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Bifurcations Dynamics of Single Neurons and Small Networks

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Definition

A bifurcation occurs when a system undergoes a qualitative change in its output as a result of a change in parameter. Under certain conditions, the voltage of a cell membrane can change from being at rest to becoming oscillatory as a result of a bifurcation. Oscillatory properties of small networks are often understood using bifurcation analysis.

Description

What Is a Bifurcation?

The word bifurcate is commonly used to denote a split, as in "up ahead, the road bifurcates into two parts." The use of the term in this context implies that a driver traveling on this road can make a real-time choice of being able to take one or the other branch of the road when the bifurcation point is reached. In mathematics, and in its application to neuroscience, the term bifurcation has an entirely different contextual meaning. While a mathematical bifurcation is similar in that it involves different branches, the decision on which branch is chosen is largely made a priori and depends on the choice of parameters.

It is instructive to first gain some insight into situations that are not bifurcations. Different initial conditions converging to different solutions of the same differential equation while all parameters are held constant are not examples of bifurcations. Instead it may be that one initial condition lies in the basin of attraction of a particular solution, while the other one does not. Think, for example, of a double well potential where each well can trap particles starting with different initial conditions. A solution to a differential equation that is perturbed and then suddenly veers off toward another attracting solution is also not an example of a bifurcation. In these examples, just because a change in behavior has occurred or a difference in convergence is observed, a bifurcation has not occurred. To qualify as a bifurcation, the change in behavior must be associated with a change in a parameter value.

Bifurcations arise in mathematical equations called dynamical systems. A dynamical system can generically be defined by the equation

$$\frac{dx}{dt} = F(x,\mu). \tag{1}$$

where x is an n-dimensional vector of unknowns, μ is an m-dimensional vector of parameters, and F is a function that depends on the two. For the time being, assume that $m = 1$ and there is only one parameter of interest. Equation 1 describes how the dependent variable x evolves in time under the flow dictated by $F(x, \mu)$. A bifurcation occurs when a system undergoes a qualitative change in its

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output as a result of a change in the parameter μ. A bifurcation analysis of Eq. 1 would involve systematically characterizing the different types of solution $x(t)$ that arise for different values of the parameter μ.

In general, a dynamical system can exhibit local and/or global bifurcations. Local ones are more prevalent in neuroscience and also easier to recognize and understand. The simplest local bifurcation involves assessing the existence and stability of fixed points of Eq. 1. A fixed point x^* is a value such that $F(x^*, \mu) = 0$ for either a specific value of μ or a set of values of μ. A fixed point can be asymptotically stable (all nearby initial conditions converge to it), stable (initial conditions that start nearby stay nearby it), or unstable (at least one nearby initial condition leaves a neighborhood of it). Often, and somewhat confusingly, the term stable is used in place of asymptotically stable. Both the existence and stability of a fixed point x^* can depend on the parameter μ in which case the possibility of a local bifurcation exists. To determine if one occurs, Eq. 1 is linearized about x^* and the eigenvalues of the ensuing Jacobian matrix are analyzed. The eigenvalues also depend on the parameter μ. Different bifurcations correspond to the eigenvalues satisfying specific mathematical conditions for different values of μ. Similarly, a periodic solution of Eq. 1 can undergo a local bifurcation as a parameter is varied. As discussed later, such bifurcations can often be studied using a discrete map rather than a continuous flow. See Guckenheimer and Holmes (1983) for a detailed analysis of both local and global bifurcations.

Bifurcation analysis is a useful tool in mathematics because it simplifies the identification of different kinds of stable and unstable solutions. Each bifurcation type has a concomitant set of stable or unstable solutions that are produced (or destroyed) as a result of it. The conditions for identifying the existence of a bifurcation are often easier to satisfy than proving the existence of an actual solution. In neuroscience, bifurcations are of importance not just at the single-cell level but also in understanding the dynamics of networks. As described below, often a bifurcation mechanism that has been identified at the single-cell level suggests how dynamical changes (not necessarily bifurcations) occur at the network level.

Typical Bifurcations in the Dynamics of Single Neurons

Perhaps the most widely studied bifurcations involving single neurons are those that give rise to oscillations. Take a neuron whose voltage is at rest. The resting membrane potential represents a stable state. If after the injection of a constant amplitude current, the membrane voltage exhibits rhythmic behavior, then a bifurcation has occurred. Mathematically, there are two typical bifurcations that characterize this change in behavior. The first is called an SNIC (saddle node on an invariant circle) bifurcation and the second is a Hopf bifurcation. Both bifurcations arise in common neuronal models such as the two-dimensional Hodgkin-Huxley (Ermentrout and Kopell 1998) or Morris-Lecar (Morris and Lecar 1981) equations.

Consider a set of two equations that depend the parameter I_{ext}.

$$\begin{aligned} \frac{dv}{dt} &= f(v, w) + I_{ext} \\ \frac{dw}{dt} &= \epsilon g(v, w). \end{aligned} \tag{2}$$

In Eq. 2, the variable v represents voltage, w a recovery variable, and ϵ a positive number used to demarcate the time scales of the two variables. When ϵ is small, then Eq. 2 effectively has a fast and a slow time scale; v is called the fast variable and w the slow. The parameter I_{ext} can be thought of as an external current that only affects the membrane voltage. The v-nullcline is defined as the set of

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points (v, w) that satisfy the equation $f(v, w) = 0$. For the two models mentioned above, the v-nullcline is a cubic-shaped curve. The w-nullcline, the points (v, w) such that $g(v, w) = 0$, is sigmoidal-shaped like a typical activation or inactivation curve.

To understand the SNIC bifurcation, suppose that at $I_{ext} = 0$, there are two intersections of the v- and w-nullclines near the local minimum of the cubic (Fig. 1a). These intersections correspond to fixed points of Eq. 2. Linearizing at them would show that under generic assumptions, the intersection on the left branch is a stable node (attracting nearby trajectories) and the one on the middle branch is a saddle point (unstable with only one attracting direction and other directions being repelled). As I_{ext} is increased, the v-nullcline moves up in the $v - w$ phase plane and the two fixed points come closer to one another. At the SNIC bifurcation value I_{SNIC}, the fixed points coincide and become one. For $I_{ext} > I_{SNIC}$ there are no longer any fixed points in a neighborhood of the local minimum and a periodic orbit arises. Figure 2a shows a bifurcation diagram associated with this situation. The diagram can be interpreted as follows. For each fixed value I_{ext}, the vertical slice at that value shows the steady-state solutions that exist. Solid curves denote stable solutions and dashed curves are unstable ones. For instance, when $I_{ext} = I_1$, there are three fixed points. The one with smallest voltage is stable, while the other two are unstable. At $I_{ext} = I_2$, there is an unstable fixed point and a stable periodic solution. The solid blue curves are the upper and lower boundaries of the voltage amplitude of the periodic solution. In this and subsequent figures, blue curves are associated with periodic solutions and black curves with fixed points. Oscillations that arise through an SNIC bifurcation can have arbitrarily low frequencies and typically are of large amplitude. The $f - I$ curve

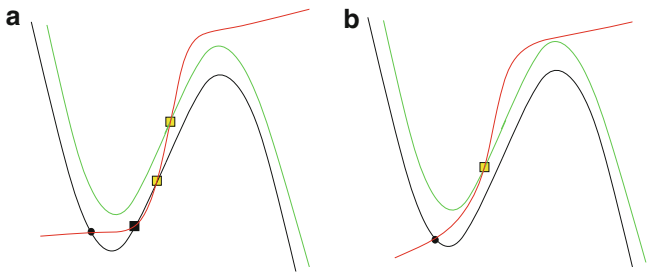

Fig. 1 Nullclines of (1). (**a**) Typical structure for an SNIC bifurcation. The *lower* black v-nullcline for $I_{ext} < I_{SNIC}$ has a stable (*black circle*) and an unstable (*black square*) fixed points near the local minima and an unstable (*yellow square*) fixed point along the middle branch. The *upper* v-nullcline for $I_{ext} > I_{SNIC}$ has only the unstable (*yellow square*) fixed point. (**b**) Typical structure for an Hopf bifurcation. Here there is only one fixed point associated with each cubic

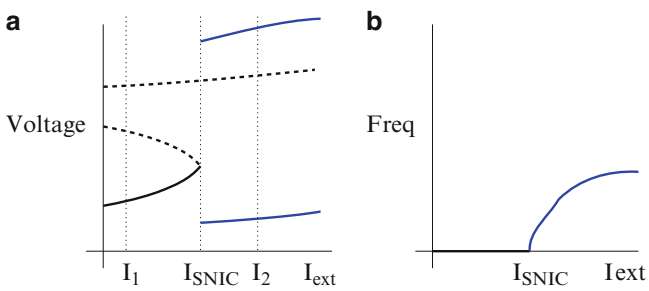

Fig. 2 SNIC bifurcation diagrams. (**a**) Stable (*solid curves*) and unstable (*dashed curves*) solutions as a function of I_{ext}. *Black curves* denote fixed points and *blue curves* periodic solutions. As I_{ext} increases, the two fixed points that meet at I_{SNIC} are destroyed. At this point a branch of stable periodic solutions arises. See text for explanations for I_1 and I_2. (**b**) The $f - I$ curve shows that oscillations begin with arbitrarily low frequency

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associated with an SNIC bifurcation is continuous at I_{SNIC} (Fig. 2b). Ermentrout (1996) has shown that neurons that oscillate through an SNIC bifurcation have type I phase response curves that are strictly of one sign.

A Hopf bifurcation can arise when the v- and w-nullclines only intersect once in a neighborhood of the local minimum (Fig 1b). Suppose when $I_{ext} = 0$, this single intersection (fixed point) is on the left branch. This fixed point is asymptotically stable. Linearization at it would show that the eigenvalues of the Jacobian matrix are complex with negative real part. As I_{ext} increases, the v-nullcline moves up and the fixed point moves toward the local minimum and eventually occurs on the middle branch. The eigenvalues depend continuously on I_{ext} and their real parts become smaller in absolute value. At some point, $I_{ext} = I_{Hopf}$, after the fixed point has moved to the middle branch, the eigenvalues at the linearization are pure imaginary. For $I_{ext} > I_{Hopf}$, the eigenvalues have positive real part. A Hopf bifurcation occurs at I_{Hopf} resulting in the creation of a periodic orbit. There are two distinct types of Hopf bifurcations: supercritical which produce stable periodic solutions and subcritical which produce unstable ones. Figure 3a shows the bifurcation diagram associated with a supercritical Hopf bifurcation. The amplitude of oscillations just after bifurcation is small. The frequency of oscillations just above the Hopf bifurcation points is bounded from below resulting in a discontinuous $f - I$ curve (Fig. 3b). Neurons that oscillate through a Hopf bifurcation mechanism typically have a type II phase response curve that is of both signs.

In some neuron models, the subcritical Hopf bifurcation is often found in conjunction with another bifurcation called the saddle node of periodic orbits (SNPO) bifurcation. Figure 4 shows

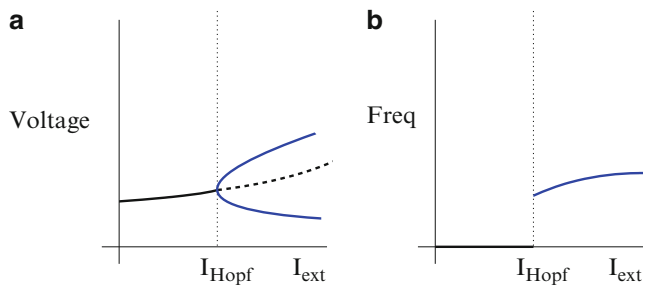

Fig. 3 Hopf bifurcation diagrams. (**a**) A single stable fixed point (*black curve*) loses stability at a supercritical Hopf bifurcation point spawning the branch of stable periodic solutions. (**b**) The $f - I$ curve shows that oscillations begin with a frequency that is bounded from below away from zero

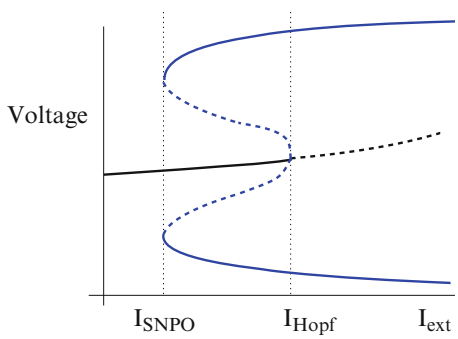

Fig. 4 Subcritical Hopf bifurcation diagram. A single stable fixed point (*black curve*) loses stability at a subcritical Hopf bifurcation point spawning the branch of unstable periodic solutions. That unstable branch merges at I_{SNPO} with a branch of stable periodic orbits. The interval $I_{SNPO} < I_{ext} < I_{Hopf}$ is a region of bistability in that both a stable fixed point and a stable periodic solution exist

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such a case where the branch of unstable orbits extends from I_{Hopf} for decreasing values of I_{ext}. Surrounding the branch of unstable periodic orbits is a branch of stable periodic orbits of larger amplitude. The stable and unstable periodic branches come together at $I_{ext} = I_{SNPO}$ which destroys the two orbits. As the bifurcation diagram shows, for $I_{SNPO} < I_{ext} < I_{Hopf}$, bistability exists between the stable fixed point on the middle branch and the larger amplitude periodic orbit. Starting at the stable rest state, as I_{ext} is increased past the Hopf bifurcation point, the solution suddenly changes to a large amplitude periodic orbit. Once on this branch of large amplitude solutions, decreasing I_{ext} shows an example of hysteresis whereby the stable branch of periodic solutions exists over a range where the stable fixed points also do.

Variations in different parameters besides I_{ext} can lead to bifurcations. For example, in a model associated with the circadian rhythm, *per1* neurons in the suprachiasmatic nuclei undergo a subcritical Hopf bifurcation as the maximal conductance of their calcium channel, g_{Ca}, is increased (Belle et al. 2009). Belle et al. show that as g_{Ca} is increased, an asymptotically stable rest state undergoes a subcritical Hopf bifurcation leading to oscillations during only a certain phase of the circadian rhythm. They also show that a second Hopf bifurcation can arise during a phase corresponding to daytime in which a highly depolarized resting state becomes stable. Mathematically, the mechanism for the creation and control of oscillations is exactly the same whether the bifurcation results from changes in g_{Ca} as in this case or from I_{ext} as shown in Fig. 4.

Bifurcation analysis is also a primary tool in understanding bursting oscillations where a neuron exhibits a sequence of (relatively) high-frequency spikes, followed by a (relatively) long interburst interval. The main idea here is to exploit the difference in time scales between the high-frequency spikes and the long interburst interval to define fast and slow variables. Consider the following set of three first-order equations:

$$\begin{aligned} x' &= f_1(x,y,z) \\ y' &= f_2(x,y,z) \\ z' &= \epsilon g(x,y,z). \end{aligned} \tag{3}$$

The small positive parameter ϵ implies that x and y are fast variables and z is the slow variable. To use bifurcation analysis, set $\epsilon = 0$ in Eq. 3 and note that now $z' = 0$, implying that z will not change. This means that z will act as a parameter in the fast equations for x' and y'. The fast subsystem can now be studied with z acting as a bifurcation parameter to see what, if any, bifurcations exist. For each z, the equations $f_1(x, y, z) = 0$ and $f_2(x, y, z) = 0$ are the nullclines of the fast subsystem. They form null surfaces in the full three-dimensional phase space. Intersections of any two null surfaces form curves of fixed points of the fast subsystem and their bifurcations can readily be studied. The mathematical technique of singular perturbation theory then shows that solutions to the actual $\epsilon > 0$, but small, problem lie close to the null surfaces except for times when they make very fast transitions between different null surfaces. The location where these fast transitions occur is computable through bifurcation and singular perturbation analysis. Rinzel (1985, 1987) first used these ideas to mathematically classify different types of bursting in single-cell models. Figure 5 shows an example of square wave bursting bifurcation diagram which illustrates this type of analysis. See (Izhikevich 2000) for a rigorous mathematical exploration of bursting in single neurons or (Ermentrout and Terman 2010) for an overview of several important types of bursting arising in neuroscience.

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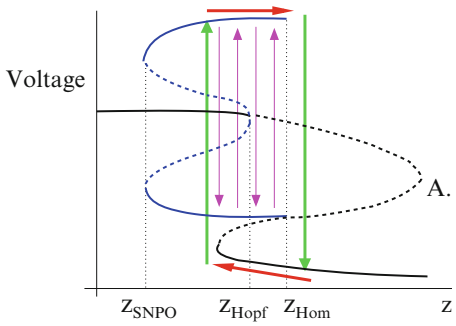

Fig. 5 Bifurcation diagram associated with square wave bursting. The variable z acts as a parameter for the $\epsilon = 0$ fast subsystem of (3). As z is increased along the *upper* branch of fixed points (*upper solid black curve* of the Z-shaped curve), the fixed point undergoes a subcritical Hopf bifurcation. The unstable periodic branch merges with a stable branch of periodic solutions at z_{SNPO}. The stable branch of periodic solutions terminates at a homoclinic bifurcation point at z_{Hom}. The actual flow of (3) for ϵ small is graphically depicted. The *red lines* pointing *left* (*right*) indicate that the solution closely follows the *lower* (*upper*) branch of the Z-shaped curve as z slowly decreases (increases). The *green lines* indicate the fast transitions between the *upper* and *lower* branches of the Z-shaped curve. *Magenta arrows* between the stable periodic branches indicate the fast spiking portion of the burst

Bifurcations in Small Neuronal Networks

Just as certain parameters intrinsic to a neuron can determine whether an individual neuron can oscillate, these parameters can also do the same for a coupled network of neurons. A small network of cells may not be able to oscillate unless some or all of the individual cells can. Thus, whatever bifurcation causes the individual cell to oscillate may, in turn, cause the network to be rhythmic. Changes in intrinsic parameters having nothing to do with the existence of oscillations can also lead to bifurcations in network output. For example, Zhang et al. (2009) show that increases in the maximal conductance of an A-current in a postsynaptic cell can cause the cell to go through a sequence of border collision bifurcations (Nusse et al. 1994), resulting in a cascade of different phase-locked solutions.

In networks, many interesting bifurcations occur with changes in synaptic parameters. Consider a network of two mutually coupled spiking neurons governed by the integrate and fire model and connected by alpha synapses $g_{syn}\alpha^2 te^{-\alpha t}$. Here g_{syn} governs the strength and α the speed of the synapse. The phase ϕ at which one cell fires with respect to the other can be used to define a function whose roots correspond to phase-locked periodic solutions. For this model of two identical cells, both the synchronous ($\phi = 0$ or 1) and antiphase ($\phi = 0.5$) solutions exist for both excitatory ($g_{syn} > 0$) and inhibitory ($g_{syn} < 0$) coupling. Van Vreeswijk et al. (1994) showed that these solutions change stability through a pitchfork bifurcation as the parameter α changes; at the pitchfork bifurcation point, three branches emerge from one. In particular, for excitatory synapses, increases in α make the antiphase solution bifurcate from being stable to unstable (Fig 6a). At the bifurcation point, a new stable out-of-phase solution arises; by symmetry there are two such solutions. Further increasing α causes these new curves of out-of-phase solutions to come closer to the curve corresponding to the synchronous solution. Note in this case, that while the synchronous solution is always unstable, as α increases and the synapse becomes faster, the phase of locking ϕ tends to synchrony. The opposite happens for inhibitory synapses (Fig. 6b). As α increases and the synapse is made faster in its rise and decay, the antiphase solution undergoes a pitchfork bifurcation taking it from unstable to stable. The curves of out-of-phase solutions that are born are unstable. The synchronous solution is stable for all values of α, but its basin of attraction shrinks as α increases.

A common way to find bifurcations in a neuronal network is to define a Poincare return map or a time T map. The Poincare map records the values of relevant variables along a defined hyperplane

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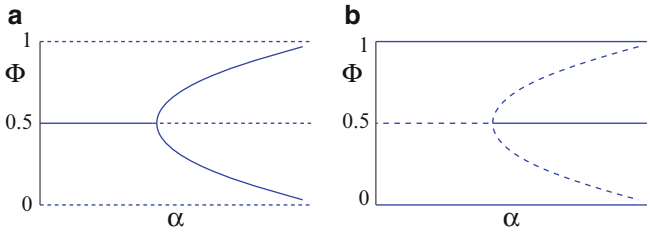

Fig. 6 Bifurcation diagram as a function of synaptic speed, (Adapted from Van Vreeswijk et al. (1994)). (**a**) For excitatory synapses, as the synaptic speed increases, the stable antiphase solution at $\phi = 0.5$ undergoes a pitchfork bifurcation. The new curve of stable out-of-phase solutions shows that solutions approach synchrony as the synapse gets faster. (**b**) For inhibitory synapses, the synchronous solution is always stable. The antiphase solution stabilizes by increasing α though the pitchfork bifurcation point

in the mathematical phase space. The time T map records the values of appropriate variables at every time nT, for $n = 1, 2, 3, \ldots$. In either case, a fixed point of the map corresponds to a periodic solution of the network. In this way, mathematical tools to study bifurcations of fixed points of maps (discrete dynamical systems) can be used to study bifurcations of periodic solutions of networks. For example, in a model consisting of an excitatory cell reciprocally coupled to an inhibitory cell whose synapse exhibits short-term synaptic depression, Bose et al. (2001) showed how changes in the maximal synaptic conductance of the inhibitory synapse give rise to saddle-node bifurcations of fixed points of a one-dimensional return map (Fig. 7). The fixed points of the map correspond to different oscillatory solutions of different frequency. Solutions on the upper branch are controlled by parameters that are intrinsic to the excitatory cell and are of high frequency. The high frequency causes the inhibitory synapse to remain in a depressed state and never recover. Solutions on the lower branch correspond to low-frequency solutions with a long interspike interval. Because of this long interval, the depressing synapse has a chance to recover between spikes and the synaptic current to the excitatory cell at each spike is large. Here the frequency is controlled by a parameter governing the decay of inhibition. Note that this network also exhibits bistability and hysteresis similar to what was seen to occur in certain single-neuron models. Perturbations can cause the solution to switch between different oscillatory solutions as seen in Fig. 7. The switch is a consequence of the bifurcation structure, but is not in and of itself a bifurcation.

As is suggested by the prior example, bifurcations in networks of neurons are also closely related to the issue of what sets of parameters control the oscillatory state. This is especially true in central pattern generating (CPG) networks where the existence of oscillations is a given. What is more relevant is what controls the existence of oscillations and their frequency. For example, in a network of two cells mutually coupled by fast inhibitory synapses, Skinner et al. (1994) describe circumstances under which the synaptic threshold is of importance in controlling the frequency of antiphase, half-center oscillations. They define the terms intrinsic escape, intrinsic release, synaptic escape, and synaptic release to indicate different ways in which the oscillators can switch orientations from being active to silent and vice versa. The synaptic threshold turns out to be irrelevant in the intrinsic escape or release mode but is highly relevant in the synaptic escape or release mode. Understanding how the synaptic threshold can play this role relies, in part, on bifurcation dynamics associated with single cells. For single cells it was earlier shown that increasing I_{ext} causes the stable solution to bifurcate from being a rest point to an oscillatory one by shifting the v-nullcline up in the phase space and removing a fixed point on its left branch. In this two-cell network, the removal of an inhibitory synaptic current to the postsynaptic cell acts similarly to increasing I_{ext} in a single cell by shifting the v-nullcline up in phase space and removing an intersection of the v- and w-nullclines.

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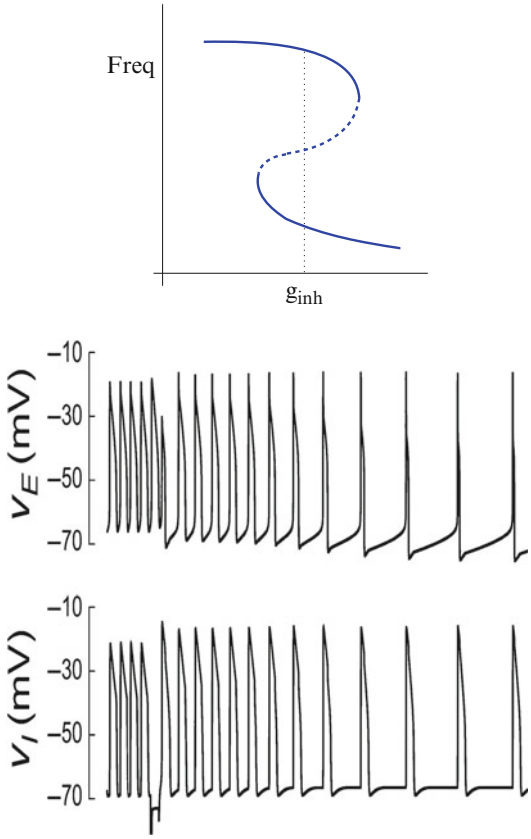

Fig. 7 Dynamics of an excitatory inhibitory network. *Upper panel* shows bifurcation diagram as a function of maximal inhibitory conductance g_{inh}. The two branches of stable periodic solutions are connected by an unstable branch. *Lower panel* shows voltage trajectories (*E* excitatory, *I* inhibitory) with g_{inh} chosen at the value of the *dotted line* in *upper panel*. The solution starts off at high frequency along the upper branch. A brief perturbation given to the inhibitory cell temporarily suppresses its activity allowing its synapse to recover from depression and strengthen. In turn, this causes the solution to switch to a lower frequency periodic orbit along the lower branch

Thus, although there is not a bifurcation in the network as the result of the application or removal of a synaptic current, the mechanism by which the postsynaptic cell fires is readily understood as a result of single-neuron bifurcation analysis. The possible application or removal of inhibition occurs only when the synaptic threshold is crossed. When the individual cells are modeled as relaxation oscillators (with cubic-shaped *v*-nullclines), then the fast transition between the silent and firing states effectively occurs at the local minima and maxima of the cubic nullcline. Thus, when the synaptic threshold lies between these two extrema, the threshold is not relevant for controlling frequency as small changes in its value have little effect on the time spent above or below it. On the other hand, if the synaptic threshold intersects either the left or right branch of the cubic, then small changes in its value can have an effect since the cell's trajectory evolves slowly there; that the evolution is slow is a consequence of the assumption of relaxation oscillations. It is through the scaffold of single-cell bifurcation analysis and fast/slow time scale decomposition that Skinner et al. are able to define intervals for the synaptic thresholds that demarcate intrinsic versus synaptic escape/release mechanisms and thereby control the frequency of oscillations.

A more complicated example of using bifurcation analysis is found in a model of a respiratory CPG due to Rubin et al. (2009). The authors consider a four-cell network of excitatory and inhibitory cells and are interested in understanding transitions between oscillatory patterns that correspond to different phasic states of the respiratory rhythm. By using fast/slow time scale analysis, they show

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how to identify certain transitional curves associated with the fast subsystem. These curves lie on equilibrium surfaces (null surfaces) of the fast subsystem. In the problem considered, there are relevant equilibrium surfaces corresponding to cells being either in the active or inactive state. When the trajectory of the system reaches one of these transitional curves, there is a switch from inspiration to expiration or vice versa. The transitional curves are themselves defined because they satisfy certain bifurcation conditions for fixed points of the fast subsystem. Through their analysis, the authors show how changes in the maximal conductance of a persistent sodium current in one of the cells play a major role in controlling the frequency and duty cycle of oscillations within the network. They also show how changing the total synaptic drive to individual cells modulates the bifurcation diagram again resulting in an understanding of how frequency and duty cycle change. The interested reader is referred to (Rubin et al. 2009) to see further details.

Concluding Remarks

Bifurcations at the single-neuron level often focus on understanding how a single fixed point is created or destroyed or how it gains or loses stability. Different kinds of bifurcations imply the existence of different kinds of oscillatory solutions, each possessing different properties. As a single-neuron model becomes more complicated, say for describing a bursting neuron, bifurcations occurring in a fast subsystem help to build the skeleton on which the dynamics of the full system can be understood. In networks, the bifurcation parameter can be either intrinsic to a cell or related to one of the synapses. Bifurcations within them are often understood by knowing the bifurcation possibilities of single neurons. But networks have the potential to be much richer and complicated in their bifurcation structure. An important concept highlighted above is that bifurcation analysis can reveal how certain parameters determine which network elements control the behavior in the network. Interestingly, a bifurcation occurring as a result of a change in an intrinsic parameter may imply that a synaptic mechanism becomes relevant for controlling the network output, or vice versa.

Bifurcations of the type described here are associated with steady-state solutions (fixed points or periodic orbits) of differential equations. They are local in the sense that the information obtained from the bifurcation only provides information in a neighborhood of the bifurcation point. While this neighborhood may in fact be mathematically large, it is important to keep in mind that the entire set of possible solutions in the global phase space are not determined through local bifurcations. Nonetheless, bifurcation analysis is a powerful tool for understanding the dynamics of neurons and the networks in which they participate.

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