Bistability in a Two-Compartment Leaky Integrate-and-Fire Neuron

Mandana Ahmadi

Nordita, Blegdamsvej 17, 2100 Copenhagen Ø, Denmark

Timothy J. Lewis

Center for Neural Science and
Courant Institute of Mathematical Sciences
New York University, 4 Washington Place, Rm 809
New York, New York, 10003

John Rinzel

Center for Neural Science and
Courant Institute of Mathematical Sciences
New York University, 4 Washington Place, Rm 809
New York, New York, 10003

January 19, 2004

Abstract

We have carried out an analytical and numerical study to explore the effects of adding a passive compartment to a point neuron spiking model. The enhanced neuron model consists of two coupled compartments, idealizing cable-like properties. The soma-like compartment has leaky integrate-and-fire (LIF) dynamics while the dendrite-like compartment is passive. Our analysis shows that the dynamics of such a two-compartment model can produce different behavior than those of a simple LIF neuron. The two-compartment model also exhibited various additional behaviors over that of a single-compartment LIF model: input resistance that can vary with cable-like parameters while leakage conductance is fixed, a non-zero minimum firing frequency, and bistability between firing and non-firing states.

1   Introduction

Simple neuron models may have the advantage of mathematical tractability but are often limited in their biological applicability. One of the most popular simplified models is the leaky integrate-and-fire (LIF) neuron. It is widely used

in analytical and computational studies (e.g, Lewis & Rinzel, 2003). There is a growing awareness of how distributed cable properties of neurons can induce complex firing properties at the single cell level (Pinsky & Rinzel, 1994; Mainen & Sejnowski, 1996). However, the LIF has rarely been implemented in a cable model. Complex neuron models employing cable theory can incorporate higher realism but are computationally much more demanding and analytically more difficult to explore. For this reason, Lansky & Rodriguez (2000) have developed a model based on simple LIF dynamics but with an extension that models dendritic influence by a passive compartment. Here, we extend their model to include the effect of the somatic spike. Using both analytical and computational methods, we found that this model, which includes with cable-like properties, can indeed show more complex behavior. We explain how this behavior of our model is caused by the interaction between the active LIF soma and the passive dendrite.

2 The Model

The equations, in dimensionless form, for the (deviations from rest of) sub-threshold membrane potentials of the two-compartment model are given by

$$\frac{dV_S}{dt} = -V_S + g_c(V_D - V_S)/\rho + I_S \tag{1}$$

$$\frac{dV_D}{dt} = -V_D - g_c(V_D - V_S)/(1 - \rho) + I_D \tag{2}$$

where V_S is the somatic voltage, V_D the dendritic voltage, g_c the coupling parameter, and I_S and I_D are external input currents to the soma and dendrite, respectively. With A_S and A_D as the somatic and dendritic membrane areas, respectively, $\rho = A_S/(A_S + A_D)$ is the fraction of somatic to total area. In our study, we use $\rho = 1/2$ (i.e. the compartments have equal membrane surface areas). When V_S reaches one (dimensionless threshold) a "spike is said to occur" and V_S is reset to the resting voltage, zero. The effect of a somatic spike on the dendrite is modeled by an instantaneous jump in the dendritic membrane potential by an amount $g_c\beta$. This treatment for the effect on an electrically connected subthreshold compartment follows that in Lewis & Rinzel (2003).

3 Results

Figure 1 shows how the additional passive dendritic compartment affects the frequency-current relationship (f-I curve). The firing threshold is shifted towards higher values of the current for the two-compartment model. In some parameter regimes, the two-compartment model has a minimum firing frequency that is greater than zero (as seen in Figure 1). In contrast, the firing frequency of the point neuron LIF model rises continuously from zero at threshold. For some other parameter values, the two-compartment model also has a monotonic and smoothly rising f-I curve.
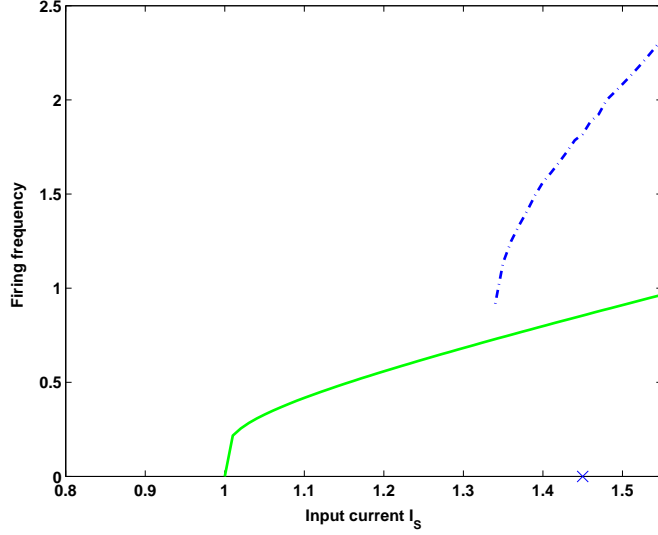
Figure 1: f-I-curves of the single compartment neuron (green solid line) and the two-compartment neuron (blue dash-dot line). The two-compartment model has a higher firing threshold for the same leakage resistance than the single compartment model, and it has non-zero minimum firing frequency. The threshold current for two compartment neuron (1.45) is indicated by the blue cross. $g_c = 0.4$.

The f-I curve in Figure 1 shows that the two-compartment neuron model is bistable. Over an I-range (near threshold) the neuron can either be firing repetitively or be at steady depolarization below threshold. We have demonstrated this bistability directly, by numerical simulation (Figure 2). Somatic voltage and the dendritic voltage are plotted as functions of time. The soma of the two compartment LIF neuron was fed with a constant current to drive the membrane potential slightly below threshold. At time step 1500, the somatic membrane potential was suddenly incremented to a level above threshold; this is equivalent to delivering a delta-pulse of depolarizing current. This caused a spike and was followed by repetitive firing, which stabilized to a constant frequency within a short time. At time step 2900, the somatic potential was increased above threshold again. This second perturbation led to only a brief transient before returning to the pre-perturbed firing state. Finally, at time step 5500, we applied a negative delta-pulse current to the soma, decreasing V_S to a value below rest. This caused the neuron to cease firing and return to the steady state with V_S just below threshold.

What is the physical mechanism underlying the bistability in the two-compartment model? Consider a model neuron that is initially at rest ($V_S = V_D = 0$). By injecting a suitable current into the soma, the somatic potential will come to
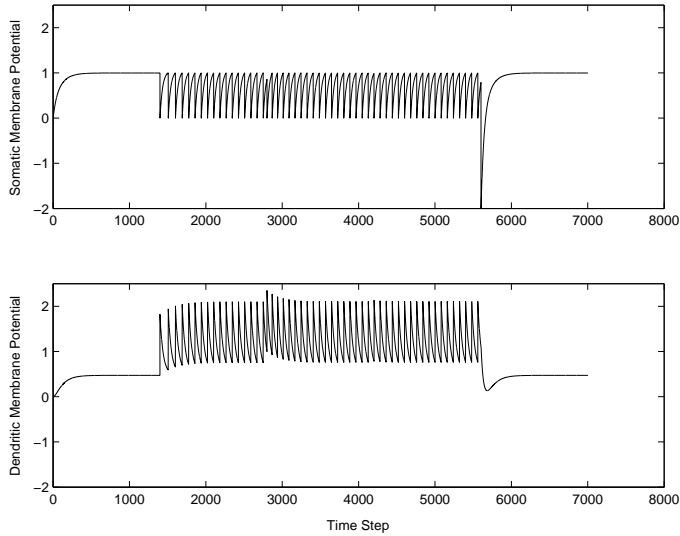
Figure 2: Bistability. A positive voltage jump at time step 1500 in the soma drives the somatic voltage into a repetitive firing pattern, which is passively followed by the dendritic voltage. At time step 5500, a negative kick forces the neuron to fall back into its steady state. Also shown is that another positive kick at time step 2900 does not have a long term effect on either the somatic firing frequency or oscillating dendritic voltage. $g_c = 0.45$.

a new steady state just below threshold ($V_S = 1$). Note that the dendritic potential will be below the somatic potential, thus the the dendritic compartment acts as a load on the soma and prevents firing. Now assume that a brief external current is applied to either the soma or the dendrite that causes a spike in the soma. The effect of this somatic spike is a flow of current from the soma to the dendrite, which raises the dendritic voltage. The amount of this dendritic membrane potential increase depends on g_c, ρ and β (i.e. parameters that determine the coupling effects between soma and dendrite and the size of the somatic spike). The spike is followed by a reset in the somatic voltage, which causes a negative potential difference between the reset soma and the newly charged dendrite. Therefore, the dendrite injects some current back into the soma. The flow of current back to the soma increases its membrane potential faster than it would given the external input current alone or with a dendritic load (i.e. when $V_S > V_D$). If the effect of the somatic spike was large enough, the somatic potential can reach threshold before the dendrite voltage dips below threshold and thus another spike can occur, increasing the potential in the passive dendrite again. This "ping-pong" process of giving charge to and taking charge from the dendritic compartment can continue infinitely, keeping the neuron firing. A negative kick to a neuron that fires due to the process described above can have the inverse effect: it can remove the extra charge which had been put into

4

the dendrite by the latest spike. This can stop the soma from producing a new spike, which interrupts the repetitive process and causes the neuron to fall back into its steady state. This argument holds only in certain parameter regimes, but is intuitively satisfying and is consistent with our mathematical results.

For fixed somatic membrane resistance, the input resistance of the two-compartment model is always smaller than that of the single-compartment model. In our dimensionless model, the input resistance R_{in} for the single-compartment model is equal to 1, while for the two-compartment model $R_{in} = (1-\rho+g_c)/(1-\rho+g_c/\rho)$. This additional conductance load due to the dendrites explains the positive shift in the current threshold for repetitive firing.

The two-compartment LIF model is analytically tractable for various aspects of its properties. For example, we have derived a single transcendental equation that describes the f-I relation. Also, we can formulate a Poincare-map (from one firing to the next) whose properties can be studied to analytically determine parameter ranges for various properties of the repetitive firing states, including bistability.

4   Discussion

Our analysis shows that adding a passive dendritic compartment to a single compartment LIF neuron can introduce additional features to the firing behavior. While a point-neuron LIF model has a monotonic f-I relation that emerges from zero frequency at threshold, in some parameter regimes the two-compartment model cannot be made to fire at arbitrarily low rates for steady input. Instead, it has a minimum firing frequency that is greater than zero. In this extended model, the passive dendritic compartment acts like a buffer: it stores a part of the charge produced by somatic firing, which is returned to the soma following the reset of the somatic potential. This ping-pong effect of charge being alternately sent between the two compartments is an important factor in enriching the firing properties of the model and leads to the non-zero minimum firing frequency that is associated with bistability near threshold. Therefore, this model may point to a simple mechanism for such complex behavior as bistability in real neurons. Cable effects from dendrites, with passive or with weak active ionic currents, can induce bistability and a finite minimum rate in neuron firing even when the spike-generating mechanism, if isolated, has no bistability or lower limit to firing rate.

References

[1] T.J. Lewis and J. Rinzel. Dynamics of spiking neurons connected by both inhibitory and electrical coupling. J. Comput. Neurosci. 14:283-309, 2003.

[2] P.F. Pinsky and J. Rinzel. Intrinsic and network rhythmogenesis in a reduced Traub model for CA3 neurons. J. Comput. Neurosci., 1:39-60, 1994.

[3] P. Lansky and R. Rodriquez. Effect of spatial extension on noise-enhanced phase locking in a leaky integrate-and-fire model of a neuron. Phys. Review E 62: 8427-8437, 2000.

[4] Z.F. Mainen and T.J. Sejnowski. Influence of dendritic structure on firing pattern in model neocortical neurons. Nature 382: 363-366, 1996.