO’s and MMO’s. Here and in the rest of the paper clustering is defined as the succession of two spikes with no period of STO’s in the corresponding ISI. Cluster fraction is given by the number of observed
spikes immediately following another spike with no STO’s in between, divided by the number of observed spikes. The fraction is computed for long time series, typically long enough to observe 500-1000 spikes in the time interval. An increased cluster fraction indicates greater noise sensitivity, as the STO’s are eliminated more frequently.

Not surprisingly, both spiking frequency and the percentage of clustering for both (2) and (3) increases with noise, similar to the case of $b$ fixed. For small to intermediate noise levels the clustering fractions for case (i) and (iii) are similar, with case (ii) somewhat below them. These levels of noise are not large enough to regularly overcome the attraction to small amplitude oscillations, so that there are usually periods of STO’s between spikes. For these smaller noise levels, case (ii) has two aspects that support STO’s and avoid clustering for small noise: the reset level is fixed at $b = 0.31$, as compared with case (iii) where $b$ often takes larger values following a spike, thus shortening the interval for STO’s in (iii) and allowing a greater chance for clustering. Even though case (i) also has a fixed reset value and $b$ increases more slowly in (2) the feedback in (3) provides some additional damping of the oscillations that is not present in case (i). For larger values of the noise, cases (i) and (ii) show increases in clustering fraction that are 2 to 3 times that of (iii). This is primarily due to the fact that the reset value is fixed, while spiking occurs for smaller values of $b$. Then on average there is a shortened ISI and a greater opportunity for noise to drive clustering in (i) and (ii). In contrast, for cases (iii) and (iv), (3) regularly yields a value of $b < 0.31$ at the start of the ISI,
yielding a greater opportunity for STO’s following damping for reduced \( b \) and thus limiting the ability of noise to drive clustering. In contrast, (i) and (ii) have fixed reset values, so the noise-driven elimination of STO’s is not damped as in (iii) and (iv). While the increase in the percentage of clustering is reduced for both cases (iii) and (iv), the overall clustering fraction is smaller for (iv) due to significant drops in the value of \( b \) following a spike and the underlying attraction to the small amplitude oscillatory state for the deterministic system, that limits the effect of the noise. Comparison of these results with the other models is given in Section 4.

![Figure 4](image)

**Figure 4.** Fraction of clusters among spiking events vs. noise level \( \sqrt{2D} \) designated by open circles for case (i), diamonds for case (ii) \((b\text{ as in (3) with reset})\), +’s for case (iii) \((b\text{ as in (3) with coefficient } c_b = 1 \text{ (no reset value)})\), and *’s for case (iv) with coefficient \( c_b = 1.2 \).

3. **Reduced model of stellate cells.** A series of papers [26, 27, 30, 31] has examined a reduced model of stellate cells, focusing on the mechanism behind the STO’s. The full single compartment seven dimensional model was introduced by Acker et al. [1] based on measurements from entorhinal cortex layer II stellate cells (see [1] for references),

\[
C \frac{dV}{dt} = I_{\text{app}} - I_{Na} - I_K - I_L - I_h - I_{Nap},
\]

\[
I_{Na} = G_{Na}m^3h(V - E_{Na}), \quad I_K = G_Kn^4(V - E_K), \quad I_L = G_L(V - E_L),
\]

\[
I_h = G_h(0.65r_f + 0.35r_s)(V - E_h), \quad I_{Nap} = G_{p}(V - E_{Na}).
\]

where \( V \) is the membrane potential, \( C \) the membrane capacitance, and \( I_{\text{app}} \) the applied current. \( I_{Na}, I_K \) and \( I_L \) are the standard Hodgkin-Huxley sodium, potassium, and leak currents respectively. In addition, two currents of interest for single cell rhythmicity at theta frequencies are \( I_{Nap} \), a persistent sodium current and \( I_h \), a hyperpolarization-activated current with both fast \( r_f \) and slow \( r_s \) components, playing a significant role as shown below. \( G_X \) and \( E_X, X = (Na, K, L, p, h) \), are respectively the maximal conductances and reversal potentials. This model (4) is dimensional and we refer the reader to a full discussion of the parameters in [26]. We mainly use the same parameter values as given there. As indicated below in
some specific cases, we vary parameters to illustrate differences due to underlying bifurcation structure.

The gating variables for the currents in (4) all evolve according to equations of the form:

\[
\frac{dx}{dt} = \frac{x_\infty - x}{\tau_x(V)} \tag{5}
\]

\[
x_\infty = \frac{\alpha_x(V)}{\alpha_x(V) + \beta_x(V)}, \quad \tau_x(V) = (\alpha_x(V) + \beta_x(V))^{-1}
\]

for \( x = (m, h, n, p, r_f, r_s) \)

The details of \( \alpha_x \) and \( \beta_x \) are given in [26], and typically are combinations of terms like \( e^{\pm(V-V)} \) for \( \dot{V} \) a constant, yielding activation and inactivation curves for these variables, with a sharp increase or decreases in the vicinity of certain voltage levels. Observations from (4) that are consistent with the full compartmental model of [11] are periods of STO’s alternating with large amplitude spikes that appear singly and in clusters.

The reduced model capturing the dynamics in the ISI of (4) was determined in [26] as

\[
C \frac{dV}{dt} = I_{app} - I_L - G_p p_\infty(V) (V - E_{Na}) - I_h
\]

\[
\frac{dr_f}{dt} = \frac{r_{f,\infty}(V) - r_f}{\tau_{r_f}(V)}
\]

\[
\frac{dr_s}{dt} = \frac{r_{s,\infty}(V) - r_s}{\tau_{r_s}(V)} \tag{7}
\]

This model is used as an IF model, so that for \( V \) above a threshold the dynamics are reset at \( V = V_0, r_f = r_f^0, r_s = r_s^0 \), corresponding to lower values that rapidly rebound to those of the ISI. The reduced model is obtained by noting that the time scales for \( \tau_p, \tau_m, \) and \( \tau_n \) are much shorter than the reference time scale \( \tau_{r_f} \), and together with the equations for \( m \) and \( n \) yields \( m \sim m_\infty \sim 0, n_\infty \sim 0, I_{Na} \sim 0, I_K \sim 0, \) and \( p \sim p_\infty \). The noise is introduced in [26] via variation in \( p_\infty \), that is, \( p_\infty(V) + \tau_p V \delta \eta(t) \) for \( \eta \) delta correlated noise \( \langle \eta(t) \eta(s) \rangle = \delta(t-s) \), based on studies of White [32] indicating that stochasticity in the persistent sodium channels could have a significant effect.

For our purposes of comparison with Section 2 and the elliptic burster in Section 4 we focus on the idea that \( r_s \) behaves as a slowly varying control parameter. As quantified in the nondimensionalized version of (7) studied in [27] its time scale of variation is an order of magnitude smaller than that of \( V \). In particular the ratio of time scales for \( V \) and \( r_f \) gives a parameter \( \epsilon_{sc} = .02 \), and the time scale for \( r_s \) is also slower than that of \( r_f \) by a factor of .3. In [26] the two dimensional subsystem underlying the predominant STO’s is obtained taking the slowest variable \( r_s \) as a fixed parameter. Then in terms of \( r_s \) as a control parameter there is a subcritical Hopf bifurcation for \( V \) at \( r_s = r_{sH} \) with a canard transition at \( r_s = r_{sc} < r_{sH} \) (see Figure 10). For sufficiently small \( \epsilon_{sc} \) this structure leads to families of periodic MMO’s in the full system (4), constructed in the reduced model (7) by combining a reset with families of solutions composed of STO’s followed by a rapid increase in \( V \) from the region near the Hopf point [30]. The bifurcation structure of the deterministic 3D reduced model is studied further in [27, 30, 31] demonstrating the funnel mechanism characteristic of higher dimensional systems with an embedded
canard structure. This feature provides the “winding in” attraction to the steady state followed by the “winding out” period evidenced by the STO’s and transition to a spike for parameter choices corresponding to a slow passage through the Hopf bifurcation in the deterministic system. In [26] the role of noise in amplifying the STO’s is demonstrated in the context of the phase plane dynamics for (7), illustrating how the STO’s and spiking behavior are sustained even when the stable steady state for the deterministic system is a quiescent state.

We review the behavior for different values of $I_{\text{app}}$ studied in [26, 30] to provide context for STO’s in terms of delay bifurcation and CR near a Hopf point. We state these in terms of the reduced model (7) but similar results are observed for the full model. For $I_{\text{app}} > -2.57$ in the absence of noise the slowest variable $r_s$ increases to values above $r_{sH}$. For $r_s < r_{sH}$ the linearized deterministic system has damped oscillations that decay towards the fixed point of the underlying 2D system. For $r_s > r_{sH}$ these oscillations grow until there is an escape to spiking. This case is analogous to a delay bifurcation, where the slowest parameter $r_s$ crosses the Hopf point, and consequently the system “winds out” from values near the steady state and does not immediately spike after the critical value is exceeded. Noise can then support additional oscillations through CR and also drive a faster escape to spiking. For $I_{\text{app}} < -2.57$ without noise there is a stable steady state, that is, a fixed point with value $r_s = r_{ss} < r_{sH}$. Without noise the oscillations are damped on the slow approach to this fixed point, while in the presence of noise CR drives these oscillations with a standard deviation inversely proportional to the square root of the distance to the Hopf point [15, 34]. Combined with the subcritical nature of the Hopf bifurcation and the unstable solution branch nearby, the noise can drive a transition to spiking before $r_s$ reaches the Hopf point. In this paper we focus on the case of CR for (7) taking $I_{\text{app}} = -2.58$, but we also compare with other parameter combinations that correspond to a bifurcation delay in the underlying deterministic system.

Figure 5 highlights how CR appears in the ISI to give behavior analogous to the delay bifurcation. Following a spike the system relaxes to nearly deterministic behavior, where $V$ drops to values well below $-55$ and then gradually approaches $-55$ on a time scale slower than the spike. The post-spike values of $r_f$ and $r_s$ are small, and they slowly rebound in the ISI to values near a steady state for the reduced two dimensional subsystem ($r_f \approx .075$ and $r_s \approx .08$). Initially in the ISI there is strong dissipation that damps other perturbations, so that even with noise the behavior follows the deterministic behavior qualitatively. As $r_s$ approaches the value of the Hopf bifurcation, even though the value of $r_s$ does not cross $r_{sH}$, the variance of the amplitude of the oscillations increases through CR, producing the winding out transition evidenced by a window of STO’s between spikes (top panels in Fig. 5). Analogous to the dynamics of a bifurcation delay, shown in Figure 1, the slow approach to the underlying critical point in (7) is reflected in noise-driven oscillations via CR.

We then seek to identify elements of the model that affect the analogous winding in/out periods as possible sources of noise sensitivity that can remove or enhance the MMO’s in the model by changing the support of oscillations in the ISI, whether through delay bifurcation or through CR. In the deterministic model, the shortening of the behavior in the funnel was explored by the variation of the deterministic values of $V$, $r_f$ and $r_s$ taken in the ISI [27] with parameter values for families of deterministic MMO’s identified in [30]. Similarly we explore how other parameter
choices related to the bifurcation structure and the return mechanism can affect the noise sensitivity of the ISI dynamics, defined in terms of increased cluster fraction.

Figure 5. Top: Time series of the full model (4) (left) and corresponding behavior in the phase plane (right), focusing on the growth of oscillations before the spike for $D = 3 \times 10^{-5}$. $I_{\text{app}} = -2.71$ is in the parameter range of CR, that is, in the absence of noise there is a stable steady state. Bottom left: Projection of the dynamics in the $V - r_f$ plane, focusing on the period in the ISI before the spike and the escape to the spike. The solid line is for the full model (4) as in the top row and the dotted line is for the reduced model (7) with $I_{\text{app}} = -2.58$.

Figure 5 contrasts the spike transition in (4) and (7), comparing the ISI dynamics where (7) is valid in the case that oscillations are driven by CR, that is, in the absence of noise there is a stable steady state. There we take $I_{\text{app}} = -2.71$ for (4) and $I_{\text{app}} = -2.58$ in (7), since between the two models there is a shift in the critical value of $I_{\text{app}}$ delineating the underlying deterministic steady state and delay bifurcation-type behaviors [30]. We note that the approach to the slowest region of the ISI for $-55 < V < -53$ and $r_f$ decreasing from $r_f \sim .75$ is the winding out region where the noise drives sustained amplitudes of the STO’s. Figure 5 illustrates the typical difference between these two models in the transition to the spike: in the reduced model (7) there is on average a longer period of winding out, that can be attributed to the lack of the gating variables $n$ and $m$ from the voltage equation in (7), as is validated by removing $n$ and $m$ from (4) in the ISI. As the attraction to the steady state of the underlying subsystem weakens, $n$ and $m$ increase slightly and provide feedback to $V$ that further amplifies the oscillations. Then the system (4) typically makes a transition to spiking at a larger value of $r_f$ than in the reduced model (7), in which $r_f$ continues to decrease as the winding out
period continues. This transition can be imitated qualitatively with increased noise in (7). This difference is captured in Figure 7, that shows the cluster fraction in the full and reduced models for comparable values of $I_{\text{app}}$ in the parameter ranges corresponding to CR and delay bifurcation. Below we consider other effects besides the feedback from gating variables that can contribute to the length of the ISI and the robustness of the STO’s to noise.

We consider first the effect of different underlying bifurcation structure as described above, with either delay bifurcation or stable fixed point. We consider different values of $C$, but this comparison could be accomplished by changing other parameters, such as $I_{\text{app}}$. From the non-dimensional model in [27, 30] we see that changes in $C$ also correspond to a change in the relative time scales of $V$, $r_f$ and $r_s$ with $\epsilon_{sc}$ proportional to $C$, and that $\epsilon_{sc}$ is an important factor in the families of oscillatory solutions for the deterministic system. The chosen values of $C$ are not different by an order of magnitude, so that the time scales of $r_s$ and $V$ differ by an order of magnitude in all three cases (by a factor between .01 and .04). Figure 6 illustrates the effect of different values of $C$ on the length of the interval of STO’s, which is directly related to the underlying dynamical structure of the deterministic system: for larger $C$ the underlying deterministic system has a stable fixed point, but for smaller $C$ the attractor is a MMO with alternating STO’s and spikes. Related to this behavior is the fact that for smaller values of $C$ the MMO’s persist through the delay bifurcation structure, while for larger values of $C$ there are no MMO’s without noise. Then in the presence of noise, the corresponding reduced winding in/ winding out period is shortened in both cases, and Figure 6 illustrates the difference via the projection of the dynamics in the $V - r_f$ plane. On the left in Figure 6 it is clear that reducing $C$ reduces the dissipation of the oscillations in the ISI for smaller values of $C$ thus heightening the spike-inducing noise sensitivity as the system follows a shorter winding in period. Then both the cluster fraction and the rate of increase of this fraction as a function of noise are larger for smaller values of $C$, indicating increased sensitivity to noise as shown in Figure 6.

Noise sensitivity related to the underlying bifurcation structure is also observed for different values of $I_{\text{app}}$. As described above, changing $I_{\text{app}}$ can change the underlying deterministic dynamics, which exhibits differences in clustering behavior in Figure 7 similar to those shown in Figure 6. From Figure 7 we again see greater noise sensitivity of the STO’s in (4) resulting in larger cluster fraction as compared with (7). There the restart value in (7) is $V_0 = -80$, $r_f0 = r_s0 = 0$ as in [26], that we reference as case (a) in our discussion of Figure 8 below. Figure 7 compares both the case of CR where $I_{\text{app}} = -2.71$ in (4) and $I_{\text{app}} = -2.58$ in (7), and the case of delay bifurcation-type deterministic dynamics where $I_{\text{app}} = -2.58$ in (4) and $I_{\text{app}} = -2.45$ in (7). As a function of the logarithm of the noise parameter $D$, the clustering fractions in the CR case are half or less than those for the delay bifurcation type behavior, and on this scale (4) yields cluster fractions 1.5-3 times larger than the analogous case for (7).

While we study the detailed dynamics of the stochastic STO’s elsewhere [6], we note that the length of the ISI and consequently the number of periods of STO’s in the ISI can vary significantly, particularly for low to intermediate noise levels, as shown in Figure 7. This variability appears to be greater in the case of CR than in the case of underlying delay bifurcation. In the case where $r_s$ passes slowly through the Hopf bifurcation value, this variability can be interpreted as the noise driving a sampling of the sectors for different STO behavior identified in [27], or the different
families of STO solutions identified in [30]. As the slowly varying control variable crosses the Hopf point into a region of instability, noise typically drives escape to spiking so that the ISI’s and variability in the number of STO’s are reduced as compared with CR. In the case of CR, the variability of the number of STO’s is related to the competition between the noise-driven coherence of the oscillations, enhancing the STO’s, and the weak attraction to the fixed point, allowing noise-driven amplification as a route to spiking.

The observations for different values of $C$ above already suggest how the reset values can allow the system to be predisposed to clustering. Trajectories that spend less time winding in to the attracting region are more susceptible to an earlier noise driven escape from this region, that is, spiking. Figure 8 illustrates the different clustering behavior for different reset values, in the context of no and random variability of the reset value $r_{s0}$. Figure 8 compares five different cases: (b) (7) with $V_0 = -61$, $r_{f0} = .04$, $r_{s0} = .05$, corresponding to a trajectory with ISI comparable to (4) for small to intermediate noise levels; (c) (7) with $V_0 = -61$, $r_{f0} = .03$, $r_{s0} = .05$, choosing a value of $r_f$ below that in b); (d) (7) with $V_0 = -70$, $r_{f0} = .025$, and $r_{s0} = .021$; (e) results from the full model (4) (no reset).

For cases (b),(c),(e) $I_{app} = -2.58$ and in (d) $I_{app} = -2.71$. We consider one additional case that has the same parameter values as in (b) with an added random
Figure 7. Left: Histograms for ISI length for the reduced model (7) that can be directly related to the number of STO’s, since the power spectral density of the ISI is concentrated near a single frequency. The critical value of $I_{\text{app}} = -2.57$ separates the two cases of a stable steady state and a delay bifurcation-type behavior for the deterministic case. The length of the intervals of STO’s for $I_{\text{app}} = -2.58$ (solid line) have a larger variance, with STO’s driven by noise via CR. In contrast, for $I_{\text{app}} = -2.45$, the STO’s are driven both by the underlying deterministic dynamics of delay bifurcation as well as noise, and there is less variability in length of the ISI.

Right: Cluster fraction observed in spiking events for different values of $I_{\text{app}}$ in both the CR and delay bifurcation settings. The full model (4) is compared with the reduced model (7) with reset values as in case (a) and in [26]. o’s and +’s correspond to the reduced model (7) with $I_{\text{app}} = -2.58$ and $I_{\text{app}} = -2.45$, respectively, while the diamonds and *’s correspond to the full model (4) with $I_{\text{app}} = -2.71$ and $I_{\text{app}} = -2.58$, respectively.

The choice of $r_{f0}$ in (b) is motivated by choosing a reset value close to the deterministic trajectory in the ISI, while (c) is motivated by choosing a reset value that is just below this deterministic trajectory, closer to a trajectory with a reduced winding in period on its approach to the noise sensitive region of the ISI.

As shown in Figure 7, cluster fractions in (7) with reset values as in (a) above are considerably less than those in (4). Cases (b)-(d) illustrate how a choice of larger reset values in the reduced model (7) can support cluster fractions close to that of (4) for lower noise values. With these increased reset values the trajectories have shorter winding in/out intervals with less dissipation, and thus allow increased clustering with increased noise. Then the different reset values in (b)-(d) produce a correction in the susceptibility of (7) for noise-driven clustering, compensating for differences between the models. For case (d) and (e) the $I_{\text{app}}$ for both models corresponds to underlying delay bifurcation dynamics. In (b) and (c) the value for $I_{\text{app}}$ corresponds to CR behavior in (7), so larger restart values are used to compensate for this additional difference compared to case (e).
While in (b)-(d) the cluster fractions are closer to those of the full model (4) for small to intermediate noise, for larger values of the noise cases (b) and (c) show increasing noise sensitivity, indicated by larger increases in the cluster fractions for increasing noise as compared with (4). Noise amplifies the reduction in winding in/out periods due to the larger restart values and thus drives increased clustering. The cluster fraction in (c) is even larger than in (b), since the restart values for (c) yield shorter and more noise-sensitive winding in/out intervals. In contrast spiking/clustering in (4) is driven by a combination of noise and the feedback from the gating variables \( n \) and \( m \) so that the larger noise levels are balanced by the dissipation in the ISI for (4) and the increase in cluster fraction is less than in (b)-(d). Compared to cases (b) and (e), there was less noise sensitivity in case (d), with lower restart values and choice of \( I_{\text{app}} \) in the delay bifurcation-type range. Then for larger noise levels the difference in increased cluster fraction between (d) and (e) was roughly half the larger difference (10\% or more) between (b) and (e) and (c) and (e), on the logarithmic scale of the noise level \( D \). Including random variation in \( r_{s0} \) yields increases in cluster fractions as a function of noise level similar to cases (b) and (c).

From Figure 8 it is clear that for lower to intermediate values of the noise it may be possible to approximate the average cluster fractions of the full model (4) by adjusting the reset values in the reduced model (7), for example, choosing a reset as in (b). However, the noise sensitivity for these choices of the reset is larger than that of the full model, as indicated by larger increases in the fraction of clustering events for larger noise levels. In contrast, choosing lower reset values as in (a) (Figure (7)) introduces significantly greater damping in the ISI that limits the noise-driven clustering as compared to (4).

The noise sensitivity of the cluster fraction to the reset mechanism is related to the observations in [11] outlining the importance of the refractory period immediately following the spike. There it was commented that the dynamics of the

![Figure 8](image-url)
$h$-current $I_h$ during the spike are not well understood, and that influence from the spike on the behavior of the $I_h$ could yield variation in the following ISI dynamics and thus influence clustering.

4. Summary of results for elliptic bursting with noise. We summarize the results for a noisy elliptic burster described by (8), based on the Wu-Baer model for activity dependent spines with a noisy input current [33]. The Wu-Baer model is essentially a FitzHugh-Rinzel oscillator coupled with a slow activity dependent conductance $G$,

$$
\begin{align*}
    dU &= [F(U, W) - G(U - f_s(U))]dt + I_{SH} + \delta dw, \\
    dW &= H(U, W)dt, \\
    dG &= \epsilon_{WB}G(U - f_s(U))dt.
\end{align*}
$$

where $(F, H)$ gives the FitzHugh-Rinzel dynamics for the membrane potential $U$ and recovery variable $W$, and $I_{SH}$ is the synaptic input current into the spine head with a noisy fluctuation given by $\delta dw$ ($w$ a standard Brownian motion). The function $H$ has the form $H = \beta(U - \gamma W)$ for $\gamma$ a constant and $\beta \ll 1$ giving the intermediate slow scale corresponding to the relaxation oscillations. Figure 9 shows a schematic for the bifurcation structure of the deterministic model (8) ($\delta = 0$). Here $\epsilon_{WB} \ll \beta \ll 1$, so that $\epsilon_{WB}$ gives the slowest time scale for the conductance $G$ that plays the role of the slowly varying bifurcation or control parameter. The function $f_s(U)$ is the potential at the spine base, and the equation for $G$ gives a nonlinear dependence of $G$ on $U$.

In Figure 9 (left) the bifurcation structure of (8) is superimposed on the dynamics in the $U - G$ plane. In the active bursting phase the conductance increases slowly, until the stability of the large amplitude oscillations is lost at the knee of this branch. During the subsequent silent phase the quiescent state is stable so that the small amplitude oscillations are damped, and the conductance $G$ decreases slowly to a critical value $G_H$ corresponding to a subcritical Hopf bifurcation in the reduced model with fixed conductance. As $G$ crosses $G_H$ the quiescent state loses stability, the oscillations slowly increase until there is a delayed transition to the active state, and the cycle repeats.

For small noise, the delay in the transition to the bursting phase is shortened dramatically, consistent with the exponential sensitivity of a ramp through the Hopf bifurcation to noise [19]. The bursting phase is also shortened by noise, due to the weak attraction to repetitive spiking for values of $G$ near the knee of the branch for large oscillations. Then larger noise values give on average a significantly larger reduction of the silent phase with STO’s than the active phase [19]. In addition, noise-driven departures from the active phase for a value of $G$ closer to the Hopf point can also reduce the length of the silent phase, since there is a shorter winding in period of the silent phase, translating into a shorter winding out phase due to the memory effect of the delay bifurcation as shown in Figure 9 [3, 4]. For increased noise, this shortening of the silent and active phases eventually leads to intermittent spiking, a transition that appears strikingly similar to bifurcations from bursting to intermittent spiking observed in the deterministic system by varying a completely different parameter [19]. Detailed analyses of (8) have been given in [19] and [29], providing methods for calculating the effect of the noise on the transition into and out of the active phase.
Comparison of the FHN, stellate cell, and elliptic bursting models. In this section we compare the results above for the stellate cell and FHN-type models with silent-active phase transitions in elliptic bursting. Figure 10 shows schematics for the bifurcation structure of (1), with a supercritical Hopf bifurcation at $b_{H}$ and canard transition at $b_{c}$, and for (7), with a subcritical Hopf bifurcation at $r_{sH}$ and canard transition at $r_{sc}$.

We compare the effect of the return mechanism on the noise sensitivity of the ISI in the three models. In (1) we considered two types of return mechanisms, described by (2) and an IF-type reset, and by (3), providing a dependence of the control parameter on the voltage-type variable. For larger values of noise, the values taken by (3) at the beginning of the ISI are typically below the reset value used for (2), so that the model using (3) was more likely to exhibit STO’s before spiking. Thus the feedback between the noise, the voltage, and the control parameter variation in (3) provided a return mechanism that gave stronger dissipation and a longer winding in period in the ISI than that for the IF model (2). As a result the IF model showed greater noise sensitivity evidenced by increased cluster fraction as compared to (3). In contrast, the noise effect in the active phase of the elliptic burster yields a return value of $G$ that is closer to the Hopf point, that in turn results in a shortened ISI. Then the noise sensitivity of the silent phase for the elliptic burster is increased in comparison with the model where the transition from the active to silent phase would be replaced by an IF-type return mechanism with fixed reset value. Comparing to the stellate cell models, the IF-type reduced model
(7) showed increased noise sensitivity when the choice of reset value decreased the winding in period in the ISI. In the full model (4), where the return mechanism depends on the voltage parameter, there was limited influence of the noise on the return value for the slow variable $r_s$, but the gating variables $n$ and $m$ contributed to a shortening of the ISI. Then the influence of the reset values in (7) imitates the feedback between the gating variables $n$ and $m$ and $V$ in (4) or the shift of the critical value of $I_{app}$, driving larger STO’s and faster transitions to spiking. However, the resulting trajectories in (7) are more sensitive to noise than the full model (4), showing larger increases in cluster fractions in (7) for larger noise levels.

Qualitative changes due to the reset mechanism were also observed in [25] for a network of resonant integrate and fire neurons. In that context, for intermediate coupling it was demonstrated that there could be a lag in the start of noise-driven synchronized firing in this network, depending on the value of the current-like recovery variable following a spike. The initial value was near zero, while the value following a spike was well below zero, providing a rebound mechanism that eliminated the lag in synchronized behavior observed for small initial values of the recovery variable.

We also compare the influence of the underlying bifurcation structure in the different models on their noise sensitivity. In both the elliptic burster and the stellate cell model, there is a subcritical Hopf bifurcation in the underlying 2D system. In the stellate cell model we considered parameter combinations where the STO’s were driven by a slow passage through this subcritical Hopf via bifurcation delay, as well as parameter combinations where the STO’s were driven by CR of oscillations about a fixed point. Even though there is not a slow passage through the Hopf point for CR, the winding in/winding out character of the delay bifurcation is imitated by the ISI behavior of attraction to the fixed point followed by CR-driven STO’s. As in the elliptic burster, there is increased noise sensitivity evidenced by
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Clustering in the delay bifurcation case of (7), due to the change of stability as the slowly varying control parameter passes through the subcritical Hopf value. Both the cluster fraction and the increase in that fraction for larger noise levels was lower for the CR case, even though the STO’s generated by CR appear similar to those generated in the delay bifurcation setting. For both the delay bifurcation and CR cases, the number of STO’s observed in an ISI varied considerably. We expect the variability of the number of STO’s to be less in the case of the delay bifurcation, due to the families of oscillatory solutions in the underlying deterministic system for that case [30]. We explore detailed features of STO’s in the stochastic models elsewhere [6].

In (1) the Hopf bifurcation is supercritical, so that there is an interval of values \( b_H < b < b_c \) of stable small oscillations in the absence of noise. For \( b \) slowly varying through \( b_H \) the noise may perturb the small amplitude oscillations but not necessarily immediately drive the system to spike. In contrast to the elliptic burster, the supercritical Hopf point in (1) does yield the possibility of a period of STO’s even if the control parameter relaxes at or near the Hopf point at the start of the ISI. For the Wu-Baer model (8) with an underlying subcritical Hopf bifurcation, \( G \) near \( G_H \) at the end of the burst would eliminate any interval of STO’s in the presence of noise.

6. Conclusion. We have considered three types of models exhibiting MMO’s composed of alternating STO’s and either spikes or bursts. In each of the three dimensional models, a FHN-type model, a reduced model for stellate cells, and a model for elliptic bursting, there are three time scales. We view the slowest variable in each model as a slowly varying bifurcation parameter, and from that viewpoint the transition from STO’s to large oscillations can be viewed as dynamics typical of bifurcation delay. That is, the ISI exhibits a winding in period where oscillations are damped followed by a winding out period where STO’s are prevalent before an escape to a spike or burst. In each model we have looked at factors that increase the noise sensitivity of the STO period, with a focus on those that lead to transitions from MMO’s to clusters of spikes. We compare the dependence on noise of the fraction of clusters among all spiking events as a measure of the noisy elimination of the STO’s in the ISI, consequently changing the MMO behavior.

While all of the models exhibit behavior in the ISI qualitatively similar to that of a delay bifurcation, there are differences in the underlying bifurcation structure that can influence the noise sensitivity. In the stellate cell model the STO’s can be driven by either coherence resonance (CR) enhancing STO’s about a fixed point in close proximity to the Hopf point, or by a slow passage through the subcritical Hopf bifurcation of the 2D subsystem. In the FHN-type model, the underlying bifurcation structure is that of a supercritical Hopf point, so that the 2D subsystem has stable STO’s for certain parameter values. Then in the settings of either CR or the subsystem with a supercritical Hopf bifurcation, there is reduced noise sensitivity in terms of increased cluster fraction as compared with cases where the underlying deterministic system is a slow ramp through a subcritical Hopf bifurcation. In the latter case the instability corresponding to the crossing of the Hopf point is a significant factor in the amplification of the STO’s leading to an escape to spiking.

We also observe increased noise sensitivity in IF-type return mechanisms in both the FHN-type model (2) and the reduced stellate cell model (7). For models where the return mechanism is influenced by feedback from the voltage-type variable to
the control variable dynamics, that is, no fixed reset, there are differences in noise sensitivity depending on this feedback. In the case of the FHN-type model with return mechanism (3) and the full stellate cell model (4), this feedback was dissipative in the initial part of the ISI, thus supporting periods of STO’s and limiting the increase of clustering rates. In the case of the elliptic bursting, the feedback of the noise in the return from the active to the silent phase limited the winding in period and consequently also the bifurcation delay, further shortening the duration of the STO’s.

This comparison of different choices of model features indicates how the concept of noise sensitivity can be used to differentiate between models that exhibit qualitatively similar behavior, in this case MMO’s, for different settings. Even though different types of noise-driven behavior can be obtained by tuning parameters within the choice of a specific model feature, the noise sensitivity obtained for different noise levels can highlight differences between models, providing a new basis for the comparison of models with experiment.

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