Bursting through interconnection of excitable circuits

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***Abstract*—We outline the methodology for designing a bursting circuit with robustness and control properties reminiscent of those encountered in biological bursting neurons. We propose that this design question is tractable when addressed through the interconnection theory of two excitable circuits, realized solely with first-order filters and sigmoidal I-V elements. The circuit can be designed and controlled by shaping its I-V curves in the relevant timescales, giving a novel and intuitive methodology for implementing single neuron behaviors in hardware.**

I. Introduction

Biological neural networks provide amazing examples of robust and highly controllable systems whose energy efficiency greatly surpasses any modern electrical devices. As such, it is of great interest to develop a design and analysis theory of neural circuits and their interconnections in order to pave the way for development of novel artificial systems.

Here, we concentrate on the phenomenon of neural bursting, a mode of neural behavior in which neurons are able to endogenously oscillate between periods of active spiking and quiescence. Such behavior has been shown to be a unique and important signaling means of many different types of neurons [1]–[3]. In addition, controlling the neural behavior between bursting and regular spiking is a central mechanism of sensory systems related to a change of scale for the sensed objects [4], suggesting it is an important property to be considered in neuromorphic design.

The well-known FitzHugh-Nagumo model [5] mimics the architecture of the more complicated conductance-based models to qualitatively capture the fundamental excitability property of neurons. FitzHugh showed that in order to realize an excitable neural circuit, it is necessary to have a fast positive and a slow negative feedback element in parallel, the essential components of a relaxation oscillator. Due to its simplicity, it has been extensively studied and designed in hardware [6]–[8].

The biological bursting neurons reveal a similar feedback structure: in addition to the fast positive and slow negative feedback currents that generate the individual action potentials, they contain slow positive and ultra-slow negative feedback currents [9], responsible for periodically transitioning the system between resting and spiking states. Nevertheless, this parallel structure has not been utilized so far in the circuit design of bursting devices. These circuits have either been implemented as detailed biophysical replicates of biological neurons [10], or have aimed at reducing the biological complexity for efficient implementation [11] at the cost of losing some of the robust modulation properties of real neurons, such as the smooth transition between different oscillatory behaviors.

Based on recent work that utilizes singularity theory to analyze and design bursting behaviors [12]–[14], we present how a bursting circuit can be realized as the parallel interconnection of elementary excitable circuits, one fast, and one slow. In order to do that, we discuss how the FitzHugh-Nagumo model can be generalized to model both fast and slow excitability. The interconnected circuit's behavior can be precisely controlled by shaping its I-V curves in distinct timescales, thus giving a powerful design framework that requires no parameter fine-tuning. As the circuit shares the same elementary feedback structure as biological bursting neurons, it is able to produce robust and controllable bursting oscillations in a simplified circuit model.

II. Excitable circuit

Excitability of a system is characterized by a specific input-output property: small input pulses elicit comparably small outputs, but pulses of magnitude above a certain threshold induce well-defined output excursions largely independent of the input; in neurons, applied current is naturally viewed as the input, while the voltage across the membrane is the output.

Here, we would like to stress the circuit interpretation of excitability. Any excitable circuit can be decomposed into three distinct elements: the passive RC circuit accounting for the small signal properties of the circuit, a fast negative conductance element that creates a hysteretic switch, and a slow positive conductance element that regulates the refractory period following the spike. A simple circuit that satisfies those properties admits the following state-space model[1] (Fig. 1):

$$C\dot{V} = -I_p^+(V) - I_f^-(V_f) - I_s^+(V_s) + I_{app} \quad (1a)$$

$$\tau_f \dot{V}_f = V - V_f \quad (1b)$$

$$\tau_s \dot{V}_s = V - V_s, \quad (1c)$$

where we are using subscripts to indicate the timescales of the currents (passive, fast, slow), while superscripts determine if the I-V characteristics are monotonically increasing $(+)$, or monotonically decreasing $(-)$. Therefore, I_p^+ and I_s^+ are monotonically increasing functions, while I_f^- is monotonically decreasing. The term $I_p^+(V)$ accounts for the passive properties of the circuit, $I_f^-(V_f)$ is the fast negative conductance element (positive feedback on the output voltage), and $I_s^+(V_s)$ is the slowly activating positive conductance element (negative feedback on the output voltage). First-order filters are used to set the characteristic timescales of the currents. Additionally,

[1]Note that the variable names are chosen to correspond to their physical correspondents in the circuit, but the equations are dimensionless.

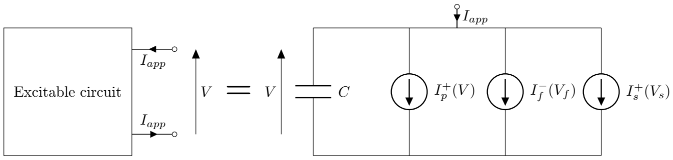

Fig. 1. Necessary components for an excitable circuit: membrane capacitor C, passive element $I_p^+(V)$, negative conductance element $I_f^-(V_f)$, and a slow positive conductance element $I_s^+(V_s)$.

we are considering the case where there is timescale separation between the fast and the slow processes, so that $\tau_f \ll \tau_s$, and set $C = 1$ for simplicity. The external input is represented by I_{app}.

Note that the familiar FitzHugh-Nagumo model is a special case of an excitable circuit where the fast positive feedback dynamics are assumed instantaneous with respect to the voltage dynamics, i.e. when $\tau_f = 0$, and the I-V functions have the standard forms: $I_p^+(V) = V^3/3$, $I_f^-(V) = -V$ and $I_s^+(V) = \alpha V$, $\alpha > 1$. The assumption that $\tau_f = 0$ is limiting when considering the design of a bursting circuit, as we will discuss further.

For implementation purposes, we will consider the case where these functions have the following forms:

$$I_p^+(V) = V \tag{2a}$$
$$I_f^-(V) = -\alpha_f \tanh(V - \delta_f) \tag{2b}$$
$$I_s^+(V) = \alpha_s \tanh(V - \delta_s), \tag{2c}$$

so that a sigmoidal function (in this case tanh) is used to define the local action of the currents, with the parameter α controlling the gain of the characteristic. The voltage offsets δ_f and δ_s are kept at 0 here, but are important parameters to control when considering interconnections of excitable behaviors.

Sigmoidal characteristics are used as the basic elements due to their ubiquity in circuit electronics; active elements such as transistors and operational amplifiers naturally saturate, providing simple realizations of such functions. Note that the negative conductance element has to be necessarily localized to a bounded voltage range, while slow positive conductance can be purely linear like in the FitzHugh-Nagumo case.

The essential property of an excitable circuit is the existence of a hysteresis in the fast subsystem that gives the circuit its switching property, with the slow adaptation regulating the refractory period. These properties are clear from the circuit's cumulative currents in each of the timescales, shown in Fig. 2. The fast cumulative current determines the bistability between the "down" and the "up" voltage, so that modifying it adapts the amplitude of the oscillations. The slow cumulative current determines the equilibrium point of the system: equilibrium is determined by the intersection with $I = I_{app}$ line, i.e. when $I_p^+(V) + I_f^-(V) + I_s^+(V) - I_{app} = 0$. When the slow cumulative current is monotonically increasing, any applied current I_{app} will define a single equilibrium. This equilibrium is either unstable if it corresponds to the negative conductance region of the fast cumulative current, or it is stable otherwise; the transition happens at the point of zero-slope in the fast cumulative current, called the threshold voltage V_{th}.

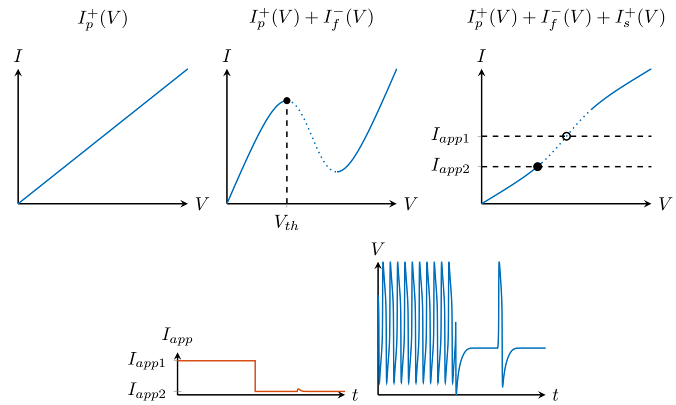

Fig. 2. Properties of an excitable circuit. Top: Cumulative instantaneous, fast and slow I-V curves of an excitable circuit. The instantaneous curve is purely passive, while the fast curve is hysteretic, with the point of zero-slope defining the threshold voltage V_{th}. The slow cumulative current is monotone and its intersection with the line $I = I_{app}$ determines the system's equilibrium. Due to timescale separation, the system is either oscillating if the equilibrium is in the unstable (dotted) region, or is stable (but excitable). Bottom: Transition between the spiking and excitable regimes through applied current.

The popular FitzHugh-Nagumo model obtained for $\tau_f = 0$ is the singular limit of a fast excitable circuit. As will be shown in the next section, the possibility of controlling the timescale τ_f of excitability is crucial for creating novel behaviors through interconnection.

III. Interconnection of Excitable Circuits

We now consider the parallel interconnection of a slow and a fast excitable circuit as described in the previous section (Fig. 3). The systems share a common voltage, and the parallel structure means that the currents are simply added in the voltage dynamics equation:

$$C\dot{V} = -I_p^+(V) - I_f^-(V_f) - I_s^+(V_s) - I_s^-(V_s) - I_{us}^+(V_{us}) + I_{app} \tag{3a}$$
$$\tau_f \dot{V}_f = V - V_f \tag{3b}$$
$$\tau_s \dot{V}_s = V - V_s \tag{3c}$$
$$\tau_{us} \dot{V}_{us} = V - V_{us}, \tag{3d}$$

where I_f^- and I_s^- are monotonically decreasing (negative conductance elements), I_s^+ and I_{us}^+ are monotonically increasing (positive conductance elements), and $\tau_f \ll \tau_s \ll \tau_{us}$. The individual passive elements are combined into a single monotonically increasing function I_p^+. The slow timescale τ_s is chosen to model simultaneously the positive conductance of the fast excitable circuit and the negative conductance of the slow excitable circuit. This choice ensures that the excitable circuits have a common timescale where they can interact.

We approach the analysis again by considering the cumulative currents in the relevant timescales: fast, slow and the ultra-slow timescale. The addition of the I_s^- current changes the previously monotonically increasing slow cumulative current by introducing a region of negative conductance, as seen in Fig. 4. In order to outline the methodology behind the synthesis of a burster, we start with a case where the slow and the fast systems do not interact in amplitude; in the I-V curves this

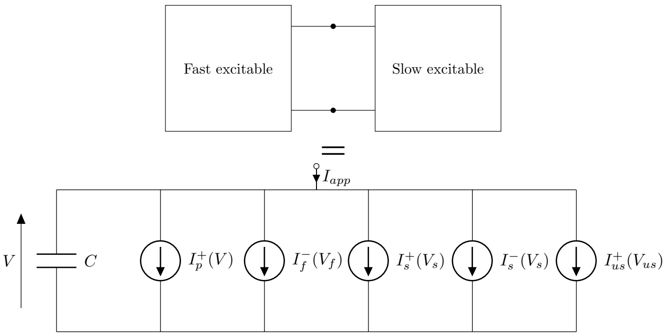

Fig. 3. Parallel interconnection of a fast and a slow exciable circuit. Top: Block diagram representation. Bottom: The complete circuit diagram of the interconnected system. In addition to the fast excitable circuit elements, the full circuit has a slow negative conductance current (I_s^-) and an ultra-slow positive conductance current (I_{us}^+).

translates to the slow bistable voltage range being outside the unstable voltage range of the fast system (Fig. 4, top). Due to the presence of both fast and slow hysteresis, the system can be either slow excitable, or fast excitable depending on the external current I_{app}; the transition between these regimes is shown (Fig. 4, bottom left).

In order for the system to be burst excitable, it is necessary to have interaction between the subsystems both in time and amplitude, which is achieved by creating an overlapping voltage range between the slow and the fast hysteresis. When this is the case, the fast excitable system is driven by the slow, so that when the system undergoes a slow action potential, it excites the fast system and a burst is generated (Fig. 4, bottom right). This can be observed in the slow cumulative I-V curve: the "up" side of the bistable range now corresponds to the unstable range of the fast system (Fig. 4, middle).

We observe therefore that it is necessary for the negative conductance element of the slow circuit to be localized so that the slow bistability is generated between resting and spiking. In addition to the localization in the voltage range, it is necessary for that element to act on a slow timescale. In order to demonstrate this, we consider a parallel interconnection of two *fast* excitable circuits, by making the element instantaneous instead (Fig. 5). The fast hysteresis is now increased due to the addition of the two negative conductance elements, and, due to the absence of the timescale separation between them, the circuit acts as if it had a single hysteretic element, and is therefore only fast excitable.

So far, we have outlined the conditions required to generate a bursting circuit: a bistable fast cumulative current that generates the spiking mechanism, as well as a bistable slow cumulative current, responsible for periodically turning the spiking on and off, thus generating bursting. As both hysteretic characteristics can be independently modified, the model is able to recreate different waveforms, the transitions captured by the different shapes of the cumulative I-V curves.

IV. Controlling the Bursting and Spiking Modes

We now show how the continuous transition between bursting and spiking modes can be robustly recreated in the model. Recent work has shown that the robustness and control

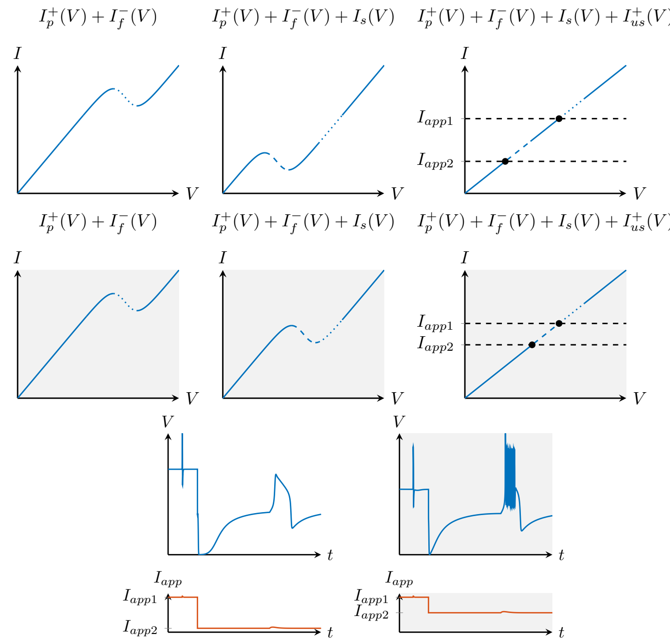

Fig. 4. Properties of the circuit interconnection. Top: Cumulative I-V curves of the interconnected circuit when there is no interaction between the systems. The slow cumulative current is bistable and the circuit experiences both fast and slow excitability (bottom left). Middle: Cumulative I-V curves of the interconnected circuit when there is interaction between the systems. The slow bistability is now between a rest point and a fast spiking state. This makes the system burst excitable (bottom right).

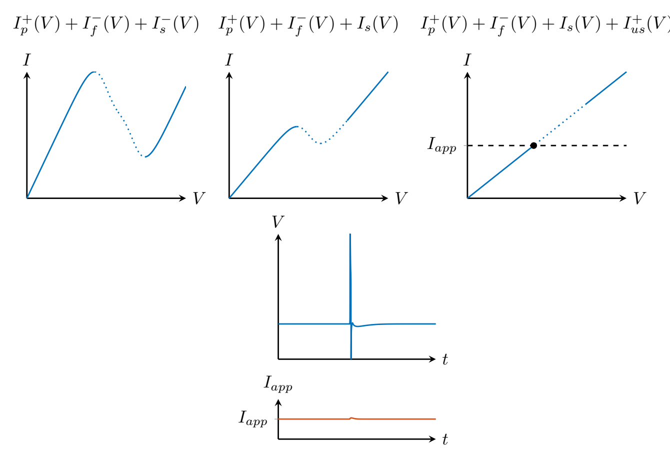

Fig. 5. Properties of the circuit interconnection when I_s^- is instantaneous. Top: Cumulative currents reveal that the two hysteresis are now joined in the fast timescale. Bottom: Due to the absence of the slow negative conductance, the circuit is now purely fast excitable.

properties of neural models can be understood through the singularity theory [12]. The gist of this analysis is that we are able to fully capture all qualitatively distinct transitions in behavior by local variations of the parameters around the degenerate conditions in the model. This is very intuitive for control between the different bursting and spiking oscillations, as we will show now.

We have shown previously that bistability in the slow cumulative current is the basic mechanism of bursting oscillations. In order to study the transition where bursting

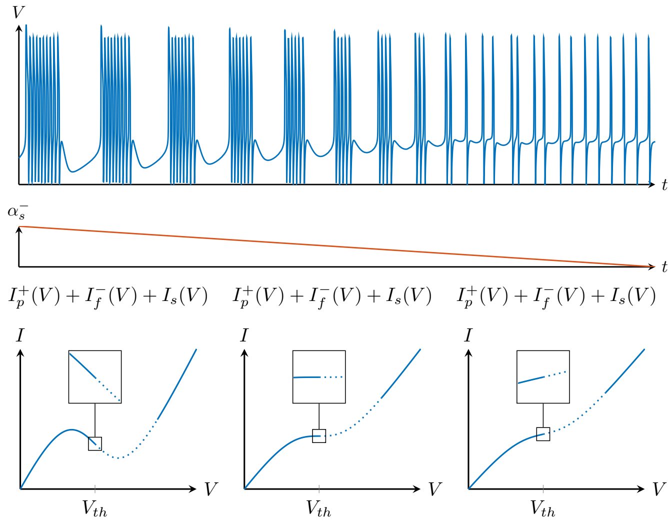

Fig. 6. Controlling the oscillation mode. Top: Transition between bursting and regular spiking modes by changing the gain of the slow negative conductance current . Bottom: The transition can be traced locally around V_{th} through the circuit's slow cumulative current (bottom). Starting from a balanced condition (middle), increasing the gain makes the slope locally negative and creates slow bistability (left), while decreasing the gain makes the slow current monotonic (right). Decreasing the size of the bistable region continuously decreases the number of spikes per burst, changing the behavior into regular spiking when bistability is lost.

is morphed into spiking, we will consider the limit when bistability is lost. We obtain this condition by imposing that the point of zero-slope of the slow current coincides with the threshold voltage of the fast system, i.e.:

$$I_s'(V_{th}) = 0. \tag{4}$$

Note that this is equivalent to the condition that the slope of the slow cumulative current is zero at V_{th}, i.e.

$$\frac{d}{dV}\Big(I_p(V) + I_f(V) + I_s(V)\Big)\Big|_{V=V_{th}} = 0. \tag{5}$$

We add an additional degeneracy condition that ensures that the slow cumulative current is exactly at the transition between a monotonic and a non-monotonic shape:

$$\frac{d^2}{dV^2}\Big(I_p(V) + I_f(V) + I_s(V)\Big)\Big|_{V=V_{th}} = 0. \tag{6}$$

By controlling the local slope of the slow cumulative current around V_{th}, we are able to transition to a non-monotone bistable characteristic (decreasing the slope), or a monotone monostable characteristic (increasing the slope). In Fig. 6, we demonstrate this by manipulating the slow negative conductance gain; other parameters of the circuit can be used as long as they affect the slope of the I-V curve at V_{th}. For large α_s^-, the bistable range is greatly increased and bursts contain many spikes as the system traverses the right unstable branch. Decreasing the gain, the bistable range is continuously shrunk giving less spikes per burst, until it is completely destroyed and the system is in the pure spiking regime.

V. Conclusion

We have outlined a circuit synthesis methodology for designing single neuron behaviors. The design is based on the interconnection of two spiking excitable circuits, and the circuit's behavior is analyzed and controlled through its I-V curves in different relevant timescales. The parallel structure of this interconnection leads to a design technique which is tractable, as the individual currents are independently summed into relevant I-V curves, while the operation of the circuit is fully determined by their shapes, as well as the points of zero-slope which determine the transitions between resting and spiking. The proposed design consists only of first order filters and sigmoidal functions, all easily realizable in hardware. The implementation of the circuit discussed here is left for future research, but recent work [13], [14] suggests that it can be achieved with elementary circuit components.

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