

8

Noisy input models: barrage of spike arrivals

Neurons in the brain receive input from thousands of other, presynaptic neurons, which emit action potentials and send their spikes to their postsynaptic targets. From the perspective of a postsynaptic neuron receiving a barrage of spikes, spike arrival times may look completely random, even under the assumption that presynaptic neurons generate their spikes by a deterministic process. Indeed, as we have seen in the preceding chapter, internal noise sources of a cell, such as spontaneous opening of ion channels, do not account for all the variability of spike-trains encountered in freely behaving animals *in vivo*. Rather, it is likely that a large fraction of the apparent variability is generated by the network. Modeling studies confirm that networks with fixed random connectivity can lead to chaos on the microscopic level, so that spike arrival times appear to be random even if generated by a deterministic network.

In this chapter, we discuss the consequences of stochastic spike arrivals for modeling. The “noise” generated by the network is often described by a noise term in the differential equation of the membrane voltage (Section 8.1). Such a noise term, typically modeled as white noise or colored noise, can be derived in a framework of stochastic spike arrival, as shown in Section 8.2. Stochastic spike arrival leads to fluctuations of the membrane potential which will be discussed in the case of a passive membrane (Section 8.2.1) – or, more generally, for neuron models in the subthreshold regime. In Section 8.3 we discuss the differences between subthreshold and superthreshold stimulation and explain its consequences for spike-train variability. We close the discussion of stochastic spike arrival models in Section 8.4 with a more mathematically oriented exposition of the diffusion limit and the Fokker–Planck equation.

8.1 Noise input

Neurons are driven by an input current $I(t)$ which summarizes the effect of synaptic input from other neurons in the network *in vivo* or the current injected by an experimenter into a cell *in vitro*. Modeling the noisiness of the input amounts to splitting the input current into two components, a deterministic and a stochastic one

$$I(t) = I^{\text{det}}(t) + I^{\text{noise}}(t), \quad (8.1)$$

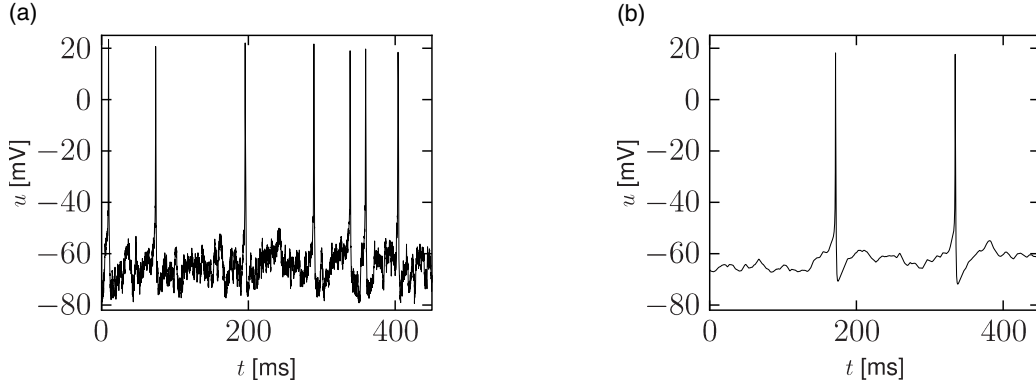


Fig. 8.1 Noisy input. (a). A Hodgkin–Huxley model with parameters as in Chapter 2 driven with white-noise input. (b). The same model driven with colored noise with time constant $\tau_s = 50$ ms. Note that the fluctuations of the membrane potential are slower.

where the deterministic term I^{det} summarizes the part of the current which is known, or at least predictable, while the stochastic term I^{noise} is the unpredictable, or noisy, part of the current.

For example, during an *in vitro* study with intracellular current injection, I^{det} would be the current that is set on the switchboard of the current generator, but the actual current fluctuates around the preset value because of finite temperature. In a neural recording during a visual psychophysics experiment *in vivo*, the part of the input current that does not change across trials with the same visual stimulus would be summarized as I^{det} , while all the remaining inputs to the neuron, which vary from one trial to the next, are treated as noise and summarized as I^{noise} .

For modeling, the noise term is simply added on the right-hand side of the differential equation of the voltage. For example, a nonlinear integrate-and-fire model with noisy input has the voltage equation

$$\tau_m \frac{d}{dt} u = f(u) + RI^{\text{det}}(t) + RI^{\text{noise}}(t). \quad (8.2)$$

If u reaches the threshold θ_{reset} , the integration is stopped and the membrane potential reset to u_r . The procedure of adding input noise is completely analogous for biophysical models of the Hodgkin–Huxley type or integrate-and-fire models with adaptation; see Fig. 8.1.

8.1.1 White noise

The standard procedure of implementing the noise term RI^{noise} in the differential equation of the membrane voltage is to formulate it as a “white noise,” $RI^{\text{noise}}(t) = \xi(t)$. White noise ξ is a stochastic process characterized by its expectation value,

$$\langle \xi(t) \rangle = 0, \quad (8.3)$$

and the autocorrelation

$$\langle \xi(t) \xi(t') \rangle = \sigma^2 \tau_m \delta(t - t'), \quad (8.4)$$

where σ is the amplitude of the noise (in units of voltage) and τ_m the time constant of the differential equation (8.2). Eq. (8.4) indicates that the process ξ is uncorrelated in time: knowledge of the value ξ at time t does not enable us to predict its value at any other time $t' \neq t$. The Fourier transform of the autocorrelation function (8.4) yields the power spectrum; see Section 7.4. The power spectrum of white noise is flat, i.e., the noise is equally strong at all frequencies.

If the white noise term is added on the right-hand side of (8.2), we arrive at a *stochastic differential equation*, i.e., an equation for a stochastic process,

$$\tau_m \frac{d}{dt} u(t) = f(u(t)) + RI^{\text{det}}(t) + \xi(t), \quad (8.5)$$

also called Langevin equation. In Section 8.2 we will indicate how the noise term $\xi(t)$ can be derived from a model of stochastic spike arrival.

In the mathematical literature, instead of a “noise term” $\xi(t)$, a different style of writing the Langevin equation dominates. To arrive at this alternative formulation we first divide both sides of Eq. (8.5) by τ_m and then multiply by the short time step dt ,

$$du = f(u) \frac{dt}{\tau_m} + RI^{\text{det}}(t) \frac{dt}{\tau_m} + \sigma dW_t, \quad (8.6)$$

where dW_t are the increments of the Wiener process in a short time dt , i.e., dW_t are random variables drawn from a Gaussian distribution with zero mean and variance proportional to the step size dt . This formulation therefore has the advantage that it can be directly used for simulations of the model in discrete time. White noise which is Gaussian distributed is called Gaussian white noise. Note for a numerical implementation of Eq. (8.6) that it is the *variance* of the Gaussian which is proportional to the step size; therefore its standard deviation is proportional to \sqrt{dt} .

Example: Leaky integrate-and-fire model with white noise input

In the case of the leaky integrate-and-fire model (with voltage scale chosen such that the resting potential is at zero), the stochastic differential equation is

$$\tau_m \frac{d}{dt} u(t) = -u(t) + RI^{\text{det}}(t) + \xi(t), \quad (8.7)$$

which is called the Ornstein–Uhlenbeck process (Uhlenbeck and Ornstein, 1930; van Kampen, 1992).

We note that the white noise term on the right-hand side is integrated by a time constant τ_m to yield the membrane potential. Therefore fluctuations of the membrane potential have an autocorrelation with characteristic time τ_m . We will refer to Eq. (8.7) as the Langevin equation of the noisy integrate-and-fire model.

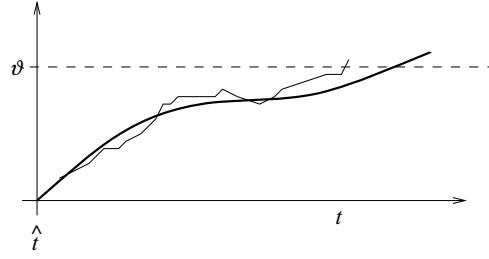


Fig. 8.2 Noisy integration. A stochastic contribution in the input current of an integrate-and-fire neuron causes the membrane potential to drift away from the reference trajectory (thick solid line). The neuron fires if the noisy trajectory (thin line) hits the threshold ϑ .

A realization of a trajectory of the noisy integrate-and-fire model defined by Eq. (8.7) is implemented in discrete time by the iterative update

$$du = (-u + RI^{\text{det}}) \frac{dt}{\tau_m} + \sigma \sqrt{dt} y, \quad (8.8)$$

where y is a random number drawn from a zero-mean Gaussian distribution of unit variance (i.e., $dW = \sqrt{dt} y$ has variance proportional to dt). Note that for small step size dt and finite current amplitude I^{det} , the voltage steps du are small as well so that, despite the noise, the trajectory becomes smooth in the limit of $dt \rightarrow 0$.

A noisy integrate-and-fire neuron is said to fire an action potential whenever the membrane potential u updated via (8.8) reaches the threshold ϑ ; see Fig. 8.2. The analysis of Eq. (8.7) in the presence of the threshold ϑ is one of the major topics of this chapter. Before turning to the problem with threshold, we determine now the amplitude of membrane potential fluctuations in the absence of a threshold.

8.1.2 Noisy versus noiseless membrane potential

The Langevin equation of the leaky integrate-and-fire model with white noise input is particularly suitable to compare the membrane potential trajectory of a noisy neuron model with that of a noiseless one.

Let us consider Eq. (8.7) for constant σ . At $t = \hat{t}$ the membrane potential starts at a value $u = u_r = 0$. Since (8.7) is a linear equation, its solution for $t > \hat{t}$ is

$$u(t) = \frac{R}{\tau_m} \int_0^{t-\hat{t}} e^{-s/\tau_m} I^{(\text{det})}(t-s) ds + \frac{1}{\tau_m} \int_0^{t-\hat{t}} e^{-s/\tau_m} \xi(t-s) ds. \quad (8.9)$$

Since $\langle \xi(t) \rangle = 0$, the expected trajectory of the membrane potential is

$$u_0(t) = \langle u(t|\hat{t}) \rangle = \frac{R}{\tau_m} \int_0^{t-\hat{t}} e^{-s/\tau_m} I^{(\text{det})}(t-s) ds. \quad (8.10)$$

In particular, for constant input current $I^{(\text{det})}(t) \equiv I_0$ we have

$$u_0(t) = u_\infty \left[1 - e^{-(t-\hat{t})/\tau_m} \right] \quad (8.11)$$

with $u_\infty = RI_0$. Note that, in the absence of a threshold, the expected trajectory is that of the noiseless model.

The fluctuations of the membrane potential have variance $\langle \Delta u^2 \rangle = \langle [u(t|\hat{t}) - u_0(t)]^2 \rangle$ with $u_0(t)$ given by Eq. (8.10). The variance can be evaluated with the help of Eq. (8.9), i.e.,

$$\langle \Delta u^2(t) \rangle = \frac{1}{\tau_m^2} \int_0^{t-\hat{t}} ds \int_0^{t-\hat{t}} ds' e^{-s/\tau_m} e^{-s'/\tau_m} \langle \xi(t-s) \xi(t-s') \rangle. \quad (8.12)$$

We use $\langle \xi(t-s) \xi(t-s') \rangle = \sigma^2 \tau_m \delta(s-s')$ and perform the integration. The result is

$$\langle \Delta u^2(t) \rangle = \frac{1}{2} \sigma^2 \left[1 - e^{-2(t-\hat{t})/\tau_m} \right]. \quad (8.13)$$

Hence, noise causes the actual membrane trajectory to drift away from the noiseless reference trajectory $u_0(t)$. If the threshold is high enough so that firing is a rare event, the typical distance between the actual trajectory and the mean trajectory approaches with time constant $\tau_m/2$ a limiting value

$$\sqrt{\langle \Delta u_\infty^2 \rangle} = \frac{1}{\sqrt{2}} \sigma. \quad (8.14)$$

In proximity to the firing threshold the above arguments break down; however, in the subthreshold regime the mean and the variance of the membrane potential are well approximated by formulas (8.11) and (8.13), respectively. The mean trajectory and the standard deviation of the fluctuations can also be estimated in simulations, as shown in Fig. 8.3 for the leaky and the exponential integrate-and-fire models.

8.1.3 Colored noise

A noise term with a power spectrum which is not flat is called colored noise. Colored noise $I^{\text{noise}}(t)$ can be generated from white noise by suitable filtering. For example, low-pass filtering

$$\tau_s \frac{dI^{\text{noise}}(t)}{dt} = -I^{\text{noise}}(t) + \xi(t), \quad (8.15)$$

where $\xi(t)$ is the white noise process defined above, yields colored noise with reduced power at frequencies above $1/\tau_s$. Eq. (8.15) is another example of an Ornstein–Uhlenbeck process.

To calculate the power spectrum of the colored noise defined in Eq. (8.15), we proceed in two steps. First we integrate (8.15) so as to arrive at

$$I^{\text{noise}}(t) = \int_0^\infty \kappa(s) \xi(t-s) ds, \quad (8.16)$$

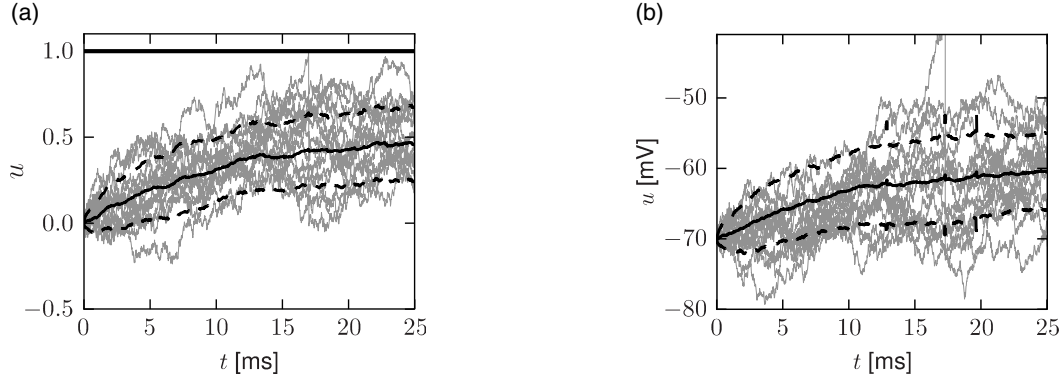


Fig. 8.3 Mean trajectory and fluctuations for (a) the leaky integrate-and-fire model and (b) the exponential integrate-and-fire model driven by white noise superimposed on a constant input that drives the neuron half-way between resting potential and firing threshold. Integration starts at $u = u_r$ and is repeated for 15 trials (gray lines). The solid line indicates mean trajectories and dashed lines indicate one standard deviation around the mean. Both models have a time constant of 10 ms. The threshold is at 1 for the leaky integrate-and-fire neuron (a) and at -50 mV for the exponential integrate-and-fire neuron (b). The numerical threshold is set at $\theta_{\text{reset}} = -30$ mV.

where $\kappa(s)$ is an exponential low-pass filter with time constant τ_s . The autocorrelation function is therefore

$$\langle I^{\text{noise}}(t) I^{\text{noise}}(t') \rangle = \int_0^\infty \int_0^\infty \kappa(s) \kappa(s') \langle \xi(t-s) \xi(t'-s') \rangle ds' ds. \quad (8.17)$$

Second, we exploit the definition of the white noise correlation function in (8.4), and find

$$\langle I^{\text{noise}}(t) I^{\text{noise}}(t') \rangle = a \exp\left(-\frac{|t-t'|}{\tau_s}\right) \quad (8.18)$$

with an amplitude factor a . Therefore, knowledge of the input current at time t gives us a hint about the input current shortly afterward, as long as $|t' - t| \ll \tau_s$.

The noise spectrum is the Fourier transform of (8.18). It is flat for frequencies $\omega \ll 1/\tau_s$ and falls off for $\omega > 1/\tau_s$. Sometimes $1/\tau_s$ is called the cut-off frequency.

The colored noise defined in (8.15) is a suitable noise model for synaptic input, if spikes arrive stochastically and synapses have a finite time constant τ_s . The relation of input noise to stochastic spike arrival is the topic of the next section.

8.2 Stochastic spike arrival

A typical neuron, for example, a pyramidal cell in the vertebrate cortex, receives input spikes from thousands of other neurons, which in turn receive input from their presynaptic neurons and so forth; see Fig. 8.4. While it is not impossible to incorporate millions of integrate-and-fire neurons into a huge network model, it is often reasonable to focus the modeling efforts on a specific subset of neurons, for example, a column in the visual cortex, and describe input from other parts of the brain as a stochastic background activity.

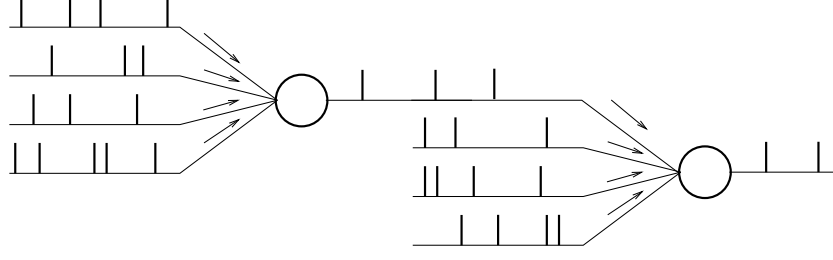


Fig. 8.4 Each neuron receives input spikes from a large number of presynaptic neurons. Only a small portion of the input comes from neurons within the model network; other input is described as stochastic spike arrival.

Let us consider a nonlinear integrate-and-fire neuron with index i that is part of a large network. Its input consists of (i) an external input $I_i^{\text{ext}}(t)$; (ii) input spikes t_j^f from other neurons j of the network; and (iii) stochastic spike arrival t_k^f due to the background activity in other parts of the brain. The membrane potential u_i evolves according to

$$\frac{d}{dt}u_i = \frac{f(u_i)}{\tau_m} + \frac{1}{C}I^{\text{ext}}(t) + \sum_j \sum_{t_j^f} w_{ij} \delta(t - t_j^f) + \sum_k \sum_{t_k^f} w_{ik} \delta(t - t_k^f), \quad (8.19)$$

where δ is the Dirac δ -function and w_{ij} is the coupling strength from a presynaptic neuron j in the network to neuron i . Input from background neurons is weighted by the factor w_{ik} . While the firing times t_j^f are generated by the threshold crossings of presynaptic integrate-and-fire neurons, the firing times t_k^f of a background neuron k are generated by a Poisson process with mean rate ν_k .

To simplify the following discussions we adopt three simplifications. First, we focus on a leaky integrate-and-fire neuron and shift the voltage so that the resting potential is at zero. Hence we can set $f(u) = -u$. Second, we concentrate on a *single* neuron receiving stochastic input from background neurons. Hence we can drop the sum over j which represents input from the network and also drop the index i of our specific neuron. We therefore arrive at

$$\frac{d}{dt}u = -\frac{u}{\tau_m} + \frac{1}{C}I^{\text{ext}}(t) + \sum_k \sum_{t_k^f} w_k \delta(t - t_k^f). \quad (8.20)$$

The membrane potential is reset to u_r whenever it reaches the threshold ϑ . Eq. (8.20) is called Stein's model (Stein, 1965, 1967b).

In Stein's model, each input spike generates a postsynaptic potential $\Delta u(t) = w_k \varepsilon(t - t_k^{(f)})$ with $\varepsilon(s) = e^{-s/\tau_m} \Theta(s)$, i.e., the potential jumps upon spike arrival by an amount w_k and decays exponentially thereafter. Integration of Eq. (8.20) yields

$$u(t|\hat{t}) = u_r \exp\left(-\frac{t - \hat{t}}{\tau_m}\right) + \frac{1}{C} \int_0^{t - \hat{t}} \exp\left(-\frac{s}{\tau_m}\right) I(t - s) ds + \sum_{k=1}^N \sum_{t_k^f} w_k \varepsilon(t - t_k^f) \quad (8.21)$$

for $t > \hat{t}$ where \hat{t} is the last firing time of the neuron. It is straightforward to generalize the model so as to include a synaptic time constant and work with arbitrary postsynaptic potentials $\varepsilon(s)$ that are generated by stochastic spike arrival; see Fig. 8.5a.

8.2.1 Membrane potential fluctuations caused by spike arrivals

To calculate the fluctuations of the membrane potential caused by stochastic spike arrival, we assume that the firing threshold is relatively high and the input weak so that the neuron does not reach its firing threshold. Hence, we can safely neglect both threshold and reset. The leaky integrate-and-fire model of Stein (Eq. (8.21)) is then equivalent to a model of a passive membrane driven by stochastic spike arrival.

We assume that each input spike evokes a postsynaptic potential $w_0 \varepsilon(s)$ of the same amplitude and shape, independent of k . The input statistics is assumed to be Poisson, i.e., firing times are independent. Thus, the total input spike train (summed across all synapses)

$$S(t) = \sum_{k=1}^N \sum_{t_k^f} \delta(t - t_k^f) \quad (8.22)$$

that arrives at neuron i is a random process with expectation

$$\langle S(t) \rangle = v_0 \quad (8.23)$$

and autocorrelation

$$\langle S(t) S(t') \rangle - v_0^2 = v_0 \delta(t - t'); \quad (8.24)$$

see Eq. (7.46).

Suppose that we start the integration of the passive membrane equation at $t = -\infty$ with initial condition $u_r = 0$. We rewrite Eq. (8.21) using the definition of the spike train in Eq. (8.22)

$$u(t) = \frac{1}{C} \int_0^\infty \exp\left(-\frac{s}{\tau_m}\right) I(t-s) ds + w_0 \int_0^\infty \varepsilon(s) S(t-s) ds. \quad (8.25)$$

Obviously, the integration over the δ -function in the last term on the right-hand side is possible and would lead back to the more compact representation $w_0 \sum_{t_k^f} \varepsilon(t - t_k^f)$. The advantage of having the spike train $S(t)$ appear explicitly is that we can exploit the definition of the random process S , in particular, its mean and variance.

We are interested in the mean potential $u_0(t) = \langle u(t) \rangle$ and the variance $\langle \Delta u^2 \rangle = \langle [u(t) - u_0(t)]^2 \rangle$. Using Eqs. (8.23) and (8.24) we find

$$u_0(t) = \frac{1}{C} \int_0^\infty \exp\left(-\frac{s}{\tau_m}\right) I(t-s) ds + w_0 v_0 \int_0^\infty \varepsilon(s) ds \quad (8.26)$$

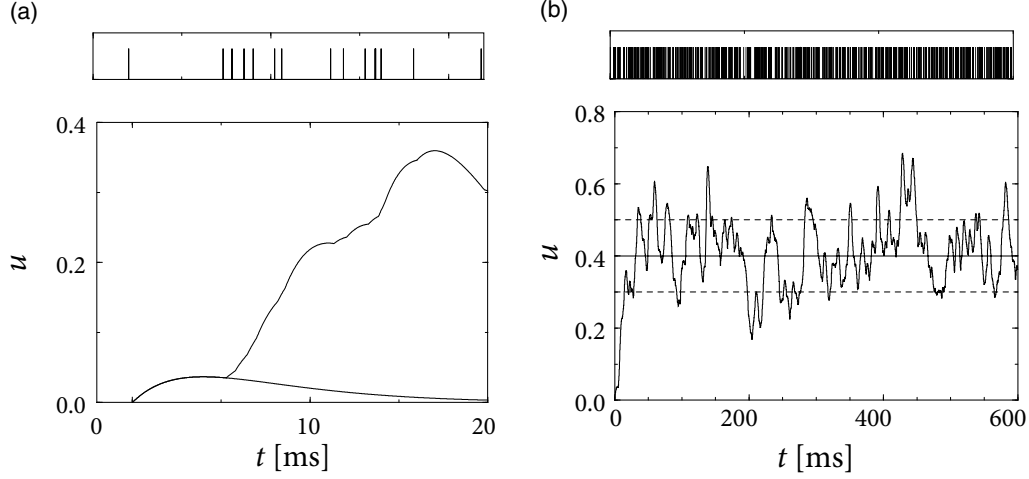


Fig. 8.5 Input spikes arrive stochastically (upper panel) at a mean rate of 1 kHz. (a). Each input spike evokes an excitatory postsynaptic potential (EPSP) $\varepsilon(s) \propto s \exp(-s/\tau)$ with $\tau = 4$ ms. The first EPSP (the one generated by the spike at $t = 0$) is plotted. The EPSPs of all spikes sum up and result in a fluctuating membrane potential $u(t)$. (b). Continuation of the simulation shown in (a). The horizontal lines indicate the mean (solid line) and the standard deviation (dashed lines) of the membrane potential.

and

$$\begin{aligned} \langle \Delta u^2 \rangle &= w_0^2 \int_0^\infty \int_0^\infty \varepsilon_0(s) \varepsilon_0(s') \langle S(t) S(t') \rangle ds ds' - u_0^2 \\ &= w_0^2 v_0 \int_0^\infty \varepsilon^2(s) ds. \end{aligned} \quad (8.27)$$

In Fig. 8.5 we have simulated a neuron which receives input from $N = 100$ background neurons with rate $v_0 = 10$ Hz. The total spike arrival rate is therefore $v_0 = 1$ kHz. Each spike evokes an EPSP $w_0 \varepsilon(s) = 0.1 (s/\tau) \exp(-s/\tau)$ with $\tau = 4$ ms. The evaluation of Eqs. (8.26) and (8.27) for constant input $I = 0$ yields $u_0 = 0.4$ and $\sqrt{\langle \Delta u^2 \rangle} = 0.1$.

Example: Stein's model with step current input

In Stein's model each background spike evokes an EPSP $\varepsilon(s) = e^{-s/\tau_m}$. In addition, we assume a step current input which switches at $t = 0$ from zero to I_0 ($I_0 < 0$).

Mean and fluctuations for Stein's model can be derived by evaluation of Eqs. (8.26) and (8.27) with $\varepsilon(s) = e^{-s/\tau_m}$. The result is

$$u_0 = I_0 [1 - \exp(-t/\tau_m)] + w_0 v_0 \tau_m, \quad (8.28)$$

$$\langle \Delta u^2 \rangle = 0.5 w_0^2 v_0 \tau_m. \quad (8.29)$$

Note that with stochastic spike arrival at excitatory synapses, as considered here, mean and variance cannot be changed independently. As we shall see in the next subsection, a

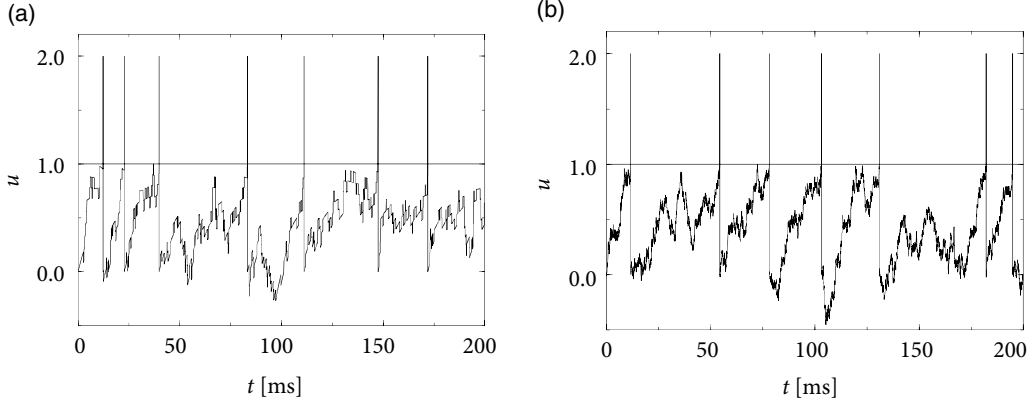


Fig. 8.6 (a). Voltage trajectory of an integrate-and-fire neuron ($\tau_m = 10\text{ms}$, $u_r = 0$) driven by stochastic excitatory and inhibitory spike input at $\nu_+ = \nu_- = 1\text{ kHz}$. Each input spike causes a jump of the membrane potential by $w_{\pm} = \pm 0.1$. The neuron is biased by a constant current $I_0 = 0.8$ which drives the membrane potential to a value just below the threshold of $\vartheta = 1$ (horizontal line). Spikes are marked by vertical lines. (b). Similar plot as in (a) except that the jumps are smaller ($w_{\pm} = \pm 0.025$) while rates are higher ($\nu_{\pm} = 16\text{ kHz}$).

combination of excitation and inhibition allows us to increase the variance while keeping the mean of the potential fixed.

8.2.2 Balanced excitation and inhibition

Let us suppose that an integrate-and-fire neuron defined by Eq. (8.20) with $\tau_m = 10\text{ms}$ receives input from 100 excitatory neurons ($w_k = +0.1$) and 100 inhibitory neurons ($w_k = -0.1$). Each background neuron k fires at a rate of $\nu_k = 10\text{ Hz}$. Thus, in each millisecond, the neuron receives on average one excitatory and one inhibitory input spike. Each spike leads to a jump of the membrane potential of ± 0.1 . The trajectory of the membrane potential is therefore similar to that of a random walk subject to a return force caused by the leak term that drives the membrane potential always back to zero; see Fig. 8.6a.

If, in addition, a constant stimulus $I^{\text{ext}} = I_0 > 0$ is applied so that the mean membrane potential (in the absence of the background spikes) is just below threshold, then the presence of random background spikes may drive u toward the firing threshold. Whenever $u \geq \vartheta$, the membrane potential is reset to $u_r = 0$.

Since firing is driven by the fluctuations of the membrane potential, the interspike intervals vary considerably; see Fig. 8.6. Balanced excitatory and inhibitory spike input could thus contribute to the large variability of interspike intervals in cortical neurons; see Section 8.3.

With the above set of parameters, the mean of the stochastic background input vanishes since $\sum_k w_k \nu_k = 0$. Using the same arguments as in the previous example, we can convince ourselves that the stochastic arrival of background spikes generates fluctuations of

the voltage with variance

$$\langle \Delta u^2 \rangle = 0.5 \tau_m \sum_k w_k^2 v_k = 0.1; \quad (8.30)$$

see Section 8.4 for a different derivation.

Let us now increase all rates by a factor of $a > 1$ and at the same time multiply the synaptic efficacies by a factor $1/\sqrt{a}$. Then both mean and variance of the stochastic background input are the same as before, but the size w_k of the jumps is decreased; see Fig. 8.6b. In the limit $a \rightarrow \infty$ the jump process turns into a diffusion process and we arrive at the stochastic model of Eq. (8.7). In other words, the balanced action of the excitatory and inhibitory spike trains, S^{exc} and S^{inh} respectively, arriving at the synapses with Poisson input rate $\langle S^{\text{exc}} \rangle = \langle S^{\text{inh}} \rangle = a v$ yields in the limit $a \rightarrow \infty$ a white noise input

$$\frac{w}{\sqrt{a}} S^{\text{exc}} - \frac{w}{\sqrt{a}} S^{\text{inh}} \longrightarrow \xi(t). \quad (8.31)$$

The above transition is called the diffusion limit and will be systematically discussed in Section 8.4. Intuitively, the limit process implies that in each short time interval Δt a large number of excitatory and inhibitory input spikes arrive, each one causing the membrane potential to jump by a tiny amount upward or downward.

Example: Synaptic time constants and colored noise

In contrast to the previous discussion of balanced input, we now assume that each spike arrival generated a current pulse $\alpha(s)$ of finite duration so that the total synaptic input current is

$$RI(t) = w^{\text{exc}} \int_0^\infty \alpha(s) S^{\text{exc}}(t-s) ds - w^{\text{inh}} \int_0^\infty \alpha(s) S^{\text{inh}}(t-s) ds. \quad (8.32)$$

If the spike arrival is Poisson with rates $\langle S^{\text{exc}} \rangle = \langle S^{\text{inh}} \rangle = a v$ and the synaptic weights are $w^{\text{exc}} = w^{\text{inh}} = w/\sqrt{a}$, then we can take the limit $a \rightarrow \infty$ with no change of mean or variance. The result is colored noise.

An instructive case is $\alpha(s) = (1/\tau_s) \exp(-s/\tau_s) \Theta(s)$ with synaptic time constant τ_s . In the limit $\tau_s \rightarrow 0$ we are back to white noise.

8.3 Subthreshold vs. superthreshold regime

One of the aims of noisy neuron models is to mimic the large variability of interspike intervals found, for example, in vertebrate cortex. To arrive at broad interval distributions, it is not just sufficient to introduce noise into a neuron model. Apart from the noise level, other neuronal parameters such as the firing threshold or a bias current have to be tuned so as to make the neuron sensitive to noise. In this section we introduce a distinction between super- and subthreshold stimulation (Abeles, 1991; Shadlen and Newsome, 1994; König *et al.*, 1996; Troyer and Miller, 1997; Bugmann *et al.*, 1997).

An arbitrary time-dependent stimulus $I(t)$ is called subthreshold if it generates a membrane potential that stays – in the absence of noise – below the firing threshold. Owing to noise, however, even subthreshold stimuli can induce action potentials. Stimuli that induce spikes even in a noise-free neuron are called superthreshold.

The distinction between sub- and superthreshold stimuli has important consequences for the firing behavior of neurons in the presence of noise. To see why, let us consider a leaky integrate-and-fire neuron with constant input I_0 for $t > 0$. Starting from $u(t=0) = u_r$, the trajectory of the membrane potential is

$$u_0(t) = u_\infty \left[1 - e^{-t/\tau_m} \right] + u_r e^{-t/\tau_m}. \quad (8.33)$$

In the absence of a threshold, the membrane potential approaches the value $u_\infty = RI_0$ for $t \rightarrow \infty$. If we take the threshold ϑ into account, two cases may be distinguished. First, if $u_\infty < \vartheta$ (subthreshold stimulation), the neuron does not fire at all. Second, if $u_\infty > \vartheta$ (superthreshold stimulation), the neuron fires regularly. The interspike interval is s_0 derived from $u_0(s_0) = \vartheta$. Thus

$$s_0 = \tau \ln \frac{u_\infty - u_r}{u_\infty - \vartheta}. \quad (8.34)$$

We now add diffusive noise. In the superthreshold regime, noise has little influence, except that it broadens the interspike interval distribution. Thus, in the superthreshold regime, the spike train in the presence of diffusive noise is simply a noisy version of the regular spike train of the noise-free neuron.

On the other hand, in the subthreshold regime, the spike train changes qualitatively if noise is switched on; see König *et al.* (1996) for a review. Stochastic background input turns the quiescent neuron into a spiking one. In the subthreshold regime, spikes are generated by the *fluctuations* of the membrane potential, rather than by its mean (Abeles, 1991; Shadlen and Newsome, 1994; Troyer and Miller, 1997; Bugmann *et al.*, 1997; Feng, 2001). The interspike interval distribution is therefore broad; see Fig. 8.7.

Example: Interval distribution in the superthreshold regime

For small noise amplitude $0 < \sigma \ll u_\infty - \vartheta$, and superthreshold stimulation, the interval distribution is centered at the deterministic interspike interval s_0 . Its width can be estimated from the width of the fluctuations $\langle \Delta u_\infty^2 \rangle$ of the free membrane potential; see Eq. (8.13). After the reset, the variance of the distribution of membrane potentials is zero and increases slowly thereafter. As long as the mean trajectory is far away from the threshold, the distribution of membrane potentials has a Gaussian shape.

As time goes on, the distribution of membrane potentials is pushed across the threshold. Since the membrane potential crosses the threshold with slope u'_0 , there is a scaling factor $u'_0 = du_0(t)/dt$ evaluated at $t = s_0$ between the (approximately) Gaussian distribution of membrane potential and the interval distribution; see Fig. 8.8. The interval

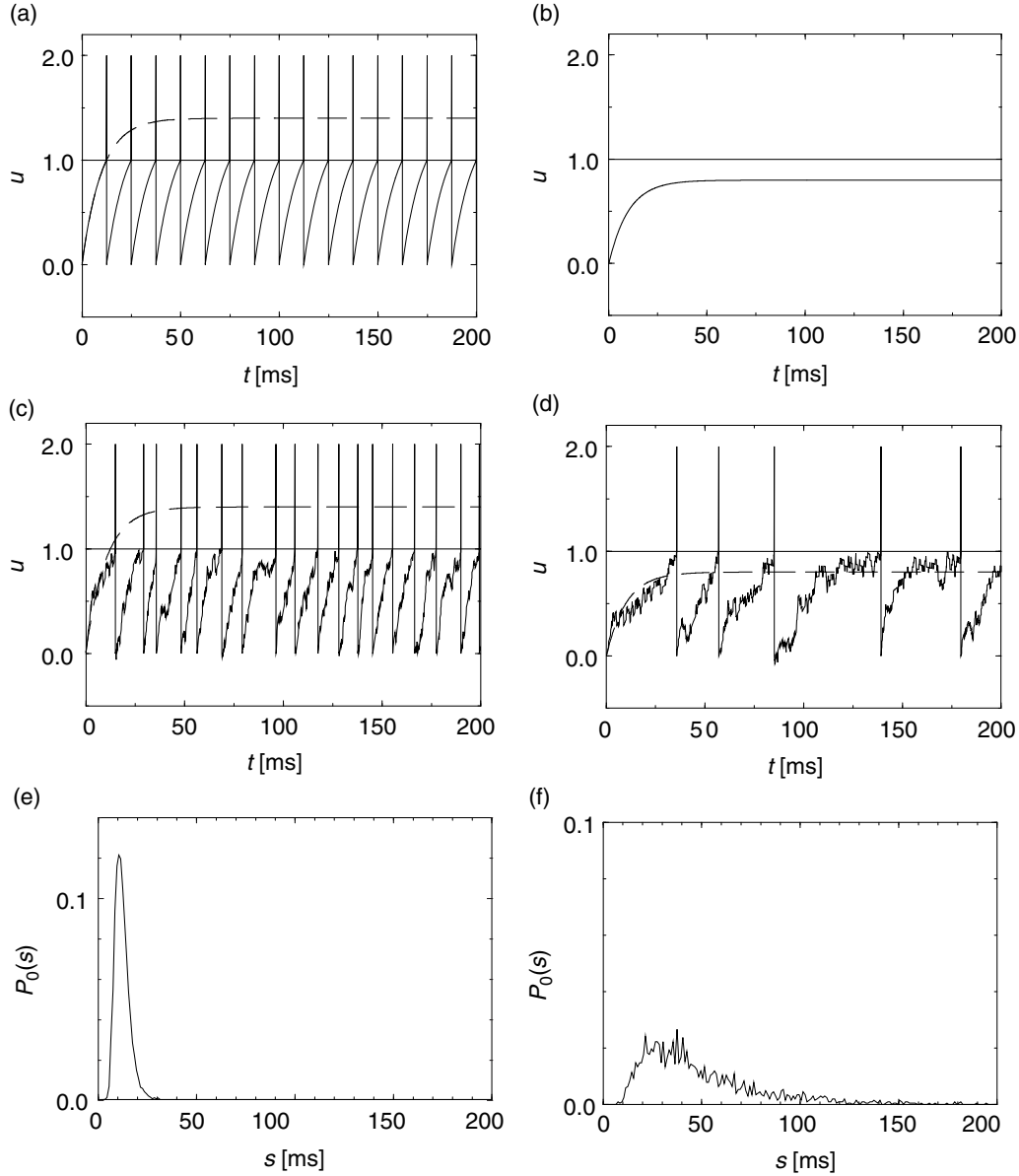


Fig. 8.7 Integrate-and-fire neuron ($\tau_m = 10$ ms) with superthreshold (left column) and subthreshold (right column) stimulation. (a). Without noise, a neuron with superthreshold stimulus I_a fires regularly. Spikes are marked by vertical lines. The threshold is indicated by a horizontal line. The dashed line shows the evolution of the membrane potential in the absence of the threshold. (b). The same neuron with subthreshold stimulation I_b does not fire. (c). If we add stochastic excitatory and inhibitory spike input ($w_{\pm} = 0.05$ at $\nu_{\pm} = 1.6$ kHz) to the constant input I_a , the membrane potential drifts away from the noise-free reference trajectory, but firing remains fairly regular. (d). The same sequence of input spikes added to the subthreshold current I_b generates irregular spiking. (e) and (f) Histogram of interspike intervals in (c) and (d), respectively, as an estimator of the interval distribution $P_0(s)$ in the super- and subthreshold regime. The mean interval $\langle s \rangle$ is 12 ms (e) and 50 ms (f); the C_V values are 0.30 and 0.63, respectively.

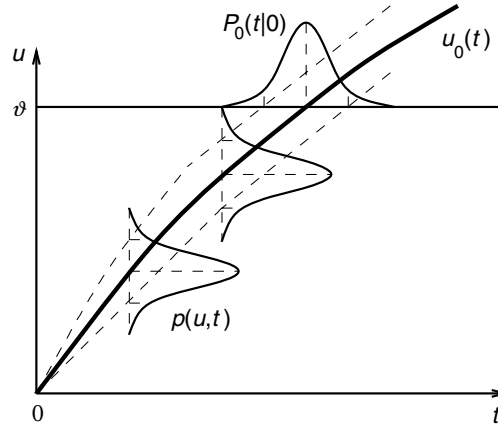


Fig. 8.8 Interval distribution $P_0(t|0)$ for superthreshold stimuli. The membrane potential distribution $p(u, t)$ is shifted across the threshold and generates an interval distribution $P_0(t|0)$ (schematic figure).

distribution is therefore also approximately given by a Gaussian with mean s_0 and width $\sigma/\sqrt{2}u'_0$ (Tuckwell, 1988), i.e.,

$$P_0(t|0) = \frac{1}{\sqrt{\pi}} \frac{u'_0}{\sigma} \exp \left[-\frac{(u'_0)^2 (t - s_0)^2}{\sigma^2} \right]. \quad (8.35)$$

8.4 Diffusion limit and Fokker–Planck equation (*)

In this section we analyze the model of stochastic spike arrival defined in Eq. (8.20) and show how to map it to the diffusion model defined in Eq. (8.7) (Gluss, 1967; Johannesma, 1968; Capocelli and Ricciardi, 1971). Suppose that the neuron has fired its last spike at time \hat{t} . Immediately after the firing the membrane potential was reset to u_r . Because of the stochastic spike arrival, we cannot predict the membrane potential for $t > \hat{t}$, but we can calculate its probability density, $p(u, t)$. The evolution of the probability density as a function of time is described, in the diffusion limit, by the Fokker–Planck equation which we derive here in the context of a *single* neuron subject to noisy input. In Part III (Section 13.1.1) the Fokker–Planck equation will be introduced systematically in the context of populations of neurons.

For the sake of simplicity, we set for the time being $I^{\text{ext}} = 0$ in Eq. (8.20). The input spikes at synapse k are generated by a Poisson process and arrive stochastically with rate $v_k(t)$. The probability that no spike arrives in a short time interval Δt is therefore

$$\text{Prob}\{\text{no spike in } [t, t + \Delta t]\} = 1 - \sum_k v_k(t) \Delta t. \quad (8.36)$$

If no spike arrives in $[t, t + \Delta t]$, the membrane potential changes from $u(t) = u'$ to $u(t + \Delta t) = u' \exp(-\Delta t/\tau_m)$. On the other hand, if a spike arrives at synapse k , the membrane

potential changes from u' to $u' \exp(-\Delta t/\tau_m) + w_k$. Given a value of u' at time t , the probability density of finding a membrane potential u at time $t + \Delta t$ is therefore given by

$$P^{\text{trans}}(u, t + \Delta t | u', t) = \left[1 - \Delta t \sum_k v_k(t)\right] \delta\left(u - u' e^{-\Delta t/\tau_m}\right) + \Delta t \sum_k v_k(t) \delta\left(u - u' e^{-\Delta t/\tau_m} - w_k\right). \quad (8.37)$$

We will refer to P^{trans} as the transition law. Since the membrane potential is given by the differential equation (8.20) with input spikes generated by a Poisson distribution, the evolution of the membrane potential is a Markov Process (i.e., a process without memory) and can be described by (van Kampen, 1992)

$$p(u, t + \Delta t) = \int P^{\text{trans}}(u, t + \Delta t | u', t) p(u', t) du'. \quad (8.38)$$

We insert Eq. (8.37) in Eq. (8.38). To perform the integration, we have to recall the rules for δ -functions, namely, $\delta(au) = a^{-1} \delta(u)$. The result of the integration is

$$p(u, t + \Delta t) = \left[1 - \Delta t \sum_k v_k(t)\right] e^{\Delta t/\tau_m} p\left(e^{\Delta t/\tau_m} u, t\right) + \Delta t \sum_k v_k(t) e^{\Delta t/\tau_m} p\left(e^{\Delta t/\tau_m} u - w_k, t\right). \quad (8.39)$$

Since Δt is assumed to be small, we expand Eq. (8.39) about $\Delta t = 0$ and find to first order in Δt

$$\frac{p(u, t + \Delta t) - p(u, t)}{\Delta t} = \frac{1}{\tau_m} p(u, t) + \frac{1}{\tau_m} u \frac{\partial}{\partial u} p(u, t) + \sum_k v_k(t) [p(u - w_k, t) - p(u, t)]. \quad (8.40)$$

For $\Delta t \rightarrow 0$, the left-hand side of Eq. (8.40) turns into a partial derivative $\partial p(u, t)/\partial t$. Furthermore, if the jump amplitudes w_k are small, we can expand the right-hand side of Eq. (8.40) with respect to u about $p(u, t)$:

$$\tau_m \frac{\partial}{\partial t} p(u, t) = -\frac{\partial}{\partial u} \left[-u + \tau_m \sum_k v_k(t) w_k \right] p(u, t) + \frac{1}{2} \left[\tau_m \sum_k v_k(t) w_k^2 \right] \frac{\partial^2}{\partial u^2} p(u, t), \quad (8.41)$$

where we have neglected terms of order w_k^3 and higher. The expansion in w_k is called the Kramers–Moyal expansion. Eq. (8.41) is an example of a Fokker–Planck equation (van Kampen, 1992), i.e., a partial differential equation that describes the temporal evolution of a probability distribution. The right-hand side of Eq. (8.41) has a clear interpretation: the first term in rectangular brackets describes the systematic drift of the membrane potential due to leakage ($\propto -u$) and *mean* background input ($\propto \sum_k v_k(t) w_k$). The second term in rectangular brackets corresponds to a “diffusion constant” and accounts for the fluctuations

of the membrane potential. The Fokker–Planck equation (8.41) is equivalent to the Langevin equation (8.7) with $RI(t) = \tau_m \sum_k v_k(t) w_k$ and time-dependent noise amplitude

$$\sigma^2(t) = \tau_m \sum_k v_k(t) w_k^2. \quad (8.42)$$

The specific process generated by the Langevin equation (8.7) with *constant* noise amplitude σ is called the Ornstein–Uhlenbeck process (Uhlenbeck and Ornstein, 1930), but Eq. (8.42) indicates that, in the context of neuroscience, the effective noise amplitude generated by stochastic spike arrival is in general time-dependent. We will return to the Fokker–Planck equation in Chapter 13.

For the transition from Eq. (8.40) to (8.41) we have suppressed higher-order terms in the expansion. The missing terms are

$$\sum_{n=3}^{\infty} \frac{(-1)^n}{n!} A_n(t) \frac{\partial^n}{\partial u^n} p(u, t) \quad (8.43)$$

with $A_n = \tau_m \sum_k v_k(t) w_k^n$. What are the conditions that these terms vanish? As in the example of Fig. 8.6a and b, we consider a sequence of models where the size of the weights w_k decreases so that $A_n \rightarrow 0$ for $n \geq 3$ while the mean $\sum_k v_k(t) w_k$ and the second moment $\sum_k v_k(t) w_k^2$ remain constant. It turns out, that, given both excitatory and inhibitory input, it is always possible to find an appropriate sequence of models (Lansky, 1984, 1997). For $w_k \rightarrow 0$, the diffusion limit is attained and Eq. (8.41) is exact. For excitatory input alone, however, such a sequence of models does not exist (Plesser, 1999).

8.4.1 Threshold and firing

The Fokker–Planck equation (8.41) and the Langevin equation (8.7) are equivalent descriptions of drift and diffusion of the membrane potential. Neither of these describe spike firing. To turn the Langevin equation (8.7) into a sensible neuron model, we have to incorporate a threshold condition. In the Fokker–Planck equation (8.41), the firing threshold is incorporated as a boundary condition

$$p(\vartheta, t) \equiv 0 \quad \text{for all } t. \quad (8.44)$$

The boundary condition reflects the fact that, under a white noise model, in each short interval Δt many excitatory and inhibitory input spikes arrive which each cause a tiny jump of size $\pm \delta$ of the membrane potential. Any finite density $p(u, t)$ at a value $\vartheta - \delta < u \leq \vartheta$ would be rapidly removed, because one of the many excitatory spikes which arrive at each moment would push the membrane potential above threshold. The white noise limit corresponds to infinite spike arrival rate and jump size $\delta \rightarrow 0$, as discussed above. As a consequence there are, in each short interval Δt infinitely many “attempts” to push the membrane potential above threshold. Hence the density at $u = \vartheta$ must vanish. The above argument also shows that for colored noise the density at threshold is finite, because the effective frequency of “attempts” is limited by the cut-off frequency of the noise.

Before we continue the discussion of the diffusion model in the presence of a threshold, let us study the solution of Eq. (8.41) without threshold.

Example: Free distribution

The solution of the Fokker–Planck equation (8.41) with initial condition $p(u, \hat{t}) = \delta(u - u_r)$ is a Gaussian with mean $u_0(t)$ and variance $\langle \Delta u^2(t) \rangle$, i.e.,

$$p(u, t) = \frac{1}{\sqrt{2\pi \langle \Delta u^2(t) \rangle}} \exp \left\{ -\frac{[u(t|\hat{t}) - u_0(t)]^2}{2 \langle \Delta u^2(t) \rangle} \right\}, \quad (8.45)$$

as can be verified by inserting Eq. (8.45) into (8.41). In particular, the stationary distribution that is approached in the limit of $t \rightarrow \infty$ for constant input I_0 is

$$p(u, \infty) = \frac{1}{\sqrt{\pi}} \frac{1}{\sigma} \exp \left\{ -\frac{[u - RI_0]^2}{\sigma^2} \right\}, \quad (8.46)$$

which describes a Gaussian distribution with mean $u_\infty = RI_0$ and variance $\sigma/\sqrt{2}$.

8.4.2 Interval distribution for the diffusive noise model

Let us consider a leaky integrate-and-fire neuron that starts at time \hat{t} with a membrane potential u_r and is driven for $t > \hat{t}$ by a known input $I(t)$. Because of the diffusive noise generated by stochastic spike arrival, we cannot predict the exact value of the neuronal membrane potential $u(t)$ at a later time $t > \hat{t}$, only the probability that the membrane potential is in a certain interval $[u_0, u_1]$. Specifically, we have

$$\text{Prob} \{u_0 < u(t) < u_1 | u(\hat{t}) = u_r\} = \int_{u_0}^{u_1} p(u, t) du, \quad (8.47)$$

where $p(u, t)$ is the probability density of the membrane potential at time t . In the diffusion limit, $p(u, t)$ can be found by solution of the Fokker–Planck equation (8.41) with initial condition $p(u, \hat{t}) = \delta(u - u_r)$ and boundary condition $p(\vartheta, t) = 0$.

The boundary is absorbing. In other words, in a simulation of a single realizations of the stochastic process, the simulation is stopped when the trajectory passes the threshold for the first time. To be concrete, imagine that we run 100 simulation trials, i.e., 100 realizations of a leaky integrate-and-fire model with diffusive noise. Each trial starts at the same value $u(\hat{t}) = u_r$ and uses the same input current $I(t')$ for $t' > \hat{t}$. Some of the trials will exhibit trajectories that reach the threshold at some point $t' < t$. Others stay below threshold for the whole period $\hat{t} < t' < t$. The expected fraction of simulations that have not yet reached the threshold and therefore still “survive” up to time t is given by the survivor function,

$$S_I(t|\hat{t}) = \int_{-\infty}^{\vartheta} p(u, t) du. \quad (8.48)$$

In other words, the survivor function in the diffusive noise model is equal to the probability that the membrane potential has not yet reached the threshold between \hat{t} and t .

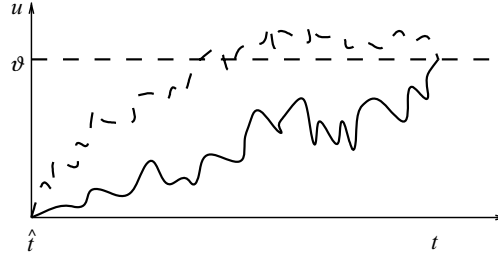


Fig. 8.9 Without a threshold, several trajectories can reach at time t the same value $u = \vartheta$ from above or below.

In view of Eq. (7.24), the input-dependent interval distribution is therefore

$$P_I(t|\hat{t}) = -\frac{d}{dt} \int_{-\infty}^{\vartheta} p(u, t) du. \quad (8.49)$$

We recall that $P_I(t|\hat{t}) \Delta t$ for $\Delta t \rightarrow 0$ is the probability that a neuron fires its next spike between t and $t + \Delta t$ given a spike at \hat{t} and input I . In the context of noisy integrate-and-fire neurons $P_I(t|\hat{t})$ is called the distribution of “first passage times.” The name is motivated by the fact, that firing occurs when the membrane potential crosses ϑ for the first time. Unfortunately, no general solution is known for the first passage time problem of the Ornstein–Uhlenbeck process. For constant input $I(t) = I_0$, however, it is at least possible to give a moment expansion of the first passage time distribution. In particular, the mean of the first passage time can be calculated in closed form.

Example: Numerical evaluation of $P_I(t|\hat{t})$

We have seen that, in the absence of a threshold, the Fokker–Planck equation (8.41) can be solved; see Eq. (8.45). The transition probability from an arbitrary starting value u' at time t' to a new value u at time t is

$$P^{\text{trans}}(u, t | u', t') = \frac{1}{\sqrt{2\pi \langle \Delta u^2(t) \rangle}} \exp \left\{ -\frac{[u - u_0(t)]^2}{2 \langle \Delta u^2(t) \rangle} \right\} \quad (8.50)$$

with

$$u_0(t) = u' e^{-(t-t')/\tau_m} + \int_0^{t-t'} e^{-s'/\tau_m} I(t-s') ds', \quad (8.51)$$

$$\langle \Delta u^2(t) \rangle = \frac{\sigma^2}{2} \left[1 - e^{-2(t-t')/\tau_m} \right]. \quad (8.52)$$

A method due to Schrödinger uses the solution of the unbounded problem in order to calculate the input-dependent interval distribution $P_I(t|\hat{t})$ of the diffusion model with threshold (Schrödinger, 1915; Plesser and Tanaka, 1997; Burkitt and Clark, 1999). The

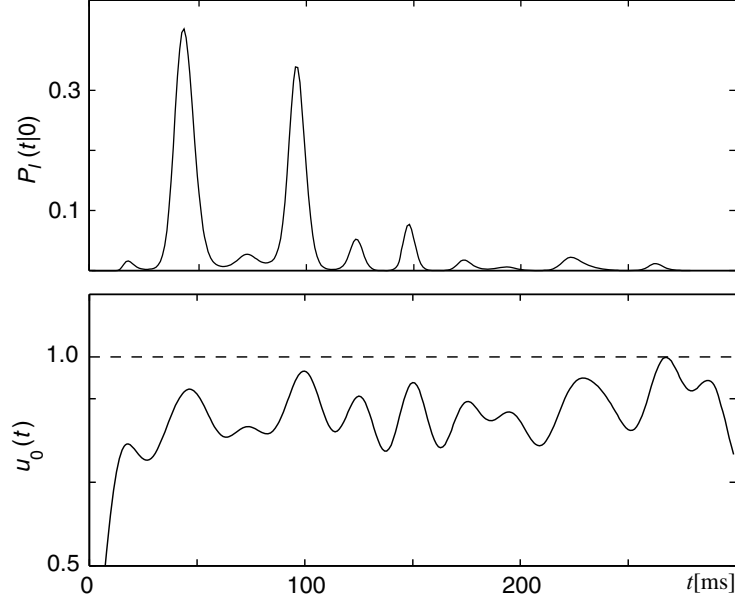


Fig. 8.10 A time-dependent input current $I(t)$ generates a noise-free membrane potential $u_0(t)$ shown in the lower part of the figure. In the presence of diffusive noise, spikes can be triggered although the reference trajectory stays below the threshold (dashed line). This gives rise to an input-dependent interval distribution $P_I(t|0)$ shown in the upper panel. Taken from Plesser and Gerstner (2000).

idea of the solution method is illustrated in Fig. 8.9. Because of the Markov property, the probability density of crossing the threshold (not necessarily for the first time) at a time t is equal to the probability of crossing it for the first time at $t' < t$ and returning back to ϑ at time t , i.e.,

$$P^{\text{trans}}(\vartheta, t | u_r, \hat{t}) = \int_{\hat{t}}^t P_I(t' | \hat{t}) P^{\text{trans}}(\vartheta, t | \vartheta, t') dt'. \quad (8.53)$$

This integral equation can be solved numerically for the distribution $P_I(t' | \hat{t})$ for arbitrary input current $I(t)$ (Plesser, 2000). An example is shown in Fig. 8.10. The probability of emitting a spike is high whenever the noise-free trajectory is close to the firing threshold. Very long intervals are unlikely, if the noise-free membrane potential was already several times close to the threshold before, so that the neuron has had ample opportunity to fire earlier.

8.4.3 Mean interval and mean firing rate (diffusive noise)

For constant input I_0 the mean interspike interval is $\langle s \rangle = \int_0^\infty s P_{I_0}(s|0) ds = \int_0^\infty s P_0(s) ds$; see Eq. (7.13). For the diffusion model Eq. (8.7) with threshold ϑ , reset potential u_r , and

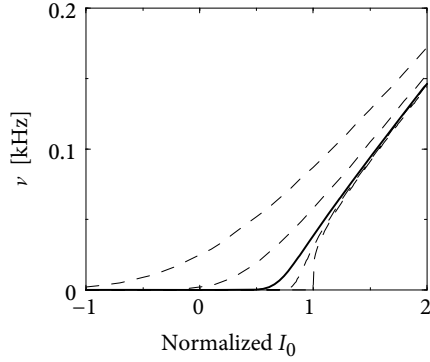


Fig. 8.11 Mean firing rate of a leaky integrate-and-fire model as a function of constant input evaluated for different levels of diffusive noise, using the Siegert formula, Eq. (8.54). From top to bottom: $\sigma = 1.0$, $\sigma = 0.5$, $\sigma = 0.2$ (solid line), $\sigma = 0.1$, $\sigma = 0.0$.

membrane time constant τ_m , the mean interval is

$$\langle s \rangle = \tau_m \sqrt{\pi} \int_{\frac{u_r - h_0}{\sigma}}^{\frac{\vartheta - h_0}{\sigma}} du \exp(u^2) [1 + \operatorname{erf}(u)], \quad (8.54)$$

where $h_0 = RI_0$ is the input potential caused by the constant current I_0 (Siegert, 1951; Johannesma, 1968). Here “erf” denotes the error function $\operatorname{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x \exp(-u^2) du$. This expression, sometimes called the Siegert formula, can be derived by several methods; for reviews see, for example, van Kampen (1992). The inverse of the mean interval is the mean firing rate. Hence, Eq. (8.54) enables us to express the mean firing rate of a leaky integrate-and-fire model with diffusive noise as a function of a (constant) input I_0 (Fig. 8.11). We will derive Eq. (8.54) in Chapter 13 in the context of populations of spiking neurons.

8.5 Summary

Each spike arrival at a synapse causes an excursion of the membrane potential of the post-synaptic neuron. If spikes arrive stochastically the membrane potential exhibits fluctuations around a mean trajectory. If the fluctuations stay in the subthreshold regime where the membrane properties can be approximated by a linear equation, the mean and the standard deviation of the trajectory can be calculated analytically, given the parameters of the stochastic process that characterize spike arrivals. In the presence of a firing threshold, the fluctuations in the membrane potential caused by stochastic spike arrivals can make the neuron fire even if the mean trajectory would never reach the firing threshold.

In the limit that the rate of spike arrival at excitatory and inhibitory synapses is high while each spike causes only a small jump of the membrane potential, synaptic bombardment can be approximated by the sum of two terms: a mean input current and a Gaussian white noise input. The white noise leads to a “diffusion” of the membrane potential trajectory around the mean trajectory. The evolution of the probability distribution $p(u, t)$ of the membrane potential over time is described by a Fokker–Planck equation. For the leaky

integrate-and-fire model and stationary input, the Fokker–Planck equation can be solved analytically. For nonlinear integrate-and-fire neurons and time-dependent input numerical solutions are possible. We will return to the Fokker–Planck equations in Chapter 13 where further results will be derived.

Literature

Stochastic spike arrival as an important source of noise has been discussed by Stein in the context of integrate-and-fire models (Stein, 1965, 1967b). The accessible review article of König *et al.* (1996) highlights how stochastic spike arrival in the input can lead to a broad interspike interval distribution in the output of a neuron. The close relation between stochastic spike arrival and diffusive noise has been known for a long time (Gluss, 1967; Johannesma, 1968). The leaky integrate-and-fire model with diffusive noise is equivalent to the Ornstein–Uhlenbeck process (Uhlenbeck and Ornstein, 1930) with an absorbing boundary. Mathematical results for integrate-and-fire models with diffusive noise are reviewed in Tuckwell (1989). An in-depth treatment of the mathematical theory of stochastic processes and Fokker–Planck equations can be found in van Kampen (1992).

Exercises

1. Colored noise.

(a) Calculate the noise spectrum of the colored noise defined by Eq. (8.15) which we repeat here:

$$\tau_s \frac{dI^{\text{noise}}(t)}{dt} = -I^{\text{noise}}(t) + \xi(t), \quad (8.55)$$

where $\xi(t)$ is white noise with mean zero and variance

$$\langle \xi(t) \xi(t') \rangle = \sigma^2 \tau_s \delta(t - t'). \quad (8.56)$$

(b) Calculate the membrane potential fluctuations $\langle (\Delta u(t))^2 \rangle$ caused by the colored noise in Eq. (8.55), using the differential equation

$$\tau_m \frac{d}{dt} u(t) = -u(t) + RI^{\text{det}}(t) + RI^{\text{noise}}(t). \quad (8.57)$$

(c) Show that the limit process of balanced excitatory and inhibitory input with synaptic time constant τ_s leads to colored noise.

2. Autocorrelation of the membrane potential. Determine the autocorrelation $\langle u(t)u(t') \rangle$ of the Langevin equation (8.7) where $\xi(t)$ is white noise.

3. Membrane potential fluctuations and balance condition. Assume that each spike arrival at an excitatory synapse causes an EPSP with weight $w^{\text{exc}} = +w$ and time course $\varepsilon^{\text{exc}}(t) = (t^2/\tau_{\text{exc}}^3) \exp(-t/\tau_{\text{exc}})$ for $t > 0$. Spike arrival at an inhibitory synapse causes an IPSP with weight $-bw^{\text{exc}}$ and, for $t > 0$, a time course $\varepsilon^{\text{inh}}(t) = (t/\tau_{\text{inh}}^2) \exp(-t/\tau_{\text{inh}})$ where $\tau_{\text{inh}} > \tau_{\text{exc}}$ and $b > 1$.

The membrane potential is

$$u(t) = w^{\text{exc}} \sum_{t^f} \varepsilon^{\text{exc}}(t - t^f) - bw^{\text{inh}} \sum_{t^f} \varepsilon^{\text{inh}}(t - t^f). \quad (8.58)$$

Excitatory and inhibitory spike arrival are generated by Poisson processes rate $v^{\text{exc}} = v_1$ and $v^{\text{inh}} = \beta v_1$, respectively.

- (a) Determine the mean membrane potential.
- (b) Calculate the variance of the fluctuations of the membrane potential.
- (c) You want to increase the rate v_1 without changing the mean or the variance of the membrane potential. Does this limit exist for all combinations of parameters b and β or do you have to impose a specific relation $b = f(\beta)$? Interpret your result.