Chapter 12

WHAT'S DIFFERENT WITH SPIKING NEURONS?

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Abstract In standard neural network models neurons are described in terms of mean firing rates, viz., an analog signal. Most real neurons, however, communicate by pulses, called action potentials or simply 'spikes'. In this chapter the main differences between spike coding and rate coding are described. The integrate-and-fire model is studied as a simple model of a spiking neuron. Fast transients, synchrony, and coincidence detection are discussed as examples where spike coding is relevant. A description by spikes rather than rates has implications for learning rules. We show the relation of a spike-time dependent learning rule to standard Hebbian learning. Finally, learning rule and temporal coding are illustrated using the example of a coincidence detecting neuron in the barn owl auditory system.

Keywords: temporal coding, coincidence detection, spikes, spiking neurons, integrate-and-fire neurons, auditory system, Hebbian learning, spike-time dependent plasticity

1. SPIKES AND RATES

In most chapters of this book, neuronal activity is described as a rate. In a simple rate model the output ν_i of a neuron i is a nonlinear transform of its input u_i:

$$\nu_i = g(u_i) \tag{1}$$

Figure 12.1. Standard rate model neuron. The output rate ν_i is a nonlinear transform g of the total input $u_i = w_{ij}\,\nu_j$ with synaptic weights w_{ij}. The nonlinear function g has a sigmoidal shape.

where

$$u_i = \sum_j w_{ij}\,\nu_j + h^{\text{ext}} \tag{2}$$

is the input which arises from other neurons and/or from external stimulation. The weight w_{ij} is the coupling strength between neuron j and neuron i. ν_i is called the firing rate of the neuron. But what is this 'rate'?

1.1. TEMPORAL AVERAGE - SPIKE COUNT

Most neurons in the cortex and in other areas of the brain communicate by short electrical pulses which are called 'action potentials' or simply 'spikes'. In experiments spikes can be recorded by an electrode which is placed close to the soma or the axon of a neuron. Most neurons in the cortex emit even in the absence of external stimulation some action potentials. This is called the 'spontaneous activity'. During spontaneous activity, the temporal sequence of action potentials (the 'spike train') is irregular. There are only few occasional spike events. If a neuron in the visual cortex is stimulated by an appropriate input at the retina, then the neuron emits more spikes. A simple concept of a rate is the *spike count* in some time window:

$$\nu_i = \frac{\text{number of spikes in } T}{T}\,. \tag{3}$$

(3) defines a temporal average and is the first and most common definition of a rate. The gain function $g(u)$ tells us that a weak stimulation leads on the average only to a few spikes in a time window T whereas strong stimulation excites more spikes; see Fig. 12.1.

The problem with (3) is that a code based on a temporal average is intrinsically slow. In order to perform a sensible average, we should have at least 5 or 10 spikes inside the averaging period. Given the typical rates of cortical neurons, the time window T should then be in the order of 100-500 ms. If we estimate that the information flow in the cortex involves at least five to ten processing steps, and if at each step the neurons have to average over 200 ms to read the code of spikes they receive, then processing would be slow - in fact much too slow to account for the reaction times of the system. Humans can recognize and classify complex scenes within 400-500 ms (Thorpe et al., 1996). In a simple reaction time experiment, where images have been classified into two groups (e.g. those that show an animal and those that do not), responses are given by pressing or releasing a button. Since movement of the finger alone takes about 200-300 ms, this leaves 200-300 ms to make the decision and classify the visual scene. Moreover, EEG signals show that the classification is in fact performed in less than 200 ms (Thorpe et al., 1996). Such a short classification time is inconsistent with the idea that each neuron in a sequence of processing steps needs to average over 200 ms to read out the code. Thus, while spike count and temporal average are useful tools for experimental data analysis, this can not be the code used by the neurons.

1.2. SPATIAL AVERAGE - POPULATION ACTIVITY

There is, however, a completely different definition of a rate which relies on averaging over a group of identical or similar neurons. To distinguish this definition from the first definition of a rate we will refer to it as the *population activity.* It may also be called a population rate. What is the idea? The visual cortex, for example, is organized in columns of neurons with similar properties. In each short time interval Δt, a certain fraction of the neurons in a column will be active. Let us suppose we measure this fraction. The population rate A is found by dividing this fraction by Δt. This idea is illustrated in Figure 12.2 which shows the spike trains of several neurons. We count the number of spikes of all neurons in a time interval Δt, divide by the number of neurons to get the fraction of active ones, and then divide by Δt to get a rate. The result is the population activity

$$A(t) = \frac{1}{\Delta t} \frac{\text{total number of spikes in } [t, t + \Delta t]}{\text{population size } N} \tag{4}$$

If the density of connections is fairly high, then a code based on population rates is also a rather natural concept. Let us consider a column of neurons in the visual cortex. A neuron in another area of cortex which

Figure 12.2. Definitions of the firing rate as a temporal average for a single neuron (a) or as a spatial average over a population of neurons (b). In (a) the spike count $n(T)$ gives the number of action potentials in an interval T. Similarly $n_i(t; t + \Delta t)$ in (b) is the number of spikes neuron i emits in the short interval between t and $t + \Delta t$. If Δt is sufficiently short, each neuron can emit at most one spike. Hence, $n_i = 1$ if neuron i fires and $n_i = 0$ otherwise. Adapted from (Gerstner, 1998b).

Figure 12.3. Examples of temporal coding schemes. a) The phase of spikes with respect to some periodic background signal could carry information which is not contained in the mean firing rate. b) The synchrony of groups of neurons could signify special events. Adapted from (Gerstner, 1998b).

receives input from a hundred neurons of the column under consideration, 'measures' the population activity of this column.

A rate defined by a population average avoids therefore the disadvantage of a temporally averaged firing rate. In fact, we will see later in the chapter that the population rate can respond rapidly to changes in the input. The problem then is, how to arrive at a useful mathematical description of the population activity. The rate model (1) is by definition a static equation. It can not capture the dynamics of the population activity. A simple generalization of (1) would be a dynamic model of the form

$$\tau \frac{dA_i}{dt} = -A_i + g\left(\sum_j w_{ij} A_j\right) . \qquad (5)$$

It is, however, not clear why (5) should give a correct description of the dynamics of the population. The gain function g introduced in (1) is defined in a static situation and for a single neuron. Moreover the time constant τ has no obvious physiological meaning. Thus the question is: What would be a correct description of the population activity?

1.3. PULSE CODING - CORRELATIONS AND SYNCHRONY

So far the discussion has focused on rate coding. But there are also theoretical coding schemes which take the temporal structure of the spike sequence generated by neurons more seriously. Two examples are shown in Fig. 12.3. The first sketch is an illustration of phase coding. Signals in the auditory nerve are found to occur preferentially with a certain phase with respect to a sinusoidal sound stimulus. The auditory system uses this phase information to localize the external sound source (Carr and Konishi, 1990). Similarly, the phase of spikes in the hippocampus contains information which is not contained in the firing rate alone (J.O'Keefe and Recce, 1993).

Fig. 12.3b gives an illustration of coding by synchrony. The fact that several neurons fire at the same time could signify that they encode the same aspect of an external stimulus. This idea has some experimental support coming from recordings in the visual cortex (Eckhorn et al., 1988; Engel et al., 1991; Gray and Singer, 1989). Exact temporal correlations of spikes on a millisecond time scale could also contain information which is not contained in the firing rate alone (Abeles, 1994).

If we do not want to exclude the possibility that temporal coding plays a role, then we must take neuronal spike trains seriously and study models which work on the level of spikes. A simple spiking neuron model is the integrate-and-fire model, which will be studied in the next section.

2. INTEGRATE-AND-FIRE MODEL

A neuron is surrounded by its cell membrane. Ions may pass through the membrane at pores or specific channels which may be open or closed. A rather simple picture of the electrical properties of a cell is the following.

Close to the inactive rest state the neuron is characterized by some resistance R in parallel with some capacitance C. The factor $RC = \tau_m$ defines the membrane time constant of the neuron. The voltage u will be measured with respect to the neuronal resting potential. If the neuron is stimulated by some current $\mathcal{I}$, the voltage u rises according to

$$\tau_m \frac{du}{dt} = -u(t) + R\mathcal{I}(t)\,. \tag{6}$$

In the absence of current ($\mathcal{I} = 0$), the membrane potential would approach the resting potential $u = 0$. On the other hand, if there is a strong current $\mathcal{I} > 0$, the voltage u may reach some threshold value ϑ. At this point an action potential is generated. During the action potential numerous ion channels in the membrane open and close. A detailed model of these biochemical processes could explain the form of the voltage pulse. In the integrate-and-fire model, however, the action potential is not described explicitly. We simply record the firing time $t^{(f)}$, which is defined by the threshold condition

$$u(t^{(f)}) = \vartheta \,. \tag{7}$$

After firing the membrane potential is immediately reset to a value u_{reset}. Thus at $t = t^{(f)} + \delta$ with $\delta > 0$ we have a limit

$$\lim_{\delta \to 0} u(t^{(f)} + \delta) = u_{\text{reset}} \tag{8}$$

Often it is assumed that the reset potential is the resting potential. In this case we may set $u_{\text{reset}} = 0$.

The current $\mathcal{I}(t)$ could be some driving current that a neurophysiologist applies artificially by an intracellular electrode. In a real cortical network the driving current is the synaptic input which arises due to the arrival of spikes from other neurons. Let us suppose that a spike of a presynaptic neuron j which was fired at time $t_j^{(f)}$ evokes some current $w_{ij}\,\alpha(t - t_j^{(f)})$ at the synapse connecting neuron j to neuron i. The factor w_{ij} determines the amplitude of the current pulse and will be called the synaptic efficacy. The function $\alpha(t - t_j^{(f)})$ describes the time course of the synaptic current. If neuron i receives input from several presynaptic neurons j, the total input current to neuron i is

$$\mathcal{I}_i = \sum_j \sum_{t_j^{(f)}} w_{ij}\,\alpha(t - t_j^{(f)}) \tag{9}$$

where the sums run over all neurons $1 \leq j \leq N$ and over all firing times $t_j^{(f)}$. We put (9) in (6):

$$\tau_m \frac{du_i}{dt} = -u_i + R \sum_j \sum_{t_j^{(f)}} w_{ij}\,\alpha(t - t_j^{(f)}) \,. \tag{10}$$

Eqs. (7) - (10) define the dynamics in a network of integrate-and-fire neurons.

The sketch in Fig. 12.4 corresponds to a simplified situation where the input current pulse $\alpha(t - t_j^{(f)})$ is a simple square pulse. More realistically, we may take an exponential pulse

$$\alpha(s) = \frac{1}{\tau_s} \exp(-s/\tau_s) \tag{11}$$

Figure 12.4. Integrate-and-fire model. A spike from neuron j which arrives at a synapse to neuron i leads to a current input into the RC circuit (dashed circle) which represents the electrical properties of the soma of i. The RC-circuit acts as a leaky integrator. The result of current integration is the voltage response $u(t - t_j^{(f)})$. If several presynaptic pulses arrive in a short interval, then the total voltage may surpass, at some time $t_i^{(f)}$ the threshold value ϑ. In this case, an output pulse is generated. At the same time, the circuit is shunted so that the voltage is reset to zero.

where τ_s is a time constant which characterizes the open time of a synaptic channel. In a detailed model, we could change the form of $\alpha(s)$ so as to include a rise time of the synaptic current, but we will not do so here. In reality the amplitude of the current pulse should also depend on the momentary membrane voltage, but this dependence will be neglected in our presentation of the model.

3. SPIKE RESPONSE MODEL

Equations (6) - (10) define the dynamics of the integrate-and-fire model. (6) and (10) are linear differential equation and can therefore be easily integrated. Moreover, linearity implies that each term in the sum on the right-hand-side of (10) can be integrated separately. The total voltage is simply the sum of all components.

For the integration of (6) several different methods can be used. A simple approach is based on the impulse response function u_{imp} (also called Greens function) of the equation. Since (6) is a first-order linear differential equation with time constant τ_m, the response of the membrane potential u to a short current pulse at $t = 0$ is of the form

$$u_{\text{imp}}(t) \propto e^{-t/\tau_m} \tag{12}$$

for $t > 0$. If the current pulse deposits exactly one unit of charge on the capacitance C, the proportionality factor is found to be $1/C$. The response to an arbitrary input current $\mathcal{I}(t)$ is given by the convolution of the input with the response function

$$\begin{aligned} u(t) &= \int_0^\infty ds\, u_{\text{imp}}(s)\, \mathcal{I}(t-s) \\ &= \int_0^\infty ds\, \frac{1}{C}\, e^{-s/\tau_m}\, \mathcal{I}(t-s) \end{aligned} \tag{13}$$

We may check by differentiation that (12) is indeed a solution to the differential equation (6).

The impulse response function (12) can be found by Laplace transform of (6) or directly from the solution of the associated initial value problem. It is instructive to recall that, as an alternative, the impulse response can also be calculated via the integration of (6) with a unit step current as input, i.e. $\mathcal{I}(t) = 0$ for $t \leq 0$ and $\mathcal{I}(t) = 1$ for $t > 0$. The result is

$$u_{\text{step}}(t) = R\left[1 - e^{-t/\tau_m}\right] \tag{14}$$

where $\tau_m = RC$. The derivative of the step response (14) yields the impulse response function (12).

Let us now return to (12) and specify the input current $\mathcal{I}(t)$. Without loss of generality we set $C = 1$. The voltage response to a synaptic current pulse of the form $\alpha(t - t_j^{(f)})$ is then

$$\epsilon(t - t_j^{(f)}) = \int_0^\infty ds\, e^{-s/\tau_m}\, \alpha(t - t_j^{(f)} - s)\,. \tag{15}$$

If α is a square pulse of amplitude $1/\tau_m$, the voltage response is roughly of the form sketched in Fig. 12.4. Specifically, we find from (14)

$$\epsilon(s) = \begin{cases} 1 - e^{-s/\tau_m} & \text{for} \quad s < \Delta t \\ \left[1 - e^{-\Delta t/\tau_m}\right] e^{-(s-\Delta t)/\tau_m} & \text{for} \quad s > \Delta t \end{cases} \tag{16}$$

If α is the exponential pulse (11), then

$$\epsilon(s) = \frac{1}{1 - (\tau_s/\tau_m)} \left[e^{-s/\tau_m} - e^{-s/\tau_s}\right] \tag{17}$$

In the case of a vanishing synaptic time constant, $\lim \tau_s \to 0$ the voltage response is a simple exponential pulse

$$\epsilon(s) = e^{-s/\tau_m}\,. \tag{18}$$

On the other hand, in the special case where $\tau_m = \tau_s = \tau$, we get

$$\epsilon(s) = \frac{s}{\tau}\, e^{-s/\tau}\,. \tag{19}$$

a) b)

Figure 12.5. The synaptic input current pulse $\alpha(s) = (1/\tau_s)\,\exp(-s/\tau_s)$ shown in (a) causes the postsynaptic potential $\epsilon(s)$ shown in (b). The time constants are $\tau_s = 4\,\mathrm{ms}$ and $\tau_m = 10\,\mathrm{ms}$.

A sketch of the voltage response $\epsilon(s)$ defined by (17) is given in Fig. 12.5 The voltage response to a synaptic input is called the postsynaptic potential (PSP). For an excitatory synapse, it is called the EPSP, for an inhibitory synapse the IPSP.

How can we include the reset in our integration of the model? The reset at time $t_i^{(f)}$ corresponds to an outgoing current pulse which removes all charge from the capacitor. Since the charge just before firing is $Q = C\,\vartheta$, a pulse

$$\mathcal{I}_{\text{reset}}(t) = -Q\,\delta(t - t_i^{(f)}) \tag{20}$$

yields a reset to zero. We now may use (12) to integrate the reset current. The result is a voltage contribution

$$\eta(t - t_i^{(f)}) = \eta_0\, e^{-(t - t_i^{(f)})/\tau_m} \tag{21}$$

where $\eta_0 = -\vartheta$. As mentioned before (6) is a linear differential equation. The total voltage is therefore the sum of all individual terms. Thus

$$u_i(t) = \sum_{t_i^{(f)}} \eta(t - t_i^{(f)}) + \sum_j \sum_{t_j^{(f)}} w_{ij}\,\epsilon(t - t_j^{(f)})\,. \tag{22}$$

Firing times are as before given by the threshold condition

$$\text{If} \quad u_i(t) = \vartheta \quad \text{then} \quad t = t_i^{(f)} \tag{23}$$

Eqs. (22) and (23) define the Spike Response Model (SRM) (Gerstner, 1991; Gerstner et al., 1996b).

Each term in (22) has a simple interpretation. The function $\eta(s)$ describes the reset of the voltage after each spike. It is the response of the neuron to a threshold crossing. Due to the reset, it is rather unlikely that the neuron fires two spikes immediately one after the other. The

Figure 12.6. Each input pulse causes an excitatory postsynaptic potential (EPSP) $\epsilon(s)$. All EPSPs are added. If the threshold is reached the voltage is reset. The reset corresponds to adding a negative kernel $\eta(s)$.

reset leads therefore to 'refractoriness'. We may call η the refractory potential.

The term $\epsilon(s)$ describes the response of the neuron to incoming spikes. In biological terms it is the (excitatory or inhibitory) postsynaptic potential (EPSP or IPSP). Since EPSPs can be measured in experiments, the form of ϵ can be chosen so as to approximate as closely as possible experimental data. A graphical interpretation of the spike response approach (22) is given in Fig. 12.6.

For the purpose of mathematical analysis, it is often convenient to neglect the sum over all preceding spikes of neuron i and to keep only the refractory potential of the *most recent* spike. Let us write $\hat{t}_i$ for the *last* spike of neuron i. This simplification has been called a short-term memory approximation (Gerstner et al., 1996b) or SRM$_0$ (Gerstner, 2000b)

$$u_i(t) = \eta(t - \hat{t}_i) + \sum_j \sum_{t_j^{(f)}} w_{ij}\, \epsilon(t - t_j^{(f)})\,. \tag{24}$$

Note that this approximation affects only the first sum on the right-hand side of (22). The sum over the *presynaptic* pulses $t_j^{(f)}$ remains.

As before, the next spike of neuron i occurs when $u_i(t) = \vartheta$. We may put (24) in the threshold condition and move the term $\eta(t - \hat{t})$ in (24)

Figure 12.7. Neurons in a state of asynchronous firing. The upper part of the figure shows the population activity in a network of 1000 neurons. In the lower part of the figure, the spike trains of six randomly selected neurons are marked as sequences of dots. Since neurons do not fire at the same time, the population average (over all 1000 neurons) yields an activity which is, apart from fluctuations, approximately constant. Taken from (Gerstner, 1998a).

to the left-hand side. The result is

$$\vartheta - \eta(t - \hat{t}_i) = \sum_j \sum_{t_j^{(f)}} w_{ij}\, \epsilon(t - t_j^{(f)})\,. \tag{25}$$

The left-hand side of (25) may be interpreted as a dynamic threshold which is *increased* after each spike. The next spike occurs when the total postsynaptic potential, defined by the right-hand side of (25) reaches this dynamic threshold. In the following sections, we will use (25) to discuss some of the results for networks of spiking neurons. We will focus on those aspects where the difference to a naive rate model (1) is most obvious. A more detailed treatment is given in (Gerstner, 2000b; Gerstner, 1998a; Gerstner, 1998b; Gerstner et al., 1998).

4. RAPID TRANSIENTS

Let us suppose that we have a large and homogeneous network. All neurons are identical and described by (24). In order to have spike trains which are not completely regular we also add artificially some noise. Since the network is large, we are interested not in the spikes of each individual neuron, but rather in the population activity $A(t)$ defined in (4). Fig. 12.7 shows an example of a network state. The spike trains of six selected neurons are plotted (bottom). If we add the spikes of all the 1000 neurons in the population, we get the population activity (top). The population activity looks noisy and fluctuates around a constant mean.

The value of the activity A depends, of course, on the size of the input. In Fig. 12.7 the input was constant. We may imagine that the presynaptic spikes which drive the neuron arrive at a constant rate. Let us now suppose that the input rate increases abruptly at time $t = 100\,\mathrm{ms}$. How does the population activity respond to this change in the input?

The answer is given by Fig. 12.8. The population activity responds quasi instantaneously to a step in the input. In fact it can be shown that the form of the transient reflects directly the time course of the postsynaptic potential $\epsilon(s)$ (Gerstner, 2000b; Gerstner, 1998a). Let us write $A(t) = A_0 + \Delta A(t)$ where A_0 is the constant mean activity for $t < 100\,\mathrm{ms}$. Immediately after the switch at $t_0 = 100\,\mathrm{ms}$ we have (Gerstner, 1998a)

$$\Delta A(t) = a_0\,\epsilon(t - t_0) \tag{26}$$

with some constant a_0. For the simulation in Fig. 12.8, we have used the ϵ defined in (18). The initial phase of the transient is therefore an exponentially decaying pulse.

An equation of the form (1) or (4) can not describe such an instantaneous transition. Thus (4) is, in general, not a useful description of the population rate. It can, however, be shown that the approximation is good in the case of a population of neurons that is subject to white-noise input of large amplitude (Gerstner, 2000b). To get a correct description in the general case, we may use an integral equation which we motivate now.

Given the last firing time $\hat{t}_i$ of a neuron i and given the input which arrives from other neurons we can always calculate the neuronal potential $u_i(t)$ from (24). Given $u_i(t)$ we may calculate its next firing time from the threshold condition. In the noisy case, we can not predict the exact firing time, but only the probability that it fires around some time t. Let us write

$$P_u(t|\hat{t}) \tag{27}$$

for the probability density that a neuron which has fired its last spike at $\hat{t}$ and which has a potential $u(t')$ for $t' > \hat{t}$ fires again at time t. In a large population, the population activity is then (Gerstner, 1998a; Gerstner, 1995; Gerstner and van Hemmen, 1994)

$$A(t) = \int_{-\infty}^{t} P_u(t|\hat{t})\, A(\hat{t})\, d\hat{t}\,. \tag{28}$$

Figure 12.8. Rapid switching. At $t = 100\,\text{ms}$ the input current was changed to a higher value. The population activity responds immediately. Solid line: simulation of a network of 1000 neurons. Dashed line: theory. Taken from (Gerstner, 2000a).

An analysis of the population activity (28) correctly predicts the rapid transients (Gerstner, 1998a; Gerstner, 2000b). In fact, the dashed line in Fig. 12.8 is the theoretical prediction which coincides nicely with the simulation result.

Fast switching in networks of spiking neurons is a well-known effect (Knight, 1972a; Knight, 1972b; Treves, 1992; Tsodyks and Sejnowski, 1995). It has important implications for potential coding schemes. First it shows that signal transmission in cortical networks can be fast and is not limited by the membrane time constant τ_m (Knight, 1972a; Knight, 1972b; Treves, 1993). Thus a firing rate in the sense of a population activity *is* a useful concept and is in accordance with the reaction time experiments of Thorpe et al. (Thorpe et al., 1996). A necessary condition for fast switching, is that the population is, just before the switch, in a state of asynchronous firing. Second, it can be shown by an analysis of the population activity dynamics, that the asynchronous state is *unstable* unless a sufficient amount of noise is present in the network (Gerstner and van Hemmen, 1993; Abbott and van Vreeswijk, 1993). Thus, noise is a necessary requirement for the functioning of the network - which may explain why the spike trains of cortical neurons look noisy.

5. PERFECT SYNCHRONY

If synchrony is important for neural coding, then we should study conditions for synchrony in a network of mutually coupled neurons. In this section we will present the essence of an argument which is more extensively discussed in (Gerstner et al., 1996b).

We study a homogeneous network of N identical neurons which are mutually coupled with strength $w_{ij} = w_0/N$ where w_0 is a constant. In other words, the interaction is scaled with one over N so that the total input to a neuron i is of order one even if the number of neurons is large ($N \to \infty$). Since we are interested in synchrony we suppose that all neurons have fired simultaneously at $\hat{t} = 0$. When will the neurons fire again?

Since all neurons are identical we expect that the next firing time will also be synchronous. Let us calculate the period T between one synchronous pulse and the next. We start from (25). Since all neurons have fired synchronously at $t = 0$, we set $\hat{t}_i = t_j^{(f)} = 0$. The result is a condition of the form

$$\vartheta - \eta(t) = w_0 \, \epsilon(t) \tag{29}$$

where $\epsilon(t)$ is a postsynaptic potential, e.g., equation (17). The graphical solution of (29) is presented in Fig. 12.9. The first crossing point of the $\vartheta - \eta(t)$ and $w_0 \, \epsilon(t)$ defines the time T of the next synchronous pulse.

What happens if synchrony at $t = 0$ was not perfect? Let us assume that one of the neurons is slightly late compared to the others; Fig. 12.9b. It will receive the input $w_0 \epsilon(t)$ from the others, thus the right-hand side of (29) is the same. The left-hand side, however is different since the last firing was at δ^0 instead of zero. The next firing time is at $t = T + \delta^1$ where δ^1 is found from

$$\vartheta - \eta(T + \delta^1 - \delta^0) = w_0 \, \epsilon(T + \delta^1) \, . \tag{30}$$

Linearisation with respect to δ^0 and δ^1 yields:

$$\delta^1 < \delta^0 \quad \Longleftrightarrow \quad \epsilon'(T) > 0 \, . \tag{31}$$

Thus the neuron which has been late is 'pulled back' into the synchronized pulse of the others, if the postsynaptic potential ϵ is rising at the moment of firing at T. (31) is a rather general condition for stable synchrony (Gerstner et al., 1996b).

6. COINCIDENCE DETECTION

In a simple rate model, the temporal order of spikes does not matter. If two presynaptic neurons fire at 100 Hz each, then the total spike arrival rate at the postsynaptic neuron i is 200 Hz which results in a certain output rate $\nu_i = g(w_{i1}\nu_1 + w_{i2}\nu_2)$; see Eq. (1). For a spiking neuron model, however, the degree of synchrony in the input matters;

a)

b)

Figure 12.9. a) Perfect Synchrony. All neurons have fired at $\hat{t} = 0$. The next spike occurs when the summed postsynaptic potential $w_0\epsilon(t)$ reaches the dynamic threshold $\vartheta - \eta(t)$. b) Stability of perfect synchrony. The last neuron is out of tune. The firing time difference at $t = 0$ is δ^0. One period later the firing time difference is reduced ($\delta^1 < \delta^0$), since the threshold is reached at a point where $w_0\epsilon(t)$ is rising. Adapted from (Gerstner et al., 1996b).

a) b)

Figure 12.10. Coincidence Detection. Each spike evokes a postsynaptic potential EPSP denoted by ϵ. The sum of all ϵ terms yields the potential $u(t)$. a) Spike trains from two different presynaptic neurons are phase shifted with respect to each other. The total potential u does not reach the threshold. There are no output spikes. b) Spikes from two different presynaptic neurons arrive synchronously. The summed EPSPs reach the threshold ϑ and cause the generation of an output spike. Schematic figure; in most neurons the amplitude of the postsynaptic potential is smaller so that two input spikes would not be sufficient to drive the neuron to threshold.

cf. Fig. 12.10. In Fig. 12.10a we have sketched the situation where input spikes from two different neurons arrive phase shifted with respect to each other. The threshold is not reached and no output spike occurs. If the same number of input spikes arrives synchronously, then output spikes occur. The neuron acts as a coincidence detector, viz. it is sensitive to inputs which arrive within a short time window.

The above arguments are rather schematic and apply to a noise-free neuron. We may wonder whether coincidence detection is still possible if input is noisy. To answer this we have simulated an integrate-and-fire neuron which receives stochastic input from N presynaptic neurons $j = 1, \dots, N$. Each input spike evokes a jump of the membrane potential by a fixed amount $w_{ij} = 0.1$. Afterwards the membrane potential decays exponentially with time constant τ_m; cf. Eq. (18). At each synapse spikes arrive with a time-dependent rate

$$\nu(t) = \nu_0 \, [1 + k \, \cos(2\pi \, f \, t) \tag{32}$$

where f is the frequency of the modulation and k the modulation amplitude. For $k = 0$, input spikes arrive at a constant rate ν_0; for $k = 1$ the rate is periodically modulated between zero and $2\,\nu_0$.

It can be shown that, in the absence of a threshold, the mean membrane potential approaches a value of $u_0 \approx \nu_0 \, \tau_m \sum_j w_{ij}$ while the fluctuations due to stochastic spike arrival cause membrane potential fluctuations with amplitude $\sigma \propto \nu_0 \, \tau_m \sum_j w_{ij}^2$. Let us now take into account the firing threshold ϑ. If $u_0 < \vartheta$ the neuron is said to be in the sub-threshold regime; see e.g., (Abeles, 1991; Shadlen and Newsome, 1994; König et al., 1996; Troyer and Miller, 1997; Bugmann et al., 1997).

a) b)

Figure 12.11. Coincidence Detection with noisy spike input. a) At 100 synapses spikes arrive stochastically at a rate of $\nu_0 = 70\,\mathrm{Hz}$. The membrane potential u fluctuates around a mean value of $u_0 = 0.7$ and reaches threshold only occasionally (mean firing rate 12 Hz). Spikes are marked by vertical lines. b) At 100 synapses spikes arrive stochastically at a rate of $\nu(t) = \nu_0\,[1 + \cos(2\pi\, t/T)$ with mean $\nu_0 = 70\,\mathrm{Hz}$ and periodic modulation with period $T = 1\,\mathrm{ms}$. Due to the modulation, the membrane potential exhibits a periodic component and reaches threshold more frequently than in a. (mean firing rate 18 Hz). Parameters: Integrate-and-fire model with $\tau_m = 1\,\mathrm{ms}$, $\vartheta = R = 1$; each spike evokes an exponentially decaying postsynaptic potential (18). Its amplitude is given by the synaptic coupling strength $w = 0.1$

In the sub-threshold regime, spikes are triggered by the fluctuations of the membrane potential. In this regime the neuron is sensitive to the timing of the input spikes and can function as a coincidence detection. Sensitivity is highest if the mean membrane potential is about one or two standard deviations below threshold, i.e. $\vartheta - 2\sigma \le u_0 \le \vartheta - \sigma$ (Kempter et al., 1998; Plesser, 1999). Coincidence detection is used by neurons in the auditory system and will be discussed below.

7. SPIKE-TIME DEPENDENT HEBBIAN LEARNING

In standard Hebbian learning (Hebb, 1949), the synaptic weight w_{ij} of a presynaptic neuron j to a postsynaptic neuron i is increased, if presynaptic and postsynaptic neurons are 'simultaneously active'. In rate models where the activity of presynaptic and postsynaptic neurons is defined by their rates ν_j^{in} and ν_i^{out}, respectively, the learning rule is usually summarized as

$$\tau_w \frac{\mathrm{d}}{\mathrm{d}t} w_{ij} = a_0(w_{ij}) + a_1^{\mathrm{in}}(w_{ij})\,\nu_j^{\mathrm{in}} + a_1^{\mathrm{out}}(w_{ij})\,\nu_i^{\mathrm{out}} + a_2^{\mathrm{corr}}(w_{ij})\,\nu_j^{\mathrm{in}}\,\nu_i^{\mathrm{out}} \tag{33}$$

which can be seen as the first terms of an expansion of a general adaptation rule $dw_{ij}/dt = F(w_{ij}; \nu_i^{\mathrm{out}}, \nu_i^{\mathrm{out}})$ that uses only information that is locally available at the synapses, i.e., the firing rates ν_j^{in}, ν_i^{out} and the momentary value of the synaptic weight w_{ij}. The correlation term

Figure 12.12. Time windows for synaptic plasticity. a) If the spikes of a presynaptic neuron j and a postsynaptic neuron i coincide within a 'learning window', the synaptic weight of the connection between the two neurons is changed. b) Simple coincidence detection window. c) Asymmetric learning window that potentiates synapses where the presynaptic spike arrives slightly before the postsynaptic one. d) Two-phase learning window. A presynaptic spike arriving slightly before postsynaptic firing leads to an increase (potentiation), a presynaptic spike that arrives after postsynaptic firing leads to an decrease of the synaptic weight (depression).

$a_2^{\mathrm{corr}}(w_{ij})$ is sensitive to the joint activity of pre- and postsynaptic neurons. A correlation term $a_2^{\mathrm{corr}}(w_{ij}) > 0$ is usually called Hebbian learning in its narrow senses, whereas $a_2^{\mathrm{corr}}(w_{ij}) < 0$ is called anti-Hebbian learning.

In spiking neurons, the notion of 'simultaneously active' that leads to a term a_2^{corr} in Eq. (33), is less well defined. A simple notion would be to define a time window of simultaneity (e.g., a few milliseconds) and change weights whenever presynaptic and postsynaptic spikes occur within the time span set by the time window; cf. Fig. 12.12b. There is, however, no need that the time window be symmetric or rectangular. More generally it could be asymmetric as in Fig. 12.12c or it could have two phases as shown in Fig. 12.12d. Such generalized learning windows have been postulated on theoretical grounds for spiking neuron models (Gerstner et al., 1993; Gerstner et al., 1996a) as well as for rate models (Herz et al., 1988; Herz et al., 1989; Abbott and Blum, 1996; Gerstner and Abbott, 1997) and have recently found in experiments (Levy and Stewart, 1983; Markram and Tsodyks, 1997; Zhang et al., 1998; Debanne et al., 1998; q. Bi and Poo, 1999). What are potential advantages of such a generalized learning window?

First, asymmetric Hebb rules like in Fig. 12.12c are a natural implementation of the 'causal' notion in Hebbs original statement (Hebb, 1949) in that these rules strengthen the synapses with those presynaptic neurons j that have potentially contributed to firing the postsynaptic neuron i; obviously only a neuron j that has fired slightly *before* the postsynaptic spike can have an influence on the firing of this very spike. Moreover, these asymmetric learning rules are useful for sequence learning (Herz et al., 1988; Herz et al., 1989; Gerstner et al., 1993; Minai and Levy, 1993; Abbott and Blum, 1996; Gerstner and Abbott, 1997). It is, for example, possible to store spatio-temporal spike patterns in a network of spiking neurons (Gerstner et al., 1993).

With an asymmetric time window as in Fig. 12.12c, synaptic plasticity can detect, enhance, and store temporal structure *on the time scale of the learning window*. In the auditory system, for example, we need to resolve temporal structure in the sub-millisecond range, but it is unlikely that learning windows have a width that is less than a few milliseconds. How is this then possible? The answer is given by a two-phase learning window as in Fig. 12.12d. The combination of potentiation and inhibition leads to an effective competition between different synapses so that synaptic growth at a connection w_{ij} is only possible at the expense of decreasing the weight of other synapses (Gerstner et al., 1996a; Song et al., 2000). Only those synapses that give the 'correct' timing are enhanced while all others are decreased. Such a mechanism is thought of playing a role in tuning the delay lines in the barn owl auditory system (Gerstner et al., 1996a).

To understand the competitiveness in a two-phase learning rule from a mathematical point of view, it is useful to study an extension of Eq. (33) to spike-based learning: (Gerstner et al., 1996a; Gerstner et al., 1998; Kempter et al., 1999; Kistler and van Hemmen, 2000):

$$\begin{aligned} \tau_w \frac{\mathrm{d}}{\mathrm{d}t} w_{ij} &= a_0 + a^{\mathrm{in}}\, S_j^{\mathrm{in}}(t) + a^{\mathrm{out}}\, S_i^{\mathrm{out}}(t) \qquad (34) \\ &+ S_j^{\mathrm{in}}(t) \int_{-\infty}^{t} \mathrm{d}t'\, W(t-t')\, S_i^{\mathrm{out}}(t') + S_i^{\mathrm{out}}(t) \int_{-\infty}^{t} \mathrm{d}t'\, W(-t+t')\, S_j^{\mathrm{in}}(t')\,, \end{aligned}$$

where $S_j^{\mathrm{in}}(t) = \sum_f \delta(t - t_j^{(f)})$ is the presynaptic spike train that arrives at the synapse w_{ij}. The learning window W that we sketched in Fig. 12.12 plays the role of the correlation term a_2^{corr} in Eq. (33). In analogy to Eq. (33), the coefficients a_0, a^{in}, a^{out}, and the learning window W in general depend on the current weight value w_i. They may also depend on other local variables such as the membrane potential or the calcium concentration. Here we drop these dependencies and assume constant coefficients. All terms have a direct biological interpretation. For example the term $a^{\mathrm{in}}\, S_j^{\mathrm{in}}(t)$ implies that each presynaptic spike of neuron j induces a weight change in the synapse w_{ij} independent of the presence or absence of an output spike of the postsynaptic neuron j.

For Poisson input and Poisson output the correlation term a_2^{corr} in Eq. (33) can be identified with the integral over the learning window W in Eq. (34) (Kempter et al., 1999). It is then easy to see that, for certain combinations of parameters, the learning rule (34) leads to an intrinsic stabilization of the output firing rate. For example a model with $a = a^{\mathrm{out}} = 0$, $a^{\mathrm{in}} = c > 0$, and $\int_{-\infty}^{\infty} W(s)\mathrm{d}s = -1$ in Eq. (34) leads, for Poisson input, to an equivalent rate model of the form

$$\tau_w \frac{\mathrm{d}}{\mathrm{d}t} w_{ij} i(t) = -[\nu_i^{\mathrm{out}} - c]\, \nu_j^{\mathrm{in}}\,. \tag{35}$$

For constant input rates, learning stops after the output rate has approached the stable fixed point $\nu_i^{\mathrm{out}} = c > 0$. These arguments can be made more precise in order to show that stabilization of output rates occurs generically over a broad range of parameters and independent of the neuron model under consideration (Kempter et al., 2000).

8. TEMPORAL CODING IN THE AUDITORY SYSTEM

The most prominent example of temporal coding is probably found in the auditory system of the barn owl (Carr and Konishi, 1990; Konishi, 1986; Konishi, 1993; Sullivan and Konishi, 1986). The barn owl is capable of localizing external sound sources in the horizontal plane with a precision of a few degrees of azimuthal angle. The localization is achieved by measuring the interaural time difference, viz., the phase difference between the sound waves in the left and right ear. A precision of 5 degrees of angle corresponds to a temporal precision of a few microseconds (!) which must be resolved by the auditory system.

The basic idea of how this could work is sketched in Fig. 12.13. An array of coincidence detection neurons receives input from both ears. The spatial position of the neuron in the array is a mirror image of the position of the sound source in the external world (Jeffress, 1948). A circuit with these properties has indeed been found in the barn owl auditory system (Carr and Konishi, 1990). Neurons in the nucleus laminaris of the barn owl auditory system play the role of coincidence detectors. Neurons in this nucleus are sensitive to the interaural time difference. The phase of the sound wave at each ear is transmitted to the coincidence detector neurons by phase locked spikes. The basic picture of coincidence detection is therefore indeed the one of Fig. 12.10, except that not only two but hundreds of spike trains arrive from the two ears - just as in Fig. 12.11. If we adapt the parameters of the model of Fig. 12.11 to the barn owl auditory system, we can check that the neuron can indeed act as a coincidence detector and is indeed sensitive to the interaural time

Figure 12.13. Jeffress model. Activity waves from both ears meet at an array of coincidence detectors (circles).

difference of a stimulating tone (Gerstner et al., 1998; Gerstner et al., 1996a; Kempter et al., 1998); cf. Fig. 12.14, bottom right.

An essential component of a model of coincidence detection in the barn owl auditory system is an adaption or learning rule that controls the timing of the transmission delays. Each coincidence detecting neuron in the nucleus laminaris of the barn owl auditory system receives about 100 synapses from the left, and 100 synapses from the right ear. If the transmission delays are different between synapses from the *same* side, then spikes do not arrive synchronously even if they have been generated at the cochlea in a perfectly synchronous fashion. In that case, the activity wave that travels from the ear to the coincidence detectors looses the information about the timing of the external stimulus.

In order to guarantee a nearly perfect timing of the transmission delays, we can use the spike-time dependent learning rule discussed in the previous section. Fig. 12.14 shows how the delay lines that arrive from the two ears are selected. At the beginning we have about 600 connections with broad distribution of delays between 1 and 4 milliseconds (top left). For a simulation with a 5 kHz tone, a small delay difference in the range of 0.2 millisecond will already completely destroy all temporal information. The postsynaptic neuron can therefore not function as a coincidence detector (top right). During learning some synapses are strengthened, others are decreased (middle). After learning all synapses have either the same delay or the delay differs by a full period (0.2 ms). The output rate of the neuron (number of spikes in a time window of 500 ms) depends now clearly on the interaural time difference (ITD) between the stimulus at the left and the stimulus at the right ear (bottom right). The neuron acts as a coincidence detector and responds maximally at ITD=0, i.e., if the spikes from the left and right ear arrive, on average, simultaneously.

9. CONCLUSION

The auditory system is one of the specific examples where temporal coding is a generally accepted principle. Related coding schemes could,

Figure 12.14. Development of tuning to a 5kHz tone. The left column shows the strength of synaptic efficacies w_{ij} of all synapses. Synapses are indexed according to the delay Δ_j of the corresponding transmission line and are plotted as $w_{ij} = w(\Delta)$. On the right, we show the output firing rate (ν) as a function of the interaural time delay (ITD). **Top**. Before learning, there are 600 synapses (300 from each ear) with different delays, chosen randomly from a Gaussian distribution with mean 2.5 ms and variance 0.3 ms. All weights have unit value. The output rate shows no dependence upon the ITD (right). **Middle**. During learning, some synapses are strengthened others decreased. Those synapses which increase have delays that are similar or that differ by multiples of the period $T = 0.2$ ms of the stimulating tone. **Bottom**. After learning, only about 150 synapses (≈ 75 from each ear) survive. The output rate ν shows the characteristic dependence upon the ITD as seen in experiments with adult owls (Carr and Konishi, 1990). The neuron has the maximal response ($\nu = 200$ Hz) for ITD $= 0$, the stimulus used during the learning session of the model neuron. Taken from (Gerstner et al., 1998).

in principle, also hold in other areas of the brain. The final decision of whether temporal codes are relevant in a given system or not must come from experiments. If we do not want to bias model approaches towards rate coding, then models on the level of spike events - like the integrate-and-fire or the Spike Response Model – must be studied.

In many areas of the brain, rate coding might be sufficient – rate coding, however, not interpreted as a temporal average but rather as a population average. Rate coding in the sense of a population activity is an important concept, since it allows fast temporal coding schemes. Models of the population activity must be capable of describing these fast signal transmission properties. A naive rate model of the form (1) or (4) is unable to do this. To get an appropriate model of the population activity, we must keep track of the spike dynamics. Thus, spikes are important even if rate should be the coding principle.

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