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Next: 4.3 From Detailed Models **Up:** 4. Formal Spiking Neuron **Previous:** 4.1 Integrate-and-fire model

Subsections

4.2 Spike response model (SRM)

The Spike Response Model (SRM) is - just like the nonlinear integrate-and-fire model - a generalization of the leaky integrate-and-fire model. The direction of the generalization is, however, somewhat different. In the nonlinear integrate-and-fire model, parameters are made *voltage* dependent whereas in the SRM they depend on the time since the last output spike. Another difference between integrate-and-fire models and the SRM concerns the formulation of the equations. While integrate-and-fire models are usually defined in terms of differential equations, the SRM expresses the membrane potential at time t as an integral over the past.

The explicit dependence of the membrane potential upon the last output spike allows us to model refractoriness as a combination of three components, viz., (i) a reduced responsiveness after an output spike; (ii) an increase in threshold after firing; and (iii) a hyperpolarizing spike after-potential. In Section 4.2.1 the Spike Response Model is introduced and its properties illustrated. Its relation to the integrate-and-fire model is the topic of Section 4.2.2. An important special case of the Spike Response Model is the simplified model SRM$_0$ that we have already encountered in Chapter 1.3.1. Section 4.2.3 will discuss it in more detail.

4.2.1 Definition of the SRM

In the framework of the Spike Response Model the state of a neuron i is described by a single variable u_i. In the absence of spikes, the variable u_i is at its resting value, $u_{rest} = 0$. Each incoming spike will perturb u_i and it takes some time before u_i returns to zero. The function ϵ describes the time course of the response to an incoming spike. If, after the summation of the effects of several incoming spikes, u_i reaches the threshold ϑ an output spike is triggered. The form of the action potential and the after-potential is described by a function η. Let us suppose neuron *i* has fired its last spike at time $\hat{t}_i$. After firing the evolution of u_i is given by

$$u_i(t) = \eta(t - \hat{t}_i) + \sum_j w_{ij} \sum_f \epsilon_{ij}(t - \hat{t}_i, t - t_j^{(f)}) + \int_0^\infty \kappa(t - \hat{t}_i, s)\, I^{ext}(t - s)\, ds \qquad (4.24)$$

where $t_j^{(f)}$ are spikes of presynaptic neurons *j* and w_{ij} is the synaptic efficacy. The last term accounts for an external driving current I^{ext}. The two sums run over all presynaptic neurons *j* and all firing times $t_j^{(f)} < t$ of neuron *j*. We emphasize that all terms depend on $t - \hat{t}_i$, i.e., the time since the last output spike.

In contrast to the integrate-and-fire neuron discussed in Section (4.1) the threshold ϑ is not fixed but may also depend on $t - \hat{t}_i$

$$\vartheta \longrightarrow \vartheta(t - \hat{t}_i)\,. \qquad (4.25)$$

During an absolute refractory period Δ^{abs}, we may for example set ϑ to a large and positive value to avoid firing and let it relax back to its equilibrium value for $t > \hat{t}_i + \Delta^{abs}$. Firing occurs whenever the membrane potential u_i reaches the dynamic threshold $\vartheta(t - \hat{t}_i)$ from below

$$t = t_i^{(f)} \quad \Leftrightarrow \quad u_i(t) = \vartheta(t - \hat{t}_i) \text{ and } \frac{du_i(t)}{dt} > 0\,. \qquad (4.26)$$

As mentioned before $\hat{t}_i$ is the *last* firing time,

$$\hat{t}_i = max\left\{ t_i^{(f)} < t \right\}. \qquad (4.27)$$

Dynamic thresholds are a standard feature of phenomenological neuron models (Fuortes and Mantegazzini, 1962; Stein, 1967b; MacGregor and Oliver, 1974; Eckhorn et al., 1990; Abeles, 1991; Geisler and Goldberg, 1966; Weiss, 1966; Horn and Usher, 1989). Models similar to Eqs. (4.24)-(4.26) can be traced back much further; see, e.g., Hill (1936).

4.2.1.1 Interpretation

So far Eqs. (4.1) and (4.24) define a mathematical model. Can we give a biological interpretation of the terms? Let us identify the variable u_i with the membrane potential of neuron *i*. The functions η, κ and ϵ_{ij} are *response kernels* that describe the effect of spike emission and spike reception on the variable u_i. This interpretation has motivated the name `Spike Response Model', SRM for short (Gerstner, 1995; Kistler et al., 1997). Let us discuss the meaning of the response kernels.

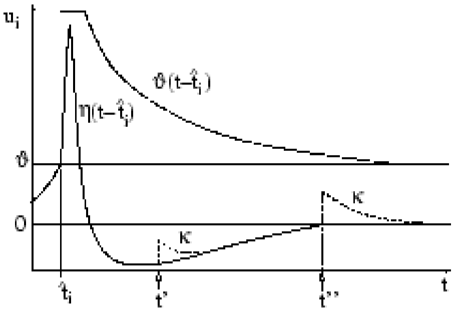

Figure 4.5: Schematic interpretation of the Spike Response Model. The figure shows the time course $u_i(t)$ of the membrane potential of neuron *i* as a function of time *t*. A spike of neuron *i* has been initiated at $\hat{t}_i$. The kernel $\eta(t - \hat{t}_i)$ for $t > \hat{t}_i$ describes the form of the action potential (positive pulse) and the (negative) spike after-potential that follows the pulse (thick solid line). If an input current pulse is applied at a time *t''* a long time after the firing at $\hat{t}_i$, it evokes a standard response described by the function $\kappa(\infty, t - t'')$ and indicated by the dashed line starting at *t''* (arrow). An input current pulse at *t'* (arrow) which arrives shortly after the postsynaptic spike at $\hat{t}_i$ evokes, due to refractoriness of the neuron, a response of significantly shorter duration. Its time course is described by the response kernel $\kappa(t - \hat{t}_i, t - t')$; see the dashed line after *t'*. Immediately after firing at $\hat{t}_i$, the threshold is increased (dot-dashed line).

The kernel η describes the standard form of an action potential of neuron *i* including the negative overshoot which typically follows a spike (after-potential). Graphically speaking, a contribution η is `pasted in' each time the membrane potential reaches the threshold $\vartheta$; cf. Fig. 4.5. Since the form of the spike is always the same, the exact time course of the action potential carries no information. What matters is whether there is the event `spike' or not. The event is fully characterized by the firing time $t_i^{(f)}$. In a simplified model, the *form* of the action potential may therefore be neglected as long as we keep track of the firing times $t_i^{(f)}$. The kernel η describes then simply the `reset' of the membrane potential to a lower value after the spike at $\hat{t}_i$ just like in the integrate-and-fire model.

The leaky integrate-and-fire model is in fact a special case of the SRM as we will see below in Section 4.2.2.

The kernel $\kappa(t - \hat{t}_i, s)$ is the *linear response* of the membrane potential to an input current. It describes the time course of a deviation of the membrane potential from its resting value that is caused by a short current pulse (``impulse response''). We have already seen in Chapters 2.2 and 3 that the response depends, in general, on the time that has passed since the last output spike at $\hat{t}_i$. Immediately after $\hat{t}_i$ many ion channels are open so that the resistance of the membrane is reduced. The voltage response to an input current pulse decays therefore more rapidly back to zero than in a neuron that has been inactive. A reduced or shorter response is one of the signatures of neuronal refractoriness. This form of refractory effect is taken care of by making the kernel κ depend, via its first argument, on the time difference $t - \hat{t}_i$. We illustrate the idea in Fig. 4.5. The response to a first input pulse at t' is shorter and less pronounced than that to a second one at t'', an effect which is well-known experimentally (Fuortes and Mantegazzini, 1962; Stevens and Zador, 1998; Powers and Binder, 1996).

The kernel $\epsilon_{ij}(t - \hat{t}_i, s)$ as a function of $s = t - t_j^{(f)}$ can be interpreted as the time course of a *postsynaptic potential* evoked by the firing of a presynaptic neuron *j* at time $t_j^{(f)}$. Depending on the sign of the synapse from *j*, to *i*, ϵ_{ij} models either an excitatory or inhibitory postsynaptic potential (EPSP or IPSP). Similarly as for the kernel κ, the exact shape of the postsynaptic potential depends on the time $t - \hat{t}_i$ that has passed since the last spike of the postsynaptic neuron *i*. In particular, if neuron *i* has been active immediately before the arrival of a presynaptic action potential, the postsynaptic neuron is in a state of refractoriness. In this case, the response to an input spike is smaller than that of an `unprimed' neuron. The first argument of $\epsilon_{ij}(t - \hat{t}_i, s)$ accounts for the dependence upon the last firing time of the postsynaptic neuron.

4.2.1.2 Total Postsynaptic Potential

In order to simplify the notation for later use, it is convenient to introduce the *total postsynaptic potential*,

(4.28)

$$h(t|\hat{t}_i) = \sum_j w_{ij} \sum_{t_j^{(f)}} \epsilon_{ij}(t - \hat{t}_i, t - t_j^{(f)}) + \int_0^\infty \kappa(t - \hat{t}_i, s)\, I_i^{\text{ext}}(t - s)\, ds\,.$$

Equation (4.24) can then be written in compact form,

$$u_i(t) = \eta(t - \hat{t}_i) + h(t|\hat{t}_i)\,. \tag{4.29}$$

4.2.1.3 Refractoriness

Refractoriness may be characterized experimentally by the observation that immediately after a first action potential it is impossible (absolute refractoriness) or more difficult (relative refractoriness) to excite a second spike (Fuortes and Mantegazzini, 1962).

Absolute refractoriness can be incorporated in the SRM by setting the dynamic threshold during a time Δ^{abs} to an extremely high value that cannot be attained.

Relative refractoriness can be mimicked in various ways; see Fig. 4.5. First, after the spike the membrane potential, and hence η, passes through a regime of hyperpolarization (after-potential)

where the voltage is *below* the resting potential. During this phase, more stimulation than usual is needed to drive the membrane potential above threshold. This is equivalent to a transient increase of the firing threshold (see below). Second, ϵ and κ contribute to relative refractoriness because, immediately after an action potential, the response to incoming spikes is shorter and, possibly, of reduced amplitude (Fuortes and Mantegazzini, 1962). Thus more input spikes are needed to evoke the same depolarization of the membrane potential as in an `unprimed' neuron. The first argument of the ϵ function (or κ function) allows us to incorporate this effect.

4.2.1.4 Removing the dynamic threshold

From a formal point of view, there is no need to interpret the variable u as the membrane potential. It is, for example, often convenient to transform the variable u so as to remove the time-dependence of the threshold. In fact, a general Spike Response Model with arbitrary time-dependent threshold $\vartheta(t - \hat{t}) = \vartheta_0 + \Delta(t - \hat{t})$, can always be transformed into a Spike Response Model with fixed threshold ϑ_0 by a change of variables

$$u(t) \longrightarrow \tilde{u}(t) = u(t) - \Delta(t - \hat{t})\,. \tag{4.30}$$

The function $\Delta(t - \hat{t})$ can easily be absorbed in the definition of the η kernel.

4.2.1.5 Example: Impulse response of the FitzHugh-Nagumo model

In Chapter 3 we have studied the FitzHugh-Nagumo model as an example of a two-dimensional neuron model. Here we want to show that the response of the FitzHugh-Nagumo model to a short input current pulse depends on the time since the last spike. Let us trigger, in a simulation of the model, an action potential at $t = 0$. This can be done by applying a short, but strong current pulse. The result is a voltage trajectory of large amplitude which we identify with the kernel $\eta(t)$. Figure 4.6 shows the hyperpolarizing spike after-potential which decays slowly back to the resting level. To test the responsiveness of the FitzHugh-Nagumo model during the recovery phase after the action potential, we apply, at a time $t^{(f)} > 0$, a second short input current pulse of low amplitude. The response to this test pulse is compared with the unperturbed trajectory. The difference between the two trajectories defines the kernel $\kappa(t - \hat{t}, t - t^{(f)})$. In Fig. 4.6 several trajectories are overlayed showing the response to stimulation at $t = 10, 15, 20, 30$ or 40. The shape and duration of the response curve depends on the time that has passed since the initiation of the action potential. Note that the time constant of the response kernel κ is always shorter than that of the hyperpolarizing spike after-potential. Analogous results for the Hodgkin-Huxley model will be discussed below in Section 4.3.1.

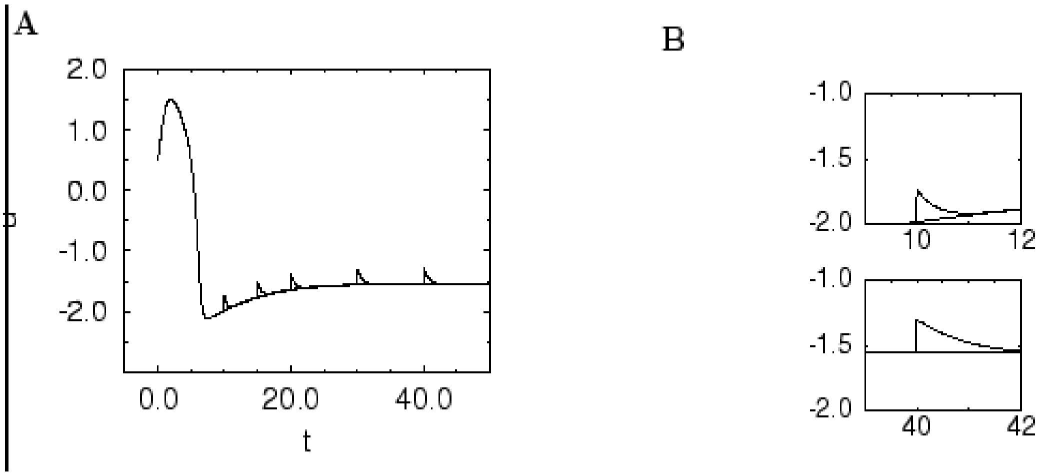

Figure 4.6: FitzHugh-Nagumo model. An action potential has been triggered at $t = 0$. After the action potential additional pulse input occurs at $t = 10, 15, 20, 30$, or 40 [arbitrary units]. In **A** the trajectories of all runs are plotted on top of each other. Part **B** shows a zoomed-in section of two trajectories. A pulse input at time t=10 after the onset of the action potential has a short lasting effect (top right) compared to a pulse at t=40 (bottom right). All parameters as in Fig. 3.5. There is no constant bias current.

4.2.1.6 Example: A motoneuron model

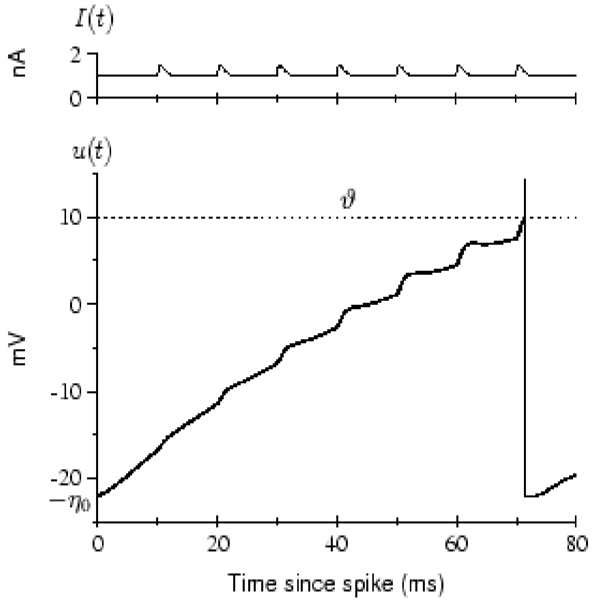

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Figure 4.7: Effect of recovery time constant $\tau_{\rm rec}$. Top: Input current consisting of a sequence of pulses superimposed on a constant bias. Bottom: The membrane potential response (thick line) to the input pulses clearly shows that the response amplitude increases as a function of the time since the last spike. Parameters: $\tau_{\rm rec} = \tau_{\rm refr}$ = 100ms; τ_m = 4ms; taken from Herrmann and Gerstner (2001b).

Motoneurons exhibit a rather slow return to the resting potential after an action potential (Powers and Binder, 1996). The time constant of the decay of the hyperpolarizing spike after-potential can be in the range of 100ms or more and is therefore much slower than the membrane time constant that characterizes the response to a short current input. On the other hand, it is found that if motoneurons are stimulated by a constant super-threshold current, their membrane potential has a roughly linear trajectory when approaching threshold. To qualitatively describe these observations, we can use a Spike Response Model with the following kernels:

$$\eta(t-\hat{t}) = -\,\eta_0\, e^{-\frac{(t-\hat{t})}{\tau_{\rm refr}}}\,\Theta(t-\hat{t}) \qquad (4.31)$$

$$\kappa(t-\hat{t},s) = \frac{R}{\tau_m}\left[1 - e^{-\frac{(t-\hat{t})}{\tau_{\rm rec}}}\right] e^{-\frac{s}{\tau_m}}\,\Theta(s)\,\Theta(t-\hat{t}-s) \qquad (4.32)$$

where τ_m is an effective passive membrane time constant, R is the input resistance, $\tau_{\rm refr}$ is the `refractory' time constant, $\tau_{\rm rec}$ is the `response recovery' time constant, η_0 is a scale factor for the refractory function. The passive membrane time constant τ_m and input resistance R characterize the membrane response to small current pulses. The refractory function η describes the return of the membrane potential to baseline after an action potential. It is characterized by a slow time constant $\tau_{\rm refr}$. For the κ-kernel we use a decaying exponential in s with time constant τ_m, modulated by the `recovery' factor $\{1 - \exp[-(t-\hat{t})/\tau_{\rm rec}]\}$. This results in a spike-time dependent scaling of the amplitude of postsynaptic potentials. The recovery time $\tau_{\rm rec}$ is taken much longer than τ_m.

The effect of the modulation of the input conductance as a function of $t-\hat{t}$ is depicted in Fig. 4.7.

An input current pulse shortly after the reset at time $\hat{t}$ evokes a postsynaptic potential of much lower amplitude than an input current pulse that arrives much later. Fig. 4.7 qualitatively reproduces the membrane trajectory of motoneurons when stimulated by the same input pattern (Poliakov et al., 1996; Powers and Binder, 1996).

4.2.2 Mapping the Integrate-and-Fire Model to the SRM

In this section, we show that the leaky integrate-and-fire neuron defined in Section 4.1 is a special case of the Spike Response Model. We consider an integrate-and-fire neuron driven by external current $I^{\rm ext}$ and postsynaptic current pulses $\alpha(t - t_j^{(f)})$. The potential u_i is thus given by

$$\tau_m \frac{{\rm d}u_i}{{\rm d}t} = - u_i(t) + R \sum_j w_{ij} \sum_f \alpha(t - t_j^{(f)}) + R\, I_i^{\rm ext}(t)\,. \qquad (4.33)$$

In order to construct a mapping of the integrate-and-fire model to the Spike Response Model, we integrate Eq. (4.33) with $u(\hat{t}_i) = u_r$ as its initial condition. The result is in analogy to Eq. (4.10)

$$\begin{aligned} u(t) = {} & u_r \exp\left(-\frac{t-\hat{t}_i}{\tau_m}\right) \qquad (4.34)\\ & + \sum_j w_{ij} \sum_f \frac{1}{C}\int_0^{t-\hat{t}_i} \exp\left(-\frac{s}{\tau_m}\right) \alpha(t - t_j^{(f)} - s)\, {\rm d}s \\ & + \frac{1}{C}\int_0^{t-\hat{t}_i} \exp\left(-\frac{s}{\tau_m}\right) I_i^{\rm ext}(t-s)\, {\rm d}s \\ = {} & \eta(t-\hat{t}_i) + \sum_j w_{ij} \sum_f \epsilon(t-\hat{t}_i, t - t_j^{(f)}) + \int_0^\infty \kappa(t-\hat{t}_i, s)\, I_i^{\rm ext}(t-s)\, {\rm d}s\,, \end{aligned}$$

with

$$\eta(s) = u_r \exp\left(-\frac{s}{\tau_m}\right), \qquad (4.35)$$

$$\epsilon(s,t) = \frac{1}{C}\int_0^s \exp\left(-\frac{t'}{\tau_m}\right) \alpha(t-t')\, {\rm d}t'\,, \qquad (4.36)$$

$$\kappa(s,t) = \frac{1}{C} \exp\left(-\frac{t}{\tau_m}\right) \Theta(s-t)\, \Theta(t)\,. \qquad (4.37)$$

As usual, $\Theta(x)$ denotes the Heaviside step function. The kernels (4.35)-(4.37) allow us to map the integrate-and-fire neuron exactly to the the Spike Response Model, as desired; cf. Eq. (4.24).

In order obtain an explicit expression for the ϵ kernel (4.36) we have to specify the time course of the postsynaptic current $\alpha(s)$. Here, we take $\alpha(s)$ as defined in (4.21), viz.,

$$\alpha(s) = \frac{q}{\tau_s} \exp\left(-s/\tau_s \right) \Theta(s) . \tag{4.38}$$

With $q = C = 1$, the integration of Eq. (4.36) yields

$$\epsilon(s, t) = \frac{\exp\left(-\frac{\max(t-s,0)}{\tau_s}\right)}{1 - \frac{\tau_s}{\tau_m}} \left[\exp\left(- \frac{\min(s,t)}{\tau_m} \right) - \exp\left(- \frac{\min(s,t)}{\tau_s} \right) \right] \Theta(s)\, \Theta(t) ; \tag{4.39}$$

cf. Fig. 4.8. If presynaptic spikes arrive before the last postsynaptic spike, then they have only a small effect on the actual value of the membrane potential because only that part of the postsynaptic current that arrives after $\hat{t}_i$ contributes to the postsynaptic potential. Spikes that arrive after $\hat{t}_i$ produce a full postsynaptic potential. Note that causality implies that the ϵ kernel has to vanishes for negative arguments.

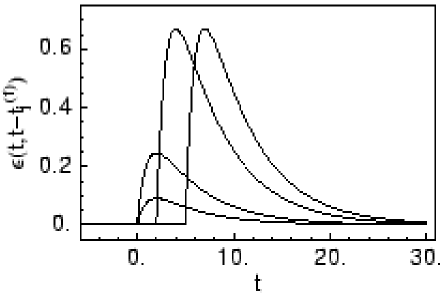

Figure 4.8: The kernel $\epsilon(t, t - t_j^{(f)})$ as a function of t for various presynaptic firing times $t_j^{(f)} = -2, -1, 2, 5$; cf. Eq. (4.39) with $\tau_s = 1$ and $\tau_m = 5$. The last postsynaptic spike was at $\hat{t} = 0$. If presynaptic spikes arrive before the last postsynaptic spike, then they have only a small effect on the membrane potential; cf. the two small EPSPs that correspond to $t_j^{(f)} = -2$ and $t_j^{(f)} = -1$. If presynaptic spikes arrive after the last postsynaptic spike then they evoke a full-blown EPSP; cf. the two large EPSPs that correspond to $t_j^{(f)} = 2$ and $t_j^{(f)} = 5$.

4.2.2.1 Example: Spike-time dependent time constant

We have seen above that the Spike Response Model contains the integrate-and-fire model as a special case. In this example, we show in addition that even a generalization of the integrate-and-fire model that has a time dependent membrane time constant can be described within the SRM framework.

To be specific, we consider an integrate-and-fire model with spike-time dependent time constant, i.e., with a membrane time constant τ that is a function of the time since the last postsynaptic spike,

$$\frac{{\rm d}u}{{\rm d}t} = -\frac{u}{\tau(t-\hat{t})} + \frac{1}{C}\, I^{\rm ext}(t)\,; \qquad (4.40)$$

cf. Stevens and Zador (1998); Wehmeier et al. (1989). As usual, $\hat{t}$ denotes the last firing time of the neuron. The neuron is insensitive to input during an absolute refractory period of duration $\Delta^{\rm abs}$.

After the refractory period, the membrane potential is reset to a value u_r. Starting the integration of Eq. (4.40) at $u(\hat{t} + \Delta^{\rm abs}) = u_r$, we find for $t > \hat{t} + \Delta^{\rm abs}$

$$u(t) = u_{\rm r} \exp\left[-\int_{\hat{t}+\Delta^{\rm abs}}^{t} \frac{{\rm d}t'}{\tau(t'-\hat{t})} \right] \qquad (4.41)$$

$$+ \frac{1}{C} \int_0^\infty \Theta(t - \hat{t} - \Delta^{\rm abs} - s) \exp\left[-\int_{t-s}^{t} \frac{{\rm d}t'}{\tau(t'-\hat{t})} \right] I^{\rm ext}(t-s)\, {\rm d}s\,,$$

which is a special case of Eq. (4.24). As we have seen above in Fig. 4.6, the effective membrane time constant of many standard neuron models is reduced immediately after a spike. The reason is that, after a spike, many ion channels are open so that conductance is increased. Since the time constant is inversely proportional to the conductance, the time constant is decreased. The relation between ion channels and spike-time dependent time constant will be discussed in more detail in Section 4.3.2.

4.2.3 Simplified Model SRM$_0$

The phenomenological neuron model SRM$_0$ introduced in Chapter 1.3.1 is a special case of the Spike Response Model. In this section we review its relation to the SRM and the integrate-and-fire model.

4.2.3.1 Relation to the SRM

A simplified version of the spike response model can be constructed by neglecting the dependence of κ and ϵ upon the first argument. We set

$$\epsilon_0(s) = \epsilon_{ij}(\infty, s)$$

$$\kappa_0(s) = \kappa_{ij}(\infty, s)$$

and use (4.24) in the form

(4.42)

$$u_i(t) = \eta(t - \hat{t}_i) + \sum_j w_{ij} \sum_{t_j^{(f)}} \epsilon_0(t - t_j^{(f)}) + \int_0^{\infty} \kappa_0(s)\, I^{\text{ext}}(t - s)\, ds .$$

Each presynaptic spike thus evokes a postsynaptic potential with the same time course, independent of the index *j* of the presynaptic neuron and independent of the last firing time $\hat{t}_i$ of the postsynaptic neuron. The amplitude of the response is scaled with the synaptic efficacy w_{ij}. The postsynaptic potentials are summed until the firing threshold ϑ is reached. In Fig. 4.9 we have assumed a constant threshold. Each output spike is approximated by a δ pulse, followed by a reset to a value below resting potential so as to account for a hyperpolarizing spike after-potential,

$$\eta(t - \hat{t}) = \delta(t - \hat{t}) - \eta_0 \exp\left(- \frac{t - \hat{t}}{\tau_{\text{recov}}} \right) , \qquad (4.43)$$

with a parameter $\eta_0 > 0$. The spike after-potential decays back to zero with a recovery time constant τ_{recov}. This simple version of the Spike Response Model (SRM$_0$ for short) has been used in the analysis of the computational power of spiking neurons (Maass, 1996,1998), of network synchronization (Gerstner et al., 1996b), and collective phenomena in locally coupled networks (Kistler et al., 1998; Kistler, 2000). The model defined in Eq. (4.42) can also be fitted to experimental data (Brillinger and Segundo, 1979; Brillinger, 1988,1992).

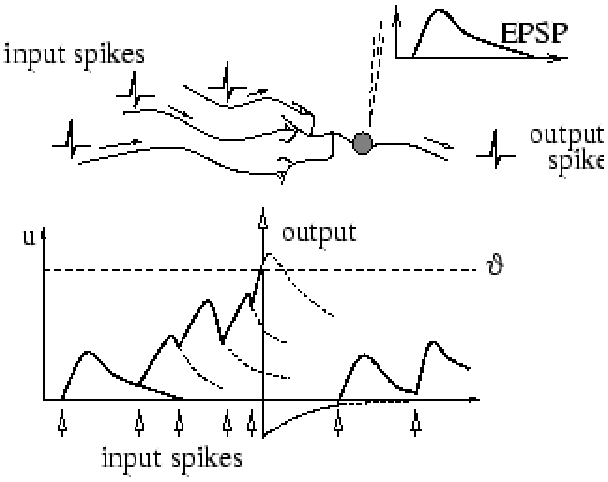

Figure 4.9: Spike Response Model SRM$_0$ with constant threshold (schematic). Each input pulse causes an excitatory postsynaptic potential (EPSP) $\epsilon_0(s)$. All EPSPs are added. If the threshold is reached an output spike is emitted (arrow) and a negative kernel $\eta(s)$ is added so that the voltage is reset.

4.2.3.2 Dynamic threshold interpretation

The simplified model SRM$_0$ defined in (4.42) with the η kernel defined in (4.43) can be reinterpreted as a model with a dynamic threshold,

$$\vartheta(t-\hat{t}) = \vartheta - \eta_0(t-\hat{t}) \,, \tag{4.44}$$

that is increased after each spike. Firing occurs if

$$h_i(t) = \vartheta(t-\hat{t}) \,, \tag{4.45}$$

where h_i is the input potential,

$$h_i(t) = \sum_j w_{ij} \sum_{t_j^{(f)}} \epsilon_0(t - t_j^{(f)}) + \int_0^\infty \kappa_0(s)\, I^{ext}(t - s)\, ds \,. \tag{4.46}$$

We emphasize that h_i depends on the input only. In particular, there is no dependence upon $\hat{t}_i$. The next spike occurs if the input potential $h_i(t)$ reaches the dynamic threshold $\vartheta(t-\hat{t})$; cf. Fig. 4.10.

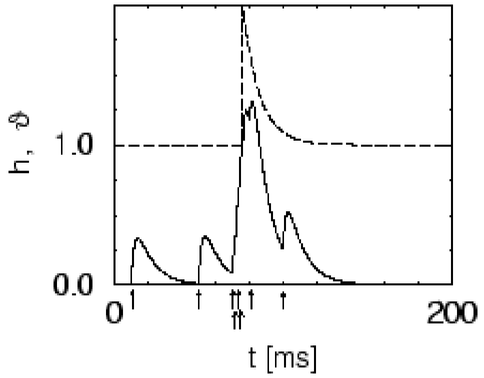

Figure 4.10: Dynamic threshold interpretation. The input potential $h(t)$ (solid line) is generated by the superposition of the EPSPs (solid line) caused by presynaptic spikes. Each spike arrival is denoted by an arrow. An output spike occurs, if h hits the dynamic threshold ϑ (dashed line). At the moment of spiking the value of the threshold is increased by one. After the spike, the threshold decays exponentially back to its resting value $\vartheta = 1$.

4.2.3.3 Relation to the integrate-and-fire model

The basic equation of the leaky integrate-and-fire model, Eq. (4.3), is a *linear* differential equation. However, because of the reset of the membrane potential after firing, the integration is not completely trivial. In fact, there are two different ways of proceeding with the integration of Eq. (4.3). In Section 4.2.2 we have treated the reset as a new initital condition and thereby constructed an exact mapping of the integrate-and-fire model to the Spike Response Model. We now turn to the second method and describe the reset as a current pulse. As we will see, the result is an approximative mapping to the simplified model SRM$_0$.

Let us consider a short current pulse $I_i^{out} = -q\,\delta(t)$ applied to the *RC* circuit of Fig. 4.1. It removes a charge q from the capacitor C and lowers the potential by an amount $\Delta u = - q/C$. Thus, a reset of the membrane potential from a value of $u = \vartheta$ to a new value $u = u_r$ corresponds to an `output' current pulse which removes a charge $q = C\,(\vartheta - u_r)$. The reset takes place every time when the neuron fires. The total reset current is therefore

$$I_i^{\rm out}(t) = - C\,(\vartheta - u_r) \sum_f \delta(t - t_i^{(f)})\,, \tag{4.47}$$

where the sum runs over all firing times $t_i^{(f)}$. We add the output current (4.47) on the right-hand side of (4.3),

$$\tau_m \frac{{\rm d}u_i}{{\rm d}t} = - u_i(t) + R\,I_i(t) + R\,I_i^{\rm out}(t)\,. \tag{4.48}$$

Here, I_i is the total input current to neuron i, generated by presynaptic spike arrival and by external stimulation $I_i^{\rm ext}(t)$. Let us assume that each presynaptic pulse evokes a postsynaptic current with time course $\alpha(t - t_j^{(f)})$. The total input current is then

$$I_i(t) = \sum_j w_{ij} \sum_f \alpha(t - t_j^{(f)}) + I_i^{\rm ext}(t)\,. \tag{4.49}$$

Since (4.48) is a linear equation, we can integrate each term separately and superimpose the result at the end. The output pulse $I_i^{\rm out}$ yields a refractory kernel η_0 while each postsynaptic current pulse α generates a postsynaptic potential ϵ_0. More specifically, we have after integration with initial condition $\lim_{t_0 \to -\infty} u_i(t_0) = 0$

$$u_i(t) = \sum_f \eta_0(t - t_i^{(f)}) + \sum_j w_{ij} \sum_f \epsilon_0(t - t_j^{(f)}) + \int_0^\infty \kappa_0(s)\, I_i^{\rm ext}(t - s)\, {\rm d}s\,, \tag{4.50}$$

with kernels

$$\eta_0(s) = - (\vartheta - u_r) \exp\left(- \frac{s}{\tau_m} \right) \Theta(s)\,, \tag{4.51}$$

$$\epsilon_0(s) = \frac{1}{C} \int_0^\infty \exp\left(- \frac{s'}{\tau_m} \right) \alpha(s - s')\, {\rm d}s'\, \Theta(s)\,, \tag{4.52}$$

$$\kappa_0(s) = \frac{1}{C} \exp\left(- \frac{s}{\tau_m} \right) \Theta(s)\,. \tag{4.53}$$

The refractory kernel $\eta_0(s)$ and the postsynaptic potential ϵ_0 are shown in Fig. 4.11.

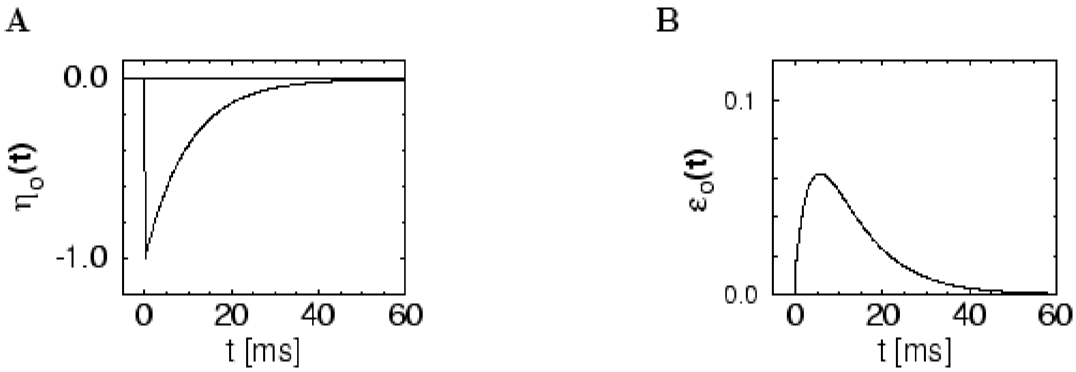

Figure 4.11: **A**. The refractory kernel η_0 of the integrate-and-fire model with membrane time constant τ_m = 10ms. **B**. The postsynaptic potential $\epsilon_0(t)$ generated by an exponential current pulse $\alpha(t) \propto \exp(-t/\tau_s)$.

We note that, in contrast to Eq. (4.42), we still have on the right-hand side of Eq. (4.50) a sum over past spikes of neuron *i*. According to Eq. (4.51) the effect of the η_0-kernel decays with a time constant τ_m. In realistic spike trains, the interval between two spikes is typically much longer than the membrane time constant τ_m. Hence the sum over the η_0 terms is usually dominated by the *most recent* firing time $t_i^{(f)} < t$ of neuron *i*. We therefore truncate the sum ofer *f* and neglect the effect of earlier spikes,

$$\sum_f \eta_0(t - t_i^{(f)}) \longrightarrow \eta_0(t - \hat{t}_i)\,, \tag{4.54}$$

where $\hat{t}_i = \max\{t_i^{(f)} < t\}$ is the last firing time of neuron *i*. The approximation (4.54) is good if the mean firing rate of the neuron is low, i.e., if the intervals between two spikes are much longer than τ_m. Loosely speaking, the neuron remembers only its most recent firing. Equation (4.54) is therefore called `short-term memory approximation' (Gerstner et al., 1996b). The final equation is

$$u_i(t) = \eta_0(t - \hat{t}_i) + \sum_j w_{ij} \sum_f \epsilon_0(t - t_j^{(f)}) + \int_0^\infty \kappa(s)\, I^{\rm ext}(t - s)\, ds\,. \tag{4.55}$$

This is exactly the equation for the model SRM$_0$, defined in (4.42). Note that we have kept, on the right-hand side of (4.55), the sum over all *presynaptic* firing times $t_j^{(f)}$. Only the sum over the η_0's has been truncated.

A careful comparison of Eq. (4.51) with Eq. (4.35) shows that the kernel η_0 is different from the kernel η derived previously for the *exact* mapping of the integrate-and-fire model to the full Spike Response Model. The difference is most easily seen if we set the reset potential to $u_r = 0$. While the kernel η in Eq. (4.35) vanishes in this case, the kernel η_0 is nonzero. In fact, whereas in the full

SRM the reset is taken care of by the definition of $\epsilon(t - \hat{t}, s)$ and $\kappa(t - \hat{t}, s)$, the reset in the simplified model SRM$_0$ is included in the kernel η_0. The relation between the kernels of the simplified model SRM$_0$ to that of the full model are discussed below in more detail.

4.2.3.4 Example: Postsynaptic potential ϵ_0

If $\alpha(s)$ is given by (4.21), then the integral on the right-hand side of (4.52) can be done and yields

$$\epsilon_0(s) = \frac{1}{1-(\tau_s/\tau_m)} \left[\exp\left(-\frac{s}{\tau_m}\right) - \exp\left(-\frac{s}{\tau_s}\right) \right] \Theta(s) \,, \tag{4.56}$$

where we have set $q = C = 1$. This is the postsynaptic potential ϵ_0 illustrated in Fig. 4.11B. We note that ϵ_0 defined in Eq. (4.56) is closely related, but not identical to the kernel ϵ introduced in Eq. (4.39).

4.2.3.5 Relation between the kernels ϵ_0 and ϵ (*)

What is the relation between the ϵ kernel derived in (4.36) and the ϵ_0 introduced in (4.52)? We will show in this paragraph that

$$\epsilon(s, t) = \epsilon_0(t) - \exp\left(-\frac{s}{\tau_m}\right) \epsilon_0(t - s) \tag{4.57}$$

holds. To this end we rewrite Eq. (4.36) as

$$\begin{aligned} \epsilon(s, t) &= \frac{1}{C}\int_0^\infty \exp\left(-\frac{t'}{\tau_m}\right) \alpha(t - t')\,\mathrm{d}t' - \frac{1}{C}\int_s^\infty \exp\left(-\frac{t'}{\tau_m}\right) \alpha(t - t')\,\mathrm{d}t' \\ &= \frac{1}{C}\int_0^\infty \exp\left(-\frac{t'}{\tau_m}\right) \alpha(t - t')\,\mathrm{d}t' \\ &\quad - \exp\left(-\frac{s}{\tau_m}\right) \frac{1}{C}\int_0^\infty \exp\left(-\frac{t'}{\tau_m}\right) \alpha(t - t' - s)\,\mathrm{d}t' \,. \end{aligned} \tag{4.58}$$

Using the definition (4.52) of ϵ_0 yields Eq. (4.57).

By a completely analogous sequence of transformations it is possible to show that

$$\kappa(x, s) = \kappa_0(s) - \exp\left(-\frac{x}{\tau_m}\right) \kappa_0(s - x) \,. \tag{4.59}$$

The total postsynaptic potential $h(t|\hat{t}_i)$ defined in (4.28) can therefore be expressed via the input potential $h_i(t)$ (Gerstner, 2000b)

$$h(t|\hat{t}_i) = h_i(t) - \exp\left(- \frac{t - \hat{t}_i}{\tau_m} \right) h_i(\hat{t}_i) \qquad (4.60)$$

As expected, the reset at $\hat{t}_i$ has an influence on the total postsynaptic potential. We emphasize that the expressions (4.58)-(4.60) hold only for the integrate-and-fire model.

Similarly we can compare the η kernel in (4.35) and the η_0 kernel defined in (4.51),

$$\eta(s) = \eta_0(s) + \vartheta \exp\left(- \frac{s}{\tau_m} \right) . \qquad (4.61)$$

We can thus write the potential in the form

$$\begin{aligned} u_i(t) &= \eta(t - \hat{t}_i) + h(t|\hat{t}_i) \\ &= \eta_0(t - \hat{t}_i) + h(t) - [h(\hat{t}_i) - \vartheta] \exp\left(- \frac{t - \hat{t}_i}{\tau_m} \right) . \end{aligned} \qquad (4.62)$$

The truncation in (4.54) is therefore equivalent to a neglection of the last term in (4.62).

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Next: 4.3 From Detailed Models **Up:** 4. Formal Spiking Neuron **Previous:** 4.1 Integrate-and-fire model

Gerstner and Kistler
Spiking Neuron Models. Single Neurons, Populations, Plasticity
Cambridge University Press, 2002