# Noise and the response of Hodgkin-Huxley-type neurons [*]

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Feb. 1, 2001

## 1 Introduction

We have previously shown how stochastic background synaptic input (synaptic noise) affects the PSTH response of an integrate-and-fire neuron to an input pulse (Herrmann & Gerstner, 1999, 2000a, 2000b). However, the integrate-and-fire neuron is highly unrealistic. Does noise have the same effect on more realistic neurons? In this paper, we apply the same methods to study the effect of noise on the response of Hodgkin-Huxley neurons. We compare predicted responses using our model with simulations of the Hodgkin-Huxley model. The results demonstrate the feasibility of the method in the above-threshold regime.

## 2 Methods

### 2.1 Neuron model: The spike-response model

The spike-response model for a point neuron (Gerstner, 1995, 1999, 2000) includes a membrane potential $u$, a threshold potential $\vartheta$, a response kernel $\varepsilon$, and a refractory function $\eta$. When $u$ reaches the threshold from below, a spike is emitted. The response kernel $\varepsilon(t - \hat{t}, s)$ describes the linear response of the membrane; the input potential resulting from a current $I(t)$ is

$$h(t|\hat{t}) = \int_0^\infty \varepsilon(t - \hat{t}, s)I(t - s)ds. \tag{1}$$

The refractory function $\eta(t - \hat{t})$ is added to the membrane potential following each spike, generating the afterhyperpotential. Thus

$$u(t) = \eta(t - \hat{t}) + h(t|\hat{t}) \tag{2}$$

where $\hat{t}$ is the last firing time of the neuron.

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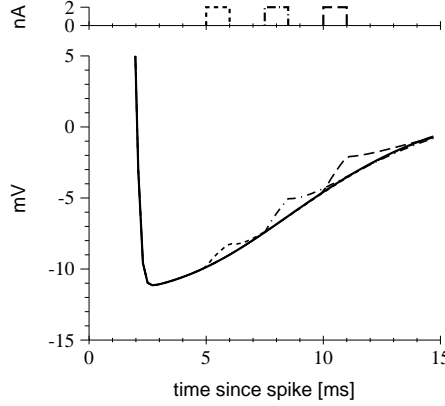
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Figure 1: Measurement of the kernels to fit the spike-response model to the Hodgkin-Huxley model. Top, pulses are applied at different delays after the spike. Bottom, the perturbed trajectories are measured. The solid curve is the reference trajectory of the membrane potential following a spike triggered by a threshold crossing at $t = 0$. Shown are three examples of perturbed trajectories, caused by square pulses applied at $t = 5$ ms (short dashes), $t = 7.5$ ms (dot-dashes), and $t = 10$ ms (long dashes). The size of the perturbation depends on the delay since the spike. After Kistler et al, 1997.

The well-known Hodgkin-Huxley equations for action potential generation (Hodgkin & Huxley, 1952) are highly nonlinear and cannot easily be analyzed. Fortunately, Kistler, Gerstner, and van Hemmen (1997) have developed a way to derive kernels of the spike-response model from the Hodgkin-Huxley equations based on Volterra kernels. The neuron model they obtained using the first-order approximation, herein called SRM-HH, produces the same three modes of response as the Hodgkin-Huxley equations, a similar $f - I$ curve, and matches the timing of about 90 percent of the spikes of a Hodgkin-Huxley neuron to within 2 ms (Kistler et al., 1997). In this paper, we use the SRM-HH neuron to predict the effect of stochastic background synaptic input (synaptic noise) on the PSTH response of a Hodgkin-Huxley neuron to an input pulse.

## 2.2   Determination of the kernels

The kernels can be determined numerically (Kistler et al., 1997) by applying test signals consisting of two short current pulses of duration $\delta t$ at times $t_1$ and $t_2$, superimposed on a constant current level $I_0$: $I_{\text{test}}^{c_1,c_2}(t) = I_0 + c_1\Delta(t - t_1) + c_2\Delta(t - t_2)$. The Hodgkin-Huxley response $u[I(t)]$ is then measured and the kernels are found from on the perturbation in the trajectory (Kistler et al., 1997).

The values of $\vartheta$ and $\delta$ are optimized to match the timing of individual spikes; Kistler et al. (1997) found that the optimal threshold was $\vartheta = 4.7$ mV. Here we use the values they give as best matching the gain function of the Hodgkin-Huxley neuron, $\delta = 2.15$ ms and $\vartheta = 9$ mV, in order to better match the baseline level of the PSTH. Fig. 2 shows examples of kernels $\eta$ and $\epsilon$.
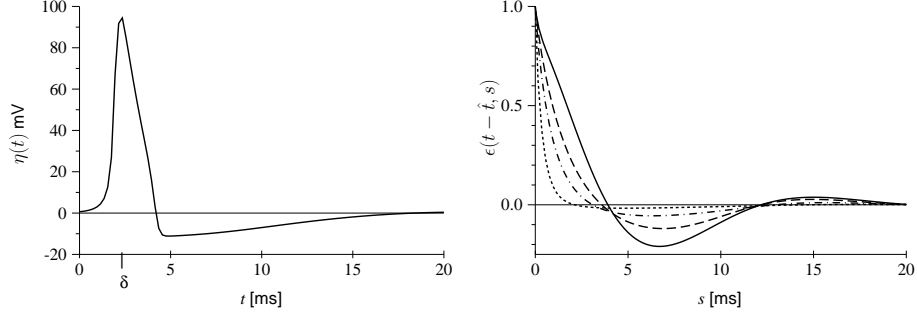
Figure 2: Kernels of the SRM-HH model calculated using the parameters in Kistler et al. (1997). **Left**, the kernel $\eta$ describes the shape of the spike and its afterpotential. There is a delay $\delta$ between the time of the threshold crossing at $t = 0$ and the maximum of the action potential. **Right**, the kernel $\epsilon$ describes the membrane response to the input (i.e., the postsynaptic potential if the input is a synaptic current). Immediately after the spike, the response is weak; it recovers with increasing $t - \hat{t}$. Solid curve, the kernel for $t - \hat{t} = \infty$; long-dashed curve, $t - \hat{t} = 10$ ms; dot-dashed curve, $t - \hat{t} = 7.5$ ms; dotted curve, $t - \hat{t} = 5$ ms.

## 2.3  Noise model

We added noise to the model using escape-rate noise (Plesser & Gerstner, 2000; Herrmann & Gerstner, 1999, 2000a) rather than diffusive noise. Supposing that the probability of a spike at time $t$ depends on the distance between the membrane potential and the threshold, we introduce an escape rate function $f$ which depends on the membrane potential $u$ and its derivative. Therefore the firing probability density given $h(t|\hat{t})$ and $\hat{t}$ (Plesser & Gerstner, 2000), $\rho_h(t|\hat{t})$, is:

$$\rho_h(t|\hat{t}) = f\left[u(t); \dot{u}(t)\right] \tag{3}$$

where $u(t) = \eta(t - \hat{t}) + h(t|\hat{t})$. We chose the escape-rate function (Herrmann & Gerstner, 2000a)

$$f(u - \theta) = w\left(\frac{1}{\tau} + 2u'H[u']\right)\frac{G(u - \theta, \sigma_u)}{\mathrm{Erfc}(\frac{u-\theta}{\sqrt{2}\sigma_u})} \tag{4}$$

where $u' = (du/dt)$ evaluated at $t$, $G(\mu, \sigma)$ is the Gaussian of width $\sigma$ centered on $\mu$, $\mathrm{Erfc}(x) = 1 - \mathrm{Erf}(x)$ is the complementary error function, and $w$ is a constant whose optimal value was been determined to be $w = 1.21$ in Herrmann and Gerstner (2000a).

## 2.4  Determining the PSTH

The theory in (Gerstner, 1995, 2000) describes the population-averaged activity $A(t)$ of a large, homogeneous, randomly initialized population of $N$ neurons, or, alternatively, the PSTH resulting from $N$ trials independently applied to a single randomly initialized neuron. By calculating $A(t)$ we can predict the PSTH of the SRM-HH neuron. $A(t)$ is defined as (Gerstner, 1995, 2000)

$$A(t) = \lim_{\Delta t \to 0}\frac{1}{\Delta t}\frac{n_{\mathrm{act}}(t; t + \Delta t)}{N} \tag{5}$$
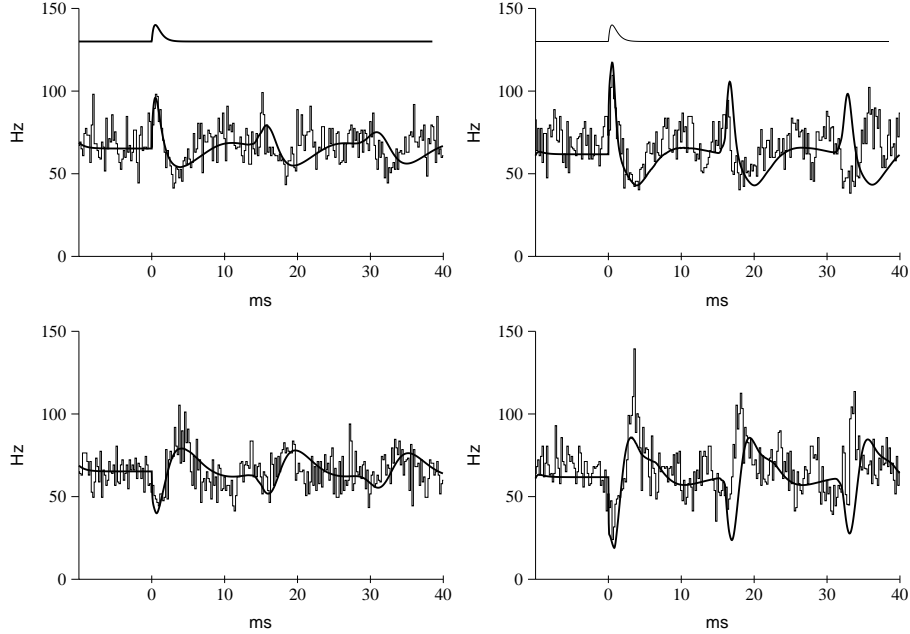
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Figure 3: Hodgkin-Huxley neuron with diffusive noise. Thin stepped lines, PSTHs obtained from simulations in which Poisson-distributed positive (top row) or negative (bottom row) current pulse stimuli were applied to the neuron superimposed on a 2 nA/cm$^2$ current step with the final current level being $I_0 = 10$ nA/cm$^2$. Thick curve: predicted PSTH response calculated by numerically integrating Eq. 6 using the kernels of the SRM-HH neuron. Left column, noise power level 2 nA$^2$/cm$^4$; right column, noise power level 0.1 nA$^2$/cm$^4$.

where $n_{\text{act}}(t; t + \Delta t)$ is the number of neurons that emitted a spike between $t$ and $t + \Delta t$. The activity dynamics are given in terms of the input $h$ and the previous firing times $\hat{t}$ in the following integral equation:

$$A(t) = \int_{-\infty}^{t} P_h(t|\hat{t})A(\hat{t})d\hat{t} \tag{6}$$

where $P_h(t|\hat{t})$ describes a neuron's firing probability density at time $t$, given that it last fired at $\hat{t}$ and that the input is $h(t|\hat{t})$. With escape noise, we have from renewal theory $P_h(t|\hat{t}) = \rho_h(t|\hat{t}) \exp\left(-\int_{\hat{t}}^{t} \rho_h(t'|\hat{t})dt'\right)$.

## 3 Results

Eq. 6, which is nonlinear, gives the exact response in the limit $N \to \infty$ and may be evaluated numerically. An algorithm for calculating the response for the integrate-and-fire neuron is given in (Herrmann & Gerstner, 2000a). We found the algorithm could be applied with only slight modifications to predict the PSTH of the SRM-HH model. For the time constant in the Gaussian-ISI escape rate function defined in Eq. 4 we used the value of $\tau = 1$ ms obtained
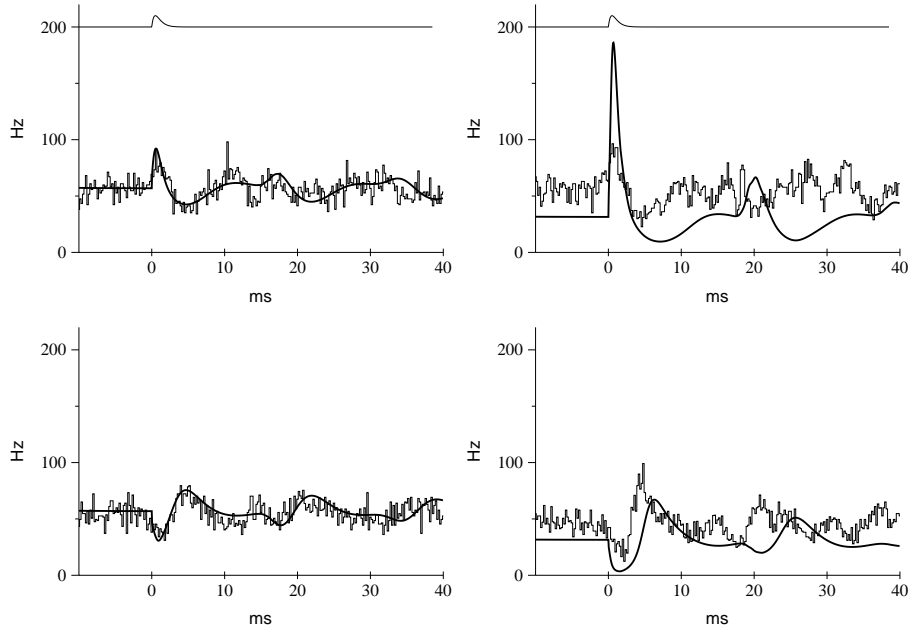
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Figure 4: Hodgkin-Huxley neuron with diffusive noise. As in the previous figure, except with $I_0 = 8$ nA/cm$^2$.

in Kistler et al. (1997) (integrate-and-fire model optimised to Hodgkin-Huxley firing times).

Note that in discretizing the SRM-HH model, we cannot eliminate the $\hat{t}$ dependence of the $\epsilon$-kernel as in the SRM-IF model. Therefore, the above method can be quite compute-intensive if the time step is very small and the kernel convolution window is long. The window length is related to the activity level, which depends on the noise level and drive level for a given value of the threshold. Because of these limitations it was impractical to use this method to predict the PSTH when the baseline activity was less than about 50 Hz.

We compared the PSTH responses predicted using the above method with those measured from simulations of the Hodgkin-Huxley model with diffusive noise. In the simulations, a 2-nA current step resulting in the final drive level $I_0$ was applied. Superimposed on this current was a Poisson-distributed train of 1-nA $\alpha$-pulse stimuli delivered at a mean rate of 50 Hz.

Figs. 3 and 4 show PSTH responses from the simulations, together with responses predicted for the SRM-HH model with the Gaussian-ISI noise model. Good agreement is seen when the drive level is clearly above threshold ($I_0 = 10$ nA/cm$^2$, Fig. 3). The amplitude of the primary peak and the asymmetry of responses to positive and negative pulses are accurately modeled. However, when the drive level is reduced to $I_0 = 8$ nA/cm$^2$, the SRM-HH model is below threshold. Consequently it predicts a much higher peak together with a much lower mean firing rate than in the simulations (cf. Fig. 4).

In this brief exploration we have shown that the SRM-HH model (Kistler et al., 1997) can be used with the theory of (Herrmann & Gerstner, 2000a) to study numerically the effect of background synaptic input on the PSTH of

Hodgkin-Huxley-like neurons. Although the model defined by Kistler et al. (1997) was devised for the subthreshold regime, we see that with our noise model it can be used to predict above-threshold responses as well. The same threshold value cannot, however, be used in both regimes.

# References

Gerstner, W. (1995). Time structure of the activity in neural network models. *Phys. Rev. E*, *51*(1), 738–758.

Gerstner, W. (1999). A framework for spiking neuron models - the spike response method. In van Hemmen, J. L. (Ed.), *Models of Neural Networks 4*. Springer-Verlag, New York.

Gerstner, W. (2000). Population dynamics of spiking neurons: Fast transients, asynchronous states and locking. *Neural Computation*, *12*, 43–89.

Herrmann, A., & Gerstner, W. (1999). Understanding the PSTH response to synaptic input. In Willshaw, D., & Murray, A. (Eds.), *ICANN'99. Ninth International Conference on Artificial Neural Networks*, Vol. 2, pp. 1012–1016 London. The Institution of Electrical Engineers.

Herrmann, A., & Gerstner, W. (2000a). Noise and the PSTH response to current transients: I. General theory and application to the integrate-and-fire neuron. *J. Comp. Neurosci.*, *submitted*.

Herrmann, A., & Gerstner, W. (2000b). Noise and the PSTH response to current transients: II. Integrate-and-fire model with slow recovery and application to motoneuron data. *J. Comp. Neurosci.*, *submitted*.

Hodgkin, A. L., & Huxley, A. F. (1952). A quantitative description of ion currents and its applications to conduction and excitation in nerve membranes.. *J. Physiol. (London)*, *117*, 500–544.

Kistler, W. M., Gerstner, W., & van Hemmen, J. L. (1997). Reduction of Hodgkin-Huxley equations to a single-variable threshold model. *Neural Comput.*, *9*, 1015–1045.

Plesser, H. E., & Gerstner, W. (2000). Noise in integrate-and-fire neurons: From stochastic input to escape rates. *Neural Computation*, *12*, 367–384.