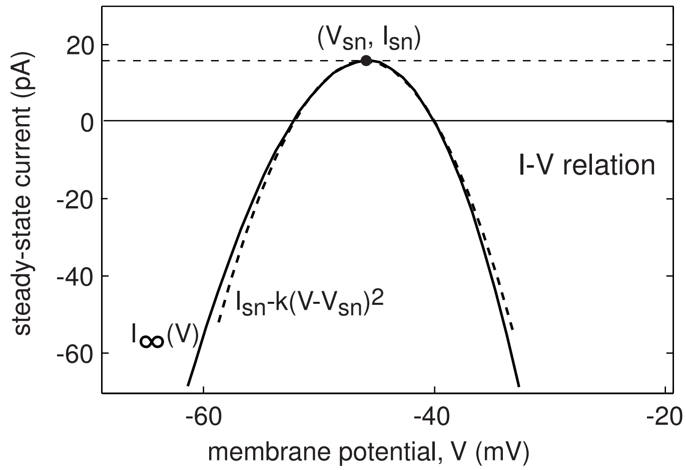

Figure 3.34: Magnification of the I-V curve in Fig.3.31 at the left knee shows that it can be approximated by a square parabola.

3.3.8 Quadratic Integrate-and-Fire Neuron

Let us consider the topological normal form for the saddle-node bifurcation (3.9). From $0 = I + V^2$ we find that there are two equilibria, $V_{\text{rest}} = -\sqrt{|I|}$ and $V_{\text{thresh}} = +\sqrt{|I|}$ when $I < 0$. The equilibria approach and annihilate each other via saddle-node bifurcation when $I = 0$, so there are no equilibria when $I > 0$. In this case, $\dot{V} \geq I$ and $V(t)$ increases to infinity. Because of the quadratic term, the rate of increase also increases, resulting in a positive feedback loop corresponding to the regenerative activation of the Na^+ current. In exercise 15 we show that $V(t)$ escapes to infinity in a finite time, which corresponds to the upstroke of the action potential. The same upstroke is generated when $I < 0$, if the voltage variable is pushed beyond the threshold value V_{thresh}.

Considering infinite values of the membrane potential may be convenient from a purely mathematical point of view, but this has no physical meaning and there is no way to simulate it on a digital computer. Instead, we fix a sufficiently large constant V_{peak} and say that (3.9) generated a spike when $V(t)$ reached V_{peak}. After the peak of the spike is reached, we reset $V(t)$ to a new value V_{reset}. The topological normal form for the saddle-node bifurcation with the after-spike resetting,

$$\dot{V} = I + V^2 , \qquad \text{if } V \geq V_{\text{peak}}, \quad \text{then } V \leftarrow V_{\text{reset}} \tag{3.10}$$

is called the *quadratic integrate-and-fire neuron*. It is the simplest model of a spiking neuron. The name stems from its resemblance to the *leaky* integrate-and-fire neuron $\dot{V} = I - V$ considered in chapter 8. In contrast to the common folklore, the leaky neuron is not a *spiking model* because it does not have a spike generation mechanism, i.e., a regenerative upstroke of the membrane potential, whereas the quadratic neuron does. We discuss this and other issues in detail in chapter 8.

In general, the quadratic integrate-and-fire model could be derived directly from the equation $C\dot{V} = I - I_\infty(V)$ through approximating the steady-state I-V curve near

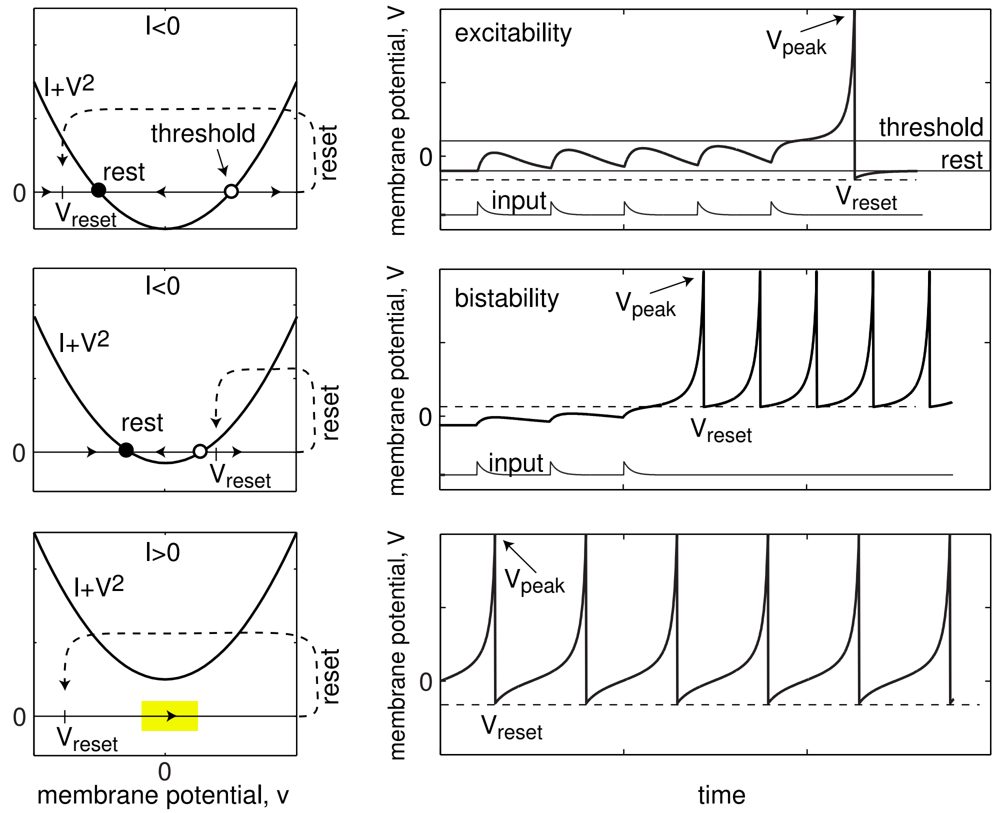

Figure 3.35: Quadratic integrate-and-fire neuron (3.10) with time-dependent input.

the resting state by the square parabola $I_\infty(V) \approx I_{\text{sn}} - k(V - V_{\text{sn}})^2$, where $k > 0$ and the peak of the curve $(V_{\text{sn}}, I_{\text{sn}})$ could easily be found experimentally (see Fig.3.34). Approximating the I-V curve by other functions – for example $I_\infty(V) = g_{\text{leak}}(V - V_{\text{rest}}) - ke^{pV}$, results in other forms of the model, such as the exponential integrate-and-fire model (Fourcaud-Trocme et al. 2003), which has certain advantages over the quadratic form. Unfortunately, the model is not solvable analytically, and it is expensive to simulate. The form $I_\infty(V) = g_{\text{leak}}(V - V_{\text{leak}}) - k(V - V_{\text{th}})_+^2$, where $x_+ = x$ when $x > 0$ and $x_+ = 0$ otherwise, combines the advantages of both models. The parameters V_{peak} and V_{reset} are derived from the shape of the spike. Normalization of variables and parameters results in the form (3.10) with $V_{\text{peak}} = 1$.

In Fig.3.35 we simulate the quadratic integrate-and-fire neuron to illustrate a number of its features, which will be described in detail in subsequent chapters using conductance-based models. First, the neuron is an integrator; each input pulse in Fig.3.35 (top), pushes V closer to the threshold value; the higher the frequency of the input, the sooner V reaches the threshold and starts the upstroke of a spike. The neuron is monostable when $V_{\text{reset}} \le 0$ and can be bistable otherwise. Indeed, the first spike in Fig.3.35 (middle) is evoked by the input, but the subsequent spikes occur because the reset value is superthreshold.

The neuron can be Class 1 or Class 2 excitable, depending on the sign of V_{reset}.

Suppose the injected current I slowly ramps up from a negative to a positive value. The membrane potential follows the resting state $-\sqrt{|I|}$ in a quasi-static fashion until the bifurcation point $I = 0$ is reached. At this moment, the neuron starts to fire tonic spikes. In the monostable case $V_{\text{reset}} < 0$ in Fig.3.35 (bottom), the membrane potential is reset to the left of the ghost of the saddle-node point (see section 3.3.5), thereby producing spiking with an arbitrary small frequency, and hence Class 1 excitability. Because of the recurrence, such a bifurcation is called saddle-node on invariant circle. Many pyramidal neurons in mammalian neocortex exhibit such a bifurcation. In contrast, in the bistable case $V_{\text{reset}} > 0$, not shown in the figure, the membrane potential is reset to the right of the ghost, no slow transition is involved, and the tonic spiking starts with a nonzero frequency. (As an exercise, explain why there is a noticeable latency [delay] to the first spike right after the bifurcation.) This type of behavior is typical in spiny projection neurons of neostriatum and basal ganglia, as we show in chapter 8.

Review of Important Concepts

- The one-dimensional dynamical system $\dot{V} = F(V)$ describes how the rate of change of V depends on V. Positive $F(V)$ means V increases; negative $F(V)$ means V decreases.
- In the context of neuronal dynamics, V is often the membrane potential, and $F(V)$ is the steady-state I-V curve taken with the minus sign.
- A zero of $F(V)$ corresponds to an equilibrium of the system. (Indeed, if $F(V) = 0$, then the state of the system, V, neither increases nor decreases.)
- An equilibrium is stable when $F(V)$ changes the sign from "plus" to "minus". A sufficient condition for stability is that the eigenvalue $\lambda = F'(V)$ at the equilibrium be negative.
- A phase portrait is a geometrical representation of the system's dynamics. It depicts all equilibria, their stability, representative trajectories, and attraction domains.
- A bifurcation is a qualitative change of the system's phase portrait.
- The saddle-node (fold) is a typical bifurcation in one-dimensional systems. As a parameter changes, a stable and an unstable equilibrium approach, coalesce, and then annihilate each other.