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Received June 6, 2002; Revised November 14, 2002; Accepted January 9, 2003

Action Editor: Xiao-Jing Wang

A a . We introduce the concept of “type I burst excitability”, which is a generalization of the “normal” excitability that is well-known in cardiac and neural systems. We demonstrate this type of burst excitability in a specific model system, a pyramidal cell from the electrosensory lateral line lobe of the weakly electric fish *Apteronotus leptorhynchus*. As depolarizing current is increased, a saddle-node bifurcation of periodic orbits occurs, which separates tonic and burst activity. This bifurcation is responsible for the excitable nature of the system, and is the basis for the “type I” designation. We verify the existence of this transition from in vitro recordings of a number of actual pyramidal cells. A scaling relationship between the magnitude and duration of a current pulse required to induce a burst is derived. We also observe this type of burst excitability and the scaling relationships in a multicompartamental model that is driven by realistic stochastic synaptic inputs mimicking sensory input. We conclude by discussing the relevance of burst excitability to communication between weakly electric fish.

: bursting, excitable systems, pyramidal cells, electric fish, bifurcation

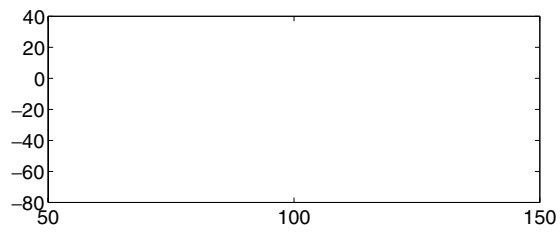
1.

Bursting, in which a cell periodically switches from quiescent behavior to a rapidly spiking state and back again, is an important and common form of electrical activity (de Vreis, 1998; Izhikevich, 2000; Keener and Sneyd, 1998; Rinzel and Ermentrout, 1998). In this paper we introduce a specific example of what we term “burst excitability”. Burst excitability is analogous to the “normal” excitability seen in neural, cardiac

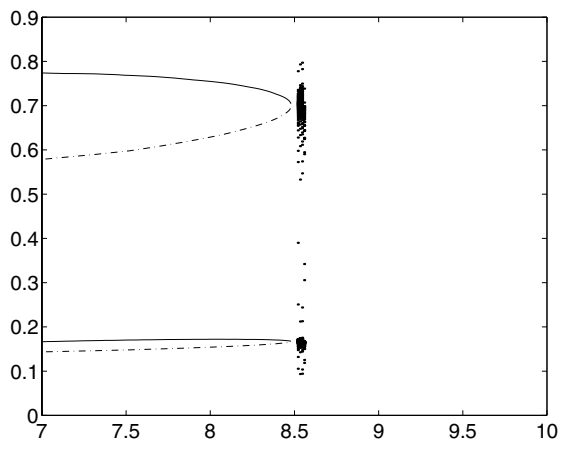
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and which also have a “global connection” which the system approximately follows during the large excursion in phase space (Ermentrout, 1996; Gutkin and Ermentrout, 1998).

We discuss burst excitability in a system which also has a saddle-node bifurcation, although of periodic orbits rather than fixed points, and which also has a “global connection” in phase space. Specifically, we discuss the “ghostburster” model of Doiron et al. (2002), a model of a pyramidal cell from the electrosensory lateral line lobe (ELL) of a weakly electric fish that



than the refractory period of the dendrite and the dendrite fails to produce an action potential in response to a somatic one, so little current flows from the dendrite to the soma, no DAP appears, and the next ISI is



space and return to a periodic orbit. We do have this “rejection”, as can be seen in the behavior of p_d during a burst (Fig. 2, bottom panel). The variable p_d gradually decreases through a burst, but cannot continue to do this forever, as eventually the effect of the dendritic refractory period come into play, the burst terminates, and p_d rapidly increases—this is the reinjection.

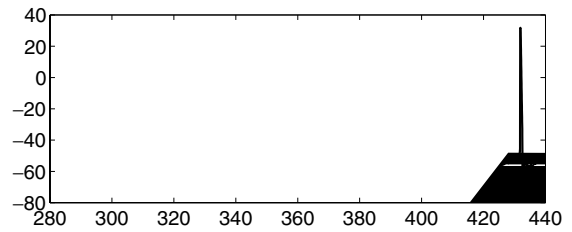
(For the study of burst excitability in the ghost-burster, we are making an analogy between the saddle-node bifurcation of fixed points in the Morris–Lecar system (Fig. 1) and the saddle-node bifurcation of periodic orbits in the ghostburster. However, for burst excitability in other bursting systems, other bifurcations may relevant.)

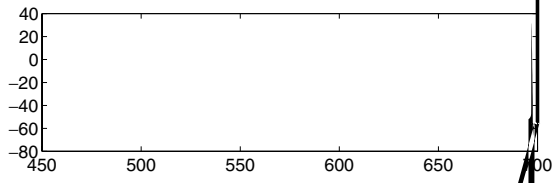
For a value of I just below that corresponding to the periodic to bursting transition, the stable manifold of the unstable periodic orbit acts as a threshold—if this is crossed, p_d starts to decrease and continues to do so until the burst terminates and the trajectory returns to the stable periodic orbit. An example of this is shown in Fig. 6. At a current of 8.3, the neuron fires periodically. The current is stepped from 8.3 to either 10.5 or 11 for 10 ms, and then returned to 8.3. The step to 10.5 fails to induce a burst and the variables return directly to their previous (periodic) values, but a step to 11 pushes the system over threshold, p_d decreases until the end of the burst, and then the variables return to their previous values. Note that most of the burst occurs after I has been returned to 8.3, another signature of the excitable nature of the system.

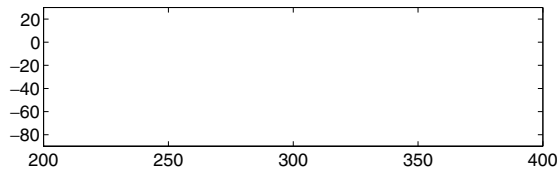
Thus, for the system (1)–(6), we have a new form of excitability, analogous to the usual form with the associations

Normal excitability	Type I burst excitability
Fixed point	Periodic firing
Action potential	Burst

However, the analogy is not exact since before the perturbation the system (1)–(6) is periodically oscillating, rather than at a fixed point, and the phase of the oscillation at which the perturbation is applied must be taken into consideration. The value of this phase can greatly affect the resulting burst. This is demonstrated in Fig. 7, where two identical current pulses are applied but at slightly different phases of the underlying oscillation (the actual difference in phases for the two situations is approximately 1/8 of a cycle). Note that the time between the onset of the pulse and the termi-







6.2. Numerical Results

In Fig. 9 we show numerical results for the system (1)–(6) that are consistent with the scaling of (13). Here, the current before a pulse (effectively ν) is held constant while the height of the pulse (effectively λ) is increased. We measured the minimum duration of a pulse needed to produce a burst with probability 0.5. We have to take this probabilistic approach for burst excitability as the “rest state” is now periodic firing, and the time of the onset of the pulse relative to the phase of the periodic firing has to be considered (see Fig. 7). (This would also be the case if, e.g. the system shown in Fig. 1 was weakly periodically forced.)

To obtain Fig. 9, a number of pulses were applied at random phases of the periodic oscillation. (The time between pulses was sufficient for the system to relax back to the periodic orbit.) The average number of bursts per pulse is a continuous function of both pulse duration and strength, and curves for probabilities other than 0.5 are similar to that shown in Fig. 9. As predicted by (13), the minimum pulse duration required to induce a burst for a fixed baseline current (effectively ν) is inversely proportional to the height of the pulse above the value needed to produce bursting. (The offset, 0.1235, in the caption of Fig. 9 is a result of the pulse height being $\nu + \lambda$, not just λ .) The baseline current was set at $I = 8.3$.

Note that a plot of the form shown in Fig. 9 but with the axes interchanged (i.e. a plot of the stimulus inten-

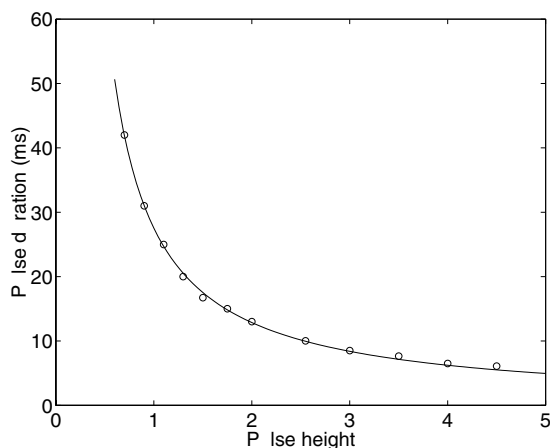


Figure 9. Minimum duration of a pulse required to generate an average of one burst per two pulses for the system (1)

ODEs:

$$\frac{du}{dt} = I - g_1 m(u)(u - 1) - g_K(u - u_K) - g_L(u - u_L) \quad (16)$$

$$\frac{dv}{dt} = \frac{\phi[v(u) - v]}{\tau(u)} \quad (17)$$

where

$$m(u) = \frac{1 + \tanh [(u - u_1)/u_2]}{2} \quad (18)$$

$$v(u) = \frac{1 + \tanh [(u - u_3)/u_4]}{2} \quad (19)$$

and

$$\tau(u) = \frac{1}{\cosh [(u - u_3)/(2u_4)]} \quad (20)$$

We use the following parameter values: $g_1 = 1$, $g_K = 2$, $u_K = -0.7$, g_L

Metzner W (1999) Neural circuitry for communication and jamming avoidance in gymnotiform electric fish. *J. Exp. Biol.* 202: 1365–1375.