神经兴奋性、峰值和簇发放的分岔机制
Section 5: 其他类型

NEURAL EXCITABILITY, SPIKING AND BURSTING

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DOI: 10.1142/S0218127400000840

Dates: Received June 9, 1999

Translated by Na Zhao, School of Mathematics, SCUT.
Link to the Journal: 10.1142/S0218127400000840

International Journal of Bifurcation and Chaos
Vol. 24, No. 8 (2014) 1440003

2023 年 3 月 28 日

* 这篇论文发表于 1999 年，引用量已经高达两千多。Izhikevich 在该文里详细介绍了神经元兴奋性、峰值和簇发放所涉及的详细分岔机制。对于神经动力学的读者而言，该文提供了详细的理论基础。由于该文内容冗长，特意将其拆封成多个部分，以便读者准确定位到自己所需。这是 Sec. 5: 其他类型.

NEURAL EXCITABILITY, SPIKING AND BURSTING

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本文综述了神经元产生动作电位 (尖峰) 所涉及的分岔机制。我们展示了分岔的类型如何决定细胞的神经计算特性。例如，当稳态接近鞍-结点分岔时，细胞可以以任意低频发放全有或全无尖峰，它具有明确定义的阈值流形，并且充当积分器；即输入脉冲的频率越高，它放电的越快。相反，当稳态接近 Andronov-Hopf 分岔时，细胞在特定频率范围内发放，其尖峰不是全有或无，它没有明确定义的阈值流形，它可以响应抑制脉冲充当谐振器；即它优先响应输入的某个 (共振) 频率。增加输入频率实际上可能会延迟或终止其触发。

我们还描述了神经簇发放现象，使用几何分岔理论扩展了现有的簇发放分类，包括许多新类型。我们讨论了 burster 的类型如何定义其神经计算属性，并且我们展示了不同的 burster 可以不同地交互、同步和处理信息。

Contents

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在这一节中，我们简要地提到不能用快慢系统 (21) 描述的簇发放事件。我们区分三种情况：周期性的、准周期性的和混沌的簇发放行为。

1. 周期性簇发放: 刺猬极限环

当一个系统具有图 113 中描述的刺猬极限环吸引子时，往往会出现周期性的簇发放。我们把这样的簇发放器称为刺猬簇发放器。上一节中考虑的许多快慢速簇发放器在 μ 小的时候与刺猬吸引子有周期性的动态关系，而当 μ 中等或大的时候，它们作为刺猬簇发放器持续存在。

即使是二维系统，例如那些具有扭曲的快速零斜线的系统，也可以表现出刺猬簇发放；见图 114。以下是两个刺猬案例。

1.1. 蓝天灾难

当神经系统接近蓝天大灾难时，也会出现刺猬吸引子 (图 30)，在相空间的尖峰区域有折叠极限环分岔。事实上，矢量场是沿着消失的周期指向的，因此解花了大部分时间围绕它旋转，从而发放了尖峰；见图 115。该系统表现出周期性的簇发放行为，尽管它不能被分解为形式为 (21) 的快速和慢速子系统。因此，这种簇发放不属于快速慢速类型。

1.2. 鞍焦点同宿轨道

现在考虑一个靠近鞍焦点同宿轨道分岔的神经系统；见图 30 的顶部。在 Shilnikov 发现的某些相当普遍的条件下 (见 [Kuznetsov, 1995])，鞍焦点有次级同宿轨道，可以 (通过次级鞍焦点同宿分岔) 为对应于两次、三次等的稳定环，见图 116。

这是 FitzHugh-Nagumo 偏微分方程 [Hastings, 1976; Evans et al., 1982; Feroe, 1982] 中产生复杂尖峰的机制，它可能与龙虾随机胃神经节的 LP 细胞的簇发放机制有关 [Guckenheimer et al., 1997]。

2. 准周期性的簇发放

如果有一个连续函数 $q(\theta_1, \cdots, \theta_k)$，在每个参数中都是 2π 周期性的，那么一个连续的节奏信号 $x(t)$ 就是准周期性的，从而

$$x(t) = q(\omega_1 t, \cdots, \omega_k t), \quad \forall t \geq 0,$$

其中 $\Omega = (\omega_1 t, \cdots, \omega_k t)^T \in \mathbb{R}^k$ 是一个频率向量 [Samoilenko, 1991; Izhikevich, 1999a]。准周期活动对应于一个环面吸引子，它通常看起来像簇发放波或主轴波；见图 117。它的形状取决于函数 q 和频率向量 Ω。

环面吸引子可能会出现，例如通过超临界的 Neimark-Sacker 分岔。它也可以通过具有同宿环面结构的折叠极限环分岔出现 (图 30)。当周期消失时，系统表现出类似于图 115 中描述的” 蓝天” 簇发放的行为。图 118 中描述了一些额外的情况。

3. 混沌的簇发放

许多混沌的信号类似于环-环的簇发放；见图 119。点-环簇发放发生，例如在 Pomeau-Manneville 间歇性的存在下。许多靠近鞍焦点同宿轨道分岔的系统也表现出点-环混沌簇发放 [Kuznetsov, 1995]，具有类似 $Rssler$ 的吸引子；见图 120。另一方面，许多快慢速簇发放器具有混沌的动力学特性。例如，” 折叠/同宿” 簇发放器可能具有鞍结构 [Terman, 1991, 1992]，因此表现为混沌的簇发放。Terman 的论点可以被推广到大多数”*/同宿” 簇发放器。

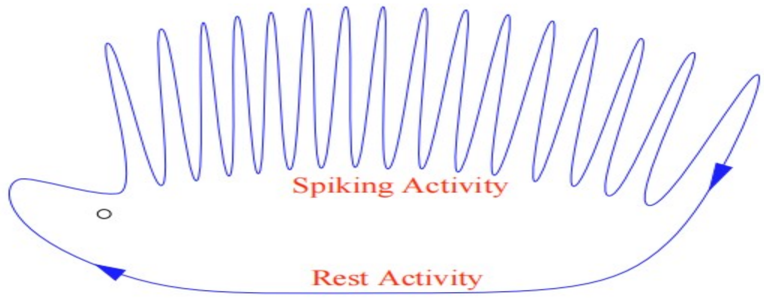

图 113. 一个刺猬状极限环吸引子通常对应于簇发放行为 (来自 [Hoppensteadt & Izhikevich, 1997])。

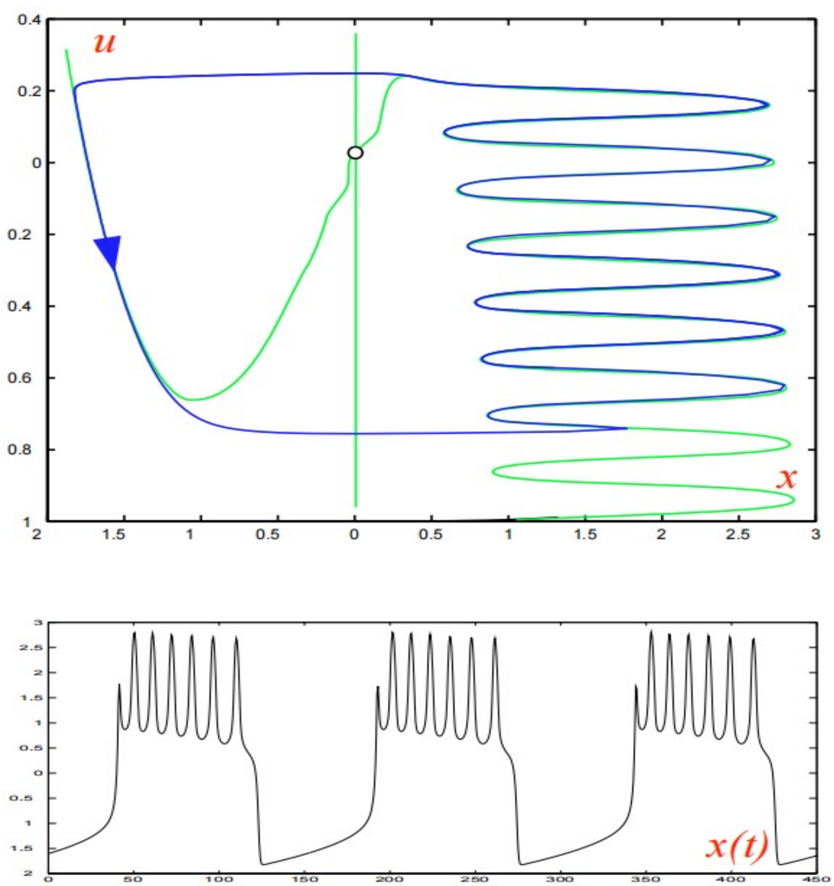

图 114. 平面松弛系统 $\dot{x} = x - x^3/3 - u + 4S(x)cos40u, \dot{u} = \mu x$, 其中 $S(x) = 1/(1 + e^{5(1-x)}), \mu = 0.01$ 中的快和慢零斜 (绿色) 和刺猬极限环吸引子 (蓝色)。

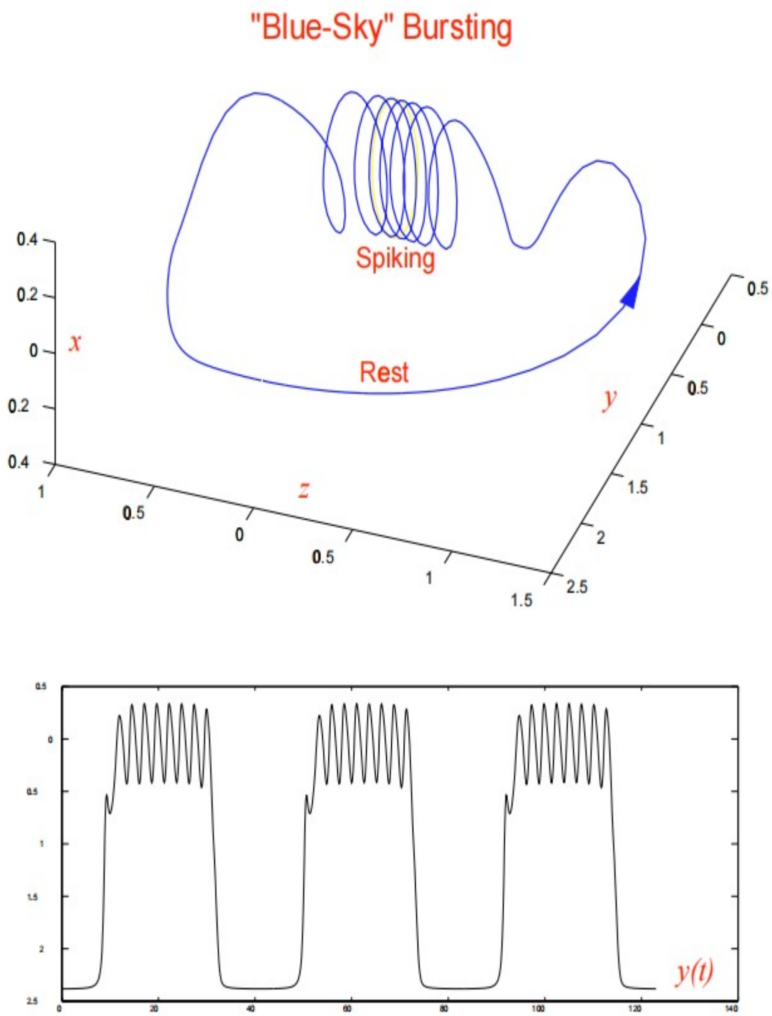

图 115. 蓝天型的刺猬簇发放。Gavrilov-Shilnikov 模型的模拟 [Kuznetsov, 1995, p. 256]。参数：$b = 10, \varepsilon = 0.02, \mu = 0.5$。

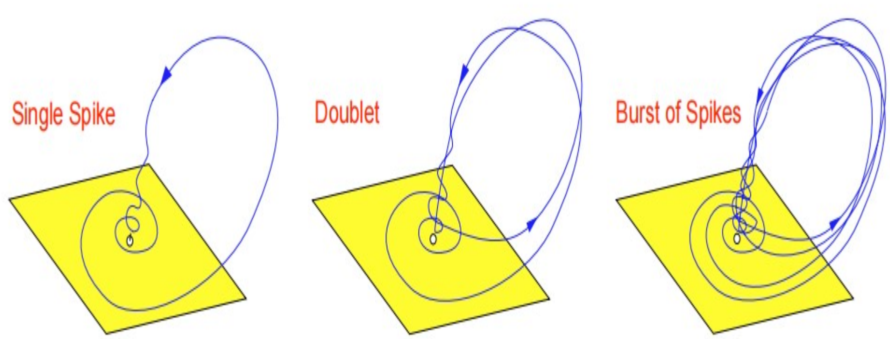

图 116. 次级同宿轨道到鞍焦点平衡可以分岔为对应于两次、三次 (未显示) 或尖峰簇发放的周期性解。

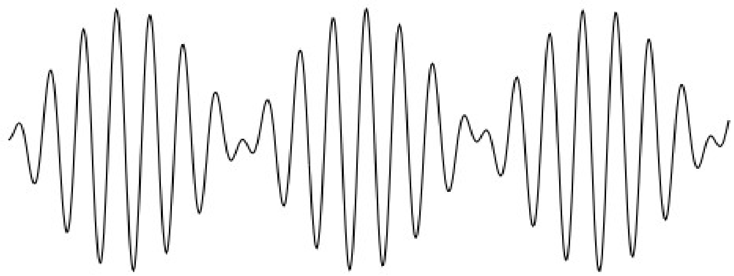

图 117. 一个准周期信号的例子。$x(t) = sin\omega_1 t sin\omega_2 t$，频率矢量 $(\omega_1, \omega_2) = (1, \sqrt{2}/20)$。

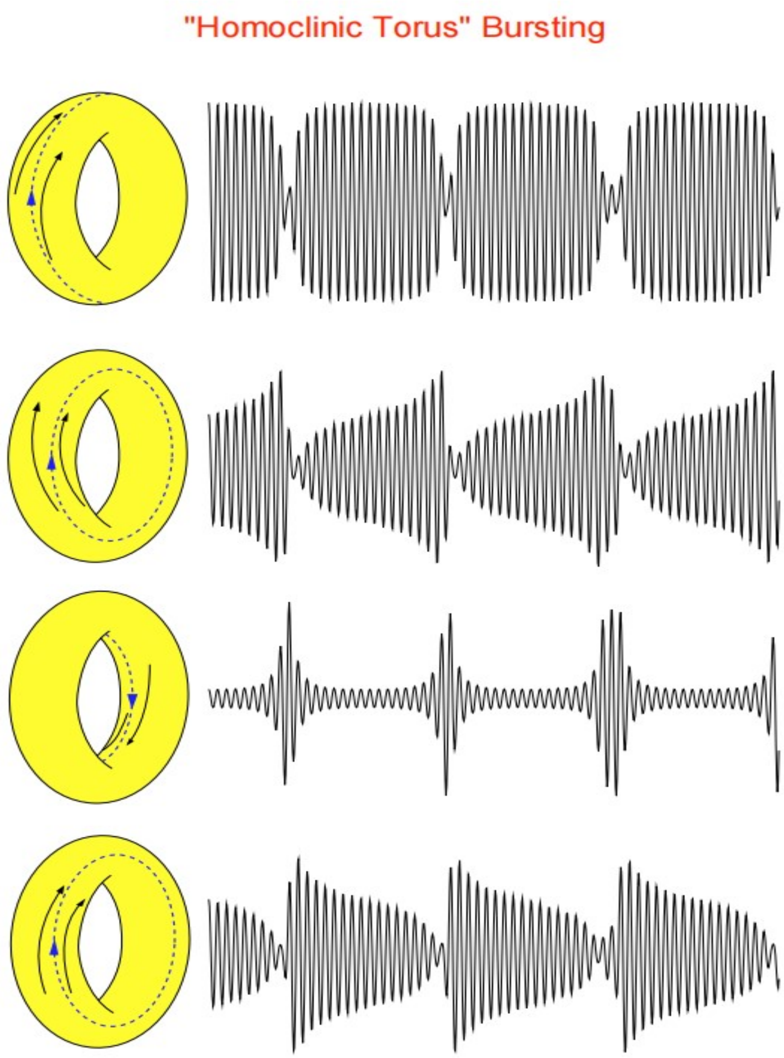

图 118. " 同宿环面" 簇发放。该模式取决于消失的折叠极限环的位置 (蓝色虚线圆)。

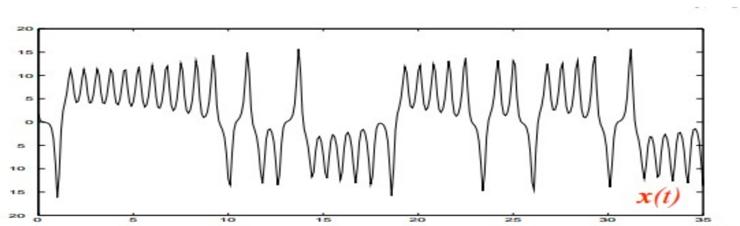

图 119. 洛伦兹系统的解类似于混沌的周期簇发放。

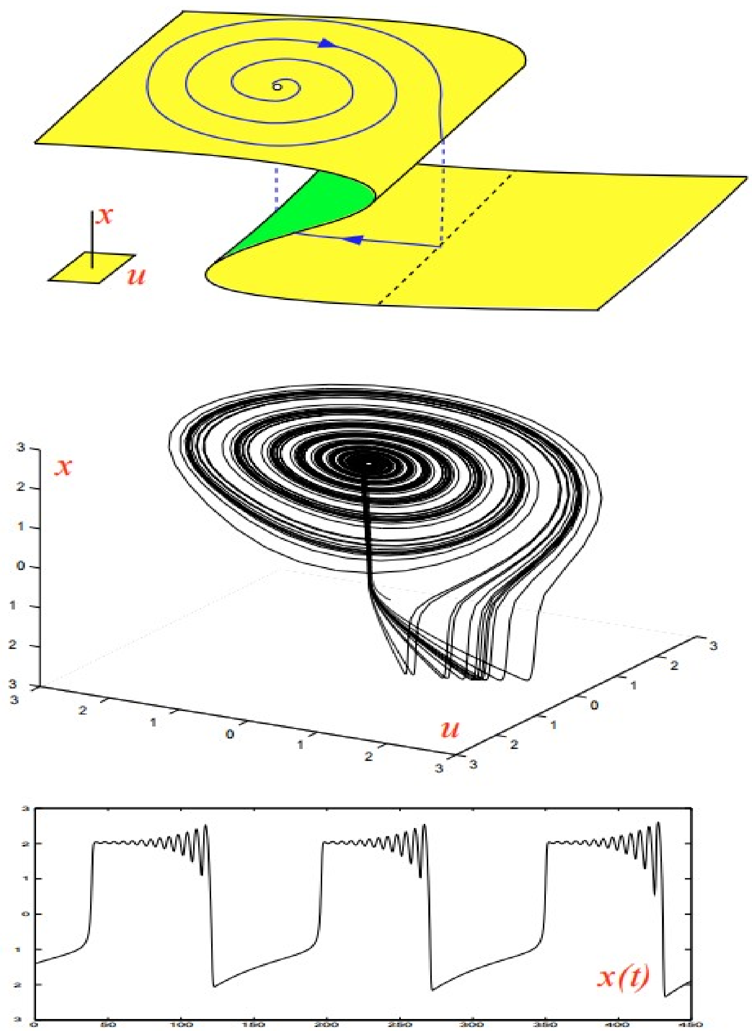

图 120. 混沌的簇发放在鞍焦点同宿轨道分岔附近。系统模拟
$\dot{x} = x - x^3/3 + I - Reu, \dot{u} = \mu(S(x)(1+\omega i)u - u/2)$, 其中 $u \in \mathbb{C}, S(x) = 1/(1+e^{-5x}), \omega = -10, I0.75, \mu = 0.1$

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