神经兴奋性、峰值和簇发放的分岔机制 *Section 6:* 簇发放的分类：为什么是 *Boster*?

NEURAL EXCITABILITY, SPIKING AND BURSTING

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* 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. 6: 簇发放的分类：为什么是 Boster?

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。

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从纯动力系统的角度来看，有许多类型的不同簇发放器。它们是否真的与神经计算的观点如此不同？答案是也许。

事实上，一些簇发放事件具有相当独特的神经计算特性。例如，环/环 (抛物线) 簇发放表现出第 1 类神经兴奋性和第 1 类尖峰，当它通过" 折/* 滞后环发生时，它可以作为神经信号的积分器。相比之下，亚 Hopf/折环 (椭圆) 簇发放器表现出第 2 类神经兴奋性和第 2 类尖峰，它作为一个谐振器。这种谐振器簇发放器之间的相互作用主要取决于它们的尖峰间频率的谐振关系 [Izhikevich, 2000a]；它们可以表现出尖峰同步、簇发放同步或两者兼而有之。相比之下，环/环-簇发放器没有明确的尖峰间频率，因此不愿意表现出尖峰同步。

因此，不同的簇发放器可以以不同的方式通信、同步和处理信息。然而，我们不能排除一对不同的簇发放器具有相同的神经计算特性的情况，因为簇发放器非常多 [见表 4]，关于它们行为的信息也很少。

1. 如何区分簇发放器？

由于不同的簇发放器可能有不同的神经计算特性，所以在实验中用标准来区分它们是很重要的。最没用的，但可能是最常见的方式，是浏览本文，并试图找到一张" 类似于" 所考虑的微电极记录的图片。这可能完全是在浪费时间，因为两个相同的簇发放器可能看起来很不一样 (图 121)，或者两个截然不同的簇发放器看起来" 相似"；比较一下图 57 中的" 环/环" 簇发放和图 86 中的" 折/同宿" 簇发放。

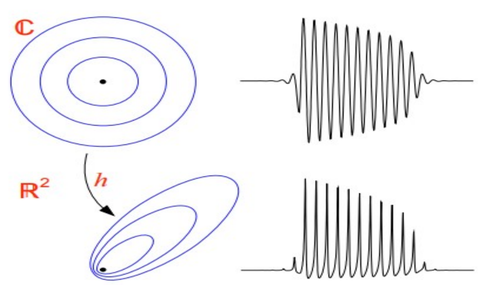

图 121. 两个拓扑上等价的 (通过同胚 h) 亚 Hopf/折环簇发放器可能" 看起来" 相当不同 (来自 [Izhikevich, 2000a])。

1.1. 出现/终止尖峰的频率

首先，我们应该检查出现和终止尖峰的频率，并将其与簇发放事件中间的尖峰间频率对比。频率的明显下降是衡量不变圆上的鞍结点和鞍同宿轨道分岔的良好指标。例如，如果我们考虑平面情况，那么小的初始频率就意味着" 环/*" 的簇发放。同样地，小的终止频率意味着"*/环" 或"*/同宿" 簇发放。如果在簇发放期间频率没有明显变化，那么可能的分岔是折或 Andronov-Hopf 型的；见表 1 和表 2。

Guckenheimer 等人。[1997] 使用启发式论证，获得了簇发放结束时尖峰间频率的详细渐近线，这可以用来区分，例如，"*/环" 与"*/同宿" 簇发放。

1.2. 出现/终止尖峰的振幅

小振幅的初始或终止尖峰是一个强有力的指标，可以防止折叠、不变圆上的鞍-结点和鞍同宿轨道分岔，因为它只发生在 Andronov-Hopf 和折叠极限环分岔期间。然而，大振幅的尖峰不能排除 Andronov-Hopf 分岔和折叠极限环分岔，因为许多靠近 (奇异)Andronov-Hopf 分岔的松弛系统只在分岔参数极其狭窄的区域表现出小的和中等的振幅尖峰；例如，见图 73 和 76。

1.3. 静止时的阻尼振荡

阻尼亚阈值振荡的存在是接近 Andronov-Hopf 分岔振荡的一个强有力的指标。它的频率是神经元的谐振频率。然而，只要系统的维度大于 2，甚至对于折叠分岔也可能存在阻尼振荡；见图 122。 这样的振荡不

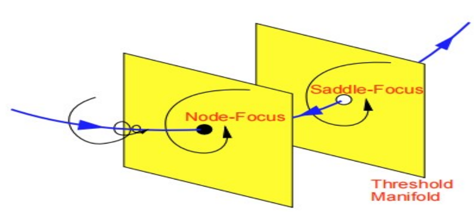

图 122. 即使系统接近折分岔点，一个小的扰动也可能表现出阻尼振荡。

会使神经元成为谐振器，因为它发生在与鞍-结点的稳

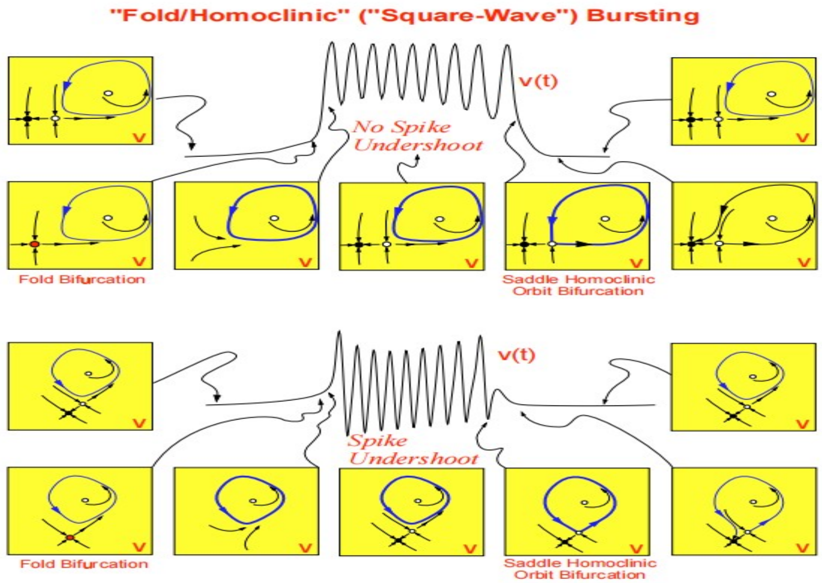

图 123. 在" 折/同宿"(" 方波" 或"Ia " 型) 簇发放中的尖峰下冲。

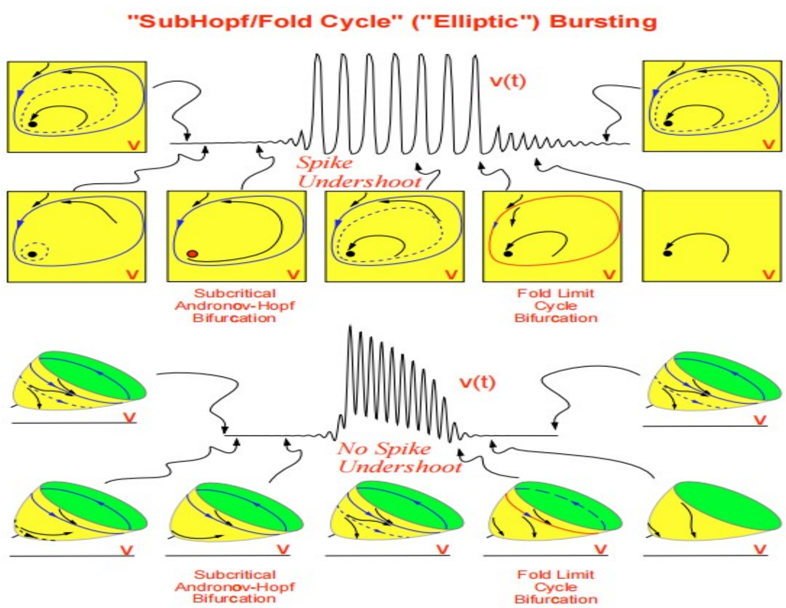

图 124. 当快速子系统为三维时，" 亚 Hopf/折环"(椭圆) 簇发放器中没有尖峰下冲。

定流形相切的子空间中。增加振荡的振幅并不明显改变与门槛流形的距离，因此不便于尖峰的出现。

1.4. 尖峰下冲

尖峰下冲的存在或不存在可以用来区分不同类型的簇发放器吗？答案是否定的。

人们普遍认为，下冲的发生是因为对应于重复尖峰的极限环吸引子包含了对应于静止状态的平衡。这确实导致了下冲，但只是在一个二维的快速子系统中。此外，正如我们在图 123 中所说明的那样，下冲可能发生在没有包围的情况下。这特别表明，著名的" 折/同宿"(" 方波" 或"Ia" 型) 簇发放可能会显示出下冲，即使快速子系统是平面的。

如果快速系统是多维的，那么极限环是否围绕着平衡点是相关的。此外，" 围绕" 的概念在这种情况下

没有很好的定义，因为它取决于观点。在图 124 中，我们说明了这个问题，并表明”折/同宿”簇发放可能不会显示出下冲。

显然，尖峰下冲取决于重复尖峰对应的极限环吸引子在电压轴上的重叠和静止状态对应的稳定平衡；见图 125。由于重叠完全取决于吸引子的位置，而不是导致它们出现或消失的分叉机制，因此峰值不足不应被用作神经爆发类型的指标。

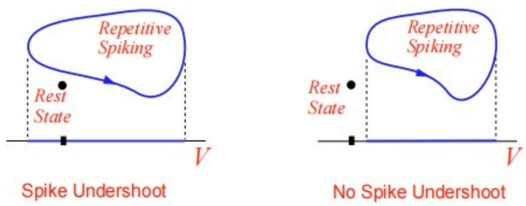

图 125. 极限环吸引子和稳定平衡在电压轴 v 上的正交投影。

1.5. 尖峰和静止状态的共存

吸引子的全局共存可能对识别簇发放类没有用处，因为任何簇发放都有稳定的静止和簇发放状态。然而，局部共存可能是有用的。

让我们详细说明一下。考虑到图 49 或 52 中的”环/环”簇发放现象，尖峰极限环吸引子与静止状态共存，因此一个合适的短扰动可以关闭尖峰状态。然而，扰动应该足够强，以将解推入下行状态的吸引域。相比之下，图 59 中”折/同宿”簇发放的重复性尖峰可以通过具有适当时间的弱扰动而过早关闭。

一般来说，在任何”*/同宿” 和”*/折环” 中的重复尖峰都可以通过弱刺激过早地关闭，而在”*/环” 和”*/Hopf” 中的重复尖峰则不能。同样，在”折/* 和”亚 Hopf/* 簇发放器中，短暂的弱刺激可以唤起重复的尖峰，而在”环/* 和”Hopf/*” 簇发放器中则不能。

最后，请注意测试吸引子的共存是一个需要刺激的侵入性过程，而上面讨论的其他标准是非侵入性的，因为它们只基于观察。

1.6. 从簇发放到强直尖峰或静止的过渡

簇发放模式的精细结构取决于许多生理参数，如温度、细胞外离子的浓度等。改变这样的参数可以扭曲簇发放模式，在极端情况下，可以完全关闭它或将其转化为强直的簇发放。这些是有趣的情况，因为它们对应于整个系统行为的分岔。测量分岔处的尖峰间期和/或簇发放间期，原则上可以确定系统可以表现出的簇发放类型。不幸的是，除了 Terman[1992] 和 Izhikevich[2000a] 讨论的一些特殊情况外，人们对从簇发放到强直加压或静止的可能机制知之甚少。因此，在对这些测量结果进行理解之前，还需要进行更多的分析。

1.7. 基于电导率的模型

我们将神经元视为一般的动态系统，对右边的形式没有限制。现在我们限制自己，考虑基于电导率的模型，其形式为

$$\dot{V} = I - \sum_{i=1}^{n} g_i(x)(V - E_i)$$

$$\dot{x} = f(V, x)$$

其中 V 是电压，$x \in \mathbb{R}^m$ 是电导率、门控变量等的矢量。基于电导率的形式是否对静止状态或极限环的可能分岔施加了任何限制？某些分岔是否总是导致尖峰过低或过冲？这些都是重要的开放性问题。

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