Maximal Information Transfer in a Spiking Neuron

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1 A neuron's bit rate

Consider a spiking neuron which communicates information only by the timing of its spikes. The information is thus encoded entirely in the train of inter-spike intervals, $s_1, s_2, \ldots$ A neuron cannot spike twice in an arbitrarily short period of time; instead there is a refractory period $\Delta > 0$ following a spike during which the neuron is quiescent. Therefore the inter-spike intervals are bounded below by $s_i \geq \Delta$.

Assuming that the neuron's code is not redundant, the joint probability distribution of the inter-spike intervals will factorize, $p(s_1, s_2, \ldots, s_n) = p_1(s_1)\, p_2(s_2) \cdots p_n(s_n)$. Assuming constant statistical properties of the signal, we have $p_i(s) = p_j(s) \equiv p(s)$.

In a physical system there must be some jitter in the spike times, so let the inter-spike intervals be corrupted by additive Gaussian noise with variance σ^2. The entropy of this noise is thus $H[\text{noise}] = \frac{1}{2} \ln 2\pi e \sigma^2$.

The probability density of finding an inter-spike interval s if one picks a random point in time is $q(s) = s\, p(s) / \langle s \rangle_s$, where $\langle f(s) \rangle_s = \int_0^\infty p(s)\, f(s)\, ds$ is the expectation over inter-spike intervals. Therefore the expectation in time of a function of the inter-spike interval is $\langle f(s) \rangle_t = \int q(s)\, f(s)\, ds = \langle s f(s) \rangle_s / \langle s \rangle_s$.

Assuming that the jitter in inter-spike intervals is much less than the refractory period, $\sigma \ll \Delta$, the amount of information encoded by a particular inter-spike interval s is $i(s) = -\ln p(s) - H[\text{noise}]$. The time taken to transmit it is of course s, so for the duration of the inter-spike interval s, the neuron's bit rate is $i(s)/s$. Taking the expectation of this in time

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gives the average amount of information flowing down the channel per unit time,

$$J[p(s)] = \left\langle \frac{i(s)}{s} \right\rangle_t = \frac{\langle i(s) \rangle_s}{\langle s \rangle_s} \tag{1}$$

2 Maximizing a neuron's bit rate

We now ask: what is the distribution $p(s)$ that maximizes the neuron's bit rate? To answer this question we will first consider distributions $p(s)$ with a given mean inter-spike interval $\langle s \rangle_s = \overline{s}$ and find the maximum of the functional $J[p(s)]$. Given that resulting distribution we then maximize $J(\overline{s})$ with respect to $\overline{s}$. Introducing the normalization condition $\int_\Delta^\infty p(s)\,ds = 1$ and the mean inter-spike interval as side conditions with Lagrange multipliers λ_0 and λ_1 respectively, we get the new functional

$$\int_\Delta^\infty \left\{ \ln p(s) + \tfrac{1}{2} \ln 2\pi e \sigma^2 + \lambda_1 s + \lambda_0 \right\} p(s)\,ds$$

The Euler-Lagrange equation is then

$$\ln p(s) + 1 + \tfrac{1}{2} \ln 2\pi e \sigma^2 + \lambda_1 s + \lambda_0 = 0$$

which, together with the normalization condition, gives

$$p(s) = \begin{cases} t < \Delta & 0 \\ t \geq \Delta & \tau^{-1} \exp -\frac{s-\Delta}{\tau} \end{cases} \tag{2}$$

and the obvious relation $\overline{s} = \Delta + \tau$. With this the information transfer rate is $J(\overline{s}) = (\ln(\overline{s} - \Delta) + 1 - \frac{1}{2} \ln 2\pi e \sigma^2)/\overline{s}$. The maximum is given in terms of the refractory period and the optimal time constant τ^* by,

$$\frac{\Delta}{\sigma} = \frac{\tau^*}{\sigma} (\ln \frac{\tau^*}{\sigma} - \frac{1}{2} \ln (2\pi e)) \tag{3}$$

The density of inter-spike intervals $p(s)$ is an exponential distribution with a "front porch" of the length of the refractory period and a time constant τ. The relation between this optimal time constant τ^* and the refractory period Δ is shown graphically in figure 1.

Rather than simply maximizing its bit rate, a neuron might also reduce the average number of spikes produced per second, since each spike consumes energy. Minimizing the expected number of spikes per second is equivalent to maximizing the expected inter-spike interval $E[s] = \int_\Delta^\infty s\, p(s)\,ds$. Introducing this constrain with a constant of proportionality α which trades off the importance of these two goals, does not change the calculation leading to the exponential distribution 2. The subsequent optimazation leads now as expected to an increased optimal time constant τ^{**},

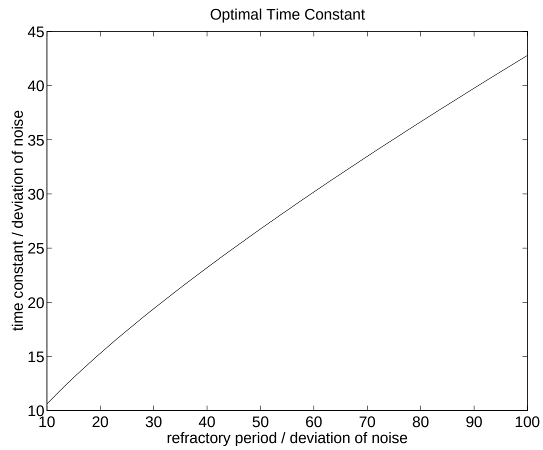

Figure 1: Optimal time constant τ^* of exponential distribution as a function of the refractory period Δ measured in multiples of noise deviation σ.

$$\frac{\Delta}{\tau^{**}} = \ln \frac{\tau^{**}}{\sigma} - \frac{1}{2} \ln (2\pi e) - \alpha \left(\frac{\tau^{**}}{\sigma} + \frac{\Delta}{\sigma} \right)^2 \tag{4}$$

These theoretical prediction relating the parameters of the distribution of inter-spike intervals to physiological characteristics of the neurons might be compared with experiments.

3 Comparison to Binary Coding

A conventional clocked binary code would have a clock, and at each tick of the clock it would either send a pulse or not. Because of the refractory period, the fastest the clock could tick is with a period of Δ. Therefore, ignoring any errors, the channel is being used to transmit Δ^{-1} bits/sec.

In contrast, the variable-ISI code yields a maximum bit rate of $1/(\tau^* \ln 2)$. So the relation between maximum information transfer rate J_{isi} with inter-spike interval coding versus the rate J_{bin} with binary coding is given by,

$$\frac{J_{isi}}{J_{bin}} = \frac{\Delta}{\tau^* \ln 2} = \frac{1}{\ln 2} (\ln \frac{\tau^*}{\sigma} - \frac{1}{2} \ln (2\pi e)) \tag{5}$$

where we used equation 3 that gives the optimal time constant. Figure 2 shows this relation graphically.

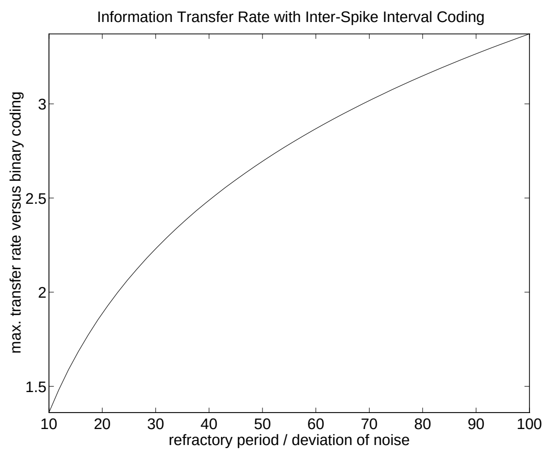

Figure 2: Maximum bit rate with inter-spike interval coding versus binary codinging.

Typical for neurons, say $\Delta = 5$ msec and $\sigma = 0.2$ msec, so we transmit about 2 times as many bits/sec.