## Transient spike adding in the presence of equilibria

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#### Abstract

Many models of neuronal activity exhibit complex oscillations in response to an input from other neurons in a network or to an input from an injected current. We consider the effect of a single short stimulus on a simple model designed to mimic some features of neuronal dynamics. We focus on the transient response induced by the stimulus, particularly on the spike-adding behaviour of the response. Our main goal is to explain how the transient response is affected by the presence of unstable equilibria. We also investigate the dependence of the number of spikes on the amplitude and duration of the stimulus. In our analysis, we use numerical continuation methods and exploit the presence of different time scales in the model.

#### 1 Introduction

An excitable system is one in which a large enough perturbation from an equilibrium state causes one or multiple large-amplitude oscillations before relaxation back to the equilibrium. Excitability is commonly due to the presence of a saddle equilibrium that lies close to the stable resting state: any perturbation large enough to push the initial condition past the so-called stable manifold of the saddle will result in a large excursion [10, 18]. The stable manifold is a codimension-one surface of trajectories that converge to the saddle equilibrium. It acts as the excitability threshold, separating orbits that make an immediate relaxation back to the equilibrium from those that make large excursions. The resulting number of large-amplitude oscillations is organised by homoclinic connections, for nearby parameters, from the equilibrium back to itself [18].

Recent work reports on a different mechanism for spike adding in neuron models that is organised by multiple time scales in the system [12, 13, 15]. Here, the response is characterised by the fact that it involves tracking of an unstable (saddle) object called the slow manifold. Numerical techniques have been reported in [13] that allow for a systematic study of spike adding in such systems. Together with these new developments, techniques from geometric singular perturbation theory (GSPT) [5, 7] provide a powerful tool to study transient dynamics and excitability.

In this paper, we study spike adding in the polynomial model from [17] that was also used in [2, 14, 15]. The authors of [15] applied a slow-fast analysis to study the spike-adding mechanism in the transient response of the model to a very short injected current. The addition of a new spike occurs in an exponentially small interval of parameters, the size of which is controlled by the difference in the time scales. The two-point boundary value problem setup presented in [13] is used to compute a detailed bifurcation set, showing the regions in a two-parameter space where different numbers of spikes occur in the transient response. In [15], the authors only considered the case for which the system has one attracting equilibrium. In this paper, we extend the results of [15] and provide a more thorough analysis of the organisation of the spike-onset curves in the region of the parameter plane where additional equilibria are present. In our setting, these equilibria are not close to the stable resting state. We explore the role of the stable manifold of one such equilibrium as an excitability threshold. We also study the effect of changing the strength and duration of the current injection.

This paper is organised as follows. In section 2, we briefly introduce the model and the typical transient response to a short current injection; we also discuss how this behaviour depends on other system parameters. Section 3 shows the organisation of the curves of spike onset. The spike-adding mechanism when additional equilibria are present is studied in section 4. In section 5, we investigate the dependence on the injected current by changing its amplitude and duration. We end the paper with a summary and discussion in section 6.

#### 2 The model and the transient response

The model we analyse here is a three-dimensional model introduced in [17], and given by the following system of ordinary differential equations:

$$\begin{cases} \dot{x} = sax^3 - sx^2 - hy - bz, \\ \dot{y} = \phi(x^2 - y), \\ \dot{z} = \varepsilon(sa_1x + b_1 - kz). \end{cases}$$
(1)

Throughout this paper, we set the parameter values  $\phi = 1$ ,  $\varepsilon = 0.01$ , a = 0.55,  $a_1 = -0.1$ ,  $b_1 = 0.01$ , k = 0.2, and s = -2, but leave b and h as free parameters. Note that  $\varepsilon$  is much smaller than 1, which means that the variable z evolves much slower than the variables x and y. System (1) was designed to mimic the qualitative behaviour of spiking neurons and was used in [14] to study and characterise different bursting behaviour. The variable x is analogous to the membrane potential (voltage), y can be regarded as the ratio of open and closed ion channels and z might represent the calcium concentration. The polynomial form of the equations makes the model amenable to analysis.

In this section, we consider b = 0.9 and h = 1 as a representative choice of parameters. Then system (1) has a unique equilibrium  $E_1 \approx (-0.04737, 0.00224, 0.00262)$ , that is the sole attractor. We are interested in the response of system (1) as it is perturbed from its rest state  $E_1$ . As in [15], we define a piecewise-continuous system by applying a fixed current  $I_{app}$  for a very short time interval to the first equation of system (1); we write this stimulus as a product of two Heaviside functions so that the system becomes:

$$\begin{cases} \dot{x} = sax^3 - sx^2 - hy - bz + I_{app}H(T_{on} - t)H(t), \\ \dot{y} = \phi(x^2 - y), \\ \dot{z} = \varepsilon(sa_1x + b_1 - kz). \end{cases}$$
(2)

Initial conditions of system (2) will be subjected to a current with amplitude  $I_{\rm app}$  for the time interval  $0 \le t \le T_{\rm on}$ ; at  $t = T_{\rm on}$ , the stimulus stops. Throughout this paper, the amplitude and duration of the current injection are fixed, with  $I_{\rm app} = 0.02$  and  $T_{\rm on} = 15$ , except in section 5 in which we study the effect of varying  $I_{\rm app}$  and  $T_{\rm on}$ .

We can predict the behaviour of system (2) by analysing system (1). We utilise the fact that z evolves on a much slower time scale than x and y and consider the limit  $\varepsilon \to 0$ . In this limit, the right-hand side of the z-equation in system (1) becomes zero and z can be viewed as a parameter of the so-called *fast subsystem*:

$$\begin{cases} \dot{x} = sax^3 - sx^2 - hy - bz, \\ \dot{y} = \phi(x^2 - y). \end{cases}$$
(3)



Figure 1: Typical bifurcation diagram of the fast subsystem (3) for the representative choice b = 0.9and h = 1. The Z-shaped curve (black) is the branch of equilibria of (3), with two saddle-node bifurcation points labelled  $SN_1$  and  $SN_2$ . A branch of periodic orbits, indicated by the maximum and minimum values of x (green), emanates from a subcritical Hopf bifurcation (HB), undergoes a saddlenode bifurcation of periodic orbits (SNP) and terminates at a homoclinic bifurcation (Hom). Stable and unstable equilibria and periodic orbits are indicated by solid and dashed curves, respectively. The z-nullcline of system (1) (magenta) is superimposed. Panel (b) shows part of panel (a) together with an orbit of (2), where  $I_{app} = 0.02$  and  $T_{on} = 15$ ; here, the two colour shades indicate when  $0 \le t \le T_{on}$  and  $t > T_{on}$ , respectively.

The equilibria of system (3) satisfy  $y = x^2$  and

$$z = \frac{sax^3 - (s+h)x^2}{b}.$$
 (4)

Note that  $E_1$  satisfies equation (4), but the fast subsystem (3) has an entire curve of equilibria in the (x, y, z)-space that projects to a Z-shaped curve in the (x, z)-plane; an example of this, for the case b = 0.9 and h = 1, is shown in Figure 1(a). The three branches of the Z-shaped curve are connected at two saddle-node bifurcation points, denoted by  $SN_1$  and  $SN_2$  in Figure 1(a). The equations of the system are such that  $SN_1$  is always fixed at the origin and  $SN_2$  satisfies:

$$x_{\mathsf{SN}_2} = \left(\frac{2(s+h)}{3as}\right).\tag{5}$$

The lower and middle branches consist of equilibria of attracting and saddle type, respectively. The equilibria on the upper branch are stable for small z and lose stability in a subcritical Hopf bifurcation, for which

$$x_{\mathsf{HB}} = \frac{s - \sqrt{s^2 + 3as}}{3as}.$$
(6)

A family of periodic orbits emanates from the Hopf bifurcation point on the upper branch. They are repelling near the Hopf bifurcation, become attracting after a saddle-node bifurcation of periodic orbits, labelled SNP, and finally terminate at a homoclinic bifurcation point, denoted Hom in Figure 1(a). We refer to [6, 11] for more details about these bifurcations.

The equilibrium  $E_1$  lies at the intersection of the z-nullcline

$$z = \frac{sa_1x + b_1}{k} \tag{7}$$

with the Z-shaped curve of equilibria of the fast subsystem (3). Since  $E_1$  lies on the lower branch, it is an attracting equilibrium. Note that the z-nullcline is a plane in (x, y, z)-space, but it only depends on x and z; hence, its projection is a straight line in the (z, x)-plane, as shown in Figure 1(a). When viewed in the (z, x)-plane, trajectories move to the right above the z-nullcline and to the left below it.

Figure 1(b) shows a solution of system (2) for a stimulus with  $I_{app} = 0.02$  and  $T_{on} = 15$ superimposed on the bifurcation diagram of the fast subsystem shown in Figure 1(a). The first segment curve (teal) corresponds to the solution of model (2) for  $0 \le t \le T_{on}$  and the other segment (orange) corresponds to the solution of system (2) with  $t > T_{on}$ . Injecting the applied current into the system leads to a shift of magnitude  $\frac{I_{app}}{h}$  to the right for the Z-shaped curve of equilibria, while the z-nullcline remains fixed. When sufficient current is injected, this moves the unique attracting equilibrium on the lower branch of the Z-shaped curve, which is very close to the origin, to the unstable middle branch. Thus, the rest state  $E_1$  becomes an ordinary initial point located to the left of  $SN_1$ . Since the evolution in the z-direction is very slow compared with the evolution in x and y, the response solution will track the z-dependent attractors of the fast subsystem. Hence, as long as  $0 \le t \le T_{\rm on}$ , the flow pushes the initial condition up towards the upper branch, which acts as an attractor provided z evolves slowly enough. For the values of  $I_{app}$  and  $T_{on}$  used in Figure 1(b), when the injected current is turned off, the response of system (2) has just reached a first maximum spike with respect to x. Even though  $E_1$  is again an attracting equilibrium, the trajectory starts oscillating around the upper branch as z increases. On the left-hand side of the Hopf bifurcation, the solution spirals towards the attracting segment of the upper branch and the spike amplitude decreases, but after passing through HB the response moves away from the now repelling upper branch. Note that  $\varepsilon$  is not small enough to give sufficient time for the solution to converge to the upper branch. When the orbit has moved sufficiently far from the upper branch of equilibria, the response drops down to the lower branch and follows it towards  $E_1$ .

#### 2.1 Two-parameter analysis of the fast subsystem

Variation of any of the parameters in system (1) may change the number or location of the intersections of the z-nullcline and the Z-shaped curve of equilibria of the fast subsystem. We focus on varying b and h, which may cause a stretching of the Z-shaped curve and, hence, change the number of equilibria of (1), even though the z-nullcline does not depend on b and h.

The effect of parameter b on the fast subsystem is fundamentally different from the effect of h because b is in the denominator of formula (4). Consequently, if all other parameters are kept fixed, and b tends to 0 then the z-coordinates of all equilibria increase to  $\infty$ , except for the points at z = 0. In particular, HB and  $SN_2$  go to  $\infty$  as b tends to 0. The locations of HB and  $SN_2$  are important because the locus of the Hopf bifurcation determines the number of oscillations of the transient response around the upper branch and the locus of the saddle-node bifurcation dictates the possible appearance of additional equilibria of the full system (1); see sections 3 and 4, respectively.

The types and order of the bifurcations for the fast subsystem change with h, in a way that will be important for the organisation of the spike onsets in section 3. Figure 2 shows how the bifurcation diagram of system (3) depends on h when b = 0.9 remains fixed. We calculated the locus of saddle-node, Hopf, homoclinic and saddle-node bifurcations of periodic orbits in the (z, h)-plane. As already mentioned,  $SN_1$  (the vertical magenta line) is always fixed at the origin. Furthermore,  $SN_2$  (black) and HB (green) are given by equations (5) and (6), respectively. As h increases, the Hopf bifurcation crosses z = 0 and later switches from subcritical to supercritical at a generalised Hopf bifurcation, denoted GH, at which the



Figure 2: A typical bifurcation set of the fast subsystem (3) in the (z, h)-plane for b = 0.9. The curves  $SN_1$ ,  $SN_2$ , HB, SNP and Hom are the continuation of their counterparts in Figure 1(a). The curve SNP (red) stops at a generalised Hopf bifurcation, labelled GH, at which the criticality of the Hopf bifurcation changes, and from the other side collides with the curve Hom (blue) at a Belyakov point, labelled B. The curve Hom ends on  $SN_1$  at  $h = h_{Hom} \approx 1.11315$  at which a SNIC interval starts. The curve SNP crosses the z-coordinate of the equilibrium  $E_1$  when  $h = h_{SNP} \approx 1.04687$ .

curve SNP of saddle-node bifurcation of periodic orbits (red) ends. The other end of the curve SNP terminates on the curve Hom of homoclinic bifurcations (blue) at a Belyakov point [1], denoted B. The curve Hom ends on  $SN_1$ , which marks the start of an interval on  $SN_1$  of saddle-node bifurcations on an invariant cycle, denoted SNIC.

### 3 The organisation of curves of spike onset

We are interested in the number of additional oscillations or spikes that arise after the applied current is switched off and how this depends on b and h. Although the injected current  $I_{app}$  and its duration  $T_{on}$  play an important role in the location of the end point of the first segment of the transient response (see section 5), after switching to the system with no applied current, only the free parameters b and h influence the behaviour of the transient response.

The moment of spike onset is difficult to define as a bifurcation point if system (1) has a unique attracting equilibrium. The spike adding occurs in an exponentially small strip in the (b, h)-plane, where the transient response, instead of dropping down to the attracting lower branch of the Z-shaped curve of equilibria of the fast subsystem, first follows the unstable (saddle) middle branch of the Z-shaped curve, or more precisely, a saddle slow manifold close to it [15]. We define the moment of spike onset as the curve of parameter values inside the exponentially small strip along which the transient response follows the saddle slow manifold for the longest time, that is, the integration time until the last maximum of the x-coordinate is maximal [12]. Along this curve, the z-coordinate also reaches (approximately) a local maximum, which we use to compute the curves of spike onset [13, 15]

We use the set-up of a two-point boundary value problem (2PBVP) to detect the spike onsets with the continuation package AUTO [3, 4] and compute 14 spike-onset curves in the (b, h)-plane; for details of the set-up, see [13, 15]. Figure 3 shows the result of this continuation. The number of spikes on either side of each curve differs by exactly one. The numbers in Figure 3 indicate the total number of spikes generated by the transient response for b- and



Figure 3: The exponentially thin strips of spike onset replaced by the numerically-defined curves of spike onset together with the loci of fold bifurcation (LP) and Hopf bifurcation (H) of system (1). The numbers indicate the number of spikes in each region. The two grey curves labelled Max and Min bound the parameter regime for which the response achieves exactly one extremum (a maximum) during the period when the applied current is switched on.

*h*-values in these regions, including the spike generated while the applied current is switched on. Here, we restrict our attention to the region bounded by the two grey curves, denoted Maxand Min. For *b*-values to the right of the curve Max, the applied current  $I_{app}$  is switched off before the response reaches the maximum of the first spike. Similarly, for *b*-values to the left of the curve Min, the applied current is switched off after the response has already started the generation of a second spike.

As mentioned in section 2, decreasing b stretches the Z-shaped curve of the equilibria of the fast subsystem and the family of periodic orbits emanating from the Hopf bifurcation on the upper branch in the z-direction. Accordingly, for the same h-value, the transient response oscillates more times around the upper branch of the Z-shaped curve of the equilibria of the fast subsystem when b decreases.

The behaviour of the curves of spike onset in Figure 3 is consistent with the changes in the bifurcation set of the fast subsystem in Figure 2. Note that we choose b = 0.9 as a representative value in Figure 2 but the behaviour of the bifurcation curves is the same for any value of b apart from a stretch or squeeze in the z-direction. We divide the h-axis in Figure 2 into three different parts. The first part is the half-line  $h < h_{SNP} \approx 1.04687$ , where  $h_{SNP}$  is the h-value for the point on the curve SNP that corresponds to the same z-coordinate as that of the h-dependent equilibrium  $E_1$ . For h-values smaller than  $h_{SNP}$ , the z-coordinate of SN<sub>2</sub> lies

to the right of the z-coordinate of  $E_1$  and the location of the Hopf (HB) and saddle-node (SN<sub>2</sub>) bifurcations of the fast subsystem determine the number of spikes. As h decreases, the curves HB and SN<sub>2</sub> move to the right and this has the same effect as decreasing b. Thus, decreasing h increases the number of spikes for b fixed.

The second part of the *h*-axis in Figure 2 is the interval  $[h_{SNP}, h_{Hom}]$ , where  $h_{Hom} \approx 1.11315$ identifies the intersection point of the curve Hom and the line z = 0. For  $h \in [h_{SNP}, h_{Hom}]$ , the saddle-node bifurcation of periodic orbits in the fast subsystem occurs to the left of the location of  $E_1$ , so that the transient response is initially attracted to a branch of stable periodic orbits of (3). In fact, this already happens for values of h slightly below  $h_{SNP}$ , because the z-coordinate of the transient response increases slightly as it leaves  $E_1$  and jumps up towards the upper attracting branch. As soon as the periodic orbits terminate at the homoclinic bifurcation (Hom in Figure 1), the response falls down to the lower branch and stops spiking. Indeed, the number of spikes is affected by the locus of the homoclinic bifurcation of the fast subsystem. Therefore, while the curve Hom in Figure 2 approaches  $SN_1$  (as h increases), a smaller value of b is needed to move the homoclinic bifurcation point in the fast subsystem sufficiently far to the right, so that the solutions have enough time to oscillate around the family of attracting periodic orbits and generate the same number of spikes. As a result, the curves of spike onset tend to smaller b as h increases. This is not a vertical asymptote, because the curves of spike-onset stop before or at the point  $(b, h) = (0, h_{Hom})$ .

The third part of the *h*-axis in Figure 2 is the SNIC regime that starts at  $h = h_{\text{Hom}}$ . For  $h > h_{\text{Hom}}$ , there is only one spike generated by the perturbation. For this interval there are no attracting equilibria or branches of periodic orbits on the upper branch with z > 0. Hence, the transient response cannot oscillate around the upper branch of the Z-shaped curve, and falls down to the lower branch as soon as the injected current is switched off. Therefore, there are no new spike onsets for  $h > h_{\text{Hom}}$ .

For very small values of b in Figure 3, the spike-onset curves cross the curve LP of fold bifurcations of system (1). The entire family of spike-onset curves accumulates on the curve of Hopf bifurcations of the full system (H). As will be discussed in section 4, there is no spike adding to the left of H.

# 4 Spike-adding mechanism in the presence of extra equilibria

For very small values of b, to the left of the fold curve LP in Figure 3, system (1) has three equilibria instead of only  $E_1$ . Since the z-nullcline of system (1) does not depend on b and remains fixed, the right-most saddle-node bifurcation point  $SN_2$  crosses it as b decreases. In fact, just before  $SN_2$  crosses the z-nullcline, the Z-shaped curve of equilibria of the fast subsystem already intersects the z-nullcline in three points. This situation is shown in Figure 4, where the two new equilibria are labelled  $E_2$  and  $E_3$ . Both  $E_2$  and  $E_3$  lie on the middle branch and are of saddle type with real eigenvalues; equilibrium  $E_2$  has two negative and one positive eigenvalues, while  $E_3$  has one negative and two positive eigenvalues.

In the presence of the additional equilibria  $E_2$  and  $E_3$ , the mechanism for spike adding is different from the case where there is just one equilibrium; when the transient response follows the middle branch of the Z-shaped curve of equilibria of the fast subsystem for parameter values in the exponentially thin strips in the (b, h)-plane, it cannot pass through  $E_2$ . Instead, the transient response forms an instantaneous connecting orbit between the attracting equilibrium  $E_1$  and the saddle  $E_2$ . In Figure 4, we chose  $b \approx 0.19517$  and h = 1 approximately at the moment of such an instantaneous spike onset. Note that the integration time until the last local maximum of the x-response is maximal (infinite) at the moment of existence of the



Figure 4: The bifurcation diagram of the fast subsystem (3) and the z-nullcline of the full system (1) for  $b \approx 0.19517$  and h = 1 with the corresponding transient response superimposed. Two additional equilibria of saddle type exist on the middle branch. The value for b changes such that the response creates a connection between  $E_1$  and the new equilibrium  $E_2$ ; compare Figure 1.

connecting orbit. Hence, our definition of spike onset does not depend on the presence of additional equilibria and we expect that the curves of spike onset are continuous across the fold LP. We note that our computational set-up detects a local maximum with respect to z, also if additional equilibria are present. As illustrated in Figure 4, the maxima of the integration time and z-coordinate seem to occur simultaneously. Hence, with our computational set-up, we expect to continue the spike onset across the fold LP. We found other parameter values for which zis not maximal at the moment for which the integration time to the last local maximum of the x-coordinate is maximal; see for example Figure 5. However, the spike-adding transition, either with or without additional equilibria, occurs in an exponentially small parameter range, which means that our numerically detected spike onset lies exponentially close to the defined value of spike onset and the computed curves are the same, up to the accuracy of the numerics.

As soon as  $SN_2$  crosses the z-nullcline,  $E_3$  lies on the upper branch, and soon after, its two positive eigenvalues become complex conjugate with positive real parts. This has no influence on the spike-adding mechanism compared to when  $E_3$  is on the middle branch. However, a difference does occur in the direction of motion just before and after a new spike onset depending on the location of  $E_2$  on the middle branch. When  $E_2$  lies on the left-hand side of the transient response as it falls off from the upper branch, the transient response follows the middle branch towards the left while one of the exponentially thin strips is crossed. This is illustrated in Figure 5 where  $E_2$  is located much closer to  $E_1$  than in Figure 4. Here,  $b \approx 0.10902$  and h = 1 are chosen just after a new spike onset. Figure 5 illustrates another phenomenon that does not occur when there is a unique attracting equilibrium. During the spike-adding transition, soon after the moment of spike onset, the transient response exhibits several new spikes because it moves up towards the branch of attracting periodic orbits of the fast subsystem, and z starts increasing again. These extra spikes only occur exponentially close to, but after the moment of spike onset and eventually, the total number of added (or deleted) spikes in this transition is always one.

The equilibrium  $E_3$  undergoes a Hopf bifurcation when *b* decreases further, namely, when *b* crosses H in Figure 3. This Hopf bifurcation is subcritical and  $E_3$  is attracting for *b*-values to the left of H. As a result, the transient response follows the upper branch until it reaches  $E_3$ , creating a connection from  $E_1$  to  $E_3$ . Therefore, spike adding cannot occur to the left of H



Figure 5: The bifurcation diagram of the fast subsystem (3) and the z-nullcline of the full system (1) for  $b \approx 0.10902$  and h = 1 with the corresponding transient response superimposed. Equilibrium  $E_2$  lies to the left of the homoclinic bifurcation and  $E_3$  now lies on the upper branch compare; Figures 1 and 4.

and the family of spike-onset curves must accumulate onto the curve H in Figure 3. Figure 6 illustrates a typical connecting transient response between  $E_1$  and  $E_3$  superimposed on the Z-shaped curve of the equilibria of (4) and the z-nullcline of (1); here b = 0.04 and h = 1.

The subcritical Hopf bifurcation H gives rise to a family of saddle periodic orbits. Our numerical calculations indicate that this family undergoes a fold and an attracting periodic orbit coexists with the attracting equilibrium  $E_3$ . This attracting periodic orbit persists for *b*-values to the right of H in Figure 3, but it and other attractors resulting from period-doubling bifurcations only exist for very small *b*-intervals. We find that the spike adding does not seem to be affected by the presence of such additional attractors for  $h < h_{SNP} \approx 1.04687$ . For such small values of *h*, the basins of attraction of these co-existing attractors are very small. We checked numerically that the stable manifold of  $E_2$ , which bounds these basins, deforms in such a way that the transient response cannot enter the basins of attraction. However, it seems that the basins boundaries can be crossed for  $h_{SNP} < h < h_{Hom}$ . This means that there may be discontinuities in the spike-onset curves in the small parameter region where an additional attractor is present. Here, the geometry of the regions with the same number of spikes could be much more complicated. A more detailed investigation of spike adding in this parameter region is beyond the scope of this paper.

#### 5 Effect of the injected current and its duration

As was mentioned in section 2, the combination of  $I_{app} = 0.02$  and  $T_{on} = 15$  is such that the response of system (2), when the injected current is on, ends somewhere between the first maximum and the subsequent minimum with respect to x in the time series. If either  $I_{app}$  or  $T_{on}$  or both are changed, the behaviour of the response varies as well, at least qualitatively.

Figure 7(a) shows the curves of spike onset in the  $(b, I_{app})$ -plane for  $T_{on} = 15$ , where h = 0.95 in panel (a1) and h = 1 in panel (a2). Figure 7(b) shows the curves of spike onset in the  $(b, T_{on})$ -plane for  $I_{app} = 0.02$ , where h = 0.95 in panel (b1) and h = 1 in panel (b2). The turn in the curves of spike onset in all panels of Figure 7 means that, for a fixed value of b, the transient response can generate a different number of spikes when  $I_{app}$  or  $T_{on}$  vary. For



Figure 6: The bifurcation diagram of the fast subsystem (3) and the z-nullcline of the full system (1) for b = 0.04 and h = 1 with the corresponding transient response superimposed. Equilibrium  $E_3$  on the upper branch is now attracting; compare Figures 1, 4 and 5.

example, for b = 1 in panel (a2), the number of spikes can be one, two, three and even four, depending on the chosen value of  $I_{app}$ . However, the effect of the amplitude and duration of the current injection on the number of spikes is not significant for small values of b since the sharp turn is absent and the spike onset curves are near vertical.

Comparison of rows (a) and (b) in Figure 7 suggests that the effects of modifying the amplitude and duration of the current injection are roughly the same. Both panels are slices of the three-dimensional surfaces of spike onsets in  $(b, h, I_{\rm app})$ - and  $(b, h, T_{\rm on})$ -space. As is expected from Figure 3, the curves of spike onset in Figure 7 are less squeezed for h = 0.95 (left column) than for h = 1 (right column). This sparseness leads to a reduced sensitivity of the number of spikes of the transient response to variation of the current injection.

## 6 Conclusions and remarks

We considered the transient response of a polynomial model to a very short current injection. The unperturbed model has an attracting equilibrium, and perturbation from this equilibrium typically results in a number of large-amplitude oscillations (spikes) before the response relaxes back to equilibrium. The number of spikes in the transient response depends on the system parameters as well as the amplitude and duration of the current injection.

The spike-adding mechanism in this model was studied in [15] for the case that the model has a unique attracting equilibrium. In this paper, we investigated the process of spike adding in the case that the model has three equilibria. The moment of spike onset can then be defined as a bifurcation, namely, as a codimension-one connection of the transient response to a saddle equilibrium. This codimension-one connection still involves a transition along a saddle slow manifold, a process that occurs within an exponentially small strip of the parameter plane. The behaviour in this exponentially small parameter regime can be very complicated. For instance, the transient response can temporarily generate several spikes during the addition of one new spike, which is not possible when there is only one equilibrium. We found that the overall spike-adding process adds one spike each time, also when additional equilibria are present.

The curves of spike onset do not exist in the regime of saddle-node bifurcation on an



Figure 7: Curves of spike onset in the  $(b, I_{app})$ -plane with  $T_{on} = 15$  (a) and the  $(b, T_{on})$ -plane with  $I_{app} = 0.02$  (b) for the two values h = 0.95 (column 1) and h = 1 (column 2). The number of spikes in the first few regions is indicated. The curves labelled Max and Min bound the parameter regime for which the response achieves exactly one extremum (a maximum) during the time interval  $0 \le t \le T_{on}$  when the applied current is switched on.

invariant cycle (SNIC) for the fast subsystem. In this regime, only one spike is generated by the injected current. Furthermore, spike adding can only occur to the right of the Hopf bifurcation H of the full system (see Figure 3). This Hopf bifurcation stops the process of addition of a new spike because the transient response converges to a different attracting equilibrium for our values of  $I_{\rm app}$  and  $T_{\rm on}$ .

We showed that the curves of spike onset are organised by the location of the Hopf and homoclinic bifurcations in the bifurcation set of the fast subsystem for the large region of parameters b and h considered here. A more complicated underlying organisation occurs for band h near the SNIC regime when additional attracting periodic orbits or other attractors exist. A detailed investigation of this parameter regime is left for future work. We also investigated whether a modification of the amplitude or duration of the current injection can change the number of spikes. This effect is not significant for small values of b.

Neuron models can exhibit a variety of underlying bifurcation structures [8, 16]. To date, most studies of transient responses in multiple-time-scale systems, including ours, have focussed on models for which the fast subsystem exhibits a very particular bifurcation structure, namely, a Z-shaped curve or surface of equilibria. This Z-shaped object is necessary for the spikeadding mechanisms studied here and in earlier work. It would be worthwhile to investigate whether similar mechanisms control the spike adding of transient responses in systems with fundamentally different underlying bifurcation structures for the corresponding fast subsystem.

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