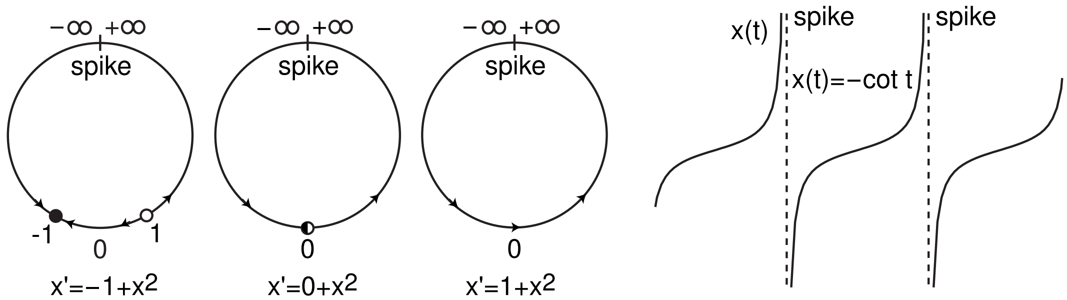

Figure 10.34: Phase portraits and typical oscillations of the quadratic integrate-and-fire neuron $\dot{x} = I + x^2$ with $x \in \mathbb{R} \cup \{\pm\infty\}$. Parameter: $I = -1, 0, +1$.

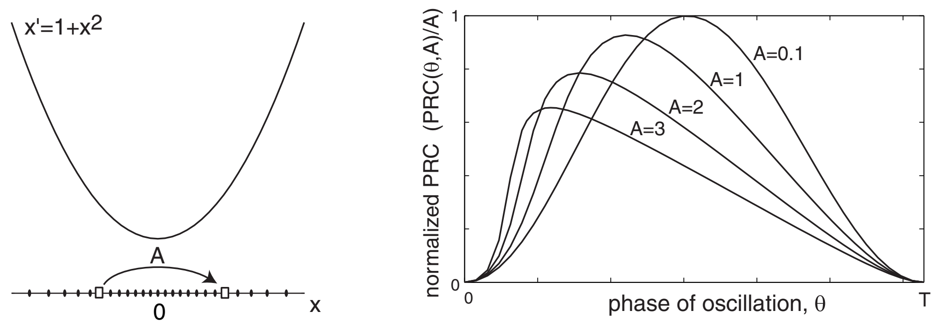

Figure 10.35: The dependence of the PRC of the quadratic integrate-and-fire model on the strength of the pulse A.

10.4.2 SNIC Oscillators

Let us go through all the steps of derivation of the phase equation using a neuron model exhibiting low-frequency periodic spiking. Such a model is near the saddle-node on invariant circle (SNIC) bifurcation studied in section 6.1.2. Appropriate rescaling of the membrane potential and time converts the model into the normal form

$$x' = 1 + x^2 \,, \qquad x \in \mathbb{R} \,.$$

Because of the quadratic term, x escapes to infinity in a finite time, producing a spike depicted in Fig.10.34. If we identify $-\infty$ and $+\infty$, then x exhibits periodic spiking of infinite amplitude. Such a spiking model is called a quadratic integrate-and-fire (QIF) neuron (see also section 8.1.3 for some generalizations of the model).

Strong Pulse

The solution of this system, starting at the spike, that is, at $x(0) = \pm\infty$, is

$$x(t) = -\cot t \,,$$

as the reader can check by differentiating. It is a periodic function with $T = \pi$; hence, we can introduce the phase of oscillation via the relation $x = -\cot\vartheta$. The corresponding PRC can be found explicitly (see exercise 9) and it has the form

$$\mathrm{PRC}\,(\vartheta, A) = \pi/2 + \operatorname{atan}(A - \cot\vartheta) - \vartheta \ ,$$

depicted in Fig.10.35, where A is the magnitude of the pulse. Note that the PRC tilts to the left as A increases. Indeed, the density of isochrons, denoted by black points on the x-axis in the figure, is maximal at the ghost of the saddle-node point $x = 0$, where the parabola $1 + x^2$ has the knee. This corresponds to the inflection point of the graph of $x(t)$ in Fig.10.34, where the dynamics of $x(t)$ is the slowest. The effect of a pulse is maximal just before the ghost because x can jump over the ghost and skip the slow region. The stronger the pulse, the earlier it should arrive; hence the tilt.

Weak Coupling

The PRC behaves as $A\sin^2\vartheta$, with $\vartheta \in [0, \pi]$, when A is small, as the reader can see in Fig.10.35 or prove by differentiating the function $\mathrm{PRC}\,(\vartheta, A)$ with respect to A. Therefore, $Z(\vartheta) = \sin^2\vartheta$, and we can use Winfree's approach to transform the weakly perturbed quadratic integrate-and-fire (QIF) oscillator

$$x' = 1 + x^2 + \varepsilon p(t)$$

into its phase model

$$x' = 1 + \varepsilon(\sin^2\vartheta)p(t) \ , \qquad \vartheta \in [0, \pi] \ .$$

The results of the previous section, $Q(\vartheta) = 1/f(x(\vartheta)) = 1/(1+\cot^2\vartheta) = \sin^2\vartheta$, confirm the phase model. In fact, any neuronal model $C\dot{V} = I - I_\infty(V)$ near saddle-node on invariant circle bifurcation point $(I_{\mathrm{sn}}, V_{\mathrm{sn}})$ has infinitesimal PRC:

$$\mathrm{PRC}\,(\vartheta) = \frac{C}{I - I_{\mathrm{sn}}}\sin^2\vartheta \ , \qquad \vartheta \in [0, \pi] \ ,$$

as the reader can prove as an exercise. The function $\sin^2\vartheta$ has the same form as $(1 - \cos\theta)$ if we change variables $\theta = 2\vartheta$ (notice the font difference). The change of variables scales the period from π to 2π.

In Fig.10.36a we compare the function with numerically obtained PRCs for the $I_{\mathrm{Na}} + I_{\mathrm{K}}$-model in the Class 1 regime. Since the ghost of the saddle-node point, revealing itself as an inflection of the voltage trace in Fig.10.36b, moves to the right as I increases away from the bifurcation value $I = 4.51$, so does the peak of the PRC.

Figure 10.36a emphasizes the common features of all systems undergoing saddle-node on invariant circle bifurcation: they are insensitive to the inputs arriving during the spike, since $\mathrm{PRC} \approx 0$ when $\vartheta \approx 0, T$. The oscillators are most sensitive to the input when they are just entering the ghost of the resting state, where PRC is maximal. The location of the maximum tilts to the left as the strength of the input increases, and may tilt to the right as the distance to the bifurcation increases. Finally, PRCs are non-negative, so positive (negative) inputs can only advance (delay) the phase of oscillation.

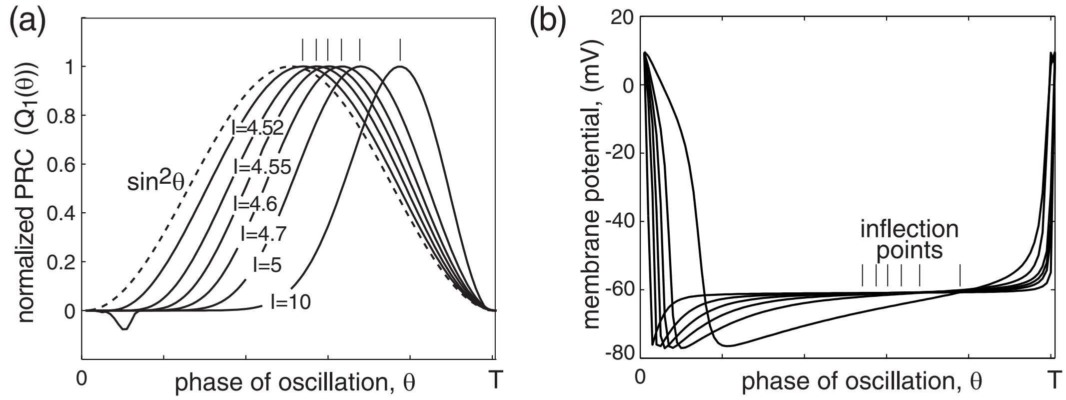

Figure 10.36: (a) Numerically found PRCs of the $I_{\mathrm{Na}} + I_{\mathrm{K}}$-oscillator in Class 1 regime (parameters as in Fig.4.1a) and various I using the MATLAB program in exercise 12. (b) Corresponding voltage traces show that the inflection point (slowest increase) of V moves right as I increases.

Gap Junctions

Now consider two oscillators coupled via gap junctions (discussed in section 2.3.4):

$$\begin{aligned} x_1' &= 1 + x_1^2 + \varepsilon(x_2 - x_1) , \\ x_2' &= 1 + x_2^2 + \varepsilon(x_1 - x_2) . \end{aligned}$$

Let us determine the stability of the in-phase synchronized state $x_1 = x_2$. The corresponding phase model (10.12) has the form

$$\begin{aligned} \vartheta_1' &= 1 + \varepsilon(\sin^2 \vartheta_1)(\cot \vartheta_1 - \cot \vartheta_2) , \\ \vartheta_2' &= 1 + \varepsilon(\sin^2 \vartheta_2)(\cot \vartheta_2 - \cot \vartheta_1) . \end{aligned}$$

The function (10.16) can be found analytically:

$$H(\chi) = \frac{1}{\pi} \int_0^\pi \sin^2 t \,(\cot t - \cot(t + \chi)) \; dt = \frac{1}{2} \sin 2\chi ,$$

so that the model in the phase deviation coordinates, $\vartheta(t) = t + \varphi$, has the form

$$\begin{aligned} \varphi_1' &= (\varepsilon/2) \sin\{2(\varphi_2 - \varphi_1)\} , \\ \varphi_2' &= (\varepsilon/2) \sin\{2(\varphi_1 - \varphi_2)\} . \end{aligned}$$

The phase difference, $\chi = \varphi_2 - \varphi_1$, satisfies the equation (compare with Fig.10.26)

$$\chi' = -\varepsilon \sin 2\chi ,$$

and, apparently, the in-phase synchronized state, $\chi = 0$, is always stable while the anti-phase state $\chi = \pi/2$ is not.