Rapid signal transmission by populations of spiking neurons

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Abstract

The dynamics of a homogeneous population of spiking neurons are analyzed. It is shown that signal transmission can be rapid. The cut-off frequency of signal transmission depends on the noise level and on synaptic time constants rather than on the membrane time constant. In the low noise limit, transients of the population activity can be immediate.

1 Introduction

Mammals can react rapidly to unknown stimuli. Humans, for example, can classify complex visual scenes into two groups (animal/not animal) within less than four hundred milliseconds [1]. If we assume that half of the time is needed for motor commands (pressing or releasing a button), this leaves about 200 milliseconds for the recognition task. Since it is generally assumed that recognition involves many processing steps, each processing step in some iterative scheme must be completed within 10 or 20 milliseconds. This implies that the network of neurons in the brain does not have the time to reach a stationary state. Most of the processing has to be done during the initial transient. If we aim for a better understanding of the brain, we must therefore be interested in the dynamics of neural systems.

While the relevance of dynamics is commonly recognized, most standard problems in artificial neural network are formulated as static tasks. In a stationary state, neurons are fully characterized by their transfer function g. The output of neuron i is simply $a_i = g(\sum_j w_{ij} a_j)$ where w_{ij} are the connection weights from j to i. A simple way to add dynamics to the model is (e.g., [2, 3]) an equation of the form

$$\tau \frac{d}{dt} a_i = -a_i + g\left(\sum_j w_{ij} a_j + h^{\text{ext}}\right) \quad (1)$$

where h^{ext} is some external stimulus. The fixed points of the dynamics (1), defined by $da_i/dt = 0$, yield the standard equations of artificial neural networks.

The dynamics (1) is completely *ad hoc.* In particular, the interpretation of the time constant τ is not clear. For a step-like stimulus which is switched on at time t_0, the time constant τ characterizes the transient of the approach to the new stationary state. Is τ the membrane time constant of the neuron? This is the central question of this paper and the answer will be negative. Before we can answer this question, we must discuss the interpretation of the variable a. Is a the temporally averaged firing rate of a single neuron? If so, τ would be related to the time window of temporal averaging and have no physical meaning. On the other hand, a may represent the activity of a population of neurons. It is this second interpretation that we will study in this contribution. We will see that transients in a population of spiking neurons can be fast compared to the time scale of the membrane time constant. It will turn out that the time constant of the transient is rather related to the level of noise than to the membrane time constant.

Formally we define the population activity A by counting the spikes in a pool of neurons averaged over an infinitesimal time window Δt

$$\begin{aligned} A(t) &= \lim_{\Delta t \to 0} \frac{1}{\Delta t} \frac{n_{\text{act}}(t; t+\Delta t)}{N} \\ &= \frac{1}{N} \sum_{t_j^{(f)}} \delta(t - t_j^{(f)}) \end{aligned} \quad (2)$$

where $n_{\text{act}}(t; t+\Delta t)$ is the number of spikes emitted by the population between t and $t+\Delta t$ and N is the size of the population. The firing times of neuron j are denoted by $t_j^{(f)}$. In section 3 we review an integral equation which replaces (1) and describes the dynamics of $A(t)$ in the limit of $N \to \infty$. For any finite population, the variable $A(t)$ fluctuates considerably around a momentary expectation value $\langle A(t) \rangle$. In the last part of the paper, we calculate the spectrum of the fluctuations and discuss its relevance for signal transmission.

2 Spike Response Model

2.1 Definition

Spikes will be treated as formal events and are characterized by their firing time $t_i^{(f)}$. Spikes of neuron i are generated if the variable $u_i(t)$ (the membrane potential) approaches a threshold ϑ from below:

$$u_i(t) = \vartheta \quad \textbf{and} \; \frac{du}{dt} > 0 \Longrightarrow t = t_i^{(f)} \quad (3)$$

At each threshold crossing we 'paste in' the effect of a spike by adding a kernel $\eta(t-\hat{t}_i)$ where $\hat{t}_i$ is the last firing time of neuron i. In a detailed model $\eta(t-\hat{t}_i)$ would include the form of the action potential and the spike afterpotential. Here we take a simple model,

$$\eta(t-\hat{t}_i) = \eta_0 \, \exp\left(-\frac{t-\hat{t}_i}{\tau}\right) \, \mathcal{H}(t-\hat{t}_i) \quad (4)$$

with $\eta_0 < 0$. In this case, η does not describe the time course of the spike itself but only the 'reset' to a lower value of the membrane potential after threshold crossing. The Heaviside step function $\mathcal{H}(s)$ is zero for $s \le 0$ and unity for $s > 0$.

A spike of a presynaptic neuron j at time $t_j^{(f)}$ evokes, for $t > t_j^{(f)}$, a postsynaptic potential at the soma of neuron i. The time course of the postsynaptic response is described by a kernel $\epsilon(t-\hat{t}_i, t-t_j^{(f)})$. The response of the postsynaptic neuron i depends on the time $t-\hat{t}_i$ which has passed since the last output spike of i. Immediately after a postsynaptic spike, most ion channels are open and the membrane resistance is practically shunted. An input spike which arrives a short time after $\hat{t}_i$ evokes therefore only a small response. If the same input spike arrived a long time after the last postsynaptic spike, it would cause a much larger response. The amplitude of the response is scaled by the synaptic efficacy w_{ij}. The total membrane potential is the sum of all postsynaptic potentials plus the spike afterpotential η

$$\begin{aligned} u(t|\hat{t}_i) &= \eta(t-\hat{t}_i) \\ &+ \sum_{t_j^{(f)}} w_{ij} \, \epsilon(t-\hat{t}_i, t-t_j^{(f)}) \\ &+ J^{\rm ext} \int_0^\infty \tilde{\epsilon}(t-\hat{t}_i, s) \mathcal{I}^{\rm ext}(t-s) ds \end{aligned} \quad (5)$$

where the sum runs over all firing times of all presynaptic neurons. The last term in (5) accounts for a potential external input current $\mathcal{I}^{\rm ext}$ which may be applied to the cell. Eqs. (3) and (5) define the Spike Response Model. With an appropriate choice of the kernels $\eta(t-\hat{t}_i)$ and $\epsilon(t-\hat{t}_i, t-t_j^{(f)})$, the Spike Response Model can reproduce ninety percent of the firing times of the Hodgkin-Huxley model with a precision of $\pm 2\,$ms [4]. With a different choice of the kernels the Spike Response Model can be mapped exactly to the integrate-and-fire model [5]. Moreover, a model of the form (5) can also be fitted to experimental data [6]. We may therefore consider (3) and (5) as a rather general framework for the dynamics of spiking neurons [7].

2.2 Simplified model SRM$_0$

The population theory discussed below is valid for the general model defined by (5) [8]. In order to simplify the notation, we neglect in the following the dependence of ϵ and $\tilde{\epsilon}$ on $t-\hat{t}_i$ and take

$$\begin{aligned} u(t|\hat{t}_i) &= \eta(t-\hat{t}_i) + \sum_{t_j^{(f)}} w_{ij} \, \epsilon(t-t_j^{(f)}) \\ &\quad + J^{\rm ext} \int_0^\infty \tilde{\epsilon}(s) \, \mathcal{I}^{\rm ext}(t-s) \, ds. \end{aligned} \quad (6)$$

Eqs. (3) and (6) define the simplified spike response model SRM$_0$.

It is convenient to introduce the total input potential

$$\begin{aligned} h_i(t) &= \sum_{t_j^{(f)}} w_{ij} \, \epsilon(t-t_j^{(f)}) \\ &\quad + J^{\rm ext} \int_0^\infty \tilde{\epsilon}(s) \, \mathcal{I}^{\rm ext}(t-s) \, ds \end{aligned} \quad (7)$$

which allows us to write the membrane potential as $u(t|\hat{t}_i) = \eta(t-\hat{t}_i) + h_i(t)$. Note that the input potential $h_i(t)$ does not depend on the last firing time $\hat{t}_i$ of neuron i.

In a simple model, the kernel $\tilde{\epsilon}$ can be approximated by a low-pass filter

$$\tilde{\epsilon}(s) = \frac{1}{\tau} e^{-s/\tau} \tag{8}$$

with the membrane time constant τ.

2.3 Noise

In the deterministic version of the model, we can calculate the next firing time of a neuron i with potential $u(t|\hat{t}_i)$ from the threshold condition (3). Let us now assume that there is some intrinsic noise source. In this case, we cannot predict the exact firing time of neuron i but only the probability density $P_h(t|\hat{t}_i)$ that a spike occurs at t given that the last spike occurred at $\hat{t}_i$. The lower index h is intended to remind the reader that the firing density at time t depends on the input potential $h_i(t')$ for $\hat{t}_i < t' < t$.

A noise model which is particularly convenient is escape noise. We assume that neuron i may emit a spike even though its membrane potential $u_i(t|\hat{t}_i)$ has formally not yet reached the threshold ϑ. Similarly, the neuron may stay quiescent even though the membrane potential is already above threshold. At each instant of time, the probability density of firing (escape rate ρ) depends only on the momentary distance between u and the threshold:

$$\rho(t) = f[u_i(t|\hat{t}_i) - \vartheta]\,. \tag{9}$$

We may for example take or $f(u-\vartheta) = (u-\vartheta)\,\mathcal{H}(u-\vartheta)\,f_0$ with some constant f_0. For $f_0 \to \infty$ we are back to the noise-free case.

We emphasize that (9) describes a noise source which is *intrinsic* to the neuronal dynamics. Given that in recordings with well-defined intracellular stimuli neurons seem to be nearly noiseless such intrinsic noise sources do not seem to play a major role. The apparent 'noisiness' of cortical neurons is probably a network effect, as supported by theoretical studies [9, 10]. Noise should then better be described as stochastic spike arrival. It can, however, be shown that stochastic spike arrival and escape noise give, under a wide range of stimulus conditions, rise to rather similar behavior [11].

The advantage of the escape noise model compared to other noise models is that we can derive a (more or less explicit) expression for the firing density $P_h(t|\hat{t}_i)$. Let us suppose that the last spike of neuron i occurred at time $\hat{t}_i$. If we know the input current and past spikes of other neurons we can calculate the membrane potential of neuron i from (6). At each moment between $\hat{t}_i$ and t there is the probability of escape across threshold proportional to $\rho(t) = f(u_i(t|\hat{t}_i) - \vartheta)$. The probability that the neurons stays quiescent from $\hat{t}_i$ up to time t is therefore

$$S_h(t|\hat{t}_i) = \exp\left\{-\int_{\hat{t}_i}^{t} \rho(t')\,dt'\right\}\,. \tag{10}$$

(10) is called the survivor function [12, 13]. The probability density of emitting the *next* spike at t (with no output spikes in between) is then the probability of 'surviving' from $\hat{t}_i$ to t times the probability of firing at t, viz.,

$$\begin{aligned} P_h(t|\hat{t}_i) &= \rho(t)\,S_h(t|\hat{t}_i) \qquad (11)\\ &= \rho(t)\,\exp\left\{-\int_{\hat{t}_i}^{t} \rho(t')\,dt'\right\}\,. \end{aligned}$$

In the following sections, we will make repeated use of (11). Survivor function and interval distribution for constant input potential $h(t) = h_0$ are plotted in Figs. 1 and 2, respectively.

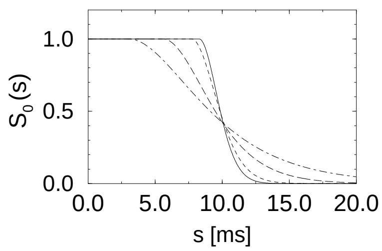

Figure 1: Survivor function for four different levels of noise. Escape rate $\rho(t) = [u(t|\hat{t}) - \vartheta]\,\mathcal{H}[u(t|\hat{t}) - \vartheta]\,f_0$ with $f_0 = 20$ (solid line), 10 (dotted line), 2 (long-dashed line), and 0.5 (dot-dashed line). The constant input potential h_0 has been adjusted so that the mean interval is always 10 ms.

3 Population dynamics

3.1 Population equations

In this section we derive the equations describing the population dynamics in a homogeneous pool of neurons. For the sake

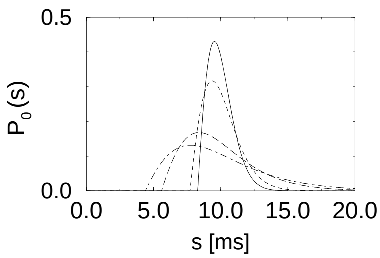

Figure 2: Interval distribution for four different levels of noise. For low noise, the interval distribution is fairly sharp (solid line). For higher noise level the distribution becomes skewed and broad (dashed and dot-dashed lines). The mean interval is 10 ms in all cases.

of simplicity we consider a single population. All neurons have identical parameters, homogeneous coupling $w_{ij} = w_0/N$, and receive the same external input $J^{\mathrm{ext}}\mathcal{I}^{\mathrm{ext}}$. Given the definition of the activity (2) we can rewrite the input potential as

$$\begin{aligned} h(t) &= w_0 \int_0^\infty \epsilon(s)\, A(t-s)\, ds \qquad (12) \\ &\quad + J^{\mathrm{ext}} \int_0^\infty \tilde{\epsilon}(s)\, \mathcal{I}^{\mathrm{ext}}(t-s)\, ds \end{aligned}$$

Note that the input potential does not depend on the neuronal index i. (12) is the first of the two population equations. It tells us how to calculate $h(t)$ given $A(t-s)$ in the past. A second equation allows us to determine the current value of the activity $A(t)$ given $h(t-s)$ in the past,

$$A(t) = \int_{-\infty}^{t} P_h(t|\hat{t})\, A(\hat{t})\, d\hat{t}\,. \qquad (13)$$

(13) has a rather intuitive interpretation. All neurons which have fired at $\hat{t}$ will contribute to the activity $A(t)$ at time $t > \hat{t}$ with a weight $P_h(t|\hat{t})$. Note that even though (13) looks like a linear equation, it is, in fact highly nonlinear since the firing density $P_h(t|\hat{t})$ defined in (11) depends nonlinearly on h and h depends via (12) on A. (12) and (13) define the population dynamics in a homogeneous pool of neurons. In the following two subsections we will analyze the equations in some special cases.

3.2 Steady state

A steady state may be defined by a constant activity $A(t) = A_0$. Given a constant input $\mathcal{I}^{\mathrm{ext}} = \mathcal{I}_0$ the input potential is

$$h_0 = w_0\, A_0 + J^{\mathrm{ext}}\mathcal{I}_0\,. \qquad (14)$$

For constant input, the firing density $P_h(t|\hat{t})$ depends only on the time difference

$$P_{h_0}(t|\hat{t}) = P_0(t-\hat{t})\,. \qquad (15)$$

We may think of $P_0(s)$ as the interspike-interval distribution. The mean interspike interval is $\langle s \rangle = \int s\, P_0(s) ds = \int S_0(s) ds$ where $S_0(s) = S_{h_0}(s|0)$ denotes the survivor function in the stationary state. The mean firing rate of a neuron is $1/\langle s \rangle$. In a stationary state the population activity is equal to the mean rate and hence

$$\begin{aligned} A_0 &= \left[\int_0^\infty S_0(s)\, ds\right]^{-1} \qquad (16) \\ &= \left[\int_0^\infty \exp\left(-\int_0^s \rho_0(s')\, ds'\right)\, ds\right]^{-1} \end{aligned}$$

with $\rho_0(s) = f[\eta(s) + h_0 - \vartheta]$.

3.3 Linearization

Let us suppose that the network activity is close to a stationary state, $A(t) = A_0 + \Delta A(t)$. We want to linearize (13) to first order in ΔA. Before we do the linearization, it is convenient to rewrite (13) in the form

$$0 = \frac{d}{dt} \int_{-\infty}^{0} S_h(t|\hat{t})\, A(\hat{t})\, d\hat{t}\,. \qquad (17)$$

Evaluation of the right-hand side with $P_h(t|\hat{t}) = -\frac{d}{dt} S_h(t|\hat{t})$ leads back to (13).

We now set $A(t) = A_0 + \Delta A(t)$ and expand to first order in ΔA. The external stimulus is $\mathcal{I}^{\mathrm{ext}}(t) = \mathcal{I}_0 + \Delta\mathcal{I}(t)$. The input potential is therefore $h(t) = h_0 + \Delta h(t)$ with $h_0 = w_0\, A_0 + J^{\mathrm{ext}}\mathcal{I}_0$ and

$$\begin{aligned} \Delta h(t) &= w_0 \int_0^\infty \epsilon(s)\, \Delta A(t-s)\, ds \qquad (18) \\ &\quad + J^{\mathrm{ext}} \int_0^\infty \tilde{\epsilon}(s)\, \Delta\mathcal{I}(t-s)\, ds \end{aligned}$$

The linearization of (17) is

$$\begin{aligned} \Delta A(t) &= \int_{-\infty}^{t} P_0(t-\hat{t})\, \Delta A(\hat{t})\, d\hat{t} \qquad (19) \\ &\quad + A_0 \int_0^\infty \mathcal{L}(x)\, \frac{d}{dt} \Delta h(t-x)\, dx\,. \end{aligned}$$

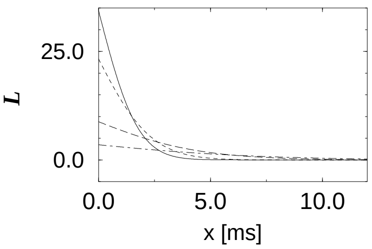

Figure 3: Example of the filter $\mathcal{L}(x)$ for four different values of noise. For low noise, the filter decays rapidly to zero and vanishes pratically for $x > 2.5\,\mathrm{ms}$ (solid line). For high noise, the filter is much broader (dashed and dot-dashed lines).

where we have introduced a filter

$$\begin{aligned}\mathcal{L}(s) &= \int_{-s}^{\infty} ds' \, \frac{\partial S_h(s'|0)}{\partial h(s'-s)}|_{h=h_0} \qquad (20)\\ &= \int_{s}^{\infty} S_0(s') \, \frac{d}{dh_0} f[\eta(s'-s)+h_0]\end{aligned}$$

The first term on the right-hand side of (19) describes the effect of previous variations ΔA on the present activity. The second term is due to variations in the input potential. We emphasize that the second term is proportional to the *derivative* of a *low-pass filtered* version of the input potential. Examples of the filter $\mathcal{L}(s)$ are shown in Fig. 3.

4 Transients

To keep things simple, we set the coupling to zero: $w_0 = 0$. Let us suppose that the input $\mathcal{I}^{\rm ext}$ is switched at time t_0 from $\mathcal{I}_0$ to a new value $\mathcal{I}_0 + \Delta\mathcal{I}$. This causes a change in the input potential $\Delta h(t) = J^{\rm ext} \int_0^{t-t_0} \tilde{\epsilon}(s) \Delta\mathcal{I} \, ds$. In (19) we need the derivative of Δh:

$$\frac{d}{dt} h(t) = J^{\rm ext} \, \Delta\mathcal{I} \, \tilde{\epsilon}(t-t_0) \qquad (21)$$

For low noise the filter $\mathcal{L}$ may be approximated by a δ-function. The change of the activity during the initial phase of the transient is therefore given by $\Delta A(t) \propto \tilde{\epsilon}(t-t_0)$. The rise time of the initial transients is therefore given by the *rise time* of the kernel $\tilde{\epsilon}$ and not by the membrane time constant. (The membrane time constant τ describes the decay of the $\tilde{\epsilon}$-kernel.)

In the presence of noise the transients are slower due to the low-pass characteristics of the filter $\mathcal{L}$. The cut-off frequency of the filter $\mathcal{L}$ determines the sharpness of the transient. Fig. 4 shows two simulations at low noise (top) and at high noise (bottom). Note that for low noise the transition is quasi immediate. For high noise we may approximate the filter $\mathcal{L}$ by an exponential $\mathcal{L}(x) = a\gamma e^{-\gamma x} \, \mathcal{H}(x)$. In this case, $\int_0^\infty \mathcal{L}(x) \, \frac{d}{dt} \Delta h(t-x) \, dx \propto [\Delta h(t) - \overline{\Delta h(t)}]$ where $\overline{\Delta h}$ is a running average with time window $1/\gamma$. During the initial phase of the transient i.e., $t - t_0 \ll 1/\gamma$, the running average $\overline{\Delta h}$ is negligible. The activity follows therefore in the *high-noise limit* the membrane potential h which changes with time constant τ. In the high-noise limit (1) can therefore be justified. For low noise, transients can be much faster.

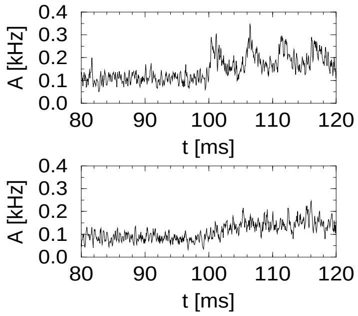

Figure 4: Transients in a network of 1000 neurons for low noise (top) and high noise (bottom). A step current input was switched on at $t = 100\,\mathrm{ms}$. In both cases, the mean activity before the current switch was about 100 Hz (mean interval $\approx 10\,\mathrm{ms}$). In the low noise case the variance of the interval was $0.5\,\mathrm{ms}$ (parameter $f_0 = 50$), in the high-noise case the variance was $5\,\mathrm{ms}$ ($f_0 = 2$)

5 Signal-transfer function

Another way of evaluating the signal transmission properties is by calculating the transfer function $S(f) = |\hat{A}(\omega)/\hat{\mathcal{I}}(\omega)|$. with $\omega = 2\pi f$. We stimulate the population with a sinusoidal current $\hat{\mathcal{I}}(\omega)$. The Fourier transform of (19) yields the response $\hat{A}(\omega)$. Thus

$$\frac{\hat{A}(\omega)}{\hat{\mathcal{I}}(\omega)} = \frac{i\omega \, J^{\rm ext} \, A_0 \, \hat{\mathcal{L}}(\omega) \, \hat{\tilde{\epsilon}}(\omega)}{1 - \hat{P}(\omega) \, - i\omega \, w_0 A_0 \hat{\mathcal{L}}(\omega) \hat{\epsilon}(\omega)} \, . \qquad (22)$$

The absolute value of (22) for $w_0 = 0$ is the signal transfer function shown in Fig. 5.

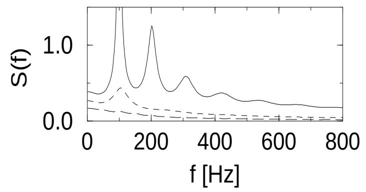

Figure 5: Signal transmission for low noise (solid line) and high noise dashed lines).

6 Finite-size effects

The above theory is valid in the limit of $N \to \infty$. For finite N we have to consider fluctuations around the expected value. Let us suppose that, for constant external input, the activity fluctuates around a constant value A_0. To mimic the effect of fluctuations, we assume that the escape rate $\rho(t)$ changes stochastically, viz., $\rho(t) = f(u - \vartheta)\,[1 + \sigma\xi(t)]$ where ξ is Gaussian white noise. Linearization with respect to σ (and as before with respect to ΔA) yields the noise spectrum in the stationary state

$$|\hat{A}(\omega)|^2 = \frac{\sigma^2 \, A_0^2 \, |\hat{\mathcal{F}}(\omega)|^2}{|\hat{S}(\omega) - w_0 \, A_0 \hat{\mathcal{L}}(\omega)\hat{\epsilon}(\omega)|^2} \tag{23}$$

where $\hat{\mathcal{F}}$ is the Fourier transform of a filter

$$\mathcal{F}(t) = \mathcal{H}(t) \int_t^\infty \rho_0(s-t)\, S_0(s)\, ds \tag{24}$$

Note that inhibitory coupling $w_0 < 0$) generates anti-correlations in the firing of the neurons. Anti-correlations lower the noise spectrum in a given frequency range. As a result, signal transmission in this frequency range has considerably less noise than would be predicted from pure Poisson firing. Thus even with as little as 100 neurons in a population signals can be transmitted rapidly and with a low noise level.

7 Discussion

The dynamics of populations of neurons has been studied by several researchers [2, 5, 14, 15, 9, 10, 16, 17, 18, 19]. The present theory aims at understanding the population dynamics from the unified point of view of an integral equation valid for renewal-type point processes [20, 13] in the limit of $N \to \infty$. Signal transmission via the population activity is a 'rate' code where the rate is defined by a spatial rather than a temporal average. Even though it is a rate code, computation by pools of spiking neurons can be fast [14, 21, 22, 8].

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