Model neurons

The rate code

Suggested reading:

- Chapter 7.1 - 7.2 in Dayan, P. & Abbott, L., Theoretical Neuroscience, MIT Press, 2001.

Model neurons: The rate code

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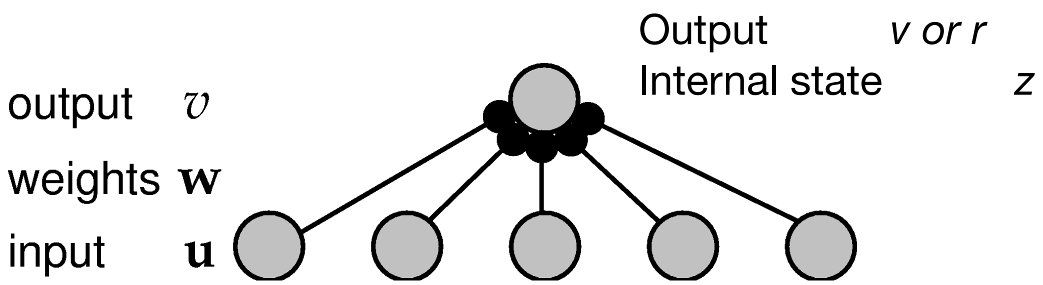
Simple model of a neuron:



Can we derive such a simple model from the knowledge we have about signal transmission in spiking neurons?

Firing-rate model

To construct a firing-rate model, we must determine how the firing rate of a neuron is related to the firing rates of the inputs that drive it.

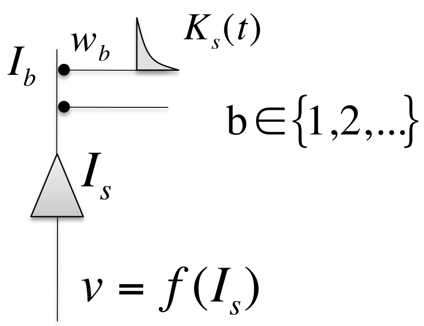
The firing-rate response curves of neurons are typically measured by injecting current into the soma of a neuron.

We therefore model the relationship between input and output firing rates by computing the total current delivered by synaptic inputs into the soma (I_s), and then computing the postsynaptic firing rate from this synaptic current.

I_b : postsynaptic current

I_s : current at the soma

The synaptic kernel, $K_s(t=0)$ describes the time course of the synaptic current in response to a presynaptic spike.



Firing-rate model

Presynaptic action potential at a synapse *b* leads to a current generated in the soma of the postsynaptic neuron:

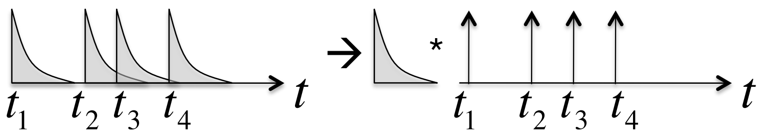
$$I_b(t) = w_b K_s(t)$$

The amplitude and sign of the synaptic current is described by the synaptic weight w_b.

Assuming that the spikes at a single synapse act independently, the total synaptic current for terminal *b* at time *t* due to a sequence of presynaptic spikes occurring at times t_i is given by

$$I_b(t) = w_b \sum_{t_i < t} K_s(t - t_i) = w_b \int_{-\infty}^{t} d\tau K_s(t-\tau)\rho_b(\tau)$$

$$\rho_b(\tau) = \sum_i \delta(\tau - t_i)$$



Firing-rate model

Assuming that there is no interaction between different terminals, the contributions of the different synapses sum linearly, and so the total synaptic current coming from all presynaptic inputs is

$$I_s = \sum_b w_b \int_{-\infty}^{t} d\tau K_s(t-\tau)\rho_b(\tau)$$

A critical assumption in the construction of firing-rate models is that we can replace the neural response function by the firing rate of the neuron.

$$I_s = \sum_b w_b \int_{-\infty}^{t} d\tau K_s(t-\tau)u_b(\tau)$$

Firing-rate model

$$\rho_b(\tau) \approx u_b(\tau)$$

<u>Justification: the large number of inputs</u>

If we sum over many synapses, the mean typically grows linearly with the number of synapses, while the standard deviation of the synaptic current grows only as the square root of the number of synapses. Thus, ignoring spike train variability at each synapse, may have a neglible effect on the total synaptic current. This assumption is equivalent to the mean-field approximation used in physics. It requires a form of central limit theorem to hold for the inputs and is invalidated if the inputs to a neuron are strongly correlated. This can occur, for example, if significant numbers of input spikes occur synchronously.

Firing-rate model

$$I_s = \sum_b w_b \int_{-\infty}^{t} d\tau K_s(t-\tau) u_b(\tau)$$

with $$K_s(t) = \frac{e^{-\frac{t}{\tau_s}}}{\tau_s}$$

K describes the temporal evolution of the synaptic current due to both synaptic conductance and dendritic cable effects.

$$\tau_s \frac{dI_s}{dt} = -I_s + \sum_b w_b u_b$$

The above equation determines the synaptic current entering the soma of a post-synaptic neuron in terms of the firing rates of the presynaptic neurons.

Firing-rate model

To finish formulating a firing-rate model, we must determine the postsynaptic firing rate from our knowledge of I_s.

For constant synaptic current, the firing rate of the postsynaptic neuron can be expressed as

$$v = f(I_s)$$

f - steady-state firing rate as a function of somatic input current.
- activation function

f - sigmoid function
- threshold function $f(I_s) = [I_s - \gamma]_+$

$$v = f(I_s) \qquad \tau_s \frac{dI_s}{dt} = -I_s + \sum_b w_b u_b$$

Firing-rate model

In the general case we obtain two ODE's. The membrane capacitance and resistance somehow implements a low-pass filter. In (A) we assume that the firing rate follows changes in the synaptic current instantaneously.

$$\tau_s \frac{dI_s}{dt} = -I_s + \sum_b w_b u_b \qquad \tau_r \frac{dv}{dt} = -v + f(I_s)$$

A If $\tau_r \ll \tau_s$

$$v = f(I_s)$$

$$\tau_s \frac{dI_s}{dt} = -I_s + \sum_b w_b u_b$$

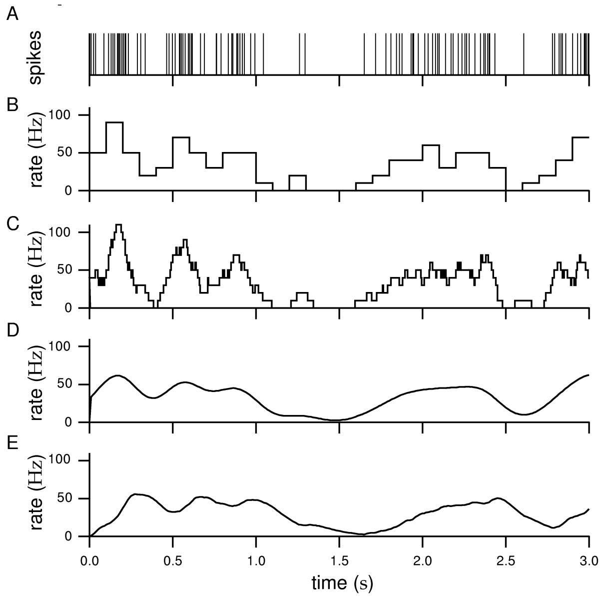
B If $\tau_s \ll \tau_r$

$$\tau_r \frac{dv}{dt} = -v + f(I_s)$$

$$I_s = \sum_b w_b u_b$$

Rate code

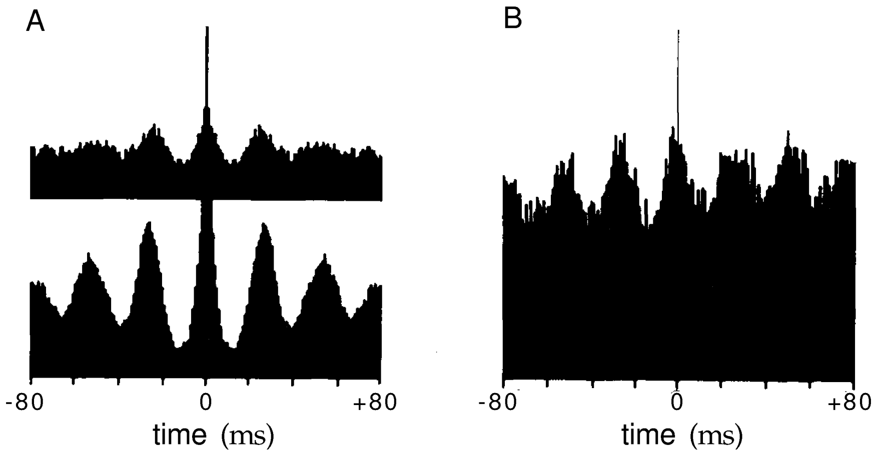
Regardles of the transmission by action potentials the information lies in the average firing rate. The rate code assumes an independent-spike code, that is, the generation of each spike is independent of all the other spikes in the



Firing rates approximated by different procedures.

Correlation code

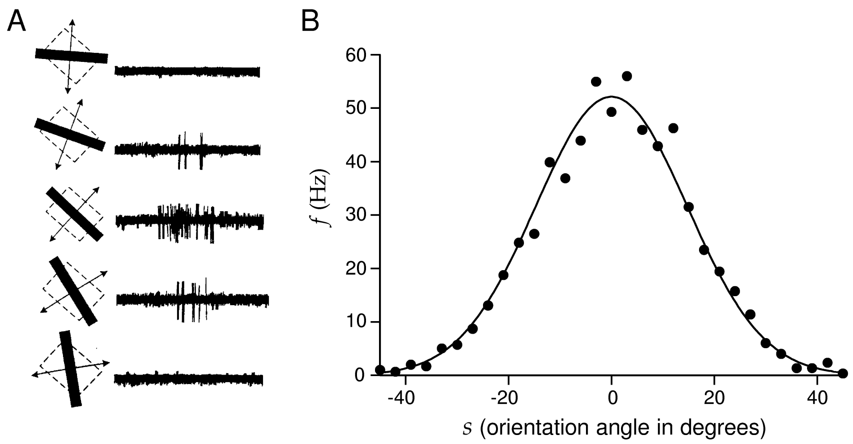
This code assumes that correlations between spike times carry additional information, e.g. synchrony and oscillations.



Autocorrelation and cross-correlation histograms for neurons in the primary visual cortex of a cat. A) Autocorrelation histograms for neurons recorded in the right (upper) and left (lower) hemispheres show a periodic pattern indicating oscillations at about 40 Hz. The lower diagram indicates stronger oscillations in the left hemisphere. B) The cross-correlation histogram for these two neurons shows that their oscillation are synchronized with little time delay.

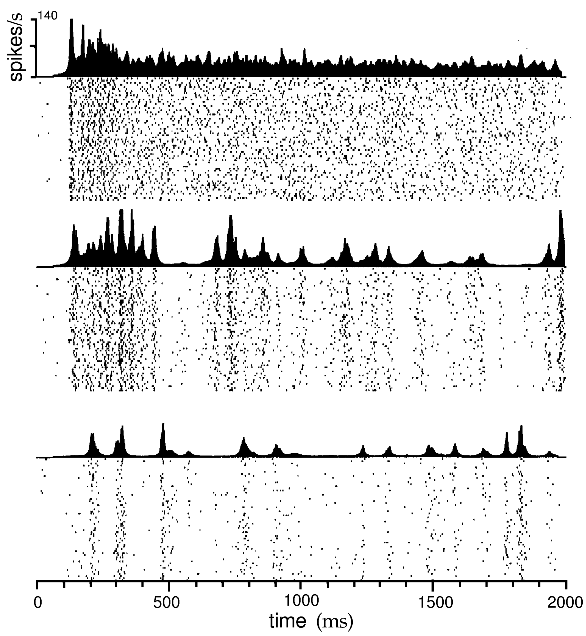
Population code

The population code suggests that information is typically encoded by neuronal populations. The analysis of population coding is easiest if the response of each neuron is considered statistically independent, and such independent-neuron coding is typically assumed. The independent-neuron hypothesis means that the cell responses can be combined without taking correlations into account.



Temporal code

When precise spike timing or high-frequency firing-rate fluctuations are found to carry information, the neural code is often identified as a temporal code.



Appendix: Model neurons

The delta function

The delta function

Despite its name, the Dirac δ function is not a properly defined function, but rather the limit of a sequence of functions. In this limit, the δ function approaches zero everywhere except where its argument is zero, and there it grows without bound. The infinite height and infinitesimal width of this function are matched so that its integral is one. Thus,

$$\int dt\, \delta(t) = 1$$

provided only that the limits of integration surround the point t = 0 (otherwise the integral is zero). The integral of the product of a δ function with any continuous function f is

$$\int dt'\, \delta(t - t') f(t') = f(t)$$

for any value of t contained within the integration interval (if t is not within this interval, the integral is zero). These two identities normally