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# Predicting spike train responses of neuron models

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**Abstract.** It is shown how neural spike train responses can be predicted by truncated Wiener series and by LN-cascade models. To prove the capability of these methods we test them on spike trains which have been generated by model neurons. The agreement of the approximated responses and the neuron response to known stimuli is analysed quantitatively by calculating least mean square errors and rates of coincidences.

## 1. Introduction

Essential properties of neural networks are results of the interaction of neurons. In biological systems this interaction is performed by means of action potentials. The ability to predict the occurrence of spikes is necessary to investigate the neural code and communication.

Wiener [7] has developed a general method to represent nonlinear systems. Adapting this technique to the circumstances of spiking neurons allows the description of impulse responses.

Here we identify truncated Wiener series which represent the spike train responses calculated with the Hodgkin-Huxley equations [2]. When these series are determined, estimated responses to new stimuli can be computed and compared with the output of the neuron.

Quantitative analyses of the model neuron with this method show that the appearance of most of the action potentials can be predicted in the range of 2 $ms$. The results are compared with approximations by means of LN-cascade models [4].

The Hodgkin-Huxley model is close to natural neurons. Therefore the results will probably hold for biological systems, too.

## 2. Representation of nonlinear systems

### Wiener theory

As Wiener has shown for a nonlinear system $S$ which processes a stationary Gaussian white noise input $x(t)$ with zero mean and variance $\sigma^2 = \langle x(t)\, x(t)\rangle$,

the output signal $y(t)$ can be written as

$$y(t) = \sum_{n=0}^{\infty} G_n[h_n; x(t)], \tag{1}$$

where $\{G_n[h_n; x(t)]\}$ is a complete set of orthogonal functionals [7]. $\{h_n\}$ is the set of Wiener kernels which characterize the system $S$. The functionals are orthogonal in the sense that the time average

$$\overline{G_n[h_n, x(t)]\, G_m[h_m, x(t)]} = 0, \qquad n \neq m. \tag{2}$$

The leading functionals for a causal system $S$ are

$$G_0 = h_0 \tag{3}$$

$$G_1 = \int_0^{\infty} h_1(\tau) x(t-\tau)\, d\tau \tag{4}$$

$$G_2 = \int_0^{\infty}\int_0^{\infty} h_2(\tau_1, \tau_2) x(t-\tau_1) x(t-\tau_2) - \sigma^2 h_2(\tau_1, \tau_2)\delta(\tau_1 - \tau_2) d\tau_1 d\tau_2. \tag{5}$$

Under well defined conditions the Wiener kernels of an unknown system can be identified by crosscorrelating the input $x(t)$ and output $y(t)$ [5, 6]. The first kernels are determined by

$$h_0 = \overline{y(t)} \tag{6}$$

$$\sigma^2\, h_1(\tau) = \overline{y(t)\, x(t-\tau)} \tag{7}$$

$$2\,\sigma^4\, h_2(\tau_1, \tau_2) = \overline{y(t)\, x(t-\tau_1) x(t-\tau_2)} - \sigma^2\, h_0\, \delta(\tau_1 - \tau_2). \tag{8}$$

### Cascade models

Expanding the input $x(t)$ by a complete set of orthogonal functions $\{\Phi_k(\tau)\}$ allows to describe the output $y(t)$ of the nonlinear system $S$ by the functional

$$y(t) = F[c_0(t), c_1(t), \ldots], \tag{9}$$

where the $\{c_k\}$ satisfy $c_k(t) = \int_0^{\infty} x(t-\tau)\Phi_k(\tau)\, d\tau$. Assuming that the nonlinear behavior depends on a weighted sum of the coefficients only instantaneously, the output may be written as

$$y(t) = f\left(\sum_{k=0}^{\infty} \gamma_k\, c_k(t)\right) = f\left(\int_0^{\infty} g(\tau)\, x(t-\tau)\, d\tau\right). \tag{10}$$

This equation describes a cascade of a dynamic linear device (L) followed by an instantaneous nonlinear device (N).

The LN-cascade model is less universal than the Wiener series expansion. The simplification from eq. 9 to eq. 10 allows the representation of only a smaller class of nonlinear systems. Consequently the output $y(t)$ of a system $S$

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characterized by a Wiener series cannot be represented in general by a LN-cascade. The function $g(\tau)$ is computed as

$$g(\tau) = h_1(\tau) \tag{11}$$

by minimizing the mean square error $\overline{[y(t) - y_C(t)]^2}$ where $y_C$ is the output of the LN-cascade. The nonlinear function $f$ has to be chosen by minimizing the above error, too. The identification of cascade models is described in detail by Korenberg [4] and Hunter and Korenberg [3].

# 3. The Hodgkin-Huxley model neuron

We use the Hodgkin-Huxley model [2] to generate spike train responses which are analysed with the above mentioned techniques. The fundamental equation describing the membrane potential $V$ is

$$C_m \frac{dV}{dt} = -F + I(t), \tag{12}$$

where $C_m$ is the membrane capacity, $F$ the membrane current and $I$ the sum of external currents. The capacity is typically $C_m = 1\ \mu F/cm^2$ per membrane area. The membrane current is the sum of potassium, sodium and leaky currents described by

$$F(V, m, h, n) = g_K\, n^4\, (V - V_K) + g_{Na}\, h\, m^3\, (V - V_{Na}) + g_L\, (V - V_L) \tag{13}$$

where the conductivities run as follows $g_K = 36\ mS/cm^2$, $g_{Na} = 120\ mS/cm^2$ and $g_L = 0.3\ mS/cm^2$ and the potentials are $V_K = -77\ mV$, $V_{Na} = 50\ mV$ and $V_L = -54.402\ mV$. Each of $m$, $h$ and $n$ satisfies the differential equation

$$\frac{d\{m,h,n\}}{dt} = \alpha_{\{m,h,n\}}(1 - \{m,h,n\}) - \beta_{\{m,h,n\}}\{m,h,n\}. \tag{14}$$

The six functions $\alpha_{\{m,h,n\}}(V)$ and $\beta_{\{m,h,n\}}(V)$ which have been determined by fitting them to experimental data are [1, 2]

$$\alpha_m = \frac{0.1(V+40)}{1 - \exp\{-0.1(V+40)\}} \qquad \beta_m = 4\exp\{-0.0556(V+65)\} \tag{15}$$

$$\alpha_h = 0.07\exp\{-0.05(V+65)\} \qquad \beta_h = \frac{1}{1+\exp\{-0.1(V+35)\}} \tag{16}$$

$$\alpha_n = \frac{0.01(V+55)}{1 - \exp\{-0.1(V+55)\}} \qquad \beta_n = 0.125\exp\{-0.0125(V+65)\} \tag{17}$$

wherein the membrane potential $V$ has to be measured in $mV$.

This model describes the release and shape of action potentials. When stimulated by appropriate currents $I(t)$ the response is a spike train.

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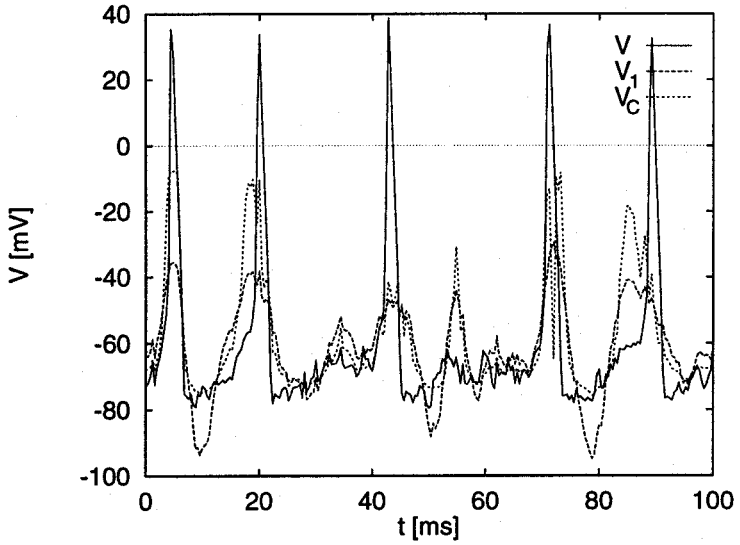


Figure 1: Response of the HH Model ($V$) and predictions by a truncated Wiener series ($V_1$) and a LN-cascade ($V_C$)

# 4. Predicting responses of the model neuron

The prediction of impulse responses generated by the Hodgkin-Huxley model requires the identification of the Wiener kernels. For that reason the system is evoked by a Gaussian white noise current which is determined by $\langle I \rangle = 0$ and $\langle I^2 \rangle = 49\ \mu^2 A^2/cm^4$.

Simulations of 1000 $s$ duration are used to calculate the Wiener kernels $h_0$, $h_1$ and $h_2$ by means of the equations 6 through 8. Previously the input current $I(t)$ and output potential $V(t)$ are sampled in steps of 0.4 $ms$. Following eq. 1 and 3 through 5 the output of the model neuron is estimated by the truncated Wiener series

$$V_1(t) = h_0 + \int_0^\infty h_1(\tau) I(t-\tau)\, d\tau \tag{18}$$

and

$$\begin{aligned} V_2(t) &= V_1(t) - \langle I^2 \rangle \int_0^\infty h_2(\tau,\tau)\, d\tau \\ &\quad + \int_0^\infty \int_0^\infty h_2(\tau_1,\tau_2) I(t-\tau_1) I(t-\tau_2)\, d\tau_1 d\tau_2. \end{aligned} \tag{19}$$

Additionally the response is approximated by the LN-cascade model using eq. 10 and 11. The nonlinear function $f$ in eq. 10 is determined by

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$f(z(t)) = \sum_{k=0}^{7} a_k\, z^k(t)$ wherein $z(t)$ satisfies $z(t) = \int_0^\infty h_1(\tau) I(t-\tau)\, d\tau$. The coefficients $\{a_k\}$ are chosen by minimizing the error

$$E = \int [V(t) - f(z(t))]^2\, dt, \tag{20}$$

Polynomials of degree higher than 7 do not reduce the error further.

Figure 1 shows responses to a Gaussian white noise stimulus which was not part of the identification procedure. Therein $V(t)$ is the response of the Hodgkin-Huxley model neuron and $V_1(t)$ and $V_C(t)$ are the estimated responses calculated by the truncated Wiener series and by the LN-cascade respectively. The potentials $V$ and $V_C$ show a similar response to the input current. The approximation by $V_2$ (not shown) is qualitative equivalent to $V_C$. Both are capable to describe action potentials whereas $V_1$ does not include the spikes.

For more evidence quantitative analysis is necessary. At first the least mean square error $\int [V(t) - V_{Approx}(t)]^2 dt$ is calculated for each approximation $V_1$, $V_2$ and $V_C$ by integrating over 4 $s$. The errors are measured in relative units of the reference error defined as $\int [V(t) - \langle V \rangle]^2\, dt$.

Furthermore, the rate of coincidences from spikes generated by the model neuron and spikes predicted by the approximations is a point of interest. The time an action potential occurs is determined by the time the potential reaches a threshold $\Theta$. If the difference of times of the events in the original and approximated response is smaller than 2 $ms$ these spikes are assumed to coincide. The threshold $\Theta$ is chosen by maximizing

$$C = \frac{2\, N_{CI}}{N_{HH} + N_{Approx}} - \frac{N_{HH}\, N_{Approx}}{K\, (N_{HH} + N_{Approx})} \tag{21}$$

where $N_{CI}$ is the number of coincidences, $N_{HH}$ the number of action potentials generated by the Hodgkin-Huxley model, $N_{Approx}$ the number of spikes described by the approximation and $K$ the number of bins which is determined by the interval of coincidence. Therefore $C$ is the relative number of coincidences without coincidences by chance. Its value is calculated by averaging the result of 6 realizations each of 0.9 $s$ duration.

The following table shows the errors and coincidences for all estimation methods.

| approximation | threshold $\theta$ | coincidence $C$ | LMS error |
|---|---|---|---|
| $V_2$ | $-44\ mV$ | 0.68 | 0.59 |
| $V_1$ | $-48\ mV$ | 0.61 | 0.73 |
| $V_C$ | $-49\ mV$ | 0.61 | 0.64 |

As expected the error of the estimation by $V_2$ is smaller than the error of $V_1$. The approximation by the LN-cascade model has to allow a better prediction than $V_1$ which was confirmed by the errors. But the cascade is obviously not able to describe all nonlinear effects which are better taken into account by the truncated Wiener series $V_2$. All the errors seem to be large but bearing in mind that a spike is a rare event the approximation by the average potential $\langle V \rangle$ will result in a small reference error which is the measure for all other errors.

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The rate of coincidences of the spikes predicted by the different approximation techniques and the spikes generated by the Hodgkin-Huxley model is very high. Nearly 70 % of the action potentials coincide if the estimation by $V_2$ is used. The coincidences predictable by $V_1$ are surprisingly good which could be explained by the knowledge that the membrane potential may be approximated by linear differential equations if the potential is close to the resting potential. The LN-cascade leads nearly to the same rate of coincidence as $V_1$ which is a consequence of the added threshold. The action potentials are assumed to coincide when placed within only 2 $ms$. If a broader time window is used the number of coincidences would increase further which is supported by fig. 1.

# 5. Conclusion

Predicting spike responses of deterministic model neurons is in principle possible by means of the infinite Wiener series. The approximation of the Hodgkin-Huxley model by truncated Wiener series results in good estimations of the impulse output. As shown in the previous sections the occurrence of most of the spikes can be determined within 2 $ms$. The considered cascade model seems to be not much more profitable than the approximation by the simplest estimation by Wiener series. Particularly the rates of coincidences are equivalent in both models whereas the shape of spikes is better realized by the LN-cascade.

The knowledge of only $h_1$ and $h_0$ makes it possible to determine 60% of the action potentials which is important for the application to biological systems where the time to look at input and output signals is limited and therefore higher Wiener kernels cannot be calculated from the data.

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