
World Scientific
Connecting Great Minds
Subject Journals Books Major Reference Works Resources For Partners Open Access About Us Help
International Journal of Bifurcation and Chaos | Vol. 10, No. 06, pp. 1171-1266 (2000) | Tutorials and Reviews
No Access
NEURAL EXCITABILITY, SPIKING AND BURSTING
EUGENE M. IZHIKEVICH
https://doi.org/10.1142/S0218127400000840 | Cited by: 1361
Next
PDF/EPUB
Tools Share Recommend To Library

神经兴奋性、峰值和簇发放的分岔机制
Section 1: 引言

NEURAL EXCITABILITY, SPIKING AND BURSTING

Author: Eugene M. Izhikevich

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. 1: 引言.

NEURAL EXCITABILITY, SPIKING AND BURSTING

EUGENE M. IZHIKEVICH

The Neurosciences Institute, 10640 John Jay Hopkins Drive,San Diego, CA 92121, USA

Center for Systems Science Engineering, Arizona State University, Tempe, AZ 85287-7606, USA[*]

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，它发射的越快。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

* Eugene.Izhikevich@nsi.edu;

1. 神经元

大脑由多种类型的细胞组成，包括神经元、神经胶质细胞和 Schwann 细胞。后两种类型几乎占大脑体积的一半，但神经元确是信号处理的关键元素。

人脑中有多达 10^{11} 个神经元，每个神经元可以与其他神经元有 10000 多个突触连接。神经元是缓慢、不可靠的模拟单元，但它们协同工作可在认知和控制方面执行高度复杂的计算。

动作电位在神经元之间的许多通信机制中起着至关重要的作用。它们是细胞膜上电位的突然变化，见图1，它们以基本恒定的形状沿着轴突从细胞体传播到与其他细胞的突触连接。

神经元信号的传播和传输问题在别处有描述 (参见例如 [Shepherd, 1983; Johnston & Wu, 1995])。在本文中，我们讨论了动作电位生成的数学理论。

2. 为何峰发放？

人们普遍认为动作电位仅由神经元产生，并且仅用于交流目的。然而，已知许多细胞会在其细胞膜上产生电压尖峰，包括来自南瓜茎、蝌蚪皮和环节动物卵的细胞。此外，动作电位在细胞分裂、受精、形态发生、激素分泌、离子转移、细胞体积控制等方面发挥一定作用 [Shepherd, 1981, 1983]，但可能与细胞信号传导无关。尽管如此，我们在本教程论文中的主要目的是回顾神经信号和信息处理背景下的各种峰发放机制。

3. 离子机制

动作电位由穿过细胞膜的离子电流产生和维持。涉及最多的离子是钠 Na^+、钙 Ca^{++} 和钾 K^+。在最简单的情况下，膜电位的增加激活 (打开) Na^+ 和/或 Ca^{2++} 通道，导致离子快速流入并进一步增加膜电位。这种正反馈导致电位的骤增。此时会触发相对较慢演化通道的失活 (关闭) 和/或 K^+ 通道的激活，从而导致 K^+ 电流增加并最终降低膜电位。这些简化的正负反馈机制负责动作电位的产生。

有十几种不同的离子流具有不同的激活和失活动力学，并在不同的时间尺度上发生 [Llinas，1988]。几乎它们的任何组合都可能导致有趣的非线性行为，例如神经兴奋性。因此，可能有数以千计不同的生物物理基于电导模型。他们都不是完全正确或错误的。

4. 动力学机制

在本文中，我们从动力系统的角度来看待神经元，并使用几何方法来说明可能的分岔及其在神经元计算特性中的作用。

如果一个神经元的膜电位处于稳态或它表现出小幅度 (阈下) 振荡，我们就说它是静止的。在动力系统术语中，这分别对应于处于平衡状态或小振幅极限环吸引子的系统。如果远离稳态的小扰动会导致神经元在返回稳态之前发生较大的电位偏移，则称该神经元是易兴奋的。本文将证明存在如此大的偏移是因为稳态分岔将至。

当存在大振幅极限环吸引子时，神经元周期性地峰发放放电，这可能与稳态共存。此外，我们还简要讨论了准周期和混沌放电。

5. 兴奋性

稳态经历的分岔类型 (图 7、29 和 30) 决定了细胞的可兴奋特性，从而确定了它的神经计算属性。例如，

- 当稳态接近不变圆分岔上的鞍-结点时，神经元可以以任意低频发放全-无尖峰，具备明确定义的临界流形，并可以区分兴奋性和抑制性输入。此时，它充当积分器；即传入尖峰的频率越高，它放电越快。

- 当稳态接近 Andronov-Hopf 分岔时，神经元在特定频率范围内放电没有全-无尖峰，没有明确定义的临界流形，可以在抑制脉冲响应下放电，此时充当谐振器；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放电。

我们在 Sec. 2 部分讨论神经元的兴奋性。并在I中总结了一些基本结果。

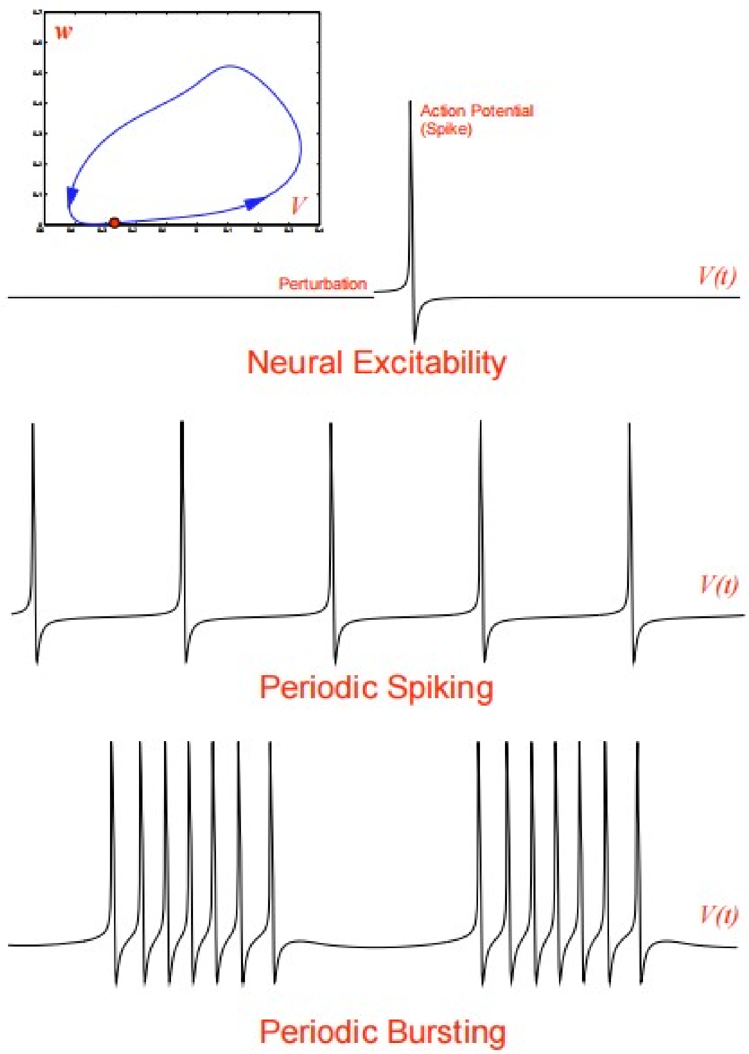

图 1: 神经兴奋性、周期性峰发放和簇发放的示例。(所示的是 Morris Lecar 模型的模拟。添加了一个慢速子系统以获得簇发放解。)

6. 周期性峰发放

细胞的神经计算特性还取决于对应于周期性尖峰脉冲的大幅度极限环的分岔。一般来说，这样的分岔不同于稳态的分岔:例如，当极限环即将通过鞍同宿轨道、折叠极限环分岔消失，或通过亚临界翻转或 Neimark-Sacker 分岔失去稳定性时，它与稳定的稳态共存。因此，具有适当时间的弱扰动可以过早地关闭周期性尖峰。我们在第 Sec. 3 讨论这些和其他问并在表II中总结了一些主要结果。

7. 簇发放

当神经元活动在稳态和重复尖峰脉冲之间交替时，神经元活动被称为簇发放；参见1。它通常是由一个缓慢的电压或钙依赖过程引起的，该过程可以调节快速尖峰活动。有两个重要的分岔 (见2) 与簇发放相关：

- 导致重复尖峰的稳态分岔；见III的左栏。
- 导致静息的尖峰吸引子分岔；见III的第一行。

我们只考虑余维 1 的分岔，因为它们是自然界中最有可能遇到的。当稳态是平衡点而尖峰状态是点-环时，我们将簇发放器称为极限环。当稳态是小振幅 (亚阈值) 振荡时，则称簇发放器为环-环。

表 I: 稳态相关余维 1 分岔的总结。参数 λ 测量到分岔点的距离。

稳态分岔		初始峰发放			阈下振荡	参考图
	行为	频率	振幅	运算		
折点	双稳	非零	定值	积分器	不相关	7, 9, 21
不变圆环上的鞍-结点	兴奋	零 ($\sqrt{\lambda}$)	定值	积分器	不相关	7, 8, 9, 11
超临界 Hopf	兴奋	非零	零 ($\sqrt{\lambda}$)	谐振器	减幅	7
亚临界 Hopf	双稳	非零	任意	谐振器	减幅	7, 16
阈下振荡分岔					阈下振荡频率	
折极限环	双稳	非零	任意	积分器 谐振器	非零	35 29, 31
鞍同宿轨	双稳 兴奋	非零	定值	谐振器	零 ($1/\lvert ln\lambda\rvert$)	29, 31,34
鞍-焦同宿轨	双稳 兴奋	非零	定值	谐振器	零 ($1/\lvert ln\lambda\rvert$)	30
焦-焦同宿轨	双稳 兴奋	非零	定值	谐振器	零 ($1/\lvert ln\lambda\rvert$)	
超临界翻转 (倍周期)	双稳	非零	任意	积分器 谐振器	非零	30
亚临界 Neimark-Sacker	双稳	非零	任意	谐振器	非零	30
蓝天灾难	兴奋	零 ($\sqrt{\lambda}$)	定值	积分器	非零	30
在同宿环面上的折极限环	兴奋	零 ($\sqrt{\lambda}$)	定值	积分器	非零	30

表 II: 大振幅尖峰的相关余维 1 分叉的总结。参数 λ 测量到分岔点的距离。

周期放电的分岔		终止	峰发放	
	行为	频率	振幅	锁
不变圆环上的鞍-结点	兴奋	零 ($\sqrt{\lambda}$)	定值	困难
超临界 Hopf	兴奋	非零	零 ($\sqrt{\lambda}$)	简单
折极限环	双稳	非零	任意	简单
鞍同宿轨	双稳	零 ($1/\lvert ln\lambda\rvert$)	定值	简单 (?)
鞍-焦同宿轨	双稳	零 ($1/\lvert ln\lambda\rvert$)	定值	简单 (?)
焦-焦同宿轨	双稳	零 ($1/\lvert ln\lambda\rvert$)	定值	简单 (?)
亚临界翻转 (倍周期)	双稳	非零	任意	简单
亚临界 Neimark-Sacker	双稳	非零	任意	简单
蓝天灾难	兴奋	零 ($\sqrt{\lambda}$)	定值	困难
准周期放电的分岔				
在同宿环面上的折极限环	兴奋	零 ($\sqrt{\lambda}$)	定值	困难

当快速尖峰子系统是二维时，我们将簇发放器称为平面的。这对可能的分岔施加了严格的限制。表III总结了 24 个平面余维 1 簇发放器。我们以所涉及的两个分岔来命名它们。其中有 16 个点-环和 8 个环-环簇发放器，分别在表格的上部和下部。我们将在 Sec. 4 详细讨论它们。

Hoppensteadt 和 Izhikevich[1997，2.9 节] 首次提供了所有 16 种平面点-环簇发放器的完整分类，尽管没有命名方案。其中包括著名的

- 折/同宿簇发放器，也称为方波或 I 型簇发放器。
- 环/环簇发放器，也称为抛物线或 II 型簇发放器。
- 亚临界 Hopf/折环簇发放器，也称为“椭圆形”或 III 型簇发放器。
- 折/折环簇发放器，也称为 IV 型簇发放器。
- 折/Hopf 簇发放器，也称为“锥形”或 V 型簇发放器。

- 折/环簇发放器，也称为“三角形”簇发放器。

表III中列出的许多其他簇发放类型都是新的。我们在 Sec. 4 展示。如果快速子系统是多维的，可能会有更多的簇发放事件。它们的分类如??所示。

簇发放的正式分类的历史始于 Rinzel [1987] 的开创性论文，他对比了方波、抛物线和椭圆簇发放的分岔机制。然后，Bertram 等人 [1995] 建议使用罗马数字来指代簇发放类型，并且他们添加了一种新的 IV 类型。Holden 和 Erneux [1993a, 1993b]、Smolen 等人 [1993] 和 Pernarowski [1994] 同时独立研究了另一种锥形簇发放。后来 Vries [1998] 建议将其称为 V 型爆破器。Rush 和 Rinzel [1994] 研究了另一种三角形类型的簇发放，使已识别的簇发放总数为 6。它们的分岔机制总结在图 126 中。

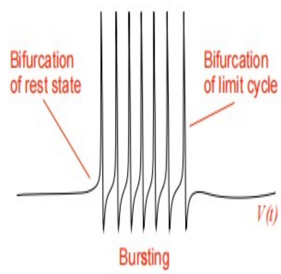

图 2: 与破裂相关的两个重要分岔。

我们的簇发放分类方法与上述科学家的分类方法存在巨大差异。他们使用自下而上的方法，也就是说，他们考虑了生物物理学上合理的基于电导的模型，这些模型描述了实验可观察到的细胞行为，然后他们试图确定这些模型表现出的簇发放类型。相比之下，我们使用自上而下的方法：我们考虑所有可能的余维 1 静止和尖峰状态分岔对，这会导致不同类型的簇发放，然后我们开发了一个基于电导的模型来展示每种簇发放类型。因此，我们的许多簇发放是理论上的，因为它们尚未在实验中看到。我们在 6.1 节讨论这个问题。

8. 零斜线和相平面分析

我们尽可能概括地阐述神经元动力学中的分岔。尽管我们使用生物物理学上详细的霍奇金-赫胥黎型神经模型来说明许多问题，但我们的大多数分岔图和相图与任何特定的方程组无关。因此，我们强调要点并省略不相关的细节。

此处讨论的大多数分岔都可以使用以下形式的二维 (平面) 系统来说明

$$\mu\dot{x} = f(x, y),$$
$$\dot{y} = g(x, y).$$

通过考虑它们的零斜线，即由条件 $f(x, y) = 0$ 或 $g(x, y) = 0$ 确定的集合，可以深入了解此类系统的行为；见3。当 $0 < \mu \preccurlyeq 1$ 时，零斜线分别称为快和慢。由于零斜线的语言在应用数学的许多领域中是通用的，因此我们在大多数插图中用它们描述 (绿色曲线)。

9. 规范模型方法

只要有可能，我们都会使用规范模型来说明神经元动力学。简而言之，如果一个动力系统族的每个成员都可以通过变量的分段连续可能不可逆的变化转化为模型，则该模型对于动力系统组是规范的；参见4。规范模型的定义概括了拓扑范式和通用展开的概念，并在 [Hoppensteadt & Izhikevich, 1997] 的第 4 章中详细讨论，在那里可以找到许多神经科学规范模型的例子。

考虑规范模型的优势在于它的普遍性，因为该模型提供了有关整个组行为的信息。例如，规范模型 (2) 描述了任何 1 类可兴奋神经元的动力学，而不管人们选择用来模拟其活动的方程的特性如何。也就是说，如果修改方程并添加更多的变量和参数以考虑更多的离子、电流、泵等，但模型仍然表现出 1 类兴奋性，那么它仍然可以转换为规范模型 (2) 变量的 (可能不同的) 变化。因此，考虑更多的生物学数据并不会改变规范模型 (2) 的形式，而只会完善我们对模型中参数 r 可能值的认识。

表 III: 一维平面快-慢簇发放的分类。表的上部（下部）对应于点-环（环-环）簇发放。也见表 4 和图 53 和 126。

分岔	不变圆环上的鞍-结点	鞍同宿轨	超临界 Andronov-Hopf	折极限环
折点	折/环	折/同宿	折/Hopf	折/折环
不变圆环上的鞍-结点	环/环	环/同宿	环/Hopf	环/折环
超临界 Andronov-Hopf	Hopf/环	Hopf/同宿	Hopf/Hopf	Hopf/折环
亚临界 Andronov-Hopf	亚临界 Hopf/环	亚临界 Hopf/同宿	亚临界 Hopf/Hopf	亚临界 Hopf/折环
折极限环	折环/环	折环/同宿	折环/Hopf	折环/折环
鞍同宿轨	同宿/环	同宿/同宿	同宿/Hopf	同宿/折环

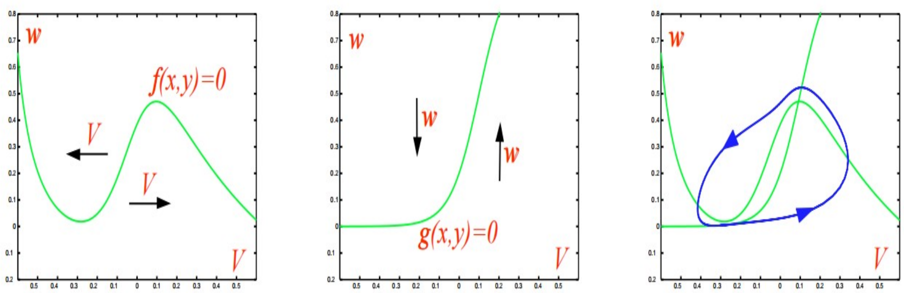

图 3: 平面神经系统的典型零斜线。(显示的是 Morris-Lecar [1981] 模型的零斜线。)

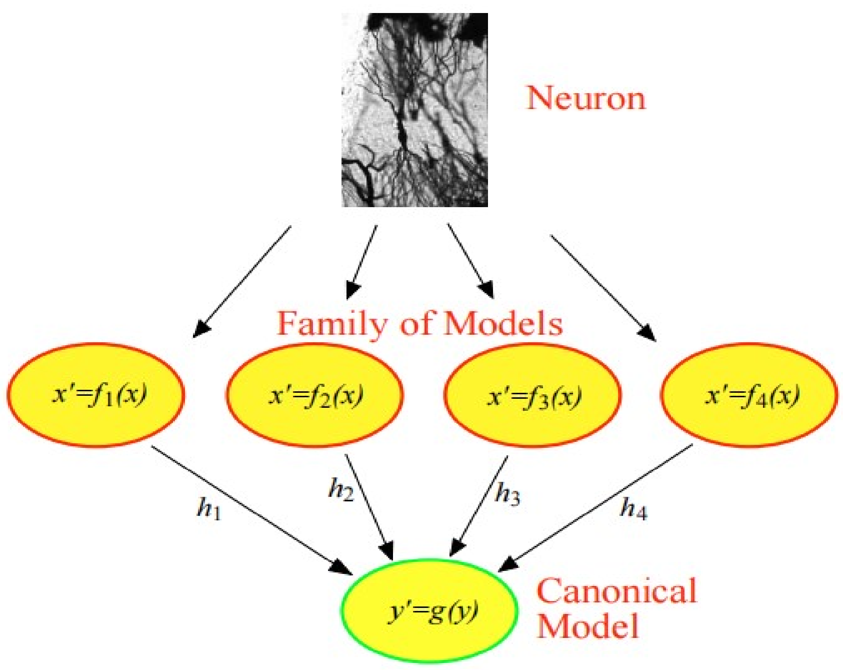

图 4: 模型 y0 = g(y) 对于神经模型家族是规范的，如果该家族的每个成员都可以通过变量的分段连续变化转化为 y0 = g(y)。

参考文献

Abarbanel, H. D. I., Huerta, R., Rabinovich, M. I., Rulkov, N. F., Rowat, P. F. & Selverston, A. I. [1996] “Synchronized action of synaptically coupled chaotic model neurons,” Neural Comput. 8, 1567-1602.

Alexander, J. C. & Cai, D. [1991] “On the dynamics of bursting systems,” J. Math. Biol. 29, 405-423.

Alexander, J. C., Doedel, E. J. & Othmer, H. G. [1990] “On the resonance structure in a forced excitable system,” SIAM J. Appl. Math. 50, 1373-1418.

Arnold, V. I. [1982] Geometrical Methods in the Theory of Ordinary Differential Equations (SpringerVerlag, NY); Russian original [1977] Additional Chapters of the Theory of Ordinary Differential Equations, Moscow.

Arnold, V. I., Afrajmovich, V. S., Il’yashenko, Yu. S. & Shil’nikov, L. P. [1994] “Bifurcation theory,” in Dynamical Systems V. Bifurcation Theory and Catastrophe Theory, ed. Arnold, V. I. (Springer-Verlag, NY).

Aronson, D. G., Ermentrout, G. B. & Kopell, N. [1990] “Amplitude response of coupled oscillators,” Physica D41, 403-449.

Baer, S. M., Erneux, T. & Rinzel, J. [1989] “The slow passage through a Hopf bifurcation: Delay, memory effects, and resonances,” SIAM J. Appl. Math. 49, 55-71.

Baer, S. M., Rinzel, J. & Carrillo, H. [1995] “Analysis of an autonomous phase model for neuronal parabolic bursting,” J. Math. Biol. 33, 309-333.

Bedrov, Y. A., Akoev, G. N. & Dick, O. E. [1992] “Partition of the Hodgkin-Huxley type model parameter space into regions of qualitatively different solutions,” Biol. Cybern. 66, 413-418.

Belair, J. & Holmes, P. [1984] “On linearly coupled relaxation oscillations,” Quarterly of Appl. Math. 42, 193-219.

Bertram, R. [1993] “A computational study of the effects of serotonin on a molluscan burster neuron,” Biol. Cybern. 69, 257-267.

Bertram, R., Butte, M. J., Kiemel, T. & Sherman, A. [1995] “Topological and phenomenological classification of bursting oscillations,” Bull. Math. Biol. 57, 413-439.

Booth, V., Carr, T. W. & Erneux, T. [1997] “Nearthreshold bursting is delayed by a slow passage near a limit point,” SIAM J. Appl. Math. 57, 1406-1420.

Butera Jr., R. J., Clark Jr., J. W. & Byrne, J. H. [1996] “Dissection and reduction of a modeled bursting neuron,” J. Comput. Neurosci. 3, 199-223.

Butera Jr., R. J., Clark Jr., J. W. & Byrne, J. H. [1997] “Transient responses of a modeled bursting neuron: Analysis with equilibrium and averaged nullclines,” Biol. Cybern. 77, 307-322.

Canavier, C. C., Clark, J. W. & Byrne, J. H. [1991] “Simulation of the bursting activity of neuron-R15 in aplysia —role of ionic currents, calcium balance, and modulatory transmitters,” J. Neurophysiol. 66, 2107-2124.

Carpenter, G. A. [1979] “Bursting phenomena in excitable membranes,” SIAM J. Appl. Math. 36, 334-372.

Chay, T. R. & Keizer, J. [1983] “Minimal model for membrane oscillations in the pancreatic -cell,” Biophys. J. 42, 181-190.

Connor, J. A. & Stevens, C. F. [1971] “Prediction of repetitive firing behavior from voltage-clamped data on an isolated neurone soma,” J. Physiol. Lond.

214, 31-53.

Del Negro, C. A., Hsiao, C.-F., Chandler, S. H. & Garfinkel, A. [1998] “Evidence for novel bursting mechanism in rodent trigeminal neurons,” Biophys. J.75, 174-182.

de Vries, G. [1998] “Multiple bifurcations in a polynomial model of bursting oscillations,” J. Nonlin. Sci.8, 281-316.

Ermentrout, G. B. [1996] “Type I membranes, phase resetting curves, and synchrony,” Neural Comput. 8, 979-1001.

Ermentrout, G. B. [1998] “Linearization of F-I curves by adaptation,” Neural Comput. 10, 1721-1729.

Ermentrout, G. B. & Kopell, N. [1986a] “Parabolic bursting in an excitable system coupled with a slow oscillation,” SIAM J. Appl. Math. 46, 233-253.

Ermentrout, G. B. & Kopell, N. [1986b] “Subcellular oscillations and bursting,” Math. Biosci. 78, 265-291.

Evans, J., Fenichel, N. & Feroe, J. [1982] “Double impulse solutions in nerve axon equations,” SIAM J. Appl. Math. 42, 219-234.

Fenichel, N. [1971] “Persistence and smoothness of invariant manifolds for flows,” Ind. Univ. Math. J. 21, 193-225.

Feroe, J. A. [1982] “Existence and stability of multiple impulse solutions of a nerve equation,” SIAM J. Appl.Math. 42, 235-246.

FitzHugh, R. [1955] “Mathematical models of threshold phenomena in the nerve membrane,” Bull. Math.Biophys. 17, 257-278.

Frankel, P. & Kiemel, T. [1993] “Relative phase behavior of two slowly coupled oscillators,” SIAM J. Appl.Math. 53, 1436-1446.

Grasman, J. [1987] Asymptotic Methods for Relaxation Oscillations and Applications (Springer-Verlag, NY).

Guckenheimer, J., Harris-Warrick, R., Peck, J. & Willms, A. [1997] “Bifurcations, bursting and spike frequency adaptation,” J. Comput. Neurosci. 4, 257-277.

Gutfreund, Y., Yarom, Y. & Segev, I. [1995] “Subthreshold oscillations and resonant frequency in guinea-pig cortical neurons: Physiology and modeling,” J. Physiol. London 483, 621-640.

Gutkin, B. S. & Ermentrout, G. B. [1998] “Dynamics of membrane excitability determine interspike interval variability: A link between spike generation mechanisms and cortical spike train statistics,” Neural Comput. 10, 1047-1065.

Hansel, D., Mato, G. & Meunier, C. [1995] “Synchrony in excitatory neural networks,” Neural Comput. 7, 307-335.

Hassard, B. D. [1978] “Bifurcation of periodic solutions of the Hodgkin-Huxley model for the squid giant axon,” J. Theoret. Biol. 71, 401-420.

Hassard, B. D., Kazarinoff, N. D. & Wan, Y. H. [1981] Theory and Applications of Hopf Bifurcation (Cambridge University Press,Cambridge).

Hastings, S. [1976] “On the existence of homoclinic and periodic orbits for FitzHugh-Nagumo equations,” Quart. J. Math. (Oxford) 27, 123-134.

Hindmarsh, J. L. & Rose, R. M. [1984] “A model of neuronal bursting using three coupled first order differential equations,” Philos. Trans. R. Soc. London, Ser. B221 87-102.

Hodgkin, A. L. [1948] “The local electric changes associated with repetitive action in a non-medulated axon,” J. Physiol. 107, 165-181.

Hodgkin, A. L. & Huxley, A. F. [1952] “A quantitative description of membrane current and application to conduction and excitation in nerve,”J. Physiol. 117, 500–544.

Holden, L. & Erneux, T. [1993a] “Slow passage through a Hopf bifurcation: Form oscillatory to steady state solutions,”SIAM J. Appl. Math. 53, 1045–1058.

Holden, L. & Erneux, T. [1993b] “Understanding bursting oscillations as periodic slow passages through bifurcation and limit points,” J. Math. Biol. 31, 351–365.

Holden, A. V., Hyde, J. & Muhamad, M. [1991] “Equilibria. Periodicity, bursting and chaos in neural activity,”Proc. 9th Summer Workshop on Mathematical Physics, Vol. 1, pp. 96–128.

Hoppensteadt, F. C. [1997] An Introduction to the Mathematics of Neurons. Modeling in the Frequency Domain (Cambridge University Press).

Hoppensteadt, F. C. [1993] Analysis and Simulations of Chaotic Systems (Springer-Verlag, NY).

Hoppensteadt, F. C. & Izhikevich, E. M. [1996] “Synaptic organizations and dynamical properties of weakly connected neural oscillators: I. Analysis of canonical model,” Biol. Cybern. 75, 117–127.

Hoppensteadt, F. C. & Izhikevich, E. M. [1997] Weakly Connected Neural Networks (Springer-Verlag, NY).

Hoppensteadt, F. C. & Izhikevich, E. M. [1998] “Thalamo-Cortical interactions modeled by weakly connected oscillators: Could brain use FM radio principles?” BioSyst. 48, 85–94.

Hutcheon, B., Miura, R. M. & Puil, E. [1996] “Models of subthreshold membrane resonance in neocortical neurons,” J. Neurophysiol. 76, 698–714.

Hutcheon, B., Miura, R. M., Yarom, Y. & Puil, E. [1994] Low-threshold calcium current and resonance in thalamic neurons: A model of frequency preference,” J.Neurophysiol. 71, 583–594.

Il’iashenko, Iu. S. & Li, W. [1999] Nonlocal Bifurcations Mathematical Surveys and Monographs (American Mathematical Society), Vol. 66.

Izhikevich, E. M. [2001] “Resonate-and-fire neurons,” Neural Networks, submitted.

Izhikevich, E. M. [2000a] “Subcritical elliptic bursting of Bautin type,” SIAM J. Appl. Math. 60, 503–535.

Izhikevich, E. M. [2000b] “Phase equations for relaxation oscillators,” SIAM J. Appl. Math., in press.

Izhikevich, E. M. [1999a] “Weakly connected quasiperiodic oscillators, FM interactions, and multiplexing in the brain,” SIAM J. Appl. Math. 59, 2193–2223.

Izhikevich, E. M. [1999b] “Class 1 neural excitability, conventional synapses, weakly connected networks, and mathematical foundations of pulse-coupled models,” IEEE Trans. Neural Networks 10, 499–507.

Izhikevich, E. M. [1999c] “Weakly pulse-coupled oscillators, FM interactions, synchronization, and oscillatory associative memory,” IEEE Trans. Neural Networks 10, 508–526.

Izhikevich, E. M. [1998] “Supercritical elliptic bursting, slow passage effect, and assistance of noise,” preprint.

Jansen, H. & Karnup, S. [1994] “A spectral analysis of the integration of artificial synaptic potentials in mammalian central neurons,” Brain Res. 666, 9–20. Johnston, D. & Wu, S. M. [1995] Foundations of Cellular Neurophysiology (The MIT Press).

Kopell, N. [1995] “Chains of coupled oscillators,” in Brain Theory and Neural Networks, ed. Arbib, M. A.(The MIT press, Cambridge, MA).

Kopell, N. & Somers, D. [1995] “Anti-phase solutions in relaxation oscillators coupled through excitatory interactions," J. Math. Biol. 33, 261-280.

Kowalski, J. M., Albert, G. L., Rhoades, B. K. & Gross, G. W. [1992] "Neuronal networks with spontaneous, correlated bursting activity: Theory and simulations," Neural Networks 5, 805-822.

Kuznetsov, Yu. [1995] Elements of Applied Bifurcation Theory 2nd edition (Springer-Verlag, NY).

Levi, M., Hoppensteadt, F. C. & Miranker, W. L. [1978] "Dynamics of the Josephson junction," Quart. J.Appl. Math. July, 167-190.

Llinas, R. R. [1988] "The intrinsic electrophysiological properties of mammalian neurons: Insights into central nervous system function," Science 242, 1654-1664.

Llinas, R. R., Grace, A. A. & Yarom, Y. [1991] "In vitro neurons in mammalian cortical layer 4 exhibit intrinsic oscillatory activity in the 10- to 50-Hz frequency range," Proc. Natl. Acad. Sci. USA 88, 897-901.

Mishchenko, E. F., Kolesov, Yu. S., Kolesov, A. Yu. & Rozov, N. K. [1994] Asymptotic Methods in Singularly Perturbed Systems (Plenum Press, NY).

Morris, C. & Lecar, H. [1981] "Voltage oscillations in the Barnacle giant muscle fiber," Biophys. J. 35, 193-213.

Nejshtadt, A. [1985] "Asymptotic investigation of the loss of stability by an equilibrium as a pair of eigenvalues slowly cross the imaginary axis," Usp. Mat. Nauk 40, 190-191.

Pernarowski, M. [1994] "Fast subsystem bifurcations in a slowly varied Li´enard system exhibiting bursting," SIAM J. Appl. Math. 54, 814-832.

Pernarowski, M., Miura, R. M. & Kevorkian, J. [1992] "Perturbation techniques for models of bursting electrical activity in pancreatic -cells," SIAM J. Appl. Math. 52, 1627-1650.

Plant, R. E. [1981] "Bifurcation and resonance in a model for bursting nerve cells," J. Math. Biol. 11, 15-32.

Puil, E., Meiri, H., Yarom, Y. [1994] "Resonant behavior and frequency preference of thalamic neurons," J.Neurophysiol. 71, 575-582.

Rinzel, J. [1987] "A formal classification of bursting mechanisms in excitable systems," Mathematical Topics in Population Biology, Morphogenesis, and Neurosciences, eds. Teramoto, E. & Yamaguti, M., Vol. 71 of Lecture Notes in Biomathematics (Springer-Verlag, Berlin).

Rinzel, J. & Ermentrout, G. B. [1989] "Analysis of neural excitability and oscillations," eds. Koch, C. & Segev, I. Methods in Neuronal Modeling (The MIT Press, Cambridge).

Rinzel, J. & Lee, Y. S. [1986] "On different mechanisms for membrane potential bursting," Nonlinear Oscillations in Biology and Chemistry, ed. Othmer, H. G., Lecture Notes in Biomathematics (Springer-Verlag).

Rinzel, J. & Lee, Y. S. [1987] "Dissection of a model for neuronal parabolic bursting," J. Math. Biol. 25, 653-675.

Rinzel, J. & Miller, R. N. [1980] "Numerical calculation of stable and unstable periodic solution to the Hodgkin-Huxley equations," Math. Biosci. 49, 27-59.

Rush, M. E. & Rinzel, J. [1995] "The potassium ACurrent, low firing rates and rebound excitation in Hodgkin-Huxley models," Bull. Math. Biol. 57, 899-929.

Rush, M. E. & Rinzel, J. [1994] "Analysis of bursting in a thalamic neuron model," Biol. Cybern. 71, 281-291.

Samoilenko, A. M. [1991] "Elements of the mathematical theory of multi-frequency oscillations," Mathematics and Its Applications (Soviet Series), Vol. 71 (Kluwer Academic, Dordrecht).

Schecter, S. [1987] "The saddle-node separatrix-loop bifurcation," SIAM J. Math. Anal. 18, 1142–1156.

Sharp, A. A., O'neil, M. B., Abbott, L. F. & Marder, E.

[1993] "Dynamic clamp: Computer-generated conductances in real neurons," J. Neurophysiol. 69, 992–995.

Shepherd, G. M. [1981] "Introduction: The nerve impulse and the nature of nervous function,"Neurones Without Impulses, eds. Roberts & Bush (Cambridge University Press).

Shepherd, G. M. [1983] Neurobiology (Oxford University Press, NY).

Shorten, P. R. & Wall, D. J. N. [2000] "A Hodgkin–Huxley model exhibiting bursting oscillations," Bull.Math. Biol., accepted.

Sivan, E., Segel, L. & Parnas, H. [1995] "Modulated excitability: A new way to obtain bursting neurons," Biol. Cybern. 72, 455–461.

Smolen, P., Terman, D. & Rinzel, J. [1993] "Properties of a bursting model with two slow inhibitory variables," SIAM J. Appl. Math. 53, 861–892.

Softky, W. R. & Koch, C. [1993] "The highly irregular firing of cortical-cells is inconsistent with temporal integration of random EPSPs," J. Neurosci. 13, 334–350.

Somers, D. & Kopell, N. [1993] "Rapid synchronization through fast threshold modulation," Biol. Cybern. 68, 393–407.

Somers, D. & Kopell, N. [1995] "Waves and synchrony in networks of oscillators or relaxation and nonrelaxation type," Physica D89, 169–183.

Soto-Trevino, C., Kopell, N. & Watson, D. [1996] "Parabolic bursting revisited,"J. Math. Biol. 35, 114–128.

Storti, D. W. & Rand, R. H. [1986] "Dynamics of two strongly coupled relaxation oscillators," SIAM J. Appl. Math. 46, 56–67.

Taylor, D. & Holmes, P. [1998] "Simple models for excitable and oscillatory neural networks," J. Math.Biol. 37, 419–446.

Terman, D. [1991] "Chaotic spikes arising from a model of bursting in excitable membranes," SIAM J. Appl.Math. 51, 1418–1450.

Terman, D. [1992] "The transition from bursting to continuous spiking in excitable membrane models," J.Nonlinear Sci. 2, 133–182.

Terman, D. & Lee, E. [1997] "Partial synchronization in a network of neural oscillators,"SIAM J. Appl. Math.57, 252–293.

Terman, D. & Wang, D. [1995] "Global competition and local cooperation in a network of neural oscillators," Physica D81, 148–176.

Traub, R. D. & Miles, R. [1991] Neuronal Networks of the Hippocampus (Cambridge University Press, Cambridge).

Troy, W. [1978] "The bifurcation of periodic solutions in the Hodgkin–Huxley equations,"Quart. Appl. Math.36, 73–83.

Wang, X.-J. [1993] "Ionic basis for intrinsic 40 Hz neuronal oscillations," NeuroReport 5, 221–224.

Wang, X.-J. [1993] "Genesis of bursting oscillations in the Hindmarsh–Rose model and homoclinicity to a chaotic saddle," Physica D62, 263–274.

Wang, X.-J. [1998] "Calcium coding and adaptive temporal computation in cortical pyramidal neurons," J.Neurophysiol. 79, 1549–1566.

Wang, X. J. & Rinzel, J. [1995] "Oscillatory and bursting properties of neurons," Brain Theory and Neural Networks, ed. Arbib, M. A. (The MIT press, Cambridge, MA).

Williams, T. L. & Sigvardt, K. A. [1995] "Spinal cord of lamprey: Generation of locomotor patterns," Brain Theory and Neural Networks, ed. Arbib, M.A. (The MIT press, Cambridge, MA).

Wilson, C. J. [1993] "The generation of natural firing patterns in neostriatal neurons," Progress in Brain Research, eds. Arbuthnott, G. W. & Emson, P. C. 99, pp. 277–297.

Wilson, C. J. & Kawaguchi, Y. [1996] "The origins of two-state spontaneous membrane potential fluctuations of neostriatal spiny neurons," J. Neurosci. 16, 2397–2410.

Wilson, H. R. & Cowan, J. D. [1972] "Excitatory and inhibitory interaction in localized populations of model neurons," Biophys J. 12, 1–24.

Wilson, M. A. & Bower, J. M. [1989] "The simulation of large scale neural networks," Methods in Neuronal Modeling, eds. Koch, C. & Segev, I. (The MIT Press, Cambridge, MA).

Wu, H.-Y. & Baer, S. M. [1998] "Analysis of an excitable dendritic spine with an activity-dependent stem conductance," J. Math. Biol. 36, 569–592.