

Quasi-renewal theory and the integral-equation approach

In the previous chapter it was shown that an approach based on membrane potential densities can be used to analyze the dynamics of networks of integrate-and-fire neurons. For neuron models that include biophysical phenomena such as refractoriness and adaptation on multiple time scales, however, the resulting system of partial differential equations is situated in more than two dimensions and therefore difficult to solve analytically; even the numerical integration of partial differential equations in high dimensions is slow. To cope with these difficulties, we now indicate an alternative approach to describing the population activity in networks of model neurons. The central concept is expressed as an integral equation of the population activity.

The advantage of the integral equation approach is four-fold. First, the approach works for a broad spectrum of neuron models, such as the Spike Response Model with escape noise and other Generalized Linear Models (see Chapter 9) for which parameters can be directly extracted from experiments (see Chapter 11). Second, it is easy to assign an intuitive interpretation to the quantities that show up in the integral equation. For example, the interspike interval distribution plays a central role. Third, an approximative mathematical treatment of adaptation is possible not only for the stationary population activity, but also for the case of arbitrary time-dependent solutions. Fourth, the integral equations provide a natural basis for the transition to classical “rate equations,” which will be discussed in Chapter 15.

In Section 14.1, we derive, starting from a small set of assumptions, an integral equation for the population activity. The essential idea of the mathematical formulation is to remain at the macroscopic level as much as possible, without reference to a specific model of neuronal dynamics. Knowledge of the interval distribution $P_I(t|\hat{t})$ for arbitrary input $I(t)$ is enough to formulate the population equations.

For didactic purposes, we begin by treating neurons without adaptation. In this case, the internal state of the neurons depends solely on the input and on the time since the last spike. The formulation of the macroscopic integral equation exploits the concepts of a time-dependent version of renewal theory that we have already encountered in Chapter 7. In the presence of adaptation, however, the state of the neuron depends not only on the last spike, but also on all the previous spike times. But since the refractoriness caused by

the last spike dominates over the effects of earlier spikes we can approximate the interval distribution for adaptive neurons by a “quasi-renewal” theory.

A theory for networks consisting of several interacting populations of spiking neurons is formulated in Section 14.2. To analyze the stability of stationary solutions of asynchronous firing with population activity A_0 in connected networks of integrate-and-fire neurons, we need to know the linear response filter. The linearization of the integral equations under the assumption of a small perturbation is presented in Section 14.3.

The integral equation of Section 14.1 is exact in the limit of a large number of neurons and can be interpreted as a solution to partial differential equations analogous to those of the previous chapter. Section 14.4, which is slightly more technical, presents the relation of the integral equation to an approach by membrane potential density equations.

Section 14.5 describes in detail how we can formulate integral equations for adaptive neurons. Finally, Section 14.6 contains variants of the theory that are applicable to populations of a finite number of neurons.

14.1 Population activity equations

The interval distribution $P_I(t|\hat{t})$, which has already been introduced in Chapter 7, plays a central role in the formulation of the population equation. Before we formulate the evolution of the population activity $A(t)$ in terms of this interval distribution $P_I(t|\hat{t})$, we specify some necessary assumptions. Two key assumptions are that the population is homogeneous and contains non-adaptive neurons so that we can work in the framework of a time-dependent renewal theory. These assumptions will eventually be relaxed in Section 14.1.4 where we extend the theory to the case of a population of adaptive neurons and in Section 14.6 where we treat populations of finite size.

14.1.1 Assumptions of time-dependent renewal theory

To formulate a first version of an integral equation for a population of neurons, we start in the framework of time-dependent renewal theory (Chapter 7). To do so, we have to assume the state of a neuron i at time t to be completely described by (i) its last firing time \hat{t}_i ; (ii) the input $I(t')$ it received for times $t' < t$; (iii) the characteristics of potential noise sources, be it noise in the input, noise in the neuronal parameters, or noise in the output.

Are these assumptions overly restrictive or can we still place an interesting and rich set of neuron models in the class of models consistent with assumptions (i)–(iii) of time-dependent renewal theory?

The state of a single-variable integrate-and-fire neuron i , for example one of the nonlinear integrate-and-fire models of Chapter 5, is completely characterized by its momentary membrane potential $u_i(t)$. After firing at a time \hat{t}_i , the membrane potential is reset, so that all information that arrived before the firing is “forgotten.” Integration continues with $u = u_r$. Therefore knowledge of the last firing time \hat{t}_i and the input current $I(t')$ for $\hat{t}_i < t' \leq t$ is sufficient to predict the momentary state of neuron i at time t and therefore (for a deterministic

model) its next firing time. If the integrate-and-fire model is furthermore subject to noise in the form of stochastic spike arrivals of known rate (but unknown spike arrival times), we will not be able to predict the neuron's exact firing time. Instead we are interested in the probability density

$$P_I(t|\hat{t}_i) \quad (14.1)$$

that the next spike occurs around time t given that the last spike was at time \hat{t}_i and the neuron was subject to an input $I(t')$ for $t' \leq t$. In practice, it might be difficult to write down an exact analytical formula for $P_I(t|\hat{t}_i)$ for noise models corresponding to stochastic spike arrival or diffusive noise (see Chapter 8), but the quantity $P_I(t|\hat{t}_i)$ is still well defined. We call $P_I(t|\hat{t}_i)$ the generalized interval distribution (see Chapter 9).

For several other noise models, there exist explicit mathematical expressions for $P_I(t|\hat{t}_i)$. Consider, for example, integrate-and-fire models with slow noise in the parameters, defined as follows. After each firing time, the value u_r for the reset or the value τ_m of the membrane time constant is drawn from a predefined distribution. Between two resets, the membrane potential evolves deterministically. As a consequence, the distribution $P_I(t|\hat{t}_i)$ of the next firing time can be predicted from the distribution of parameters and the deterministic solution of the threshold crossing equations (Gerstner, 2000). Such a model of slow noise in the parameters can also be considered as an approximation to a heterogeneous population of neurons where different neurons in the population have slightly different, but fixed, parameters.

Another tractable noise model is the “escape noise” model, which is also the basis for the Generalized Linear Models of spiking neurons already discussed in Chapter 9. The short-term memory approximation SRM_0 of the Spike Response Model with escape noise (see Eq. (9.19)) is a prime example of a model that fits into the framework of renewal theory specified by assumptions (i)–(iii).

The escape noise model can be used in combination with any linear or nonlinear integrate-and-fire model. For a suitable choice of the escape function f it provides also an excellent approximation to diffusive noise in the input; see Section 9.4. An example of how to formulate a nonlinear integrate-and-fire model with escape noise is given below.

The major limitation of time-dependent renewal theory is that, for the moment, we need to exclude adaptation effects, because the momentary state of adaptive neurons depends not only on the last firing time (and the input in the past) but also on the firing times of earlier spikes. Section 14.1.4 shows that adaptation can be included by extending the renewal theory to a quasi-renewal theory. The treatment of adaptive neurons is important because most cortical neurons exhibit adaptation (Chapter 6).

Example: Escape noise in integrate-and-fire models

Consider an arbitrary (linear or nonlinear) integrate-and-fire model with refractoriness. The neuron has fired its last spike at \hat{t} and enters thereafter an absolute refractory

period of time Δ^{abs} . Integration of the differential equation of the membrane potential u ,

$$\tau \frac{d}{dt} u = f(u) + R(u)I(t), \quad (14.2)$$

restarts at time $\hat{t} + \Delta^{\text{abs}}$ with initial condition u_r . The input current $I(t)$ can have an arbitrary temporal structure.

In the absence of noise, the neuron would emit its next spike at the moment when the membrane potential reaches the numerical threshold θ^{reset} . In the presence of escape noise, the neuron fires in each short time interval $\Delta t \rightarrow 0$, a spike with probability $P_F(t; t + \Delta t) = \rho(t)\Delta t$ where

$$\rho(t) = f(u(t) - \theta^{\text{reset}}, \dot{u}(t)) \quad (14.3)$$

is the escape rate which typically depends on the distance between the membrane potential and the threshold, and potentially also on the derivative $\dot{u} = (du/dt)$ of the membrane potential; see Section 9.4.

Knowledge of the input $I(t')$ for $t' > \hat{t} + \Delta^{\text{abs}}$ is sufficient to calculate the membrane potential $u(t)$ by integration of Eq. (14.2). The time course of $u(t)$ is inserted into Eq. (14.3) to get the instantaneous rate or firing “hazard” $\rho(t)$ for all $t > \hat{t} + \Delta^{\text{abs}}$. By definition, the instantaneous rate vanishes during the absolute refractory time: $\rho(t) = 0$ for $\hat{t} < t < \hat{t} + \Delta^{\text{abs}}$. With this notation, we can use the results of Chapter 7 to arrive at the generalized interval distribution

$$P_I(t|\hat{t}) = \rho(t) \exp \left[- \int_{\hat{t}}^t \rho(t') dt' \right]. \quad (14.4)$$

Note that, in order to keep notation light, we simply write $\rho(t)$ instead of the more explicit $\rho(t|\hat{t}, I(t'))$ which would emphasize that the hazard depends on the last firing time \hat{t} and the input $I(t')$ for $\hat{t} < t' \leq t$; for the derivation of Eq. 14.4, see also Eq. (7.28).

14.1.2 Integral equations for non-adaptive neurons

The integral equation (Gerstner, 1995, 2000; Wilson and Cowan, 1972) for activity dynamics with time-dependent renewal theory states that the activity at time t depends on the fraction of active neurons at earlier times \hat{t} multiplied by the probability of observing a spike at t given a spike at \hat{t} :

$$A(t) = \int_{-\infty}^t P_I(t|\hat{t}) A(\hat{t}) d\hat{t}. \quad (14.5)$$

Equation (14.5) is easy to understand. The kernel $P_I(t|\hat{t})$ is the probability density that the next spike of a neuron, which is under the influence of an input I , occurs at time t given that its last spike was at \hat{t} . The number of neurons which have fired at \hat{t} is proportional to $A(\hat{t})$ and the integral runs over all times in the past. The interval distribution $P_I(t|\hat{t})$ depends on the total input (both the external input and the synaptic input from other neurons in the population). For an unconnected population, $I(t)$ corresponds to the external drive.

For connected neurons, $I(t)$ is the sum of the external input and the recurrent input from other neurons in the population; the case of connected neurons will be further analyzed in Section 14.2.

We emphasize that $A(t)$ on the left-hand side of Eq. (14.5) is the *expected* activity at time t , while $A(\hat{t})$ on the right-hand side is the *observed* activity in the past. In the limit of the number N of neurons in the population going to infinity, the fraction of neurons that actually fire in a short time Δt is the same as its expected value $A(t)\Delta t$. Therefore, Eq. (14.5) becomes exact in the limit of $N \rightarrow \infty$, so that we can use the same symbol for $A(t)$ on both sides of the equation. Finite-size effects are discussed in Section 14.6.

We conclude this section with some final remarks on the form of Eq. (14.5). First, we observe that we can multiply the activity value A on both sides of the equation with a constant c and introduce a new variable $A' = cA$. If $A(t)$ solves the equation, then $A'(t)$ will solve it as well. Thus, Eq. (14.5) cannot predict the correct normalization of the activity A . This reflects the fact that, instead of defining the activity by a spike count divided by the number N of neurons, we could have chosen to work directly with the spike count per unit of time or any other normalization. The proper normalization consistent with our definition of the population activity $A(t)$ is derived below in Section 14.1.3.

Second, even though Eq. (14.5) is linear in the variable A , it is in fact a highly nonlinear equation in the drive, because the kernel $P_I(t|\hat{t})$ depends nonlinearly on the input $I(t)$. However, numerical implementations of the integral equations lead to rapid schemes that predict the population activity in response to changing input, even in the highly nonlinear regime when strong input transiently synchronizes neurons in the population (Fig. 14.1).

Example: Leaky integrate-and-fire neurons with escape noise

Using appropriate numerical schemes, the integral equation can be used to predict the activity in a homogeneous population of integrate-and-fire neurons subject to a time-dependent input. In each time step, the fraction of neurons that fire is calculated as $A(t)\Delta t$ using (14.5). The value of $A(t)$ then becomes part of the observed history and we can evaluate the fraction of neurons in the next time step $t + \Delta t$. For the sake of the implementation, the integral over the past can be truncated at some suitable lower bound (see Section 14.1.5). The numerical integration of Eq. (14.5) predicts well the activity pattern observed in a simulation of 4000 independent leaky integrate-and-fire neurons with exponential escape noise (Fig. 14.1).

14.1.3 Normalization and derivation of the integral equation

To derive Eq. (14.5), we recall that $P_I(t|\hat{t})$ is the probability density that a neuron fires at time t given its last spike at \hat{t} and an input $I(t')$ for $t' \leq t$. Integration of the probability density over time $\int_{\hat{t}}^t P_I(s|\hat{t})ds$ gives the probability that a neuron which has fired at \hat{t} fires its next spike at some arbitrary time between \hat{t} and t . Just as in Chapter 7, we can define a

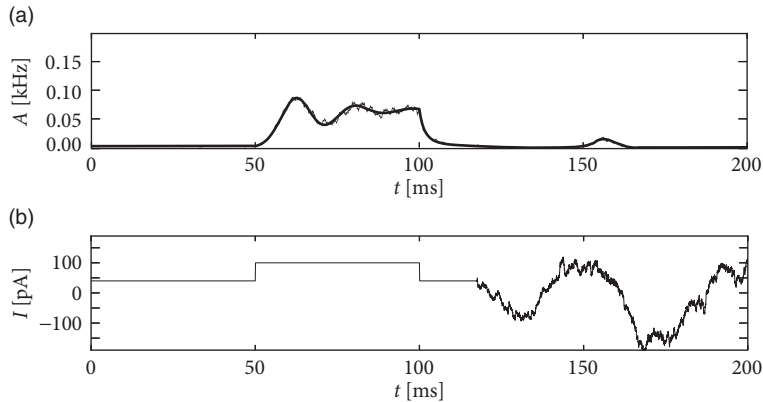


Fig. 14.1 Population activity $A(t)$ (top) in a population of leaky integrate-and-fire neurons with escape noise in response to a time-dependent input (bottom). After a strong step, neurons in the population synchronize, which leads to a transient oscillation. The numerical solution of the integral equation is compared with a simulation of 4000 neurons.

survival probability,

$$S_I(t|\hat{t}) = 1 - \int_{\hat{t}}^t P_I(s|\hat{t})ds, \quad (14.6)$$

i.e., the probability that a neuron which has fired its last spike at \hat{t} “survives” without firing up to time t .

We now return to the homogeneous population of neurons in the limit of $N \rightarrow \infty$ and assume that the firing of different neurons at time t is independent, given that we know the history (the input and last spike) of each neuron. The technical term for such a situation is “conditional independence.” We consider the network state at time t and label all neurons by their last firing time \hat{t} . The proportion of neurons at time t which have fired their last spike between t_0 and $t_1 < t$ (and have not fired since) is expected to be

$$\left\langle \frac{\text{number of neurons at } t \text{ with last spike in } [t_0, t_1]}{\text{total number of neurons}} \right\rangle = \int_{t_0}^{t_1} S_I(t|\hat{t})A(\hat{t})d\hat{t}. \quad (14.7)$$

For an interpretation of the integral on the right-hand side of Eq. (14.7), we recall that $A(\hat{t})d\hat{t}$ is the fraction of neurons that have fired in the interval $[\hat{t}, \hat{t} + \Delta\hat{t}]$. Of these a fraction $S_I(t|\hat{t})$ are expected to survive from \hat{t} to t without firing. Thus among the neurons that we observe at time t the proportion of neurons that have fired their last spike between t_0 and t_1 is expected to be $\int_{t_0}^{t_1} S_I(t|\hat{t})A(\hat{t})d\hat{t}$; see Fig. 14.2.

Finally, we use the fact that the total number of neurons remains constant. All neurons have fired at *some* point in the past.¹ Thus, if we extend the lower bound t_0 of the integral on the right-hand side of Eq. 14.7 to $-\infty$ and the upper bound to t , the left-hand side becomes

¹Neurons which have never fired before are assigned a formal firing time $\hat{t} = -\infty$.

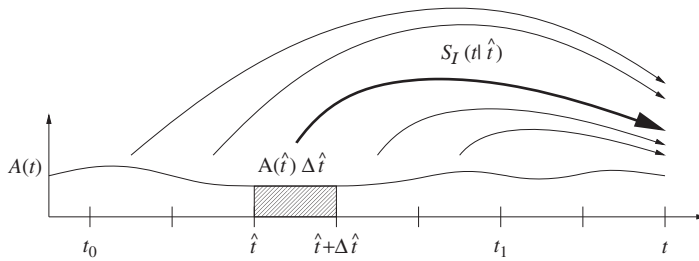


Fig. 14.2 Derivation of the population equation in discretized time. Of the $NA(\hat{t})\Delta\hat{t}$ neurons that have fired between \hat{t} and $\hat{t} + \Delta\hat{t}$, a fraction $S_I(t|\hat{t})$ is expected to “survive” up to time t without firing another spike. Thus (with $t_1 = \hat{t}_0 + k^{\max}\Delta\hat{t}$) the Riemann sum $\sum_{k=0}^{k^{\max}} S(t|t_0 + k\Delta\hat{t})A(t_0 + k\Delta\hat{t})\Delta\hat{t} \approx \int_{t_0}^{t_1} S_I(t|\hat{t})A(\hat{t})d\hat{t}$ gives the expected fraction of neurons at time t that have fired their last spike between t_0 and t_1 .

equal to one,

$$1 = \int_{-\infty}^t S_I(t|\hat{t})A(\hat{t})d\hat{t}, \quad (14.8)$$

because all N neurons have fired their last spike in the interval $[-\infty, t]$. Since the number of neurons remains constant, the normalization of Eq. 14.8 must hold at arbitrary times t . Eq. (14.8) is an implicit equation for the population activity A and the starting point for the discussions in this and the following chapters.

Since Eq. (14.8) is rather abstract, we will put it into a form that is easier to grasp intuitively. To do so, we take the derivative of Eq. (14.8) with respect to t . We find

$$0 = S_I(t|t)A(t) + \int_{-\infty}^t \frac{\partial S_I(t|\hat{t})}{\partial t} A(\hat{t})d\hat{t}. \quad (14.9)$$

We now use $P_I(t|\hat{t}) = -\frac{\partial}{\partial t}S_I(t|\hat{t})$ and $S_I(t|t) = 1$, which is a direct consequence of Eq. (14.6). This yields the activity dynamics of Eq. (14.5).

We repeat an important remark concerning the normalization of the activity. Since Eq. (14.5) is defined as the *derivative* of Eq. (14.8), the integration constant on the left-hand side of Eq. (14.8) is lost. This is most easily seen for constant activity $A(t) = A_0$. In this case the variable A_0 can be eliminated on both sides of Eq. (14.5) so that it yields the trivial statement that the interval distribution is normalized to unity. Equation (14.5) is therefore invariant under a rescaling of the activity $A_0 \rightarrow cA_0$ with any constant c , as mentioned earlier. To get the correct normalization of the activity we have to return to Eq. (14.8).

Example: Absolute refractoriness and the Wilson–Cowan integral equation

Let us consider a population of Poisson neurons with an absolute refractory period Δ^{abs} . A neuron that is not refractory fires stochastically with a rate $f[h(t)]$ where $h(t) = \int_0^\infty \kappa(s)I(t-s)ds$ is the total input potential caused by an external driving current or synaptic input from other neurons. After firing, a neuron is inactive during a time

Δ^{abs} . The population activity of a homogeneous group of Poisson neurons with absolute refractoriness is (Wilson and Cowan, 1972)

$$A(t) = f[h(t)] \left\{ 1 - \int_{t-\Delta^{\text{abs}}}^t A(t') dt' \right\}. \quad (14.10)$$

Eq. (14.10) represents a special case of Eqs. (14.5) and (14.8) (see Exercises).

The Wilson–Cowan integral equation (14.10) has a simple interpretation. Neurons stimulated by a total postsynaptic potential $h(t)$ fire with an instantaneous rate $f[h(t)]$. If there were no refractoriness, we would expect a population activity $A(t) = f[h(t)]$. However, not all neurons may fire, since some of the neurons are in the absolute refractory period. The fraction of neurons that participate in firing is $1 - \int_{t-\Delta^{\text{abs}}}^t A(t') dt'$, which explains the factor in curly brackets.

The function f in Eq. (14.10) was introduced here as the stochastic intensity of an inhomogeneous Poisson process describing neurons in a *homogeneous* population. In this interpretation, Eq. (14.10) is the exact equation for the population activity of neurons with absolute refractoriness in the limit of $N \rightarrow \infty$. In their original paper, Wilson and Cowan motivated the function f by a distribution of threshold values in an *inhomogeneous* population. In this case, the population equation (14.10) is only an approximation since correlations are neglected (Wilson and Cowan, 1972).

For constant input potential, $h(t) = h_0 = I_0 \int_0^\infty \kappa(s) I(t-s) ds$, the population activity has a stationary solution (see Fig. 14.3)

$$A_0 = \frac{f(h_0)}{1 + \Delta^{\text{abs}} f(h_0)} = g(h_0). \quad (14.11)$$

For the last equality sign we have used the definition of the gain function of Poisson neurons with absolute refractoriness in Eq. (7.50). Equation (14.11) tells us that in a homogeneous population of neurons the population activity in a stationary state is equal to the firing rate of individual neurons, as expected from the discussion in Chapter 12.

Sometimes the stationary solution from Eq. (14.11) is also used in the case of time-dependent input. However, the expression $A_0(t) = g(h(t))$ [with g from Eq. (14.11)] does not correctly reflect the transients that are seen in the solution of the integral equation (14.10); see Fig. 14.3b and Chapter 15.

14.1.4 Integral equation for adaptive neurons

The integral equations presented so far are restricted to non-adapting neurons, because we assumed that the knowledge of the input and of the last firing time was sufficient to characterize the state of a neuron. For adapting neurons, however, the whole spiking history can shape the interspike interval distribution. In this section we extend the integral equation (14.5) to the case of adapting neurons.

For an *isolated* adaptive neuron in the presence of noise, the probability density of firing around time t will, in general, depend on its past firing times $\hat{t}_n < \hat{t}_{n-1} \cdots < \hat{t}_2 < \hat{t}_1 = \hat{t} < t$

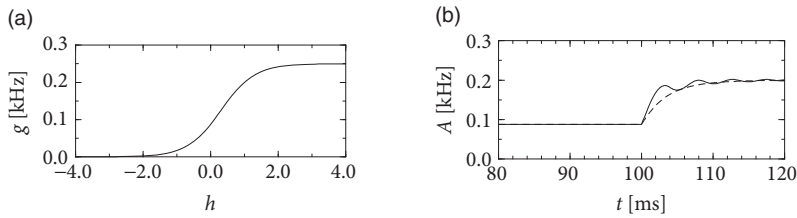


Fig. 14.3 Wilson–Cowan model. (a) Stationary activity calculated from the gain function $A_0 = g(h)$ of Poisson neurons with absolute refractoriness of $\Delta^{\text{abs}} = 4$ ms; see Eq. (14.11). (b) The response of the population activity to an abrupt change of the input current shows an oscillatory behavior (solid line) in the approach to the new stationary state. The oscillations are absent in a quasi-stationary approximation $A_0(t) = g(h(t))$ where the stationary solution from Eq. (14.11) is applied to explain time-dependent behavior (dashed line). The input potential vanishes for $t_0 < 100$ ms and is $h(t) = 1 - \exp[-(t - t_0)/\tau_m]$ for $t > t_0$ with $\tau_m = 4$ ms. The exponential escape rate $f(h) = \tau_0^{-1} \exp[\beta(h - \vartheta)]$ with $\vartheta = 1$, $\tau_0 = 1$ ms, and $\beta = 2$. No lateral coupling ($w_0 = 0$).

where $\hat{t} = \hat{t}_1$ denotes the *most recent* spike time. The central insight is that, in a *population* of neurons, we can approximate the past firing times by the population activity $A(\hat{t})$ in the past. Indeed, the probability of one of the neurons having a past spike time $\hat{t}_k = t'$ in the interval $\hat{t} < t' < \hat{t} + \Delta t$ is $A(\hat{t})\Delta t$.

Just as in the time-dependent renewal theory, we will treat the most recent spike $\hat{t}_1 = \hat{t}$ of each neuron explicitly. For all spikes \hat{t}_k with $k \geq 2$ we approximate the actual spike-train history of an individual by the *average* history as summarized in the population activity $A(t)$. Let $P_{t,A}(t|\hat{t})$ be the probability of observing a spike at time t given the last spike at time \hat{t} , the input current *and* the activity history $A(t)$ until time t ; then we can rewrite Eq. (14.5) in a form suitable for adaptive neurons

$$A(t) = \int_{-\infty}^t P_{t,A}(t|\hat{t})A(\hat{t})d\hat{t}. \quad (14.12)$$

In Section 14.5 we explain the methods to describe populations of adaptive neurons in more detail. Appropriate numerical schemes (Section 14.1.5) make it possible to describe the response of a population of adaptive neurons to arbitrary time-dependent input; see Fig. 14.4.

14.1.5 Numerical methods for integral equations (*)

Integral equations can be solved numerically. However, the type of equation we face in Eq. (14.5) or Eq. (14.12) cannot be cast in the typical Volterra or Fredholm forms for which efficient numerical methods have been extensively studied (Linz, 1985; Atkinson, 1997). In what follows, we describe a method that can be used to solve Eq. (14.5), Eq. (14.12) or

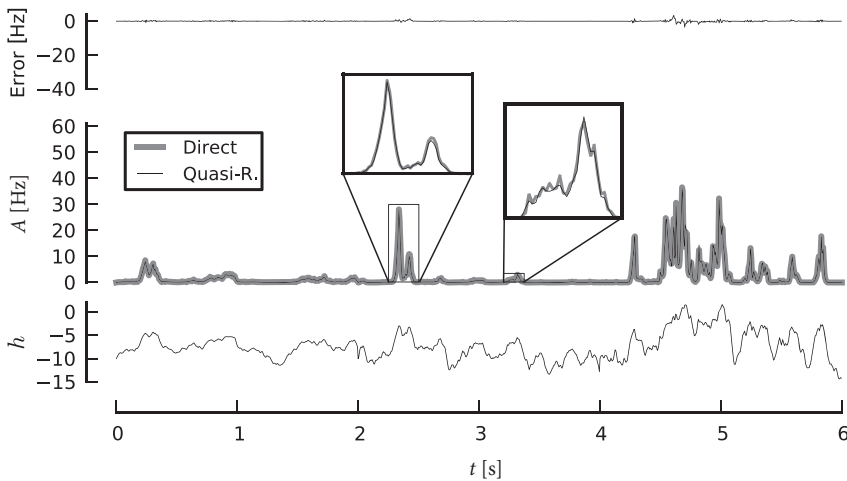


Fig. 14.4 Population of adaptive neurons. Middle: The solution (black solid line) of the integral equation for adaptive neurons (14.12) is compared with the population activity during a simulation of 25 000 model neurons (thick gray line). Model neurons are Generalized Linear Models of spiking neurons with parameters from cortical cells; see Chapter 11. Top: Error (theory minus simulations) in the prediction of the population activity. Bottom: Driving stimulus $h(t) = \int_0^\infty \exp(-s/\tau_m) I(t-s) ds$ in arbitrary units. Threshold in the limit of deterministic neurons located at $h = 0$ so that $h < 0$ indicates the subthreshold regime. Modified from Naud and Gerstner (2012a).

Eq. (14.8), but we take as an example the quasi-renewal equivalent of Eq. (14.8)

$$1 = \int_{-\infty}^t S_{I,A}(t|\hat{t}) A(\hat{t}) d\hat{t}. \quad (14.13)$$

To derive a numerical algorithm, we proceed in three steps: first, truncation of the integral in Eq. (14.13) at some lower bound; second, the discretization of this integral; and, third, the discretization of the integral defining the survivor function. Here we will use the rectangle rule for the discretization of every integral. Note that adaptive quadratures or Monte-Carlo methods could present more efficient alternatives.

The first step is the truncation. The probability of surviving a very long time is essentially zero. Let τ_c be a period of time such that the survivor $S_{I,A}(t|t - \tau_c)$ is very small. Then, we can truncate the infinite integral in (14.13)

$$1 = \int_{t-\tau_c}^t S_{I,A}(t|\hat{t}) A(\hat{t}) d\hat{t}. \quad (14.14)$$

Next, we proceed to discretize the integral on small bins of size Δt . Let $\mathbf{m}^{(t)}$ be the vector made up of the fraction of neurons at t with last spike within \hat{t} and $\hat{t} + \Delta t$. This definition means that the k th element is $m_k^{(t)} = S(t|t - k\Delta t) A(t - k\Delta t) \Delta t$. The element with $k = 0$ is then the momentary population activity in the time step starting at time t , $m_0^{(t)} = A_t \Delta t$, since

$S(t|t) = 1$. Therefore we arrive at

$$A_t \Delta t = 1 - \sum_{k=1}^K m_k^{(t)}. \quad (14.15)$$

Finally, we discretize the integral defining the survival function to obtain $m_k^{(t)}$ as a function $m_k^{(t-\Delta t)}$. Because of $S(t|\hat{t}) = \exp[-\int_{\hat{t}}^t \rho(t'|\hat{t})dt'] = \exp[-\int_{t-\Delta t}^t \rho(t'|\hat{t})dt']S(t-\Delta t|\hat{t})$, we find for sufficiently small time steps

$$m_k^{(t)} = m_{k-1}^{(t-\Delta t)} \exp[-\rho(t|t-k\Delta t)\Delta t] \quad \text{for } k \geq 1. \quad (14.16)$$

Note that we work in a moving coordinate because the index k always counts time steps backward starting from the present time t . Therefore $m_k^{(t)}$ and $m_{k-1}^{(t-\Delta t)}$ refer to the same group of neurons, i.e., those that have fired their last spike around time $\hat{t} = t - k\Delta t = (t - \Delta t) - (k-1)(\Delta t)$. Equation (14.16) indicates that the number of neurons that survive from \hat{t} up to t decreases in each time step by an exponential factor. In Eq. (14.16), $\rho(t|t')$ can be either the renewal conditional intensity of a non-adaptive neuron model (e.g., Eq. (14.3)) or the effective “quasi-renewal” intensity of adaptive neurons (see Section 14.5). Together, Eqs. (14.15) and (14.16) can be used to solve A_t iteratively.

14.2 Recurrent networks and interacting populations

The integral equation (14.5) derived in the previous section can be applied to interacting populations of connected neurons. In Section 14.2.1 we present the mathematical framework of the integral equations so as to describe several populations that interact with each other.

Using the methods discussed in Chapter 12, we can find the activity A_0 of a recurrent network in the regime of stationary asynchronous firing (Section 14.2.2). Using the linear response filter, which will be derived in Section 14.3, the stability of the solutions can further be analyzed for different levels of noise and arbitrary delays (Section 14.2.3).

14.2.1 Several populations and networks with self-interaction

In Section 14.1 we discussed a single homogeneous population of N neurons. The formalism of integral equations introduced there can readily be adapted to several populations with recurrent interactions within and across populations.

We consider a coupled network of spiking neurons of the renewal type, such as nonlinear (or leaky) integrate-and-fire neurons with escape noise or a Spike Response Model SRM₀. Neurons within a population have the same set of parameters whereas neurons of different populations can have different parameters. The activity of population k is described by Eq. (14.5)

$$A_k(t) = \int_{-\infty}^t P_k(t|\hat{t})A_k(\hat{t})d\hat{t}, \quad (14.17)$$

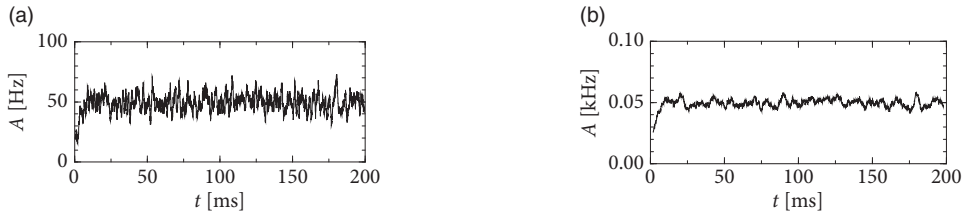


Fig. 14.5 Asynchronous firing. For a sufficient amount of noise, the population activity in a network of coupled spiking neurons with constant external input approaches a stationary value A_0 . (a) The population activity of 1000 neurons has been filtered with a time window of 1 ms duration. (b) Same parameters as before, but the size of the population has been increased to $N = 4000$. Fluctuations decrease with N and approach the value of $A_0 = 50$ Hz predicted by theory.

where $P_k(t|\hat{t})$ is the input-dependent interval distribution of population k . The input to population k is

$$I_k(t) = \sum_n N_n w_{kn} \int_0^\infty \alpha_{kn}(s) A_n(t-s) ds + I_k^{\text{ext}}. \quad (14.18)$$

Here N_n is the number of neurons in the presynaptic population n , w_{kn} is the strength of a synaptic connection of a neuron in population n to a neuron in population k , and α_{kn} the time course of the postsynaptic current into a neuron in population k , caused by spike firing of a neuron in population n . Conductance-based synapses are treated in the current-based approximation (see Section 13.6.3). Connections can be excitatory or inhibitory, depending on the choice of w_{kn} . Because the overall strength of the connection is incorporated in w_{kn} , we can, without loss of generality, assume a normalization $\int_0^\infty \alpha_{kn}(s) ds = 1$.

The noise level of each neuron in population k is fixed to a value of σ_k . The choice of noise is arbitrary. If our aim is to mimic stochastic spike arrivals in randomly connected networks by an escape rate, a suitable choice of escape function has been given in Chapter 9. In practice this implies that noise in the *input* to a neuron is effectively described and replaced by escape noise in its *output*.

In the following we assume a fully connected network with interaction strength $w_{kn} = J_{kn}/N_n$; see Chapter 12. If the theory is applied to a random network where each neuron in population k has a fixed number of presynaptic partners C_{kn} in population n , we can use the same theory, except that (i) we use $w_{kn} = J_{kn}/C_{kn}$; and (ii) we increase the noise level σ in the escape rate function so as to mimic the additional noise caused by stochastic spike arrival; see Section 9.4.

14.2.2 Stationary states and fixed points of activity

We are interested in the value $A_k(t) = A_{k,0}$ of the population activity in the stationary state of asynchronous firing. We recall from Chapter 12 that stationary activity means that the *expected* value of the population activity is constant whereas in a simulation the actual value $A(t)$ always fluctuates (Fig. 14.5). To lighten the notation, we consider a single

population k with self-interaction $w_{kk} = J_0/N_k$ and drop the index k subsequently. The input from other populations is summarized as a constant external input I^{ext} . According to our assumptions, all neurons in the population have the same parameters and can be described by time-dependent renewal theory. The level of noise is indicated by an index σ .

A stationary state of asynchronous firing requires that the total input I_0 is constant (or at least stationary). In Chapter 12, we have seen that the population activity A_0 in the state of asynchronous firing is given by the single-neuron firing rate $v = g_\sigma(I_0)$. We thus have

$$A_0 = v = g_\sigma(I_0). \quad (14.19)$$

Given constant activity A_0 of the population and constant external input I_0^{ext} , the total input I_0 to each neuron is constant. From Eq. (14.18) we find the total input to a neuron in population k

$$I_0 = I_0^{\text{ext}} + J_0 \int_0^\infty \alpha(s) A_0(t-s) ds = I_0^{\text{ext}} + J_0 A_0. \quad (14.20)$$

Equations (14.19) and (14.20) together yield the following equation for the population activity A_0

$$A_0 = g_\sigma(J_0 A_0 + I_0^{\text{ext}}). \quad (14.21)$$

This result agrees with the general result found in Chapter 12 for the stationary state in a network with self-coupling. Solutions can be found graphically (Fig. 14.6) using the same method as in Chapter 12.

The advantage of the integral equation approach is two-fold. First, for the integral equations we have transparent mathematical tools to analyze the stability of the stationary solution, as shown in Section 14.2.3.

Second, we can write down the gain function $g_\sigma(I)$ and an expression for A_0 in a compact form, as will be shown now. Because the input is constant, the state of each neuron depends only on the time since the last spike $t - \hat{t}$. We are thus in the situation of stationary renewal theory. Therefore, the survivor function and the interval distribution cannot depend explicitly upon the absolute time, but only on the time difference $s = t - \hat{t}$. Hence we set

$$S_I(\hat{t} + s | \hat{t}) \rightarrow S_0(s), \quad (14.22)$$

$$P_I(\hat{t} + s | \hat{t}) \rightarrow P_0(s). \quad (14.23)$$

The value of the stationary activity A_0 now follows directly from the normalization Equation (14.8),

$$1 = A_0 \int_0^\infty S_0(s) ds. \quad (14.24)$$

We use $\frac{d}{ds} S_0(s) = -P_0(s)$ and integrate by parts

$$1 = A_0 \int_0^\infty s P_0(s) ds = A_0 \langle T \rangle, \quad (14.25)$$

where the last equality follows from the definition of the mean interspike interval

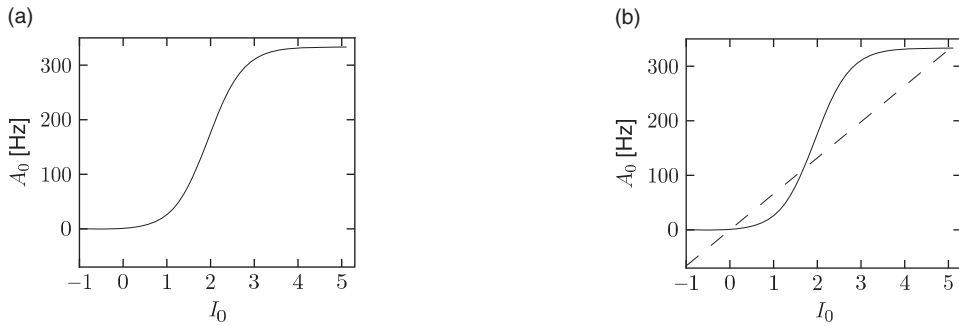


Fig. 14.6 Gain function and stationary activity in a population of SRM neurons with exponential escape noise. (a) Gain function (single neuron firing frequency ν as a function of constant current I_0) for neurons with refractoriness given by Eq. (14.29). (b) Self-consistent solution for the population activity $A(t) = A_0$ in a recurrent network of SRM neurons coupled to itself with strength J_0 . Neurons are characterized by the same gain function as in part (a) of the figure.

(see Chapter 9). Hence

$$A_0 = \frac{1}{\int_0^\infty S_0(s) ds} = \frac{1}{\langle T \rangle} = \nu. \quad (14.26)$$

The result has an intuitively appealing interpretation: if everything is constant, then averaging over time (for a single neuron) is the same as averaging over a population of identical neurons; see the discussion in Chapter 12.

Example: Population of SRM neurons with escape noise

Consider a population of SRM₀ neurons with exponential escape noise and membrane potential

$$u(t) = \eta(t - \hat{t}) + \int_0^\infty \kappa(s) I(t - s) ds = \eta(t - \hat{t}) + h(t). \quad (14.27)$$

We assume that the input current is constant so that $h(t) = h_0 = RI_0$ with $R = \int_0^\infty \kappa(s) ds$. With exponential escape noise, the hazard function (Chapter 9) is $\rho(t - \hat{t}) = \rho_0 \exp[\beta(h_0 + \eta(t - \hat{t}))]$ and the gain function is given by Eq. (14.26)

$$A_0 = \left[\int_0^\infty dx \exp \left(- \int_0^x \rho_0 e^{\beta[h_0 + \eta(s)]} ds \right) \right]^{-1} = g_\sigma(I_0) \quad (14.28)$$

where $\sigma = 1/\beta$ indicates the level of noise.

We now set $\beta = 1$ and consider a specific choice of η that includes absolute and relative refractoriness

$$\eta(t) = \begin{cases} -\infty & \text{if } t < \Delta^{\text{abs}} \\ \ln [1 - e^{-(t - \Delta^{\text{abs}})/\tau}] & \text{otherwise.} \end{cases} \quad (14.29)$$

With this choice of η it is possible to calculate the gain function in terms of the incomplete gamma function $\gamma(a, x) = \int_0^x t^{a-1} e^{-t} dt$.

$$A_0 = g_\sigma(I_0) = \left(\Delta^{\text{abs}} + \frac{\tau \gamma(r, r)}{r^r e^{-r}} \right)^{-1}, \quad (14.30)$$

where $r = \tau \rho_0 e^{h_0}$ (see Exercises). The result is shown in Fig. 14.6a.

If the population of neurons is coupled to itself with synapses $w_0 = J_0/N$, the stationary value of asynchronous activity can be found graphically by plotting on the same graph $A_0 = g_\sigma(I_0)$ and

$$A_0 = [I_0 - I_0^{\text{ext}}]/J_0, \quad (14.31)$$

which follows from Eq. (14.20); see Fig. 14.6b.

14.2.3 Oscillations and stability of the stationary state (*)

In the previous subsection we assumed that the network is in a state of asynchronous firing. In this section, we study whether asynchronous firing can indeed be a stable state of a fully connected population of spiking neurons – or whether the connectivity drives the network toward oscillations. For the sake of simplicity, we restrict the analysis to SRM₀ neurons; the same methods can, however, be applied to integrate-and-fire neurons or spiking neurons formulated in the framework of Generalized Linear Models.

For SRM₀ neurons (see Chapter 9), the membrane potential is given by

$$u_i(t) = \eta(t - \hat{t}_i) + h(t), \quad (14.32)$$

where $\eta(t - \hat{t}_i)$ is the effect of the last firing of neuron i (i.e., the spike-afterpotential) and $h(t)$ is the total postsynaptic potential caused by presynaptic firing. If all presynaptic spikes are generated within the homogeneous population under consideration, we have

$$h(t) = \sum_j w_{ij} \sum_f \varepsilon_0(t - t_j^f) = J_0 \int_0^\infty \varepsilon_0(s) A(t - s) ds. \quad (14.33)$$

Here $\varepsilon_0(t - t_j^f)$ is the time course of the postsynaptic potential generated by a spike of neuron j at time t_j^f and $w_{ij} = J_0/N$ is the strength of lateral coupling within the population. The second equality sign follows from the definition of the population activity, i.e., $A(t) = N^{-1} \sum_j \sum_f \delta(t - t_j^f)$; see Chapter 12. For the sake of simplicity, we have assumed in Eq. (14.33) that there is no external input.

The state of asynchronous firing corresponds to a fixed point $A(t) = A_0$ of the population activity. We have already seen in the previous subsection as well as in Chapter 12 how the fixed point A_0 can be determined either numerically or graphically. To analyze its stability we assume that for $t > 0$ the activity is subject to a small perturbation,

$$A(t) = A_0 + A_1 e^{i\omega t + \lambda t} \quad (14.34)$$

with $A_1 \ll A_0$. This perturbation in the activity induces a perturbation in the input potential,

$$h(t) = h_0 + h_1 e^{i\omega t + \lambda t}. \quad (14.35)$$

The perturbation of the potential causes some neurons to fire earlier (when the change in h is positive) and others to fire later (whenever the change is negative). The perturbation may therefore build up ($\lambda > 0$, the asynchronous state is unstable) or decay back to zero ($\lambda < 0$, the asynchronous state is stable). At the transition between the region of stability and instability the amplitude of the perturbation remains constant ($\lambda = 0$, marginal stability of the asynchronous state). These transition points, defined by $\lambda = 0$, are determined now.

We start from the population integral equation $A(t) = \int_{-\infty}^t P_I(t|\hat{t}) A(\hat{t}) d\hat{t}$ that was introduced in Section 14.1. Here $P_I(t|\hat{t})$ is the input-dependent interval distribution, i.e., the probability density of emitting a spike at time t given that the last spike occurred at time \hat{t} . The linearized response of the population activity to a small change ΔI in the input can, under general smoothness assumptions, always be written in the form

$$A(t) = A_0 + \int_0^\infty G(s) \Delta I(t-s) ds, \quad (14.36)$$

where $G(s)$ is the linear response filter in the time domain. The Fourier transform $\hat{G}(\omega)$ is the frequency-dependent gain function. The explicit form of the filter will be derived in the framework of the integral equations in Section 14.3.

Instead of thinking of a stimulation by an input current $\Delta I(t)$, it is more convenient to work with the input potential $h(t) = \int_0^\infty \kappa(s) I(t-s) ds$, because the neuron model equations have been defined on the level of the potential; see Eq. (14.32). We use $\Delta A(t) = A_1 e^{i\omega t + \lambda t}$ and $\Delta h(t) = h_1 e^{i\omega t + \lambda t}$ in Eq. (14.36) and search for the critical value $\lambda = 0$ where the stable solution turns into an unstable one. After cancellation of a common factor $A_1 \exp(i\omega t)$ the result can be written in the form

$$1 = J_0 \frac{\hat{G}(\omega) \hat{\epsilon}(\omega)}{\hat{\kappa}(\omega)} = S_f(\omega) \exp[i\Phi(\omega)]. \quad (14.37)$$

Here, $\hat{\kappa}(\omega)$ and $\hat{\epsilon}(\omega)$ are the Fourier transform of the membrane kernel $\kappa(s)$ and the time course of the postsynaptic potential $\epsilon_0(s)$ caused by an input spike, respectively. Typically, $\kappa(s) = (R/\tau_m) \exp(-s/\tau_m)$ where τ_m is the membrane time constant. If the synaptic input is a short current pulse of unit charge, ϵ_0 and κ are identical, but we would also like to include the case of synaptic input currents with arbitrary time dependence and therefore keep separate symbols for ϵ_0 and κ . The second equality sign defines the real-valued functions $S_f(\omega)$ and $\Phi(\omega)$.

Equation (14.37) is thus equivalent to

$$S_f(\omega) = 1 \quad \text{and} \quad \Phi(\omega) \bmod 2\pi = 0. \quad (14.38)$$

Solutions of Eq. (14.38) yield bifurcation points where the asynchronous firing state loses its stability toward an oscillation with frequency ω .

We have written Eq. (14.38) as a combination of two requirements, i.e., an *amplitude*

condition $S_f(\omega) = 1$ and a *phase* condition $\Phi(\omega) \bmod 2\pi = 0$. Let us discuss the general structure of the two conditions. First, if $S_f(\omega) \leq 1$ for all frequencies ω , an oscillatory perturbation cannot build up. All oscillations decay and the state of asynchronous firing is stable. We conclude from Eq. (14.37) that by increasing the absolute value $|J_0|$ of the coupling constant, it is always possible to increase $S_f(\omega)$. The amplitude condition can thus be met if the excitatory or inhibitory feedback from other neurons in the population is sufficiently strong. Second, for a bifurcation to occur we need in addition that the phase condition is met. Loosely speaking, the phase condition implies that the feedback from other neurons in the network must arrive just in time to keep the oscillation going. Thus the axonal signal transmission time and the rise time of the postsynaptic potential play a critical role during oscillatory activity (Abbott and van Vreeswijk, 1993; Gerstner and van Hemmen, 1993; Treves, 1993; Tsodyks *et al.*, 1993; Gerstner, 1995; Brunel and Hakim, 1999; Brunel, 2000; Gerstner, 2000).

Example: Slow noise and phase diagram of instabilities

Let us apply the above results to leaky integrate-and-fire neurons with slow noise in the parameters. After each spike the neuron is reset to a value u_r which is drawn from a Gaussian distribution with mean \bar{u}_r and width $\sigma_r \ll [\vartheta - \bar{u}_r]$. After the reset, the membrane potential evolves deterministically according to

$$\tau_m \frac{du}{dt} = -u + RI(t). \quad (14.39)$$

The next firing occurs if the membrane potential hits the threshold ϑ .

We assume that neurons are part of a large population $N \rightarrow \infty$ which is in a state of asynchronous firing with activity A_0 . In this case, each neuron receives a constant input I_0 . For constant input, a neuron which was reset to a value \bar{u}_r will fire again after a period T_0 . Because of the noisy reset with $\sigma_r \ll [\vartheta - \bar{u}_r]$, the interval distribution is approximately a Gaussian centered at T_0 . We denote the standard deviation of the interval distribution by σ . The stationary population activity is simply $A_0 = 1/T_0$. The width of the Gaussian interval distribution σ is linearly related to σ_r with a proportionality factor that represents the (inverse of the) slope of the membrane potential at the firing threshold (Gerstner, 2000).

In order to analyze the stability of the stationary state, we have to specify the time course of the excitatory or inhibitory postsynaptic potential ε_0 . For the sake of simplicity we choose a delayed alpha function,

$$\varepsilon_0(s) = \frac{s - \Delta^{\text{ax}}}{\tau^2} \exp\left(-\frac{s - \Delta^{\text{ax}}}{\tau}\right) \Theta(s - \Delta^{\text{ax}}). \quad (14.40)$$

The Fourier transform of ε has an amplitude $|\hat{\varepsilon}(\omega)| = (1 + \omega^2 \tau^2)^{-1}$ and a phase $|\psi(\omega)| = \omega \Delta^{\text{ax}} + 2 \arctan(\omega \tau)$. Note that a change in the delay Δ^{ax} affects only the phase of the Fourier transform and not the amplitude.

Figure 14.7 shows S_f defined in the second equality sign of Eq. (14.37) as a function of ωT_0 . Since $S_f = 1$ is a necessary condition for a bifurcation, it is apparent that bifurcations can occur only for frequencies $\omega \approx \omega_n = n 2\pi/T_0$ with integer n where $T_0 = 1/A_0$ is the typical interspike interval. We also see that higher harmonics are only relevant for low levels of noise. At a high noise level, however, the asynchronous state is stable even with respect to perturbations at $\omega \approx \omega_1$.

A bifurcation at $\omega \approx \omega_1$ implies that the period of the perturbation is identical to the firing period of individual neurons. Higher harmonics correspond to instabilities of the asynchronous state toward cluster states (Golomb *et al.*, 1992; Gerstner and van Hemmen, 1993; Ernst *et al.*, 1995; Golomb and Rinzel, 1994; Brunel, 2000): each neuron fires with a mean period of T_0 , but the population of neurons splits up in several groups that fire alternately so that the overall activity oscillates several times faster. In terms of the terminology introduced in Chapter 13, the network is in the synchronous regular (SR) state of fast oscillations.

Figure 14.7 illustrates the amplitude condition for the solution of Eq. (14.38). The numerical solutions of the full equation (14.38) for different values of the delay Δ^{ax} and different levels of the noise σ are shown in the bifurcation diagram of Fig. 14.8. The insets show simulations that illustrate the behavior of the network at certain combinations of transmission delay and noise level.

Let us consider, for example, a network with transmission delay $\Delta^{\text{ax}} = 2$ ms, corresponding to an x -value of $\Delta^{\text{ax}}/T_0 = 0.25$ in Fig. 14.8. The phase diagram predicts that, at a noise level of $\sigma = 0.5$ ms, the network is in a state of asynchronous firing. The simulation shown in the inset in the upper right-hand corner confirms that the activity fluctuates around a constant value of $A_0 = 1/T_0 = 0.125$ kHz.

If the noise level of the network is significantly reduced, the system crosses the short-dashed line. This line is the boundary at which the constant activity state becomes unstable with respect to an oscillation with $\omega \approx 3(2\pi/T_0)$. Accordingly, a network simulation with a noise level of $\sigma = 0.1$ exhibits an oscillation of the population activity with period $T^{\text{osc}} \approx T_0/3 \approx 2.6$ ms.

Keeping the noise level constant but reducing the transmission delay corresponds to a horizontal move across the phase diagram in Fig. 14.8. At some point, the system crosses the solid line that marks the transition to an instability with frequency $\omega_1 = 2\pi/T_0$. Again, this is confirmed by a simulation shown in the inset in the upper left corner. If we now decrease the noise level, the oscillation becomes even more pronounced (bottom left).

In the limit of low noise, the asynchronous network state is unstable for virtually all values of the delay. The region of the phase diagram in Fig. 14.8 around $\Delta^{\text{ax}}/T_0 \approx 0.1$, which looks stable, hides instabilities with respect to the higher harmonics ω_6 and ω_5 , which are not shown. We emphasize that the specific location of the stability borders depends on the form of the postsynaptic response function ε . The qualitative features of the phase diagram in Fig. 14.8 are generic and hold for all kinds of response kernels.

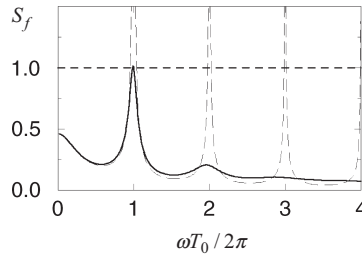


Fig. 14.7 Amplitude condition for instabilities in the asynchronous state. The amplitude S_f is plotted as a function of the normalized frequency ωT_0 for two different values of the noise: $\sigma = 1$ ms (solid line) and $\sigma = 0.1$ ms (dashed line). Instabilities of the asynchronous firing state are possible at frequencies where $S_f > 1$. For low noise S_f crosses unity (broken horizontal line) at frequencies $\omega \approx \omega_n = n2\pi/T_0$. For $\sigma = 1$ ms there is a single instability region for $\omega T_0 \approx 1$. For the plot we have set $T_0 = 2\tau$.

What happens if the excitatory interaction is replaced by inhibitory coupling? A change in the sign of the interaction corresponds to a phase shift of π . For each harmonic, the region along the delay axis where the asynchronous state is *unstable* for excitatory coupling (see Fig. 14.8) becomes *stable* for inhibition and vice versa. In other words, we simply have to shift the instability tongues for each harmonic frequency $\omega_n = 2n\pi/T_0$ horizontally by half the period of the harmonic, i.e., $\Delta/T_0 = 1/(2n)$. Apart from that the pattern remains the same.

14.3 Linear response to time-dependent input

We consider a homogeneous population of independent neurons. All neurons receive the same time-dependent input current $I(t)$ which varies about the mean I_0 . For constant input I_0 the population would fire at an activity A_0 which we can derive from the neuronal gain function. We require that the variations of the input

$$I(t) = I_0 + \Delta I(t) \quad (14.41)$$

are small enough for the population activity to stay close to the value A_0

$$A(t) = A_0 + \Delta A(t), \quad (14.42)$$

with $|\Delta A| \ll A_0$.

In that case, we may expand the right-hand side of the population equation $A(t) = \int_{-\infty}^t P_I(t|\hat{t}) A(\hat{t}) d\hat{t}$ into a Taylor series about A_0 to linear order in ΔA . In this section, we want to show that for spiking neuron models (either integrate-and-fire or SRM₀ neurons) the linearized population equation can be written in the form

$$\Delta A(t) = \int_{-\infty}^t P_0(t - \hat{t}) \Delta A(\hat{t}) d\hat{t} + A_0 \frac{d}{dt} \int_0^\infty \mathcal{L}(x) \Delta h(t - x) dx, \quad (14.43)$$

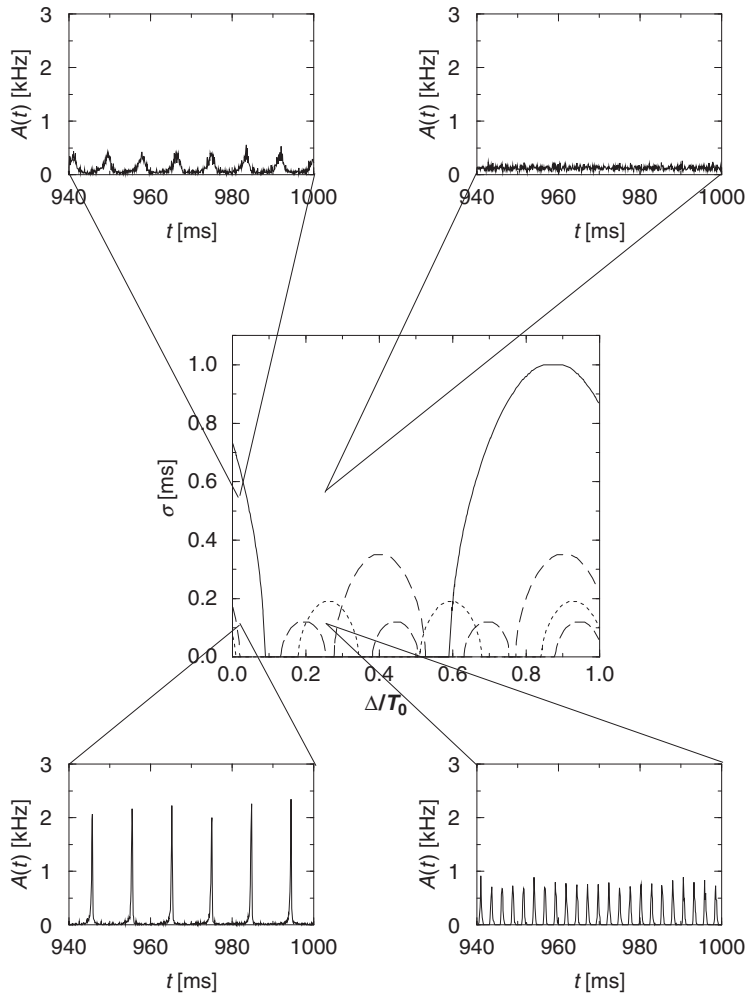


Fig. 14.8 Stability diagram (center) for the state of asynchronous firing in a network of SRM₀ neurons with reset noise as a function of the noise level (y-axis) and the delay Δ^{ax} (x-axis). The noise level is characterized by the standard deviation σ_{ISI} of the interspike-interval distribution divided by the mean interval T_0 . The diagram shows the borders of the stability region with respect to $\omega_1, \dots, \omega_4$. For high values of noise, the asynchronous firing state is always stable. If the noise is reduced, the asynchronous state becomes unstable with respect to an oscillation either with frequency ω_1 (solid border lines), or ω_2 (long-dashed border lines), ω_3 (short-dashed border lines), or ω_4 (long-short-dashed border lines). Four insets show typical patterns of the activity as a function of time taken from a simulation with $N = 1000$ neurons. Parameters are $\sigma_{\text{ISI}} = 0.5$ ms and $\Delta^{\text{ax}} = 0.2$ ms (top left); $\sigma_{\text{ISI}} = 0.5$ ms and $\Delta^{\text{ax}} = 2.0$ ms (top right); $\sigma_{\text{ISI}} = 0.1$ ms and $\Delta^{\text{ax}} = 0.2$ ms (bottom left); $\sigma_{\text{ISI}} = 0.1$ ms and $\Delta^{\text{ax}} = 2.0$ ms (bottom right). Neuronal parameters are $J_0 = 1$ and $\tau = 4$ ms. The threshold ϑ was adjusted so that the mean interspike interval is $T_0 = 2\tau = 8$ ms. Adapted from Gerstner (2000).

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

$$\Delta h(t) = \int_0^\infty \kappa(s) \Delta I(t-s) ds \quad (14.44)$$

is the input potential generated by the time-dependent part of the input current. The first term of the right-hand side of Eq. (14.43) takes into account that previous perturbations $\Delta A(\hat{t})$ with $\hat{t} < t$ have an after-effect one interspike interval later. The second term describes the immediate response to a change in the input potential. 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 main task of this section is therefore the calculation of $\mathcal{L}(x)$ to be performed in Section 14.3.1.

The linearization of the integral equation (Gerstner, 2000) is analogous to the linearization of the membrane potential density equations (Brunel and Hakim, 1999) that was presented in Chapter 13. In order to arrive at the standard formula for the linear response,

$$A(t) = A_0 + \int_0^\infty G(s) \Delta I(t-s) ds, \quad (14.45)$$

we insert Eq. (14.44) into Eq. (14.43) and take the Fourier transform. For $\omega \neq 0$ we find

$$\hat{A}(\omega) = i\omega \frac{A_0 \hat{\mathcal{L}}(\omega) \hat{\kappa}(\omega)}{1 - \hat{P}(\omega)} \hat{I}(\omega) = \hat{G}(\omega) \hat{I}(\omega). \quad (14.46)$$

Hats denote transformed quantities, i.e., $\hat{\kappa}(\omega) = \int \kappa_0(s) \exp(-i\omega s) ds$ is the Fourier transform of the response kernel; $\hat{P}(\omega)$ is the Fourier transform of the interval distribution $P_0(t - \hat{t})$; and $\hat{\mathcal{L}}(\omega)$ is the transform of the kernel \mathcal{L} . Note that for $\omega \neq 0$ we have $\hat{A}(\omega) = (\hat{\Delta A})(\omega)$ and $\hat{I}(\omega) = (\hat{\Delta I})(\omega)$ since A_0 and I_0 are constant.

The frequency-dependent gain $\hat{G}(\omega)$ describes the linear response of the population activity to a periodic input current $\hat{I}(\omega)$. The linear response filter $G(s)$ in the time domain is found by inverse Fourier transform

$$G(s) = \frac{1}{2\pi} \int_{-\infty}^\infty \hat{G}(\omega) e^{+i\omega s} d\omega. \quad (14.47)$$

A_0 is the mean rate for constant drive I_0 . The filter G plays an important role for the analysis of the stability of the stationary state in recurrent networks (Section 14.2).

Example: Leaky integrate-and-fire with escape noise

The frequency-dependent gain \hat{G} depends on the filter $\mathcal{L}(s)$, which in turns depends on the width of the interval distribution $P_0(s)$ (Fig. 14.9b and a, respectively). In Fig. 14.9c we have plotted the signal gain $\hat{G}(\omega)$ for integrate-and-fire neurons with escape noise at different noise levels. At low noise, the signal gain exhibits resonances at the frequency that corresponds to the inverse of the mean interval and multiples thereof. Increasing the noise level, however, lowers the signal gain of the system. For high noise

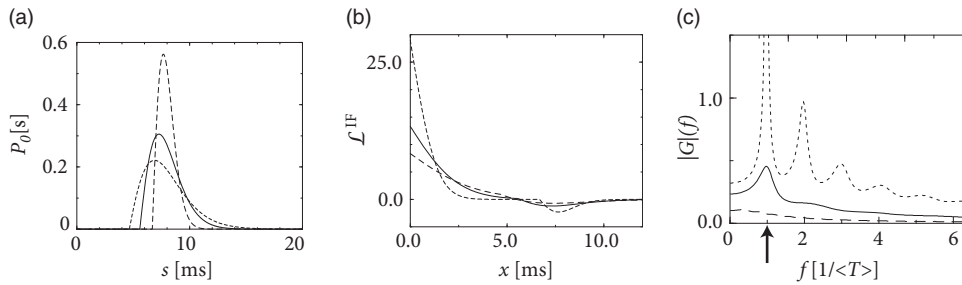


Fig. 14.9 Response properties of a population of leaky integrate-and-fire neurons with escape noise. (a) Interval distribution for three different noise levels. The escape rate has been taken as piecewise linear $\rho = \rho_0 [u - \vartheta] \Theta(u - \vartheta)$. The value of the bias current I_0 has been adjusted so that the mean interval is always $\langle T \rangle = 8$ ms. (b) The corresponding kernel $\mathcal{L}^{\text{IF}}(x)$. The dip in the kernel around $x = \langle T \rangle$ is typical for integrate-and-fire neurons. (c) Frequency-dependent gain $|G(f)| = |\hat{G}(\omega = 2\pi f)|$. Low noise (short-dashed line): the sharply peaked interval distribution (standard deviation 0.75 ms) and rapid fall-off of kernel \mathcal{L} lead to a linear response gain \hat{G} with strong resonances at multiples of the intrinsic firing frequency $1/\langle T \rangle$. High noise (long-dashed line): the broad interval distribution (standard deviation 4 ms) and broad kernel \mathcal{L} suppress resonances in the frequency dependent gain. Medium noise (solid line): a single resonance for an interval distribution with standard deviation 2 ms. Adapted from Gerstner (2000).

(long-dashed line in Fig. 14.9c) the signal gain at 1000 Hz is ten times lower than the gain at zero frequency. The cut-off frequency depends on the noise level. The gain at zero frequency corresponds to the slope of the gain function $g_\sigma(I_0)$ and changes with the level of noise.

14.3.1 Derivation of the linear response filter (*)

In order to derive the linearized response ΔA of the population activity to a change in the input we start from the conservation law,

$$1 = \int_{-\infty}^t S_I(t|\hat{t}) A(\hat{t}) d\hat{t}; \quad (14.48)$$

compare Eq. (14.8). As we have seen in Section 14.1 the population equation (14.5) can be obtained by taking the derivative of Eq. (14.8) with respect to t , i.e.,

$$0 = \frac{d}{dt} \int_{-\infty}^t S_I(t|\hat{t}) A(\hat{t}) d\hat{t}. \quad (14.49)$$

For constant input I_0 , the population activity has a constant value A_0 . We consider a small perturbation of the stationary state, $A(t) = A_0 + \Delta A(t)$, that is caused by a small change in the input current, $\Delta I(t)$. The time-dependent input generates a total postsynaptic potential, $h(t) = h_0 + \Delta h(t, \hat{t})$ where h_0 is the postsynaptic potential for constant input I_0 and

$$\Delta h(t, \hat{t}) = \int_0^{b(\hat{t})} \kappa(s) \Delta I(t-s) ds \quad (14.50)$$

is the change of the postsynaptic potential generated by ΔI . Note that we keep the notation general and include a dependence upon the last firing time \hat{t} . For leaky integrate-and-fire neurons, we set $b(\hat{t}) = t - \hat{t}$ whereas for SRM₀ neurons we set $b(\hat{t}) = \infty$. We expand Eq. (14.49) to linear order in ΔA and Δh and find

$$0 = \frac{d}{dt} \int_{-\infty}^t S_0(t - \hat{t}) \Delta A(\hat{t}) d\hat{t} + A_0 \frac{d}{dt} \left\{ \int_{-\infty}^t ds \int_{-\infty}^t d\hat{t} \Delta h(s, \hat{t}) \left. \frac{\partial S_I(t | \hat{t})}{\partial \Delta h(s, \hat{t})} \right|_{\Delta h=0} \right\}. \quad (14.51)$$

We have used the notation $S_0(t - \hat{t}) = S_{I_0}(t | \hat{t})$ for the survivor function of the asynchronous firing state. To take the derivative of the first term in Eq. (14.51) we use $dS_0(s)/ds = -P_0(s)$ and $S_0(0) = 1$. This yields

$$\Delta A(t) = \int_{-\infty}^t P_0(t - \hat{t}) \Delta A(\hat{t}) d\hat{t} - A_0 \frac{d}{dt} \left\{ \int_{-\infty}^t ds \int_{-\infty}^t d\hat{t} \Delta h(s, \hat{t}) \left. \frac{\partial S_I(t | \hat{t})}{\partial \Delta h(s, \hat{t})} \right|_{\Delta h=0} \right\}. \quad (14.52)$$

We note that the first term on the right-hand side of Eq. (14.52) has the same form as the population integral equation (14.5), except that P_0 is the interval distribution in the stationary state of asynchronous firing.

To make some progress in the treatment of the second term on the right-hand side of Eq. (14.52), we now restrict the choice of neuron model and focus on either SRM₀ or integrate-and-fire neurons.

(i) For SRM₀ neurons, we may drop the \hat{t} dependence of the potential and set $\Delta h(t, \hat{t}) = \Delta h(t)$ where Δh is the input potential caused by the time-dependent current ΔI ; compare Eqs. (14.44) and (14.50). This allows us to pull the variable $\Delta h(s)$ in front of the integral over \hat{t} and write Eq. (14.52) in the form

$$\Delta A(t) = \int_{-\infty}^t P_0(t - \hat{t}) \Delta A(\hat{t}) d\hat{t} + A_0 \frac{d}{dt} \int_0^\infty \mathcal{L}(x) \Delta h(t - x) dx, \quad (14.53)$$

with a kernel

$$\mathcal{L}(x) = - \int_x^\infty d\xi \frac{\partial S(\xi | 0)}{\partial \Delta h(\xi - x)} \equiv \mathcal{L}^{\text{SRM}}(x). \quad (14.54)$$

(ii) For leaky integrate-and-fire neurons we set $\Delta h(t, \hat{t}) = \Delta h(t) - \Delta h(\hat{t}) \exp[-(t - \hat{t})/\tau]$, because of the reinitialization of the membrane potential after the reset (Gerstner, 2000). After some rearrangements of the terms, Eq. (14.52) becomes identical to Eq. (14.53) with a kernel

$$\mathcal{L}(x) = - \int_x^\infty d\xi \frac{\partial S(\xi | 0)}{\partial \Delta h(\xi - x)} + \int_0^x d\xi e^{-\xi/\tau} \frac{\partial S(x | 0)}{\partial \Delta h(\xi)} \equiv \mathcal{L}^{\text{IF}}(x). \quad (14.55)$$

Let us discuss Eq. (14.53). The first term on the right-hand side of Eq. (14.53) is of the same form as the dynamic equation (14.5) and describes how perturbations $\Delta A(\hat{t})$ in the

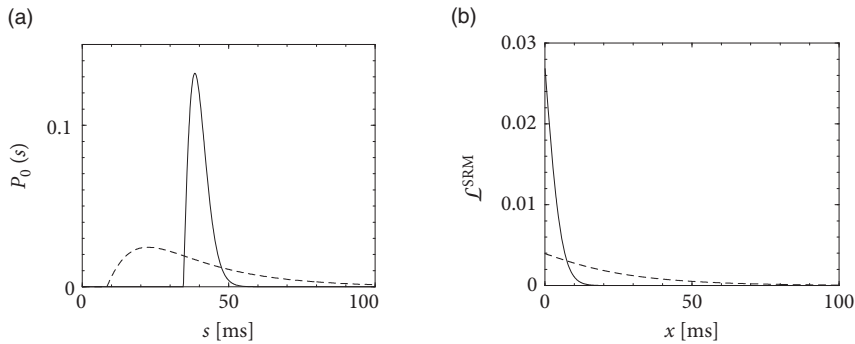


Fig. 14.10 Interval distribution (a) and the kernel $\mathcal{L}^{\text{SRM}}(x)$ (b) for SRM_0 neurons with escape noise. The escape rate has been taken as piecewise linear $\rho = \rho_0 [u - \vartheta] \Theta(u - \vartheta)$. For low noise (solid lines in (a) and (b)) the interval distribution is sharply peaked and the kernel \mathcal{L}^{SRM} has a small width. For high noise (dashed line) both the interval distribution and the kernel \mathcal{L}^{SRM} are broad. The value of the bias current I_0 has been adjusted so that the mean interval is always 40 ms. The kernel has been normalized to $\int_0^\infty \mathcal{L}(x) dx = 1$.

past influence the present activity $\Delta A(t)$. The second term gives an additional contribution which is proportional to the derivative of a *filtered* version of the potential Δh .

We see from Fig. 14.10 that the width of the kernel \mathcal{L} depends on the noise level. For low noise, it is significantly sharper than for high noise.

Example: The kernel $\mathcal{L}(x)$ for escape noise (*)

In the escape noise model, the survivor function is given by

$$S_I(t|\hat{t}) = \exp \left\{ - \int_{\hat{t}}^t f[\eta(t' - \hat{t}) + h(t', \hat{t})] dt' \right\}, \quad (14.56)$$

where $f[u]$ is the instantaneous escape rate across the noisy threshold; see Chapter 7. We write $h(t, \hat{t}) = h_0(t - \hat{t}) + \Delta h(t, \hat{t})$. Taking the derivative with respect to Δh yields

$$\left. \frac{\partial S_I(t|\hat{t})}{\partial \Delta h(s, \hat{t})} \right|_{\Delta h=0} = -\Theta(s - \hat{t}) \Theta(t - s) f'[\eta(s - \hat{t}) + h_0(s - \hat{t})] S_0(t - \hat{t}), \quad (14.57)$$

where $S_0(t - \hat{t}) = S_{h_0}(t|\hat{t})$ and $f' = df(u)/du$. For SRM_0 neurons, we have $h_0(t - \hat{t}) \equiv h_0$ and $\Delta h(t, \hat{t}) = \Delta h(t)$, independent of \hat{t} . The kernel \mathcal{L} is therefore

$$\mathcal{L}^{\text{SRM}}(t - s) = \Theta(t - s) \int_{-\infty}^s d\hat{t} f'[\eta(s - \hat{t}) + h_0] S_0(t - \hat{t}). \quad (14.58)$$

Example: Absolute refractoriness (*)

Absolute refractoriness is defined by a refractory kernel $\eta(s) = -\infty$ for $0 < s < \delta^{\text{abs}}$ and zero otherwise. We take an arbitrary escape rate $f(u) \geq 0$. The only condition on f is

that the escape rate goes rapidly to zero for voltages far below threshold: $\lim_{u \rightarrow -\infty} f(u) = 0 = \lim_{u \rightarrow -\infty} f'(u)$.

This yields $f[\eta(t - \hat{t}) + h_0] = f(h_0) \Theta(t - \hat{t} - \delta^{\text{abs}})$ and hence

$$f'[\eta(t - \hat{t}) + h_0] = f'(h_0) \Theta(t - \hat{t} - \delta^{\text{abs}}). \quad (14.59)$$

The survivor function $S_0(s)$ is unity for $s < \delta^{\text{abs}}$ and decays as $\exp[-f(h_0)(s - \delta^{\text{abs}})]$ for $s > \delta^{\text{abs}}$. Integration of Eq. (14.58) yields

$$\mathcal{L}(t - t_1) = \Theta(t - t_1) \frac{f'(h_0)}{f(h_0)} \exp[-f(h_0)(t - t_1)]. \quad (14.60)$$

As we have seen in Section 14.1, absolute refractoriness leads to the Wilson–Cowan integral equation (14.10). Thus \mathcal{L} defined in (14.60) is the kernel relating to Eq. (14.10). It could have been derived directly from the linearization of the Wilson–Cowan integral equation (see Exercises). We note that it is a low-pass filter with cut-off frequency $f(h_0)$, which depends on the input potential h_0 .

14.4 Density equations vs. integral equations

In this section we relate the integral equation (14.5) to the membrane potential density approach for integrate-and-fire neurons that we discussed in Chapter 13. The two approaches are closely related. For noise-free neurons driven by a constant suprathreshold stimulus, the two mathematical formulations are, in fact, equivalent and related by a simple change of variables. Even for noisy neurons with subthreshold stimulation, the two approaches are comparable. Both methods are linear in the densities and amenable to efficient numerical implementations. The formal mathematical relation between the two approaches is shown in Section 14.4.3.

We use Section 14.4.1 to introduce a “refractory density” which is analogous to the membrane potential density that we saw in Chapter 13. In particular, the dynamics of refractory density variables follow a continuity equation. The solution of the continuity equation (14.4.2) transforms the partial differential equation into the integral equations that we saw in Section 14.1.

14.4.1 Refractory densities

In this section we develop a density formalism for spike response neurons, similar to the membrane potential density approach for integrate-and-fire neurons that we discussed in Chapter 13. The main difference is that we replace the membrane potential density $p(u, t)$ by a refractory density $q(r, t)$, to be introduced below.

We study a homogeneous population of neurons with escape noise. The neuron model should be consistent with time-dependent renewal theory. In this case, we can write the membrane potential of a neuron i in general form as

$$u_i(t, \hat{t}) = \eta(t - \hat{t}_i) + h(t, \hat{t}_i). \quad (14.61)$$

For example, a nonlinear integrate-and-fire model which has fired the last time at \hat{t}_i and follows a differential equation $\dot{u}(t) = [f(u) + RI(t)]$ has for $t > \hat{t}_i$ a potential $u_i(t, \hat{t}_i) = h(t, \hat{t}_i) = u_r + \int_{\hat{t}_i}^t \dot{u}(t') dt'$ and $\eta = 0$. An SRM₀ neuron has a potential $u_i(t, \hat{t}) = \eta(t - \hat{t}) + h(t)$ with an arbitrary spike-afterpotential $\eta(t - \hat{t})$ and an input potential h .

The notation in Eq. (14.61) emphasizes the importance of the last firing time \hat{t} . We denote the refractory state of a neuron by the variable

$$r = t - \hat{t} \geq 0, \quad (14.62)$$

i.e., by the time that has passed since the last spike. If we know r and the total input current in the past, we can calculate the membrane potential, $u(t) = \eta(r) + h(t, t - r)$. Given the importance of the refractory variable r , we may wonder how many neurons in the population have a refractory state between r_0 and $r_0 + \Delta r$. For a large population ($N \rightarrow \infty$) the fraction of neurons with a momentary value of r in the interval $[r_0, r_0 + \Delta r]$ is given by

$$\lim_{N \rightarrow \infty} \left\{ \frac{\text{neurons with } r_0 < r(t) \leq r_0 + \Delta r}{N} \right\} = \int_{r_0}^{r_0 + \Delta r} q(r, t) dr, \quad (14.63)$$

where $q(r, t)$ is the *refractory density*. The aim of this section is to describe the dynamics of a population of SRM neurons by the evolution of $q(r, t)$.

We start from the continuity equation (see Chapter 13),

$$\frac{\partial}{\partial t} q(r, t) = - \frac{\partial}{\partial r} J_{\text{refr}}(r, t), \quad (14.64)$$

where we have introduced the flux J_{refr} along the axis of the refractory variable r . As long as the neuron does not fire, the variable $r = t - \hat{t}$ increases at a speed of $dr/dt = 1$. The flux is the density q times the velocity, hence

$$J_{\text{refr}}(r, t) = q(r, t) \frac{dr}{dt} = q(r, t). \quad (14.65)$$

The continuity equation (14.64) expresses the fact that, as long as a neuron does not fire, its trajectories $r(t)$ can neither start nor end. On the other hand, if a neuron fires, the trajectory stops at the current value of r and “reappears” at $r = 0$. In the escape rate formalism, the instantaneous firing rate of a neuron with refractory variable r is given by the hazard

$$\rho(t|t-r) = f[\eta(r) + h(t|t-r)]. \quad (14.66)$$

If we multiply the hazard (14.66) with the density $q(r, t)$, we get the loss per unit of time,

$$J_{\text{loss}} = -\rho(t|t-r) q(r, t). \quad (14.67)$$

The total number of trajectories that disappear at time t due to firing is equal to the population activity, i.e.,

$$A(t) = \int_0^\infty \rho(t|t-r) q(r, t) dr. \quad (14.68)$$

The loss (14.67) has to be added as a “sink” term on the right-hand side of the continuity equation, while the activity $A(t)$ acts as a source at $r = 0$. The full dynamics is

$$\frac{\partial}{\partial t} q(r, t) = - \left[\frac{\partial}{\partial r} q(r, t) \right] - \rho(t|t-r) q(r, t) + \delta(r) A(t). \quad (14.69)$$

This partial differential equation is the analog of the Fokker–Planck equation (13.16) for the membrane potential density of integrate-and-fire neurons. The relation between the two equations will be discussed in Section 14.4.3.

Equation (14.69) can be integrated analytically and rewritten in the form of an integral equation for the population activity. The mathematical details of the integration will be presented below. The final result is

$$A(t) = \int_{-\infty}^t P_I(t|\hat{t}) A(\hat{t}) d\hat{t}, \quad (14.70)$$

where

$$P_I(t|\hat{t}) = \rho(t|\hat{t}) \exp \left[- \int_{\hat{t}}^t \rho(t'|\hat{t}) dt' \right] \quad (14.71)$$

is the interval distribution of neurons with escape noise; see Eq. (7.28). Thus, neurons that have fired their last spike at time \hat{t} contribute with weight $P_I(t|\hat{t})$ to the activity at time T . Integral equations of the form (14.70) are the starting point for the formal theory of population activity presented in Section 14.1.

14.4.2 From refractory densities to the integral equation (*)

All neurons that have fired together at time \hat{t} form a group that moves along the r -axis at constant speed. To solve Eq. (14.69) we turn to a frame of reference that moves along with the group. We replace the variable r by $t-r \equiv \hat{t}$ and define a new density

$$Q(\hat{t}, t) = q(t - \hat{t}, t), \quad (14.72)$$

with $\hat{t} \leq t$. The total derivative of Q with respect to t is

$$\frac{d}{dt} Q(\hat{t}, t) = \frac{\partial}{\partial r} q(r, t)|_{r=t-\hat{t}} \frac{dr}{dt} + \frac{\partial}{\partial t} q(r, t)|_{r=t-\hat{t}} \quad (14.73)$$

with $dr/dt = 1$. We insert Eq. (14.69) on the right-hand side of (14.73) and obtain for $t > \hat{t}$

$$\frac{d}{dt} Q(\hat{t}, t) = -\rho(t|\hat{t}) Q(\hat{t}, t). \quad (14.74)$$

The partial differential equation (14.69) has thus been transformed into an ordinary differential equation that is solved by

$$Q(\hat{t}, t) = Q(\hat{t}, t_0) \exp \left[- \int_{t_0}^t \rho(t'|\hat{t}) dt' \right], \quad (14.75)$$

where $Q(\hat{t}, t_0)$ is the initial condition, which is still to be fixed.

From the definition of the refractory density $q(r, t)$ we conclude that $q(0, t)$ is the proportion of neurons at time t that have just fired, i.e., $q(0, t) = A(t)$ or, in terms of the new refractory density, $Q(t, t) = A(t)$. We can thus fix the initial condition in Eq. (14.75) at $t_0 = \hat{t}$ and find

$$Q(\hat{t}, t) = A(\hat{t}) \exp \left[- \int_{\hat{t}}^t \rho(t'|\hat{t}) dt' \right]. \quad (14.76)$$

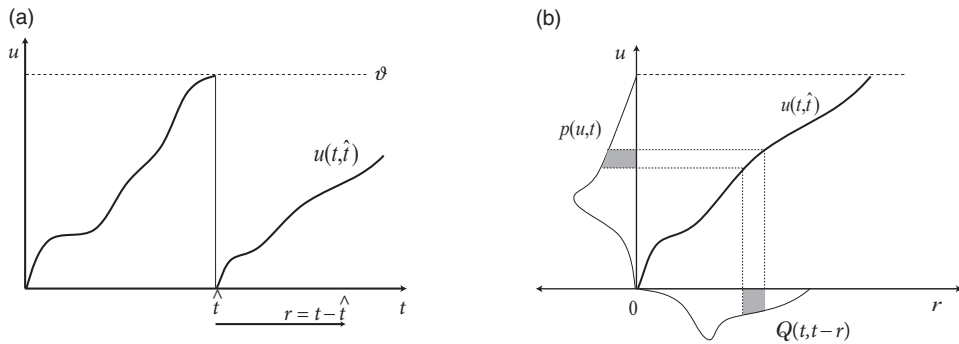


Fig. 14.11 (a) In a noise-free (nonlinear) integrate-and-fire neuron we define a refractory variable $r = t - \hat{t}$ and write the trajectory as $u(t, \hat{t})$. (b) The membrane potential density $p(u, t)$ at time t is plotted to the left as a function of the membrane potential u (vertical axis). The fraction of neurons $p(u, t) \Delta u$ with membrane potentials around u (gray shaded area) is proportional to the refractory density $Q(t, \hat{t}) \Delta \hat{t}$ (shaded area at the bottom).

On the other hand, from (14.68) we have

$$A(t) = \int_{-\infty}^t \rho(t|\hat{t}) Q(\hat{t}, t) d\hat{t}. \quad (14.77)$$

If we insert (14.76) into (14.77), we find

$$A(t) = \int_{-\infty}^t \rho(t|\hat{t}) \exp \left[- \int_{\hat{t}}^t \rho(t'|\hat{t}) dt' \right] A(\hat{t}) d\hat{t}, \quad (14.78)$$

which is the population equation (14.70) mentioned above. It has been derived from refractory densities in Gerstner and van Hemmen (1992) and similarly in the appendix of the papers by Wilson and Cowan (1972). If we insert Eq. (14.76) into the normalization condition $1 = \int_{-\infty}^t Q(\hat{t}, t) d\hat{t}$ we arrive at

$$1 = \int_{-\infty}^t \exp \left[- \int_{\hat{t}}^t \rho(t'|\hat{t}) dt' \right] A(\hat{t}) d\hat{t}. \quad (14.79)$$

Both the population equation (14.78) and the normalization condition (14.79) play an important role in the general theory outlined in Section 14.1.

For a numerical implementation of population dynamics, it is more convenient to take a step back from the integral equations to the iterative updates that describe the survival $Q(\hat{t}, t)$ of the group of neurons that has fired the last time at time \hat{t} . In other words, efficient numerical implementation schemes work directly on the level of the density equations (14.74). A simple discretization scheme for numerical implementations has been discussed above in Section 14.1.5.

14.4.3 From refractory densities to membrane potential densities (*)

In this section we want to show the formal relation between the dynamics of $p(u, t)$ and the evolution of the refractory densities $q(r, t)$. We focus on a population of nonlinear or leaky integrate-and-fire neurons with escape noise. For a known time-dependent input we can calculate the membrane potential $u(t, \hat{t})$ where the notation with \hat{t} highlights that, in addition to external input, we also need to know the last firing time (and the reset value u_r) in order to predict the voltage at time t . We require that the input is constant or only weakly modulated so that the trajectory is increasing monotonously ($\partial u / \partial t > 0$).

To stay concrete, we focus on leaky integrate-and-fire neuron for which the membrane potential is

$$u(t, \hat{t}) = u_r \exp\left(-\frac{t - \hat{t}}{\tau_m}\right) + \frac{R}{\tau_m} \int_{\hat{t}}^t \exp\left(-\frac{t - t'}{\tau_m}\right) I(t') dt'. \quad (14.80)$$

Knowledge of $u(t, \hat{t})$ can be used to define a transformation from voltage to refractory variables: $u \longleftrightarrow r = t - \hat{t}$; see Fig. 14.11a. It turns out that the final equations are even simpler if we take \hat{t} instead of r as our new variable. We therefore consider the transformation $u \longrightarrow \hat{t}$.

Before we start, we calculate the derivatives of Eq. (14.80). The derivative with respect to t yields $\partial u / \partial t = [-u + RI(t)] / \tau_m$ as expected for integrate-and-fire neurons. According to our assumption, $\partial u / \partial t > 0$ or $RI(t) > u$ (for all neurons in the population). The derivative with respect to \hat{t} is

$$-\frac{\partial u}{\partial \hat{t}} = \frac{RI(t) - u_r}{\tau_m} \exp\left(-\frac{t - \hat{t}}{\tau_m}\right) = F(t, \hat{t}) > 0, \quad (14.81)$$

where the function F is defined by Eq. (14.81).

The densities in the variable \hat{t} are denoted as $Q(\hat{t}, t)$. From $Q(\hat{t}, t) |d\hat{t}| = p(u, t) |du|$ we have

$$Q(\hat{t}, t) = p[u(t, \hat{t}), t] F(t, \hat{t}). \quad (14.82)$$

We now want to show that the differential equation for the density $Q(\hat{t}, t)$ that we derived in (14.74),

$$\frac{\partial}{\partial t} Q(\hat{t}, t) = -\rho(t|\hat{t}) Q(\hat{t}, t), \quad \text{for } \hat{t} < t, \quad (14.83)$$

is equivalent to the partial differential equation for the membrane potential densities. If we insert Eq. (14.82) into Eq. (14.83) we find

$$\frac{\partial p}{\partial u} \frac{\partial u}{\partial t} F + \frac{\partial p}{\partial t} F + p \frac{\partial F}{\partial t} = -\rho p F. \quad (14.84)$$

For the linear integrate-and-fire neuron and $I(t) = \text{const.}$ we have $\partial F / \partial t = -F / \tau_m$. Furthermore, according to our assumption of monotonously increasing trajectories, we have $F \neq 0$. Thus we can divide (14.84) by F and rewrite Eq. (14.84) in the form

$$\frac{\partial p(u, t)}{\partial t} = -\frac{\partial}{\partial u} \left[\frac{-u + RI(t)}{\tau_m} p(u, t) \right] - f(u - \vartheta) p(u, t), \quad \text{for } u_r < u < \vartheta, \quad (14.85)$$

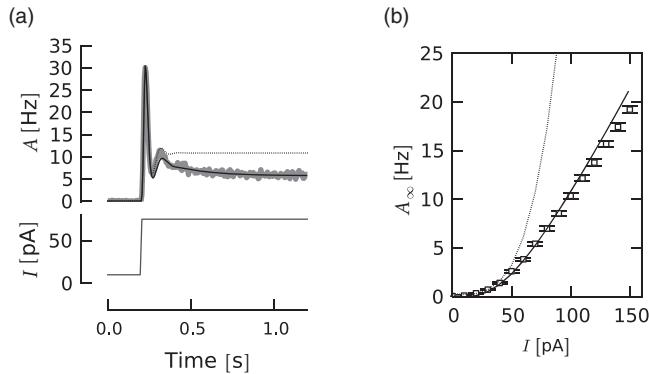


Fig. 14.12 Population of adaptive neurons in response to a step stimulus. The results from quasi-renewal theory are compared to a direct simulation of 25 000 neurons with parameters optimized for cortical cells. (a) The solution of the integral equation Eqs. (14.86) and (14.96) for the population activity (thin black line) is overlaid on the population activity calculated by simulating 25 000 SRM neurons with parameters capturing properties of cortical cells (see Chapter 11). The dotted line, which gives the solution of the integral equation of non-adapting neurons (time-dependent renewal theory, Eq. (14.5)), indicates that adaptation makes a major contribution to the observed population activity. (b) Comparing adapted activity A_∞ from simulations (squares, error bars correspond to one standard deviation) to predictions from renewal (dotted line) and quasi-renewal (black line) theory. Modified from Naud and Gerstner (2012a).

where we have used the definition of the hazard via the escape function $\rho(t|\hat{t}) = f[u(t, \hat{t}) - \vartheta]$ and the definition of the reset potential $u_r = \eta_0$. If we compare Eq. (14.85) with the Fokker–Planck equation (13.16), we see that the main difference is the treatment of the noise. For noise-free integrate-and-fire neurons (i.e., $\rho(t|\hat{t}) = 0$ for $u \neq \vartheta$) the equation (13.16) for the membrane potential densities is therefore equivalent to the density equation $\partial Q(\hat{t}, t)/\partial t = 0$; see Eq. (14.83).

14.5 Adaptation in population equations

The integral equations presented so far apply only to neurons whose state does not depend on the spiking history, except on the most recent spike. Cortical neurons, however, show pronounced adaptation, as discussed in Chapter 11. Since time-dependent renewal theory cannot account for adaptation, the predicted population activity does not match the one observed in simulations; see Fig. 14.12.

As indicated in Eq. (14.12), the intuitions that have led to the integral equation (14.5) of time-dependent renewal theory, are still applicable, but the interval distribution must take into account the past history.

Let $P_{I,A}(t|\hat{t})$ be, again, the probability of observing a spike at time t given the last spike at time \hat{t} , the input current *and* the activity history $A(t)$ until time t ; then the integral equation

for adapting neurons is Eq. (14.12), which we recall here for convenience

$$A(t) = \int_{-\infty}^t P_{I,A}(t|\hat{t})A(\hat{t})d\hat{t}. \quad (14.86)$$

In this section, we develop the methods necessary to describe adapting neuron populations. First we present the systematic derivation of the integral equation Eq. (14.86). Then, in Section 14.5.2 we describe the event-based moment expansion which provides a framework for approximating $P_{I,A}(t|\hat{t})$.

14.5.1 Quasi-renewal theory (*)

Chapter 12 discussed the concept of a homogeneous population. We have seen that the activity of a homogeneous population of uncorrelated neurons can be seen as an average of the spike trains across the population, $A(t) = \langle S(t) \rangle_N$ where the subscript N denotes an average across the N neurons. Because neurons are stochastic, all neurons have different spiking histories. Accordingly, an average over a population is equivalent to an average over all possible past spike trains,

$$A(t) = \langle \rho(t|S) \rangle_S, \quad (14.87)$$

where $\rho(t|S)$ is the hazard (or instantaneous firing rate) at time t given the previous spikes in the spike-train $S(t)$ and the average $\langle \cdot \rangle_S$ is over all spike-train histories. In other words, $A(t)$ can be calculated as the expected activity averaged over *all* possible spike train histories, whereas $\rho(t|S)$ gives the stochastic intensity of generating a spike around time t given the *specific* history summarized by the past spike train S (Naud and Gerstner, 2012a).

The spike train S consists of a series of spikes $\hat{t}_1, \hat{t}_2, \dots, \hat{t}_n$. To average over all possible spike trains requires that we consider spike trains made of $n = 0$ to ∞ spikes. Moreover, for a given number n of spikes, all possible time sequences of the n spikes must be considered. This average takes the form of a path integral (Feynman *et al.*, 2010) where the *path* here is the spike trains. Therefore, the average in Eq. (14.87) is

$$A(t) = \sum_{n=0}^{\infty} \int_{-\infty}^t \int_{-\infty}^{\hat{t}_1} \dots \int_{-\infty}^{\hat{t}_{n-1}} \rho(t|\hat{t}_1, \hat{t}_2, \dots, \hat{t}_n) P(\hat{t}_1, \hat{t}_2, \dots) d\hat{t}_n \dots d\hat{t}_1. \quad (14.88)$$

We emphasize that in Eq. (14.88) the spikes are ordered counting backward in time; therefore \hat{t}_1 is the most recent spike so that $t > \hat{t}_1 > \hat{t}_2 > \dots > \hat{t}_n$.

Each spike train can occur with a probability entirely defined by the hazard function

$$P(\hat{t}_1, \hat{t}_2, \dots, \hat{t}_n) = \left[\prod_{\hat{t}_i \in S_n} \rho(\hat{t}_i | S_n) \right] e^{-\int_{-\infty}^t \rho(x|S_n) dx}. \quad (14.89)$$

The equality follows from the product of two probabilities: the probabilities of observing the spikes at the times \hat{t} given the rest of the history (the hazard function) and the probability of not spiking between each of the spikes (the survivor function). Again, it

is a generalization of the quantities seen in Chapters 7 and 9. Writing the complete path integral, we have

$$A(t) = \rho(t) e^{-\int_{-\infty}^t \rho(x) dx} + \sum_{n=1}^{\infty} \int_{-\infty}^t \int_{-\infty}^{\hat{t}_1} \dots \int_{-\infty}^{\hat{t}_{n-1}} \left[e^{-\int_{\hat{t}_1}^t \rho(x|\hat{t}_1, \dots, \hat{t}_n) dx} \rho(t|\hat{t}_1, \dots, \hat{t}_n) \right] \\ \times \rho(\hat{t}_1|\hat{t}_2, \dots, \hat{t}_n) \rho(\hat{t}_2|\hat{t}_3, \dots, \hat{t}_n) \dots \rho(\hat{t}_n) e^{-\int_{\hat{t}_2}^{\hat{t}_1} \rho(x|\hat{t}_2, \dots, \hat{t}_n) dx - \dots - \int_{-\infty}^{\hat{t}_n} \rho(x) dx} d\hat{t}_n \dots d\hat{t}_2 d\hat{t}_1. \quad (14.90)$$

The case with zero spikes in the past (the first term on the right-hand-side of Eq. (14.90)) can be neglected, because we can always formally assign a firing time at $\hat{t} = -\infty$ to neurons that have not fired in the recent past. We now focus on the factor enclosed in square brackets on the right-hand side of Eq. (14.90). This factor resembles $P_I(t|\hat{t})$. In fact, if, for a moment, we made a renewal assumption, the most recent spike were the only one that mattered. This would imply that we could set $\rho(t|\hat{t}_1, \dots, \hat{t}_n) = \rho(t|\hat{t})$ inside the square brackets (where $\hat{t} = \hat{t}_1$ is the most recent spike) and shift the factor enclosed by square brackets in front of the $n-1$ integral over $\hat{t}_2, \hat{t}_3, \dots, \hat{t}_n$. In this case, the factor in square brackets would become exactly $P_I(t|\hat{t})$. The remaining integrals over the $n-1$ variables can be recognized as the average of $\rho(\hat{t}_1|S)$ over the possible histories, i.e., $A(\hat{t}_1)$. Therefore the renewal assumption leads back to Eq. (14.5), as it should.

In quasi-renewal theory, instead of assuming $\rho(t|S) = \rho(t|\hat{t}_1)$ we assume that

$$\langle \rho(t|S) \rangle \approx \langle \rho(t|\hat{t}_1, S') \rangle_{S'}, \quad (14.91)$$

where S' is made of all the spikes in S but \hat{t}_1 . This assumption is reasonable given the following two observations in real neurons. First, the strong effect of the most recent spike needs to be considered explicitly. Second, the rest of the spiking history only introduces a self-inhibition that is similar for all neurons in the population and that depends only on the expected distribution of spikes in the past (Naud and Gerstner, 2012a). The approximation (14.91) is not appropriate for intrinsically bursting neurons, but should apply well to other cell types (fast-spiking, non-fast-spiking, adapting, delayed, ...). If we insert Eq. (14.91) into the terms inside the square brackets of Eq. (14.90), we can define the interspike interval distribution

$$P_{I,A}(t|\hat{t}) = \langle \rho(t|\hat{t}, S') \rangle_{S'} \exp \left(- \int_{\hat{t}}^t \langle \rho(x|\hat{t}, S') \rangle_{S'} dx \right), \quad (14.92)$$

such that Eq. (14.90) becomes Eq. (14.86).

14.5.2 Event-based moment expansion (*)

The development in the previous subsection is general and does not rely on a specific neuron model nor on a specific noise model. In this section, we now introduce approximation methods that are valid for the broad class of Generalized Linear Models of spiking neurons with exponential escape noise, for example the Spike Response Model (see Chapter 9). The aim is to find theoretical expressions for $P_{I,A}(t|\hat{t})$ according to quasi-renewal theory

(Eq. (14.92)). In particular we need to evaluate the average of the likelihood over the past history $\langle \rho(t|\hat{t}_1, S') \rangle_{S'}$.

We recall the SRM model with exponential escape noise (Chapter 9). The instantaneous stochastic intensity at time t , given the spike history, is

$$\rho(t|S) = \bar{\rho} \exp \left(h(t) + \sum_{\hat{t}_k \in S} \eta(t - \hat{t}_k) \right) = \bar{\rho} e^{h(t) + [\eta * S](t)}. \quad (14.93)$$

Here, $h(t) = \int_0^\infty \kappa(s) I(t-s) ds$ is the input potential, $\eta(s)$ describes the spike-afterpotential introduced by each spike and $u(t) = h(t) + \sum_{\hat{t}_k \in S} \eta(t - \hat{t}_k)$ is the total membrane potential. The standard formulation of exponential escape noise, $\rho(t) = f(u(t) - \vartheta) = \rho_0 \exp[\beta(u(t) - \vartheta)]$, contains two extra parameters (ϑ for the threshold and $1/\beta$ for the noise level), but we can rescale the voltage and rate units so as to include the parameters β and ϑ in the definition of u and $\bar{\rho}$, respectively. The time course of η and κ and the parameter $\bar{\rho}$ can be optimized so as to describe the firing behavior of cortical neurons; see Chapter 11.

In the model defined by Eq. (14.93), all the history dependence is contained in a factor, $e^{\eta * S}$, which can be factorized into the contribution from the last spike and that of all previous spikes,

$$\langle \rho(t|I, \hat{t}, S') \rangle_{S'} = \bar{\rho} e^{h(t) + \eta(t - \hat{t})} \langle e^{[\eta * S'](t)} \rangle_{S'}. \quad (14.94)$$

In order to evaluate the expected values on the right-hand side of Eq. (14.92), we need to calculate the quantity $M_S[\eta] = \langle e^{\eta * S} \rangle_S$.

M_S is called a moment-generating functional because the functional derivative with respect to $\eta(t)$ and evaluated at $\eta(t) = 0$ yields the moments of S : $\frac{\delta M_S}{\delta \eta}[\eta = 0] = \langle S(t) \rangle$, $\frac{\delta^2 M_S}{\delta \eta^2}[\eta = 0] = \langle S(t)S(t') \rangle$, Explicit formulas for the moment-generating functional are known (van Kampen, 1992). One of the expansion schemes unfolds in terms of the correlation functions $g_k(t_1, t_2, \dots, t_k)$ and provides a useful framework for the approximation of our functional at hand.

We have already seen two examples of such correlation functions in various chapters of the book. The first term is simply the population activity $g_1(t_1) = \langle S(t_1) \rangle = A(t_1)$, i.e., the expectation value or “mean” of the spike count in a short interval $\Delta t \rightarrow 0$. The second term in the expansion scheme is the second-order correlation function which we encountered in Chapter 7 in the context of autocorrelation and the noise spectrum. There, the quantity $C_{ii}^0(s)$ is the stationary version of the slightly more general time-dependent correlation term $g_2(t_1, t_2) = \langle S(t_1)S(t_2) \rangle - \langle S(t_1) \rangle \langle S(t_2) \rangle$. Higher orders would follow the same pattern (van Kampen, 1992), but they will play no role in what follows.

Using the moment expansion, the expected value in Eq. (14.94) becomes

$$\langle e^{[\eta * S'](t)} \rangle_{S'} = \exp \left(\sum_{m=1}^{\infty} \frac{1}{m!} \int_{-\infty}^{\hat{t}} \left(e^{\eta(t-s_1)} - 1 \right) \dots \left(e^{\eta(t-s_m)} - 1 \right) g_m(s_1, \dots, s_m) ds_1 \dots ds_m \right). \quad (14.95)$$

We call the expansion the event-based moment expansion. As a physical rule of thumb, the

contribution of terms $m \geq 2$ in Eq. (14.95) decreases rapidly with increasing m , whenever the events (i.e., spike times at times t and t') are weakly coupled. For the purpose of Eq. (14.92), we can effectively ignore all second- and higher-order correlations and keep only the term with $m = 1$. This gives

$$\langle \rho(t|\hat{t}, S') \rangle_{S'} = \bar{\rho} e^{h(t) + \eta(t - \hat{t}) + \int_{-\infty}^{\hat{t}} (e^{\eta(t-z)} - 1) A(z) dz}. \quad (14.96)$$

Eq. (14.96) can be used as an excellent approximation in the survivor function as well as in the formula for the interval distribution $P_{I,A}(t|\hat{t})$ in Eq. (14.92). Used within the integral equation (14.12) it gives an implicit description of the population activity for infinite an population of adapting neurons.

14.6 Heterogeneity and finite size

Neuronal populations in biology are neither completely homogeneous nor infinitely large. In order to treat heterogeneity in local neuronal parameters, the variability of a parameter between one neuron and the next is often replaced by slow noise in the parameters. For example, a population of integrate-and-fire neurons where the reset value u_r is different for each neuron is replaced by a population where the reset values are randomly chosen after each firing (and not only once at the beginning). Such a model of slow noise in the parameters has been discussed in the example of Section 14.3. The replacement of heterogeneity by slow noise neglects, however, correlations that would be present in a truly heterogeneous model. To replace a heterogeneous model by a noisy version of a homogeneous model is somewhat ad hoc, but common practice in the literature.

The second question is whether we relax the condition of a *large network*. For $N \rightarrow \infty$ the population activity shows no fluctuations and this fact has been used for the derivation of the population equation. For systems of finite size fluctuations are important since they limit the amount of information that can be transmitted by the population activity. For a population without internal coupling ($J_0 = 0$), fluctuations can be calculated directly from the interval distribution $P_I(t|\hat{t})$ if the population consists of neurons that can be described by renewal theory; see Chapter 9. For networks with recurrent connections, several attempts toward a description of the fluctuations have been made (Spiridon *et al.*, 1998; Meyer and van Vreeswijk, 2002; Lindner *et al.*, 2005). Here we present a different approach.

If we consider a network with a finite number N of neurons, the integral equation (14.5), which describes the evolution of the population activity $A(t)$ in terms of the input-dependent interval distribution $P_I(t|\hat{t})$, should be written more carefully with expectation signs,

$$\langle A(t) \rangle = \int_{-\infty}^t P_I(t|\hat{t}) A(\hat{t}) d\hat{t} \quad (14.97)$$

so as to emphasize that the left-hand side is the *expected* population activity at time t , given the observed population activity at earlier times \hat{t} . In other words $N \langle A(t) \rangle \Delta t = N \langle m_0(t) \rangle$ is

the expected number of spikes to occur in a short interval Δt . Here we have defined $m_0(t)$ as the fraction of neurons that fire in a time step Δt , just as in Section 14.1.5. Given the past input for $t' < t$ (which is the same for all the N neurons in the group), the firing of the neurons is independent in the next time step (“conditional independence”). Therefore in the limit of $N \rightarrow \infty$ the observed variable $m_0(t)$ approaches $\langle m_0(t) \rangle$ and we can drop the expectation signs.

For finite N , the variable $m_0(t)$ fluctuates around $\langle m_0(t) \rangle$. To determine these fluctuations, we assume that N is large, but finite. For finite N the population activity $A(t)$ can be written in the form of a “noisy” integral equation

$$A(t) = \langle A(t) \rangle + \sigma(t)\xi(t) = \int_{-\infty}^t \rho^{\text{noise}}(t|\hat{t}) S_I^{\text{noise}}(t|\hat{t}) A(\hat{t}) d\hat{t}, \quad (14.98)$$

where $\xi(t)$ is a Gaussian colored noise, $A(\hat{t})$ is the observed activity in the past, $S_I^{\text{noise}}(t|\hat{t})$ is the fraction of neurons that have survived up to time t after a last spike at time \hat{t} , and $\rho(t|\hat{t})^{\text{noise}}$ is the stochastic intensity of that group of neurons. Starting from discrete time steps, and then taking the continuum limit, it is possible to determine the amplitude of the fluctuations as $\sigma(t) = \sqrt{\langle A(t) \rangle / N}$. Equation (14.98) can be used to evaluate the correlations $\langle A(t) A(t') \rangle$, in coupled networks of finite size (Deger *et al.*, 2013).

14.6.1 Finite number of neurons (*)

For the development of the arguments, it is convenient to work in discrete time. We use the formalism developed in Section 14.1.5. We introduce the variable $m_k^N(t) = N m_k^{(t)}$ to denote the number of neurons that have fired in the interval $[t - k\Delta t, t - (k-1)\Delta t]$ and have “survived” up to time t without firing again. With this definition, $m_0^N(t) = N A(t) \Delta t$ denotes the number of neurons that fire in the time step from t to $t + \Delta t$.

We start with the normalization condition in the quasi-renewal equivalent of Eq. (14.8) and multiply both sides by the number of neurons

$$N = \int_{-\infty}^t S_{I,A}(t|\hat{t}) N A(\hat{t}) d\hat{t}. \quad (14.99)$$

This normalization must hold at any moment in time, therefore

$$m_0^N(t) = N - \sum_{k=1}^K m_k^N(t), \quad (14.100)$$

where K is chosen big enough so that all neurons have fired at least once in the last K time bins.

In order to determine the value of $m_k^N(t)$ for $k \geq 2$, we focus on the group of neurons that has fired at time $\hat{t} \approx t - (k-1)\Delta t$. The number of neurons that have “survived” up to time $t - \Delta t$ without emitting a further spike is $m_{k-1}^N(t - \Delta t)$. In the time step starting at time t , all of these neurons have the same stochastic intensity $\rho(t|\hat{t})$ and fire independently with probability $p_F(t|\hat{t}) = 1 - \exp[-\rho(t|\hat{t})\Delta t]$. In a finite- N discrete-time update scheme, the

actual number of neurons $n_k(t)$ of neurons that fire in time step t is therefore drawn from the binomial distribution

$$P(n_k) = \left(\frac{[m_{k-1}^N(t - \Delta t)]!}{[n_k]! [m_{k-1}^N(t - \Delta t) - n_k]!} \right) [p_F(t|\hat{t})]^{n_k} [1 - p_F(t|\hat{t})]^{m_{k-1}^N(t - \Delta t) - n_k}. \quad (14.101)$$

In the time step starting at time t , the number of neurons that have last fired at \hat{t} is therefore (for $k \geq 2$)

$$m_k^N(t) = m_{k-1}^N(t - \Delta t) - n_k(t). \quad (14.102)$$

Because of the shifting time frame used for the index k , neurons that are at time $t - \Delta t$ in group $(k - 1)$ will be at time t in group k , except those that fired in the previous time step – and this is expressed in Eq. (14.102). Note that $m_k^N(t)$ is the *actual* number of neurons remaining in the group of neurons that fired the last spike at \hat{t} . Its *expected* value is

$$\langle m_k^N(t) \rangle = m_{k-1}^N(t - \Delta t) \exp[-\rho(t|t - k\Delta t)\Delta t] \quad \text{for } k > 1 \quad (14.103)$$

as already discussed in Eq. (14.16). In the limit $N \rightarrow \infty$, the actual value will approach the expectation value, but for finite N the actual value fluctuates. The finite- N update scheme in discrete time is given by the iteration of Eqs. (14.102) and (14.100).

To arrive at an equation in continuous time, two further steps are needed. First, the binomial distribution in Eq. (14.101) is approximated by a Gaussian distribution with the same mean and variance. Second, we take the limit of Δt to zero and keep track of terms to order $1/N$ but not $1/N^2, 1/N^3, \dots$. The result is Eq. (14.98). Note that for an uncoupled network of N neurons in the stationary case, fluctuations can also be directly calculated from the interval distribution as discussed in Chapter 7. The advantage of the approach presented here is that it works also for coupled networks.

14.7 Summary

Relating the microscopic level of single neurons to the macroscopic level of neuronal populations, the integral equation approach offers an interpretation of neuronal activity in terms of the interspike interval distribution. The integral approach can be related to partial differential equations. The formulation of partial differential equations with refractory densities exhibits a close formal relation with the membrane potential density equations of Chapter 13. In a direct comparison of the two theories, the first one developed in Chapter 13, the second here, it turns out that the integral equation approach is particularly useful in modeling populations of neurons that have multiple intrinsic time scales in refractoriness, synapses, or adaptation and escape noise as the model of stochasticity.

Population equations can be formulated for several coupled populations. At the steady state, the population can be in a state of asynchronous and irregular firing, but the stability of these solutions against emergence of oscillations needs to be checked. Stability can be analyzed using the linearization of the integral equations around a stationary state.

Heterogeneity in the population can be treated as slow noise in the parameters and finite size effects can be analyzed and included in the numerical integration scheme.

Literature

The original paper of Wilson and Cowan (1972) can be recommended as the classical reference for population equations. The paper contains the integral equation for neurons with absolute refractoriness as well as, in the appendix, the case of relative refractoriness. Note, however, that the paper is most often cited for a differential equation for an “ad hoc” rate model that does not correctly reflect the dynamics of neurons with absolute refractoriness. It is worth while also consulting the papers of Knight (1972) and Amari (1972) that each take a somewhat different approach toward a derivation of population activity equations.

The presentation of the integral equations for time-dependent renewal theory (Eqs. (14.5) and (14.8)) in this chapter follows the general arguments developed in Gerstner (1995, 2000) emphasizing that the equations do not rely on any specific noise model. The same integral equations can also be found in the appendix of Wilson and Cowan (1972) as an approximation to a model with heterogeneity in the firing thresholds and have been derived by integration of the partial differential equations for refractory densities with escape noise in Gerstner and van Hemmen (1992). The integral approach for adaptive neurons and the approximation scheme based on the moment-generating function were introduced in Naud and Gerstner (2012a).

The linearization of the integral equation can be found in Gerstner (2000) and Gerstner and van Hemmen (1993). The model of slow noise in the parameters is taken from Gerstner (2000). The escape noise model – which turns out to be particularly convenient for the integral equation approach – is intimately linked to the noise model of Generalized Linear Models, as discussed in Chapter 9, where references to the literature are given.

Exercises

1. Integral equation of neurons with absolute refractory period

(a) Apply the population equation (14.5) to SRM neurons with escape noise which have an absolute refractory period

$$\eta(t) = \begin{cases} -\infty & \text{if } t < \Delta^{\text{abs}} \\ 0 & \text{otherwise.} \end{cases} \quad (14.104)$$

(b) Introduce the normalization condition Eq. (14.8) so as to arrive at the Wilson–Cowan integral equation (14.10).

(c) Use Eq. (14.8) to show that the mean interspike interval of neurons firing stochastically with a rate $f(h_0)$ is

$$A_0^{-1} = \Delta^{\text{abs}} + f(h_0)^{-1}, \quad (14.105)$$

where h_0 is a constant input potential.

2. **Gain function of SRM neurons.** Consider SRM neurons with escape noise such that the hazard function is given by $\rho(s) = \bar{\rho}e^{h+\eta(s)}$ with $\eta(s) = \ln[1 - e^{-s/\tau}]$.

(a) Show that the survivor function in the asynchronous state is

$$S_0(t) = \exp\left(-\frac{rt}{\tau} + r(1 - e^{-t/\tau})\right), \quad (14.106)$$

where $r = \tau\bar{\rho}e^h$.

(b) Using your results in (a), find the gain function $A_0 = g(h_0)$ for neurons.

Hint: Remember that the mean firing rate for fixed h_0 is the inverse of the mean interval. You will have to use the lower incomplete gamma function $\gamma(a, x) = \int_0^x t^{a-1}e^{-t}dt$.

(c) Suppose that you have SRM₀ neurons with an absolute and a relative refractory period as in Eq. (14.29). Calculate A_0 using your result from (b) and compare with Eq. (14.30).

3. **Linearization of the Wilson–Cowan integral equation.** The aim is to find the frequency-dependent gain $\hat{G}(\omega)$ for a population of neurons with absolute refractoriness.

(a) Start from the Wilson–Cowan integral equation and linearize around a stationary state A_0 .

(b) Start with the filter in Eq. (14.60) and derive directly the filter \hat{G} .

4. **Slow noise in the parameters.** Consider a population of leaky integrate-and-fire neurons with time constant τ_m and resistance R , driven by a constant superthreshold input I_0 . After each firing, the membrane potential is reset to u_r , which is chosen randomly from a distribution $P(u_r)$ with mean $\langle u_r \rangle$.

(a) Calculate the interspike interval T_0 for a neuron i which was reset at time t_0 to a value $u_i(t_0) = \langle u_r \rangle$ and that of another neuron j which was reset at t_0 to $u_j(t_0) = \langle u_r \rangle + \Delta u$.

(b) Suppose a Gaussian distribution of reset values with standard deviation σ_r . Show that the standard deviation σ_{ISI} of the interval distribution is $\sigma_{ISI} = \sigma_r/\dot{u}(T_0)$ where $\dot{u}(T_0)$ is the derivative of the membrane potential at the moment of threshold crossing.

5. **Linear response filter with step-function escape rate.** Consider $f(u) = \rho\Theta(u - \vartheta)$, i.e., a step-function escape rate. For $\rho \rightarrow \infty$ neurons fire immediately as soon as $u(t) > \vartheta$ and we are back to a noise-free sharp threshold. For finite ρ , neurons respond stochastically with time constant ρ^{-1} . The neuron mode is an SRM₀ with arbitrary refractoriness $\eta(t - \hat{t})$ driven by a constant input h_0 and a time-dependent component $h_1(t)$. The total membrane potential at time t is $u(t) = \eta(t - \hat{t}) + h_0 + h_1(t)$ where $h_1(t) = \int_0^\infty \exp(-s/\tau_m) I_1(t - s) ds$.

(i) Show that the kernel $\mathcal{L}(x)$ for neurons with step-function escape rate is an exponential function.

Hint: Denote by T_0 the time between the last firing time \hat{t} and the formal threshold crossing, $T_0 = \min\{s | \eta(s) + h_0 = \vartheta\}$. The derivative of f is a δ -function in time. Use a short-hand notation $\eta' = \frac{d\eta(s)}{ds}|_{s=T_0}$ and exploit Eq. (14.58).

(ii) Calculate the linear filter $G(s)$ and the response to an input current $I_1(t)$.