

Fast transients and rate models

The mathematical formalism necessary for a correct description of the population activity $A(t)$ in homogeneous networks of neurons is relatively involved – as we have seen in Chapters 13 and 14. However, the population activity A_0 in a *stationary* state of asynchronous firing can simply be predicted by the neuronal gain function $g_\sigma(I)$ of isolated neurons; see Chapter 12. It is therefore tempting to extend the results that are valid in the stationary state to the case of time-dependent input. Let us write

$$A(t) = F(h(t)), \quad (15.1)$$

where F is the gain function expressed with the input *potential* $h(t)$ as an argument, as opposed to input *current*. We choose a different symbol, because the units of the argument are different, but the relation of $F(h)$ to the normal frequency–current curve is simply $F(h) = g_\sigma(h/R)$ where $g_\sigma(I_0)$ is the single-neuron gain function for constant input I_0 at some noise level σ and R the membrane resistance.

The input potential h in the argument on the right-hand side of Eq. (15.1) is the contribution to the membrane potential that is caused by the input

$$h(t) = \frac{R}{\tau_m} \int_0^\infty e^{-\frac{s}{\tau_m}} I(t-s) ds, \quad (15.2)$$

where τ_m is the membrane time constant. Eq. (15.2) can also be written in the form of a differential equation

$$\tau_m \frac{dh(t)}{dt} = -h + RI(t). \quad (15.3)$$

Integration of Eq. (15.3) with initial conditions $h(-\infty) = 0$ in the far past leads back to Eq. (15.2) so that the two formulations are equivalent.

By construction, Eqs. (15.1) and (15.2) predict the correct population activity for a *constant* mean input I_0 . From Eq. (15.2) we have $h_0 = RI_0$ so that Eq. (15.1) yields the stationary activity $A_0 = F(h_0) = g_\sigma(I_0)$, as it should.

The question arises whether the rate model defined by Eqs. (15.1) and (15.2) (or, equivalently, by Eqs. (15.1) and (15.3)) is also a valid description for *time-dependent* stimuli. In other words, we ask whether the stationary solution of the population activity can be

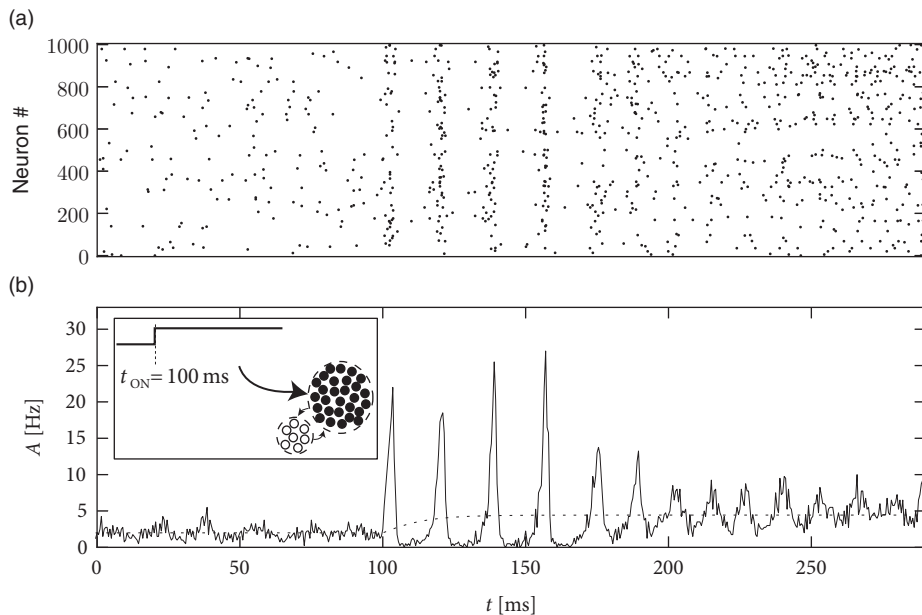


Fig. 15.1 Transients and rate models. All neurons receive the same step current stimulus at time $t_{\text{ON}} = 100$ ms. A randomly connected network of 8000 excitatory and 2000 inhibitory neurons exhibits an abrupt response to the change in the input. (a) The spike trains of 1000 excitatory neurons are shown. Vertical bands of greater spike density are short periods of high activity as shown in the population activity A to the right. Scale bars are 200 ms and 10 Hz. (b) The population activity $A(t)$ exhibits fast transients (full line). In a Standard Rate Model with population activity $A(t) = F(h(t))$, the new stationary state is approached on the time scale defined by the membrane time constant τ_m (here $\tau_m = 4$ ms, dotted line). The response to the input switch at $t_0 = 200$ ms is therefore comparatively slow.

extended to a “quasi-stationary” rate model of the population activity. To answer this question we focus in this chapter on the special case of step stimuli. Strong step stimuli cause a transient response, which can be abrupt in networks of spiking neurons (Fig. 15.1a), but is systematically smooth and slow in the rate model defined above (Fig. 15.1b).

Therefore the question arises whether the “normal” case for neurons *in vivo* is that of an abrupt and *fast* response (which would be absent in the rate model), or that of a smooth and *slow* response as predicted by the rate model. To answer this question, we start in Section 15.1 by taking a closer look at experimental data.

In Section 15.2 we use modeling approaches to give an answer to the question of whether the response to a step stimulus is fast or slow. As we shall see, the response of generalized integrate-and-fire models to a step input can be rapid, if the step is either strong and the noise level is low or if the noise is slow, i.e., not white. However, if the noise is white and the noise level is high, the response to the step input is slow. In this case the rate model defined above in Eqs. (15.1) and (15.2) provides an excellent approximation to the population dynamics.

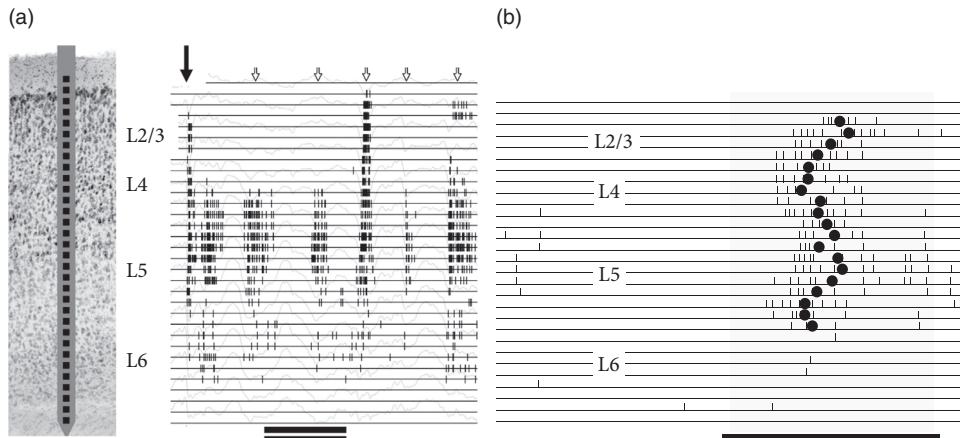


Fig. 15.2 Response of auditory neurons across different layers to short stimuli. (a) Left: Schematic drawing of an electrode with 32 sites overlaid on top of stained cortical tissue in order to show that the electrode crosses all cortical layers. Right: Spike responses of multiple neurons to a short click stimulus (solid arrows) and during spontaneous activity (open arrows). Horizontal scale bar: 500 ms. (b) Responses to a tone sustained during the shaded period. Solid circles indicate estimated peak of response. Scale bar: 50 ms. Neuron recordings in (a) and (b) are from primary auditory cortex. Figures adapted from Sakata and Harris (2009) with permission from Elsevier.

Finally, in Section 15.3, we discuss several variants of rate models. We emphasize that all of the rate models discussed in this section are intended to describe the response of a *population* of neurons to a changing input – as opposed to rate models for single neurons. However, it is also possible to reinterpret a population model as a rate model of a single stochastically firing neuron. Indeed, the single-neuron PSTH accumulated over 200 repetitions of the same time-dependent stimulus is identical to the population activity of 200 neurons in a single trial.

15.1 How fast are population responses?

Simultaneous measurements from many neurons *in vivo* with spike-time resolution are difficult. Fig. 15.2 shows two examples of simultaneous recordings across different layers in the primary auditory cortex. Each of the 32 recording sites is able to pick up activity of several neurons (Fig. 15.2a). The group of recorded neurons in layer 4 responds to a short tone stimulus with a delay of about 15 ms (Fig. 15.2b); the neurons in other layers follow shortly thereafter. Based on several such experiments, we may conclude that population activity in layer 4 exhibits an initial sharp peak less than 20 ms after stimulus onset (Sakata and Harris, 2009). Unfortunately, the number of neurons that are recorded simultaneously in one layer is limited so that an interpretation in terms of population activity is difficult; nevertheless, the data suggests that transients can be fast and reliable on the time scale of 10 ms.

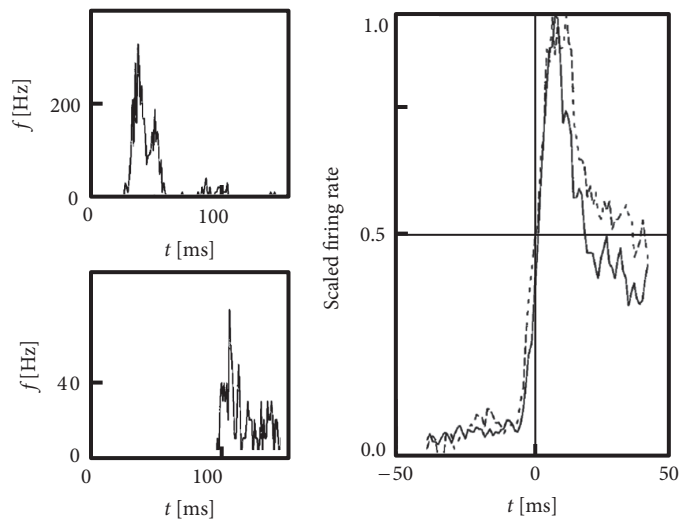


Fig. 15.3 Transient response of neurons in the visual cortex. At $t = 0$ a high-contrast grating is flashed on a gray screen. Top left: A neuron in visual cortex V1 of a behaving monkey responds with a sharp onset after a latency of 27 ms, as shown by the PSTH. Bottom left: Another neuron in V1 responds after a latency of 99 ms. Right: PSTHs of 73 neurons in V1 (solid line) and of 183 neurons in V4 (dashed line) were normalized to an amplitude of 1.0 and onsets were aligned at half the peak value (horizontal and vertical solid lines) and finally averaged. The rise time of the averaged PSTH is less than 10 ms. After the first peak, the firing rate drops off rapidly; adapted from Marsalek *et al.* (1997).

Alternatively, one can attempt to study population activity across many experiments with single-neuron recordings. Neurons in visual cortex V1 and V4 respond reliably to the onset of spatial gratings (Fig. 15.3), as seen in the PSTH accumulated over several repetitions of the stimulus presentation (Marsalek *et al.*, 1997). However, different neurons have different delays. If the PSTHs from many neurons are aligned onto the moment of the sharp rise of the PSTH response, then the resulting population activity exhibits an extremely sharp and abrupt onset peak, followed by a rapid decrease (Marsalek *et al.*, 1997). However, if the responses of different cells were aligned on the moment of stimulus onset, then the population response would look slower, which is not surprising given that the recordings do not come from a single homogeneous population.

In an *in vitro* preparation, the same step current input can be repeatedly given to the same neuron. In order to mimic additional stochastic spike arrivals that would be present *in vivo*, during each repetition a different realization of a noisy current can be added to the step current. Fig. 15.4 shows the response of pyramidal neurons in cortical layer 2/3 to such noisy step inputs, averaged over 12 different cells. The population activity in Fig. 15.4a exhibits a rapid transient, followed by a strongly damped oscillation (Tchumatchenko *et al.*, 2011). As we shall see in the following sections, the oscillatory component indicates

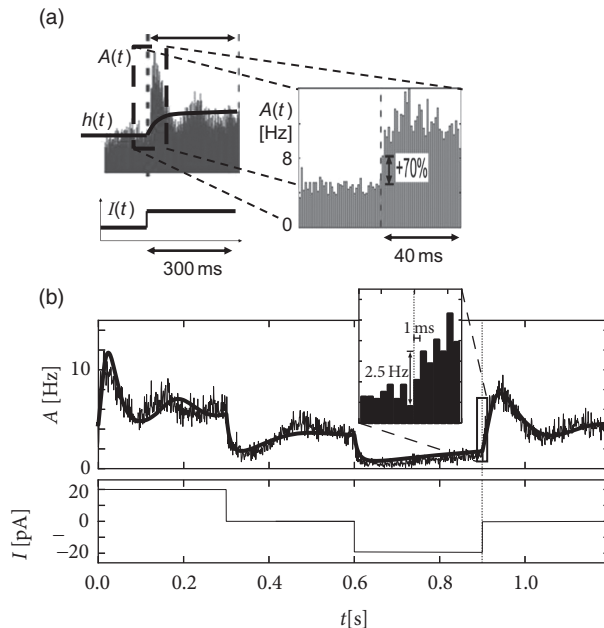


Fig. 15.4 Response of pyramidal cells *in vitro* to step input. (a) The PSTH response of pyramidal cells in cortical layers 2 and 3 averaged across 12 cells gives an estimate of the population activity $A(t)$. The step current ($I(t)$, bottom) generates an input potential $h(t)$ which responds much slower than the population activity $A(t)$. Right: Zoom into $A(t)$. Vertical dashed line indicates stimulus onset. Adapted from Tchumatchenko *et al.* (2011). (b) Experimental data from Tchumatchenko *et al.* (2011) are compared with the numerical integration of the integral equations for adaptive neurons (see Section 14.5). The input current is shown below.

that the noise level of the stochastic input component was chosen fairly low. For low noise, those neurons that fire together at stimulus onset enter together into a state of refractoriness and fire again after a time corresponding to the mean interspike interval. We can therefore conclude that populations of neurons *in vitro* exhibit, in the regime of low noise, a sharp transient, indicating a very fast response to step current input.

The theory of population activity (Fig. 15.4b) enables us to understand the responses found in the experiments, as we shall see in the next section.

15.2 Fast transients vs. slow transients in models

Populations of model neurons can exhibit fast abrupt responses or slow responses to a step current input. To predict whether the response is fast or slow, knowledge of the type and magnitude of noise turns out to be more critical than the details of the neuron model.

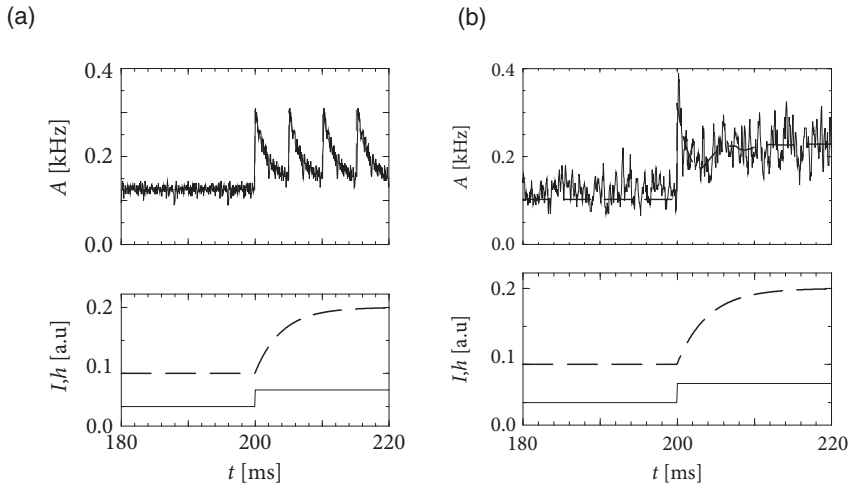


Fig. 15.5 The response is rapid for low noise or slow noise. Response of the population activity (top) to the step current $I(t)$ (bottom) and the input potential $h(t)$ caused by the step at $t = 100$ ms. (a) Leaky integrate-and-fire neurons at a very low noise level. Solid line: simulation of a population of 1000 neurons without coupling, all receiving the same step input. Dashed line: numerical integration of the integral equation (14.5) of time-dependent renewal theory in the low-noise limit; see Chapter 14. (b) Slow noise. Transients for SRM₀ neurons with noisy reset in response to the same step current. The results of a simulation of 1000 SRM₀-neurons (solid line) are compared with a numerical integration (dashed line) of the integral equation; see Eq. (14.5). The instantaneous response is typical for “slow” noise models. Bottom: Step current input I (solid line) and input potential $h(t)$ (dashed line). Note that the population responds instantaneously to the input switch at $t_0 = 100$ ms even though the membrane potential responds only slowly; taken from Gerstner (2000).

15.2.1 Fast transients for low noise or “slow” noise

A homogeneous population of independent leaky integrate-and-fire neurons with a low level of noise exhibits a sharp transient after the onset of a step current as shown in Fig. 15.5a. The onset transiently synchronizes a subgroup of neurons. Since all the neurons are of the same type and have the same parameters, the synchronized subgroup fires again some time later, such that the population activity oscillates with a period corresponding to the interspike interval of single neurons.

The oscillation is suppressed, and neurons desynchronize, if the population is heterogeneous or, for a homogeneous population, if neurons have slow noise in the parameters (Fig. 15.5b). The abrupt onset, however, remains, so that the transient after a switch in the input is extremely fast.

We can conclude that *fast transients* occur in a population of leaky integrate-and-fire neurons:

- (i) at a low noise level and strong step current stimulation;
- (ii) at a high level of “slow” noise, for example, slow variations in the parameters of the neurons or heterogeneity across the group of neurons.

In the first case, the onset triggers oscillations, while in the second case the oscillations are suppressed. The rapid transients in spiking models without noise or with slow noise have been reported by several researchers (Knight, 1972; Gerstner, 2000; Brunel *et al.*, 2001; Moreno-Bote and Parga, 2004).

Note that the time course of the response in the simulations with slow noise in Fig. 15.5b is reminiscent of the neuronal responses measured in the visual cortex; see Fig. 15.3. In particular, we find in the simulations that the rapid onset is followed by a decay of the activity immediately thereafter. This indicates that the decay of the activity is due to the reset or, more generally, to refractoriness after firing, and not due to adaptation or input from inhibitory neurons.

Whereas the low-noise result is independent of the specific noise model, the results for high noise depend on the characteristics of the noise. We analyze in Sections 15.2.2 and 15.2.3 the response to step currents for two different noise models. We start with escape noise and turn thereafter to diffusive noise. Before we do so, let us discuss a concrete example of slow noise.

Example: Fast transients with noise in parameters

We consider a population of SRM₀ neurons with noise in the duration of the absolute refractoriness. The membrane potential is $u(t) = \eta_r(t - \hat{t}) + h(t)$ where $h(t)$ is the input potential and

$$\eta_r(s) = \begin{cases} -c & \text{for } 0 < s \leq \Delta^{\text{abs}} + r \\ \eta_0(s - \Delta^{\text{abs}} - r) & \text{for } s > \Delta^{\text{abs}} + r. \end{cases}$$

The constant c is large enough to prevent firing during absolute refractoriness. After each spike the reset variable r is chosen independently from a Gaussian distribution $\mathcal{G}_\sigma(r)$ with variance $\sigma_r \ll \Delta^{\text{abs}}$. This is an example of a “slow” noise model, because a new value of the stochastic variable r is chosen only once per interspike interval. The approach of the neuron to the threshold is noise-free.

A neuron which was reset at time \hat{t} with a value r fires again after an interval $T(\hat{t}, r)$ which is defined by the next threshold crossing $u(t) = \vartheta$. The interval distribution of the noisy reset model is

$$P_I(t|\hat{t}) = \int_{-\infty}^{\infty} dr \delta[t - \hat{t} - T(\hat{t}, r)] \mathcal{G}_\sigma(r). \quad (15.4)$$

The population equation (14.5) from Chapter 14 is thus

$$A(t) = \int_{-\infty}^t d\hat{t} \int_{-\infty}^{\infty} dr \delta[t - \hat{t} - T(\hat{t}, r)] \mathcal{G}_\sigma(r) A(\hat{t}). \quad (15.5)$$

A neuron that has been reset at time \hat{t} with value r behaves identically to a noise-free neuron that has fired its last spike at $\hat{t} + r$. In particular we have the relation $T(\hat{t}, r) = r + T_0(\hat{t} + r)$ where $T_0(t')$ is the next interspike interval of a noiseless neuron ($r = 0$) that

has fired its last spike at t' . The integration over \hat{t} in Eq. (15.5) can therefore be done and yields

$$A(t) = \left[1 + \frac{h'}{\eta'} \right] \int_{-\infty}^{\infty} dr \mathcal{G}_{\sigma}(r) A[t - T_b(t) - r], \quad (15.6)$$

where $T_b(t)$ is the backward interval, i.e., the distance to the previous spike for a noiseless neuron ($r = 0$) that fires at time t . The factor $[1 + (h'/\eta')]$ arises due to the integration over the δ -function. We use the short-hand h' for the derivative $dh(t)/dt$ and η' for $d\eta_0(T(\hat{t}, 0))/dt$. We remind the reader that the interval $T(\hat{t}, r)$ is defined by the threshold condition $u(t) = \vartheta$ which gives, more explicitly, $\eta_r(T(\hat{t}, r)) + h(\hat{t} + T(\hat{t}, r)) = \vartheta$ (see Exercises).

We can interpret Eq. (15.6) as follows.

(i) The activity at time t is proportional to the activity $A(t - T_b(t))$ one interspike interval earlier.

(ii) Compared to $A(t - T_b(t))$, the activity is smoother, because interspike intervals vary across different neurons in the population, which gives rise to an integration over the Gaussian \mathcal{G}_{σ} .

(iii) Most importantly, compared to the activity $A(t - T_b(t))$ one interspike interval earlier, the activity at time t is increased by a factor $[1 + \frac{h'}{\eta'}]$. This factor is proportional to the *derivative* of the input potential as opposed to the potential itself. As we can see from Eq. (15.3), the derivative of h is discontinuous at the moment when the step current switches. Therefore, the response of the population activity $A(t)$ to a step current is instantaneous and exhibits an abrupt change, as confirmed by the simulation of Fig. 15.5b. We emphasize that the mathematical arguments that lead to Eq. (15.6) require neither an assumption of small input steps nor a linearization of the population dynamics, but are applicable to arbitrary time-dependent and strong inputs.

15.2.2 Populations of neurons with escape noise

For neurons with escape noise, the level of noise determines whether transients are sharp and fast or smooth and slow. For low noise the response to a step current is fast (Fig. 15.6a) whereas for a high noise level the response is slow and follows the time course of the input potential $h(t)$ (Fig. 15.6b). Analogous results hold for a large class of generalized integrate-and-fire models with escape noise, including SRMs and leaky integrate-and-fire models (Gerstner, 2000).

To analyze the response to step current inputs, we assume that the step amplitude ΔI of the input is small so that the population activity $A(t)$ after the step can be considered as a small perturbation of the asynchronous firing state with activity A_0 before the step. With these assumptions, we can use the linearized population activity equations (14.43) that were derived in Section 14.3. For the sake of convenience we copy the equation here

$$\Delta A(t) = \int_{-\infty}^t P_0(t - \hat{t}) \Delta A(\hat{t}) d\hat{t} + A_0 \frac{d}{dt} \int_0^{\infty} \mathcal{L}(x) \Delta h(t - x) dx. \quad (15.7)$$

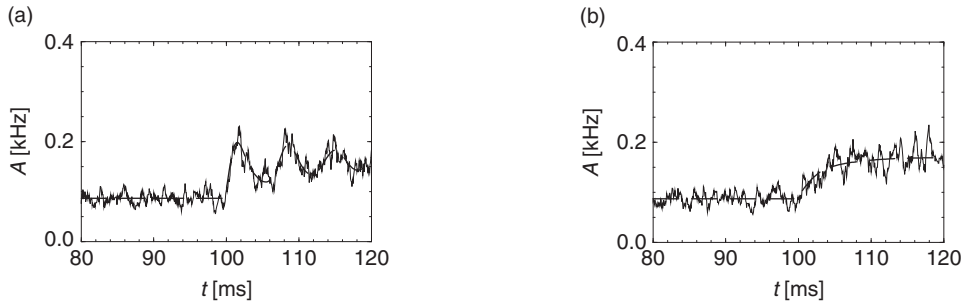


Fig. 15.6 Escape noise. Response of a network of 1000 SRM_0 neurons with exponential escape noise to step current input. The input is switched at $t = 100$ ms. Simulations (fluctuating solid line) are compared to the numerical integration of the integral equation (14.5) (thick dashed line). (a) For low noise the transition is comparatively sharp. (b) For high noise the response to the change in the input is smooth and slow.

We recall that $P_0(t - \hat{t})$ is the interval distribution for constant input I_0 before the step; $\mathcal{L}(x)$ is a real-valued function that plays the role of an integral kernel; and

$$\Delta h(t) = \int_0^{t-t_0} \frac{R}{\tau_m} e^{-\frac{s}{\tau_m}} \Delta I \, ds = R \Delta I \left[1 - \exp\left(-\frac{t-t_0}{\tau_m}\right) \right] \quad \text{for } t > t_0 \quad (15.8)$$

is the input potential generated by step input of amplitude ΔI , switched on at time t_0 .

The first term on the right-hand side of Eq. (15.7) describes that perturbations $\Delta A(\hat{t})$ in the past ($\hat{t} < t$) have an after-effect about one interspike interval later. Thus, if the switch in the input at time t_0 has caused a momentary increase of the population activity $A(t)$, then the first peak in A around t_0 can generate a second, slightly broader, peak one interspike interval later – exactly as seen in the experimental data of Fig. 15.4a. If the second peak is again prominent, it can cause a further peak one period later, so that the population activity passes through a phase of transient oscillations; see Fig. 15.6a. The oscillation decays rapidly, however, if the noise level is high, because a high noise level corresponds to a broad interspike interval distribution $P_0(t - \hat{t})$ so that successive peaks are “smeared out.” Thus, the first term on the right-hand side of Eq. (15.7) explains the potential “ringing” of the population activity after a momentary synchronization of neurons around time t_0 ; it does not, however, predict whether the transient at time t_0 is sharp or not.

It is the second term on the right-hand side of Eq. (15.7) which predicts the immediate response to a change in the input potential Δh . In what follows, we are mainly interested in the *initial* phase of the transient, i.e., $0 < t - t_0 \ll T$ where $T = 1/A_0$ is the mean interspike interval. During the initial phase of the transient, the first term on the right-hand side of Eq. (15.7) does not contribute, since $\Delta A(\hat{t}) = 0$ for $\hat{t} < t_0$. Therefore, Eq. (15.7) reduces to

$$\Delta A(t) = A_0 \frac{d}{dt} \int_0^{t-t_0} \mathcal{L}(s) \Delta h(t-s) \, ds, \quad \text{for } t - t_0 \ll T. \quad (15.9)$$

In the upper bound of the integral we have exploited that $\Delta h = 0$ for $t < t_0$.

If we want to understand the response of the population to an input current $\Delta I(t)$, we need to know the characteristics of the kernel $\mathcal{L}(x)$. The explicit form of the filter $\mathcal{L}(x)$ has been derived in Section 14.3. Here we summarize the main results that are necessary to understand the transient response of the population activity to a step current input.

- (i) In the low-noise limit, the kernel $\mathcal{L}(x)$ can be approximated by a Dirac δ -function. The dynamics of the population activity ΔA has therefore a term proportional to the *derivative* of the input potential; see Eq. (15.9). This result implies a fast response ΔA to any change in the input. In particular, for step current input, the response in the low-noise limit is discontinuous at the moment of the step.
- (ii) For a large amount of escape noise, the kernel $\mathcal{L}(x)$ is broad. This implies that the dynamics of the population activity is proportional to the *input potential* h rather than to its derivative. Therefore the response to a step input is slow and consistent with that of a rate model, $A(t) = F(h(t))$.

A summary of the mathematical results for the filter $\mathcal{L}(x)$ is given in Table 15.1. The formulas for leaky integrate-and-fire models differ slightly from those for SRM₀, because of the different treatment of the reset.

Example: Slow response for large escape noise

To understand how the slow response to a step at time t_0 arises, we focus on the right-hand side of Eq. (15.9) and approximate the kernel $\mathcal{L}(x)$ by a small constant c over the interval $0 < x < 1/c$. For $t - t_0 < 1/c$ (and as before $t - t_0 \ll T$), the integral then simplifies to $\int_0^\infty \mathcal{L}(s) \Delta h(t-s) ds \approx c \int_{t_0}^t \Delta h(t') dt'$; i.e., a simple integral over the input potential.

In front of the integral on the right-hand side of Eq. (15.9) we see the temporal derivative. The derivative undoes the integration so that

$$\Delta A(t) \propto \Delta h(t). \quad (15.10)$$

This implies that the response to a change in the input is as slow as the input potential and controlled by the membrane time constant.

15.2.3 Populations of neurons with diffusive noise

Simulation results for a population of integrate-and-fire neurons with diffusive noise are similar to those reported for escape noise. For a small to medium amount of diffusive noise, the transient is fairly sharp and followed by a damped oscillation (Fig. 15.7a). For a large amount of noise, the oscillation is suppressed and the response of the population activity $A(t)$ is slower (Fig. 15.7b).

In the discussion of escape noise in the preceding section, we saw that the response to a

Definition	$\mathcal{L}^{\text{SRM}}(x) = -\int_x^\infty d\xi \frac{\partial S(\xi 0)}{\partial \Delta h(\xi-x)}$ $\mathcal{L}^{\text{IF}}(x) = \mathcal{L}^{\text{SRM}}(x) + \int_0^x d\xi e^{-\xi/\tau} \frac{\partial S(x 0)}{\partial \Delta h(\xi)}$
No noise	$\mathcal{L}_0^{\text{SRM}}(x) = \delta(x)/\eta'$ $\mathcal{L}_0^{\text{IF}}(x) = [\delta(x) - \delta(x-T_0)e^{-T_0/\tau}] / u'$
Escape noise	$\mathcal{L}^{\text{SRM}}(x) = \int_x^\infty d\xi f'[u(\xi-x)] S_0(\xi)$ $\mathcal{L}^{\text{IF}}(x) = \mathcal{L}^{\text{SRM}}(x) - S_0(x) \int_0^x d\xi e^{-\xi/\tau} f'[u(\xi)]$
Reset noise	$\mathcal{L}^{\text{SRM}}(x) = \delta(x)/\eta'$ $\mathcal{L}^{\text{IF}}(x) = [\delta(x) - \mathcal{G}_\sigma(x-T_0)e^{-T_0/\tau}] / u'$

Table 15.1 The kernel $\mathcal{L}(x)$ that appears in Eq. (15.7) is given each time for integrate-and-fire neurons and SRM₀ neurons (upper index IF and SRM, respectively). Top row: The general case (“Definition”). Second row: Deterministic neuron model without noise. Third row: Neuron model with escape noise. Bottom: Neuron model with slow noise in the form of “reset noise,” where the value of the reset has a small jitter. $S_0(s)$ is the survivor function in the asynchronous state and \mathcal{G}_σ a normalized Gaussian with width σ . Primes denote derivatives with respect to the argument.

step input is fast if the population activity reflects the *derivative* h' of the input potential. To understand when and how the derivative h' can play a role with diffusive noise, it is convenient to consider for a moment not a step current input but a current *pulse*. According to Eq. (15.3), a current pulse $I(t) = q\delta(t-t_0)$ which deposits at time t_0 a charge q causes a discontinuous jump of the input potential

$$\Delta h(t) = \begin{cases} 0 & \text{for } t \leq t_0, \\ Rq/\tau_m & \text{for } t > t_0. \end{cases} \quad (15.11)$$

The central idea of the following arguments is shown schematically in Fig. 15.8. According to Eq. (15.11), all membrane potential trajectories jump at time t_0 by the amount $\Delta u = Rq/\tau_m$. The distribution of membrane potentials across the different neurons in the population, just before t_0 , is described by $p(u)$. The step increase in the membrane potential kicks all neurons i with membrane potential u_i in the range $\vartheta - \Delta u < u_i < \vartheta$ instantaneously across the threshold which generates an activity pulse

$$\Delta A(t_0) \propto \frac{N_F(t_0)}{N} \delta(t-t_0), \quad (15.12)$$

where $N_F(t_0)/N = \int_{\vartheta-\Delta u}^{\vartheta} p(u)du$ is the fraction of neurons that fire because of the input

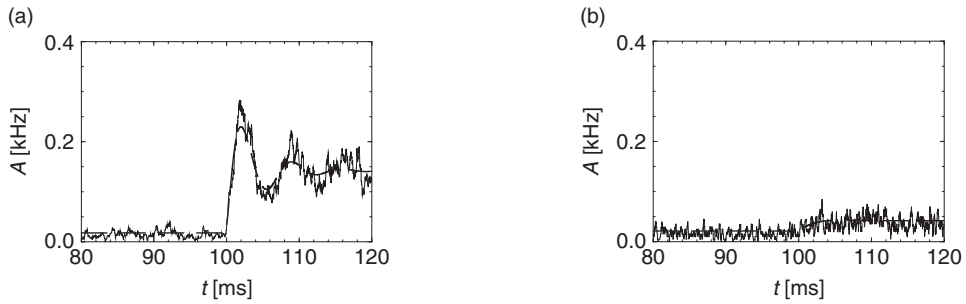


Fig. 15.7 Diffusive noise. Response of a network of 1000 integrate-and-fire neurons with diffusive noise to step current input. Simulations (fluctuating solid line) are compared to a numerical integration of the density equations (thick dashed line). (a) For low noise and a big (superthreshold) current step the response is rapid. (b) For high noise and a small current step the response is slower and does not exhibit oscillations.

current pulse. The Dirac δ -pulse in the activity indicates that $\Delta A(t)$ is proportional to the derivative h' of the input potential of Eq. (15.11). A population response proportional to h' is the signature of an immediate response to step currents.

The above argument assumes that the jump size is finite. The linearization of the membrane potential density equations (see Chapter 13) corresponds to the limit where the jump size goes to zero. Two different situations may occur, which are visualized in Figs. 15.8a and b. Let us start with the situation depicted in Fig. 15.8b. As the jump size Δu goes to zero, the fraction of neurons that fire (i.e., the shaded area under the curve of $p(u)$) remains proportional to Δu . Therefore, even in the limit of Δu to zero the linearized population equations predict a rapid response component. The fast response component is proportional to $p(\vartheta)$, i.e., to the density of the membrane potential at the threshold. For colored noise, the density at threshold is finite. Therefore, for colored noise, the response is fast (Fig. 15.9), even after linearization of the equations of the population dynamics (Brunel *et al.*, 2001; Fourcaud and Brunel, 2002).

For diffusive noise with white-noise characteristics, however, the membrane potential density vanishes at the threshold. The area under the curve therefore has the shape of a triangle (Fig. 15.8a) and is proportional to $(\Delta u)^2$. In the limit as Δu tends to zero, a linearization of the equation thus predicts that the response loses its instantaneous component (Brunel and Hakim, 1999; Lindner and Schimansky-Geier, 2001; Richardson, 2007).

The linearization of the membrane potential density equations leads to the linear response filter $G(s)$. The Fourier transform of G is the frequency-dependent gain $\hat{G}(\omega)$; see Chapter 13. After linearization of the population activity equations, the question of fast or slow response to a step input is equivalent to the question of the high-frequency behavior of $\hat{G}(\omega)$. Table 15.2 summarizes the main results from the literature. A cut-off frequency proportional to $1/\tau_m$ implies that the dynamics of the population activity is “slow” and roughly follows the input potential. Exponential integrate-and-fire neurons, which we identified in

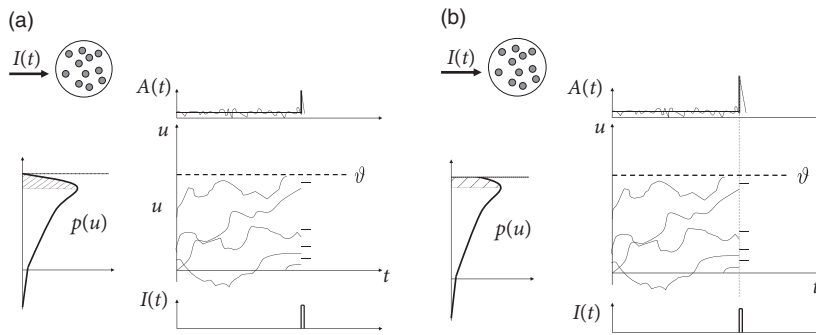


Fig. 15.8 Transients in a population of neurons with diffusive noise. (a) Rapid response to strong stimuli. A population of neurons (top left) is characterized by its distribution of membrane potentials (below left). Four representative trajectories are shown (right). In the stationary state of asynchronous firing, the population activity $A(t)$ fluctuates about a constant value A_0 . Bottom right: If all neurons receive a common current pulse at time t_0 , the membrane potential jumps by a small amount Δu . Therefore, all neurons with a membrane potential just below threshold (shaded area below $p(u)$) fire synchronously at time t_0 , which gives rise to an instantaneous peak in $A(t)$. With white diffusive noise, the density $p(u)$ vanishes at the threshold ϑ . Therefore, the amplitude of the peak vanishes quadratically as the charge deposited by the current pulse decreases. (b) Rapid response to strong and weak stimuli. Same as in (a), except that the noise is slow, either slow noise in the parameters or colored diffusive noise. In this case, the area under the curve and therefore the amplitude of the peak in $A(t)$ vanishes linearly with the charge delivered by the current pulse. This gives rise to a rapid linear response. Schematic figure.

Chapter 5 as a good model of cortical neurons, are always slow in this sense. If there is no cut-off, the population activity can respond rapidly. With this definition, leaky integrate-and-fire neurons respond rapidly to a change in the input variance σ^2 of the diffusive noise (Lindner and Schimansky-Geier, 2001; Silberberg *et al.*, 2004; Richardson, 2007). A cut-off proportional to $1/\sqrt{\tau_m}$ means that the response of a population of leaky integrate-and-fire neurons to a step is slightly faster than that of the membrane potential but must still be considered as “fairly slow” (Brunel and Hakim, 1999).

We close with a conundrum: Why is the linear response of the leaky integrate-and-fire model fairly slow for all noise levels, yet the noise-free response that we have seen in Fig. 15.5a is fast? We emphasize that the linearization of the noise-free population equations does indeed predict a fast response, because, if there is no noise, the membrane potential density at the threshold is finite. However, already for a very small amount of white diffusive noise, the formal membrane potential density at the threshold vanishes, so that the linearized population equations predict a slow response. This is, however, to a certain degree an artifact of the diffusion approximation. For a small amount of diffusive noise, the layer below ϑ over which the membrane potential density drops from its maximum to zero becomes very thin. For any finite spike arrival rate and finite EPSP size in the background input or finite signal amplitude ΔI , the immediate response is strong and fast – as seen from the general arguments in Fig. 15.8.

	$G_I(\omega)$	$G_\sigma(\omega)$	$G_g(\omega)$
LIF	$A_0 \frac{R}{\sigma} \frac{1}{\sqrt{\omega \tau_m}}$	$A_0 \frac{1}{\sigma^2} \left(1 + \frac{\vartheta - h_0}{\sigma \sqrt{\omega \tau_m}} \right)$	$A_0 \frac{1}{g_0} \frac{\vartheta - h_0}{\sigma \sqrt{\omega \tau_m}}$
EIF	$A_0 \frac{R}{\Delta_T} \frac{1}{\omega \tau_m}$	$A_0 \frac{1}{(\Delta_T)^2} \frac{1}{\omega \tau_m}$	$A_0 \frac{1}{g_0} \frac{1}{\omega \tau_m} \log(\omega \tau_m)$

Table 15.2 *High-frequency response in the presence of diffusive noise. The frequency-dependent gain of leaky integrate-and-fire neurons (LIF) and exponential integrate-and-fire neurons (EIF) in response to a periodic modulation of the input current G_I , of the noise variance G_σ , or of the input conductance G_g . The neurons are subject to diffusive noise and described by the Fokker–Planck equation; see Chapter 13. The response G_σ of the LIF to modulations in the noise level is rapid, since it approaches a finite value for $\omega \rightarrow \infty$. The response G_I or G_g of the LIF to changes in input current or input conductance is fairly slow, since it decays at high frequencies with $1/\sqrt{\omega \tau_m}$. The response of the EIF is always slow (decay with $1/\omega \tau_m$) whatever the type of input. Parameters denote the input resistance R , membrane time constant τ_m , noise level σ_0 , population activity in the stationary state A_0 , and slope factor Δ_T of the exponential integrate-and-fire model (see Chapter 5). The table (adapted from Richardson (2007)) summarizes mathematical results of various sources (Brunel and Hakim, 1999; Lindner and Schimansky-Geier, 2001; Fourcaud and Brunel, 2005; Richardson, 2007).*

15.3 Rate models

The gain function $F(h)$ of rate models can always be chosen such that, for constant input $h_0 = RI_0$, the population activity $A_0 = F(h_0)$ in the stationary state of asynchronous firing is correctly described. The dynamic equations that describe the approach to the stationary state in a rate model are, however, to a certain degree ad hoc. This means that the analysis of transients as well as the stability analysis in recurrent networks will, in general, give different results in rate models than in spiking neuron models.

15.3.1 Rate models have slow transients

In Section 15.2 we saw that spiking neuron models with a large amount of escape noise exhibit a population activity $A(t)$ that follows the input potential $h(t)$. In this case, it is therefore reasonable to define a rate model $A(t) = F(h(t))$ in which the momentary activity $A(t)$ reflects the momentary input potential $h(t)$. An example is Eq. (15.1), which corresponds to a “quasi-stationary” treatment of the population activity, because the transform F is identical to the stationary gain function, except for a change in the units of the argument, as discussed in the text after Eq. (15.1). A similar argument can also be made for

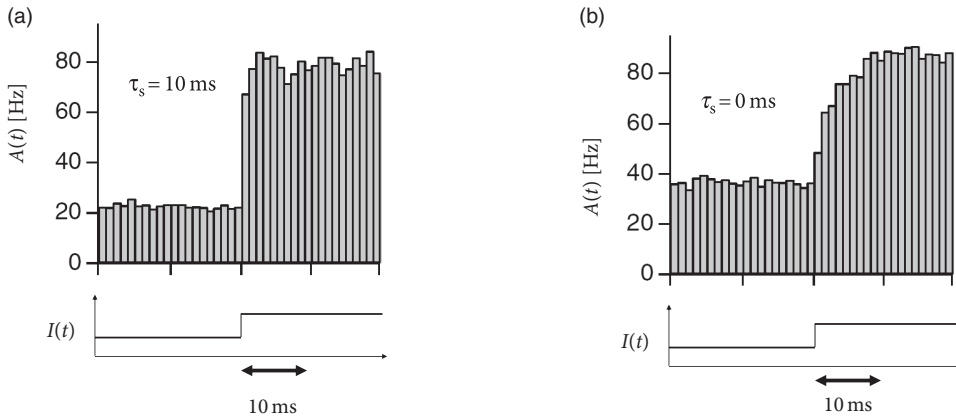


Fig. 15.9 Slow (colored) diffusive noise versus white diffusive noise. A population of integrate-and-fire models with a time constant of $\tau_m = 20$ ms was simulated and responses to a step stimulus reported in time bins of 1 ms. (a) Colored noise with a filtering time constant $\tau_s = 10$ ms leads to an abrupt, instantaneous response. (b) White noise leads to a smoothly increasing, fairly slow response. Figures adapted from Brunel *et al.* (2001). Copyright (2001) The American Physical Society.

exponential integrate-and-fire neurons with diffusive noise, as we shall see later in this section.

If we insert Eq. (15.2) into Eq. (15.1) we obtain

$$A(t) = F[h(t)] = F \left[\frac{R}{\tau_m} \int_0^\infty \exp \left(-\frac{s}{\tau_m} \right) I(t-s) ds \right]. \quad (15.13)$$

Eq. (15.13) makes explicit that the population activity in the rate model reflects a *low-pass filtered* version of the input current. The transient response to a step in the input current is therefore slow.

Since differential equations are more convenient than integrals, we rewrite the input potential in the form of Eq. (15.3), which we repeat here for convenience

$$\tau_m \frac{dh(t)}{dt} = -h + RI(t). \quad (15.14)$$

The input potential $h(t)$ resulting from the integration of Eq. (15.14) is to be inserted into the function F to arrive at the population activity $A(t) = F[h(t)]$. Note that the input current $I(t)$ in Eq. (15.14) can arise from external sources, from other populations or from recurrent activity in the network itself.

Example: Wilson–Cowan differential equation

Sometimes one finds in the literature rate models of the form

$$\tau_A \frac{d\bar{A}(t)}{dt} = -\bar{A}(t) + F(h(t)), \quad (15.15)$$

which have an additional time constant τ_A . Therefore the transient response to a step in the input would be even slower than that of the rate model in Eq. (15.13).

In the derivation of Wilson and Cowan (1973) the time constant τ_A arises from time-averaging over the “raw” activity variable with a sliding window of duration τ_A . Thus, even if the “raw” activity has sharp transients, the time-averaged variable $\bar{A}(t)$ in Eq. (15.15) is smooth. In the theory of Wilson and Cowan, the differential equation for the population activity takes the form (Wilson and Cowan, 1972, 1973)

$$\tau_A \frac{d\bar{A}(t)}{dt} = -\bar{A}(t) + (1 - \Delta^{\text{abs}}) F(h(t)) \quad (15.16)$$

so as to account for absolute refractoriness of duration Δ^{abs} ; see the integral equation (14.10) in Chapter 14. F has a sigmoidal shape. The input potential $h(t)$ comprises input from the same population as well as from other populations.

Since there is no reason to introduce the additional low-pass filter with time constant τ_A , we advise against the use of the model defined in Eqs. (15.15) or (15.16). However, we may set

$$\tau_m \frac{dA(t)}{dt} = -A(t) + g_\sigma(I(t)), \quad (15.17)$$

where $I(t)$ is the input *current* (as opposed to the input potential). The current can be attributed to input from other populations or from recurrent coupling within the population. The low-pass filter in Eq. (15.17) replaces the low-pass filter in Eq. (15.14) so that the two rate models are equivalent after an appropriate rescaling of the input, even for complex networks (Miller and Fumarola, 2012); see also Exercises.

15.3.2 Networks of rate models

Let us consider a network consisting of K populations. Each population contains a homogeneous population of neurons. The input into population k arising from other populations n and from recurrent coupling within the population is described as

$$I_k(t) = \sum_n C_{kn} w_{kn} \int_0^\infty \alpha(s) A_n(t-s) ds. \quad (15.18)$$

Here $A_n(t)$ is the activity of population n and C_{kn} is the number of presynaptic neurons in population n that are connected to a typical neuron in population k ; the time course and strength of synaptic connections are described by α and w_{kn} , respectively; see Chapter 12.

We describe the dynamics of the input potential h_k of population k with the differential equation (15.14) and use for each population the quasi-stationary rate model $A_n(t) = F_n(h_n)$ where F_n is the gain function of the neurons in population n . The final result is

$$\tau_m \frac{dh_k(t)}{dt} = -h_k + R \sum_n C_{kn} w_{kn} \int_0^\infty \alpha(s) F_n(h_n(t-s)) ds. \quad (15.19)$$

Eq. (15.19) is the starting point for some of the models in Part IV of this book.

Example: Population with self-coupling

If we have a single population, we can drop the indices in Eq. (15.19) so as to arrive at

$$\tau_m \frac{dh(t)}{dt} = -h + J_0 \int_0^\infty \alpha(s) F(h(t-s)) ds, \quad (15.20)$$

where J is the strength of the feedback. Thus, a single population with self-coupling is described by a single differential equation for the input potential h . The population activity is simply $A(t) = F(h(t))$.

Stationary states are found as discussed in Chapter 12. If there are three fixed points, the middle one is unstable while the other two (at low and high activity) are stable under the dynamics (15.20). The fixed points calculated from Eq. (15.20) are correct. However, stability under the dynamics (15.20) does *not* guarantee stability of the original network of spiking neurons. Indeed, as we have seen in Chapters 13 and 14, the fixed points of high and low activity may lose stability with respect to oscillations, even in a single homogeneous population. The rate dynamics of Eq. (15.20) cannot correctly account for these oscillations. In fact, for instantaneous synaptic current pulses $\alpha(s) = q\delta(s)$, where δ denotes the Dirac δ -function, Eq. (15.20) reduces to a one-dimensional differential equation which can never give rise to oscillatory solutions.

15.3.3 Linear-Nonlinear-Poisson and improved transients

To improve the description of transients, we start from Eq. (15.13), but insert an arbitrary filter κ ,

$$A(t) = F(h(t)) = F \left[\int_0^\infty \kappa(s) I(t-s) ds \right]. \quad (15.21)$$

Equation (15.21) is called the Linear-Nonlinear-Poisson (LNP) model (Chichilnisky 2001; Simoncelli *et al.* 2004). It is also called a cascade model because it can be interpreted as a sequence of three processing steps. First, input is filtered with an arbitrary linear filter κ , which yields the input potential h . Second, the result is passed through a nonlinearity F . Third, in case of a single neuron, spikes are generated by an inhomogeneous Poisson process with rate $F(h(t))$. Since, in our model of a homogeneous population, we have many similar neurons, we drop the third step and interpret the rate $F(h(t))$ directly as the population activity.

For $\kappa(s) = (R/\tau_m) \exp(-s/\tau_m)$ we are back at Eq. (15.13). The question arises whether we can make a better choice of the filter κ than a simple low-pass with the membrane time constant τ_m . In Chapter 11 it was shown how an optimal filter κ can be determined experimentally by reverse correlation techniques.

Here we are interested in deriving the optimal filter from the complete population dynamics. The LNP model in Eq. (15.21) is an approximation of the population dynamics that

is more correctly described by the Fokker–Planck equations in Chapter 13 or by the integral equation of time-dependent renewal theory in Chapter 14. Let us recall that, in both approaches, we can linearize the population equations around a stationary state of asynchronous firing A_0 which is obtained with a mean input I_0 at some noise level σ . The linearization of the population dynamics about A_0 yields a filter $G_I(s)$. We use this filter, and arrive at a variant of Eq. (15.21)

$$A(t) = \tilde{F} \left(\int_0^\infty G_I(s) I(t-s) ds \right), \quad (15.22)$$

where $\tilde{F}(x) = g_\sigma(x/c)$ is a scaled version of the frequency–current curve $g_\sigma(I)$ and $c = \int_0^\infty G_I(s) ds$ is a constant which matches the slope of the gain function at the reference point for the linearization (Ostojic and Brunel, 2011). Models with this, or similar, choices of \tilde{F} describe transient peaks in the population activity surprisingly well (see, e.g., Herrmann and Gerstner, 2001; Aviel and Gerstner, 2006; Ostojic and Brunel, 2011). Rate models based on Eq. (15.22) can also be used to describe coupled populations. Stability of a stationary state A_0 is correctly described by Eq. (15.22), if the filter $G_I(s)$ in the argument on the right-hand-side reflects the linearization of the full population dynamics around A_0 , but not if the filter is derived by linearization around some other value of the activity.

Example: Effective rate model for exponential integrate-and-fire neurons

We denote the stationary gain function of exponential integrate-and-fire neurons by $g_\sigma(I)$ and the linear filter arising from linearization around a stationary activity A_0 by $G_I(s)$. For exponential integrate-and-fire neurons $G_I(s)$ has the high-frequency behavior of a low-pass filter that varies as $A_0 \frac{R}{\Delta_T \tau_m} \frac{1}{\omega}$; see Table 15.2.

We recall that the Fourier transform of an exponential filter also yields a high-frequency behavior that varies as $1/\omega$ with the inverse filter time constant as cut-off frequency. This suggests that, for the exponential integrate-and-fire model, we can approximate the time course of $G_I(s)$ as an exponential filter with an effective time constant $\tau_{\text{eff}} \propto \tau_m/A_0$. This leads back to Eq. (15.22), but with an *exponential* filter $G(s)$. Hence, we are now nearly back to Eq. (15.13), except that the time constant of the exponential is different.

We now switch from the frequency current curve $g_\sigma(I)$ to the equivalent description of the gain function $F(h) = g_\sigma(h/R)$ where the argument of F has units of a potential. It is convenient to implement the exponential filter in the form of a differential equation for the effective input potential (Ostojic and Brunel, 2011)

$$\tau_{\text{eff}}(t) \frac{dh}{dt} = -h + RI(t), \quad (15.23)$$

with an effective time constant

$$\tau_{\text{eff}}(t) = \tau_m \frac{\Delta_T F'}{A_0(t)}, \quad (15.24)$$

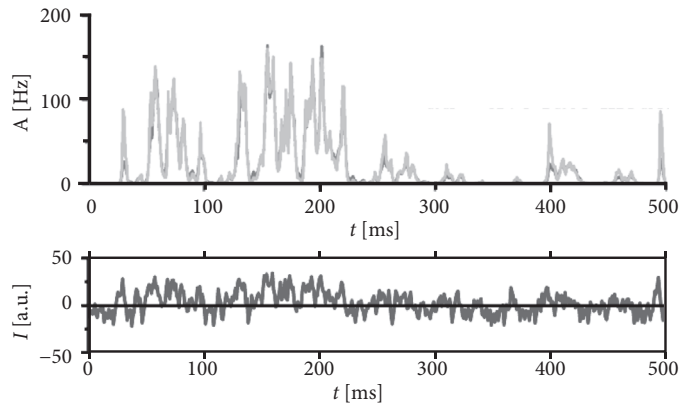


Fig. 15.10 Population of exponential integrate-and-fire neurons. The population activity $A(t)$ arising from an explicit simulation of N model neurons (black solid line) can be approximated by a rate model with effective time constant $\tau_{\text{eff}}(t)$ (gray overlaid). The stimulation is shown in the bottom panel. Figure adapted from (Ostojic and Brunel, 2011).

where $A_0(t)$ is the activity averaged over one or a few previous time steps and $F' = dF/dh$ is the derivative of the gain function at an appropriately chosen reference point h_0 , so that $F(h_0) \approx \langle A_0(t) \rangle$ is the long-term average of the activity.

In each time step, we update the input using Eq. (15.23) and calculate the activity as $A(t) = F(h(t))$ with $F(h) = g_\sigma(h/R)$. Such a rate model gives an excellent approximation of the activity in a population of exponential integrate-and-fire neurons (Fig. 15.10). Note that fast transients are well described, because the effective time constant is shortened as soon as the population activity increases.

15.3.4 Adaptation

So far we have focused on the initial transient after a step in the input current. After the initial transient, however, follows a second, much slower phase of adaptation during which the population response decreases, even if the stimulation is kept constant. For single neurons, adaptation has been discussed in Chapter 6.

In a population of neurons, adaptation can be described as an effective decrease in the input potential. If a population of non-adaptive neurons has an activity described by the gain function $A(t) = F(h(t))$, then the population rate model for adaptive neurons is

$$A(t) = F(h(t) - a(t)), \quad (15.25)$$

where $a(t)$ describes the amount of adaptation that neurons have accumulated, and

$$\tau_a(A) \frac{da}{dt} = a_\infty(A) - a, \quad (15.26)$$

where $a_\infty(A)$ is the asymptotic level of adaptation that is attained if the population continu-

ously fires at a constant rate A . The asymptotic level is approached with a time constant τ_a . Eqs. (15.25) and (15.26) are a simplified version of the phenomenological model proposed in Benda and Herz (2003).

Example: Effective adaptation filter

Suppose that $a_\infty(A) = cA$ is linear in the population activity with a constant $c > 0$ and $\tau_a(A) = \tau_a$ is independent of A . Then Eq. (15.26) can be integrated and yields $a(t) = \int_0^\infty \gamma(s)A(t-s)ds$ with a filter $\gamma(s) = (c/\tau_a) \exp(-s/\tau_a)$. We insert the result in Eq. (15.25) and find

$$A(t) = F \left(h(t) - \int_0^\infty \gamma(s)A(t-s)ds \right). \quad (15.27)$$

Equation (15.27) nicely describes the adaptation process but it misses, like other rate models, the sharp initial transient, and potential transient oscillation, caused by the synchronization of the population at the moment of the step (Naud and Gerstner, 2012a).

15.4 Summary

The population activity of spiking neuron models responds to a big and rapid change in the input current much faster than the input potential. The response of the input potential is characterized by the membrane time constant τ_m and therefore exhibits the properties of a low-pass filter. In an asynchronously firing population of neurons, however, there are always a few neurons with membrane potential just below the threshold. These neurons respond quasi-instantaneously to a step in the input current, despite the fact that the input potential, i.e., the contribution to the membrane potential that is caused by the input, responds slowly.

The details of the response depend on the neuron model as well as on the amplitude of the signal and the type of noise. With slow noise as the dominant noise source, model neurons respond quickly and reliably to a step input. For white noise, the picture is more complicated.

For Spike Response Model neurons with escape noise, the speed of the response depends on the noise level. While the response is fast for low noise, it is as slow as the membrane potential in the limit of high noise.

For a large amount of diffusive white noise and a small amplitude of the input signal, the choice of neuron model plays an important role. Leaky integrate-and-fire models respond fairly slowly, but faster than the input potential. The response of exponential integrate-and-fire models follows that of the effective membrane potential, but the effective membrane time constant depends on the population activity.

The fact that spiking neuron models in the high-noise limit respond slowly can be used to derive rate models for the population activity. Such rate models are the basis for the analysis of cognitive dynamics in Part IV of the book. Nevertheless, it should be kept in

mind that standard rate models miss the rapid transients that a population of spiking models exhibits in response to signals that are strong compared to the level of noise.

Literature

The rapid transients in spiking models without noise or with slow noise have been reported by several researchers, probably first by Knight (1972) and have later been rediscovered several times (Gerstner, 2000; Brunel *et al.*, 2001; Moreno-Bote and Parga, 2004).

The analysis of transients in the escape rate has been performed in Gerstner (2000), where the limits of high noise and low noise are also discussed. For the linearization of the membrane potential density equations and analysis of transient behavior in neuron models with diffusive noise see Brunel and Hakim (1999); Lindner and Schimansky-Geier (2001); Fourcaud and Brunel (2005); and Richardson (2007). Experimental data on transients in the linearized regime can be found in Silberberg *et al.* (2004) and Tchumatchenko *et al.* (2011).

Simoncelli *et al.* (2004) give an authoritative summary of LNP models. How generalized integrate-and-fire models can be mapped to LNP models has been discussed in Aviel and Gerstner (2006) and Ostojic and Brunel (2011). An excellent overview of the central concepts of rate models with adaptation can be found in Benda and Herz (2003).

Exercises

1. Population of noise-free neurons

(a) Show that for noise-free neurons the population activity equation yields

$$A(t) = \frac{1}{1 + T'(\hat{t})} A(\hat{t}), \quad (15.28)$$

where $T(\hat{t})$ is the interspike interval of a neuron that has fired its last spike at time \hat{t} , and the prime denotes the derivative.

Hints: In the limit of no noise, the input-dependent interval distribution $P_I(t|\hat{t})$ reduces to a Dirac δ -function, i.e.,

$$P_I(t|\hat{t}) = \delta[t - \hat{t} - T(\hat{t})], \quad (15.29)$$

where $T(\hat{t})$ is given implicitly by the threshold condition

$$T(\hat{t}) = \min\{(t - \hat{t}) | u(t) = \vartheta; \dot{u} > 0, t > \hat{t}\}. \quad (15.30)$$

Recall from the rules for δ -functions that

$$\int_a^b \delta[f(x)] g(x) dx = \frac{g(x_0)}{|f'(x_0)|}, \quad (15.31)$$

if f has a single zero-crossing $f(x_0) = 0$ in the interval $a < x_0 < b$ with $f'(x_0) \neq 0$.

(b) Assume SRM₀ neurons with $u(t) = \eta(t - \hat{t}) + h(t)$. Show that

$$A(t) = \frac{h'(t)}{\eta'T} A(\hat{t}). \quad (15.32)$$

Hint: Use the results from (a).

(c) An input current of amplitude I_1 is switched on at time $t = 0$. Assume an input potential $h(t) = h_0$ for $t < 0$ and $h(t) = (R/\tau) \int_0^t \exp(-s/\tau) I_1$ for $t > 0$. Show that the transient of the population activity after the step at $t = 0$ is instantaneous, despite the fact that the input potential responds slowly.

2. **LNP and frequency–current curve.** Around Eq. (15.22), it was argued that a model

$$A(t) = \hat{F} \left(\int_0^\infty G_I(s) I(t-s) ds \right) \quad (15.33)$$

with a choice $\hat{F}(x) = g_\sigma(x / [\int_0^\infty G_I(s) ds])$ is optimal. The aim is to make the notion of optimality more precise.

(a) Show that for constant, but arbitrary, input I_0 , Eq. (15.33) leads to $A_0 = g_\sigma(I_0)$, consistent with the general results of Chapter 12.

(b) Suppose that $G_I(s)$ is the linearization of the population activity equations around A_0 which is achieved for a constant input I_0 . Show that linearization of Eq. (15.33) leads to $\Delta A(t) = \int_0^\infty G(s) \Delta I(t-s) ds$.

Hint: Recall that the response at zero frequency, $\hat{G}(0) = \int_0^\infty G(s) ds$, is related to the slope of the gain function.

(c) Interpret the results from (a) and (b) and explain the range of validity of the model defined in Eq. (15.33). What can happen if the input varies about a mean $I_1 \neq I_0$? What happens if the variations around I_0 are big?

3. **Leaky integrate-and-fire with white diffusive noise.** According to the results given in Table 15.2, the linear filter $G_I(s)$ of leaky integrate-and-fire neurons has a high-frequency behavior $\tilde{G}_I(\omega) = A_0 \frac{R}{\sigma} \frac{1}{\sqrt{\omega \tau_m}}$.

(a) Calculate the response to a step current input.

Hint: Use $\Delta A(t) = \int_0^\infty G(s) \Delta I(t-s) ds$. Insert the step current, take the Fourier transform, perform the multiplication in frequency space, and finish with the inverse Fourier transform.

(b) Compare with the simulation results in Fig. 15.9b.

4. **Rate model for a population of exponential integrate-and-fire with white diffusive noise.**

The aim is to derive the effective time constant given in Eq. (15.24) which characterizes a population of exponential integrate-and-fire neurons.

(a) Write $A(t) = F[h(t)]$. Linearize about a reference value $A_0 = F(h_0)$ and prove that $dA/dt = F' dh/dt$.

(b) Assume that Eq. (15.23) holds with the unknown time constant τ_{eff} . Assume periodic stimulation $I(t) = I_0 + \Delta I \exp(i\omega t)$ with a high frequency ω . This will lead to a periodic perturbation $\Delta A \exp[i(\omega t + \phi)]$. Find the ratio $c(\omega) = \Delta A / \Delta I$.

(c) Match the high-frequency behavior of $c(\omega)$ to $\tilde{G}_I(\omega)$ so as to find the time constant τ_{eff} .

Hint: Recall from Table 15.2 that the linear filter $G_I(s)$ of the exponential integrate-and-fire neurons has a high-frequency behavior $\tilde{G}_I(\omega) = A_0 \frac{R}{\Delta_T} \frac{1}{\omega \tau_m}$.

5. **Equivalence of rate models.** We use the rate model defined in Eqs. (15.1) and (15.3) with $R = 1$ in order to describe coupled populations

$$\tau_m \frac{dh_i}{dt} = -h_i + I_i + \sum_k w_{ik} F(h_k). \quad (15.34)$$

Compare this model to another rate model

$$\tau_m \frac{dA_i}{dt} = -A_i + F \left(\sum_k w_{ik} A_k + \hat{I}_i \right). \quad (15.35)$$

Show that Eq. (15.35) implies Eq. (15.34) under the assumption that $I = \hat{I} + \tau_m d\hat{I}/dt$.

Hint: Set $h_i = \sum_k w_{ik} A_k + I$ and take the derivative (Miller and Fumarola, 2012).