Firing Rate Models with Feedback and Attractors

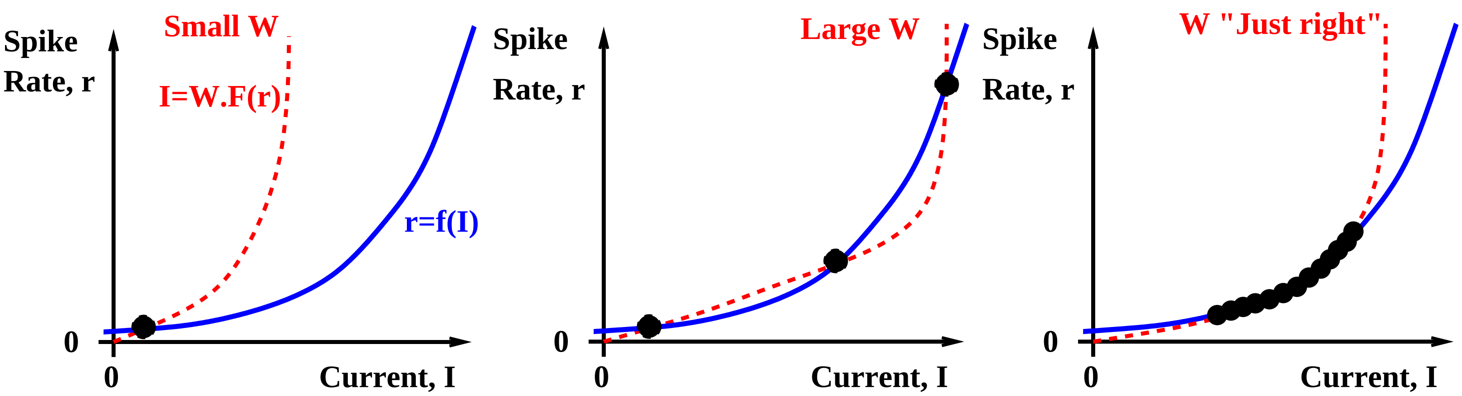
Recall that the average rate, r of a single group of neurons and the average current, I, vary in a firing rate model according to:

$$\tau_r \frac{dr}{dt} = -r + f(\{I\}) \qquad \tau_s \frac{dI}{dt} = -I + W.F(r) \tag{1}$$

where $f(I)$ is the steady-state firing rate as a function of current input and $W.F(r)$ is the total feedback current given an average firing rate, r, since W represents the product of number of synapses and their average synaptic strength.

Fixed points of the system where $dr/dt = 0$ and $dI/dt = 0$ require $r = f(I)$ and $I = W.F(r)$. These two equations describe curves that can be plotted. Where the two curves cross is where both equations are true and there is no change in rate or current.

The following 3 curves have differnet levels of feedback, W. On the left small W (only a low firing rate stable state) on the right much larger W leads to two stable states (the middle one is unstable). Note that the larger W means following the red-dashed curve, more current for a given firing rate. The final curve suggests that if the feedback strenght (and offsets/thresholds) are just right then the two curves can cross along a line, suggesting a series even continuum of stable points. This is what is needed for perfectly graded memory or an integrator.



The fine-tuning problem

Assume the simplest possible firing rate model, where the steady-state firing rate is threshold-linear in the current, and the feedback current is proportional to the firing rate:

$$\tau_r dr/dt = -r + [WI - I_{th}]_+ \qquad ; \qquad \tau_s dI/dt = -I + r. \tag{2}$$

If $\tau_s << \tau_r$ we can assume the current, I changes quickly to follow the rate, r and write from the second equation: $I = r$. If we now look at the first equation and consider only when the rate is above threshold we have:

$$\tau_r dr/dt = -r + Wr - I_{th} = -r(1 - W) - I_{th} \tag{3}$$

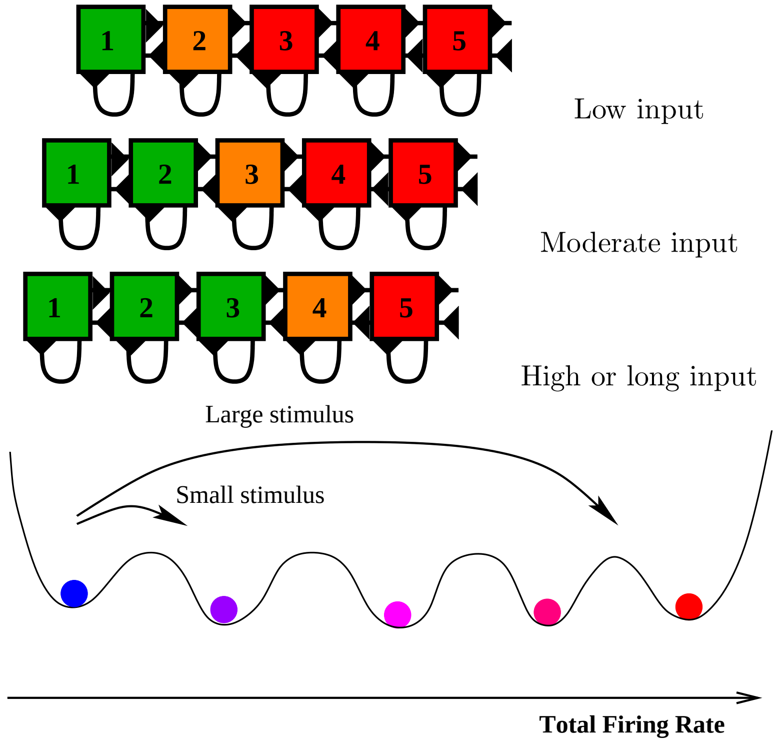
if I_{th} is positive this equation has one steady state, $r = -I_{th}/(1 - W)$ if $W > 1$ and must have $r = 0$ if $W < 1$. If I_{th} is negative it has the same stable solution, $r = -I_{th}/(1 - W)$ if $W < 1$ but rises indefinitely if $W \geq 1$. In the speacial case $I_{th} = 0$ we have:

$$dr/dt = (-r + Wr)/\tau_r = -r(1 - W)/\tau_r = -r/\tau_{eff} \tag{4}$$

where the effective time constant is $\tau_{eff} = \tau_r/(1 - W)$. So if W is only slightly less than one, the rate approaches zero very slowly with a long time constant. At precisely $W = 1$ the rate does not change and we have a continuum of stable states (a line attractor) that is also an integrator.

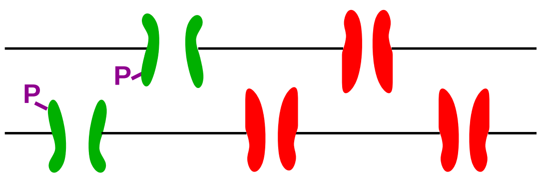
Discrete Integrators

Many bistable groups can be used to form a discrete integrator. Advantages: less fine tuning; more robust to noise.



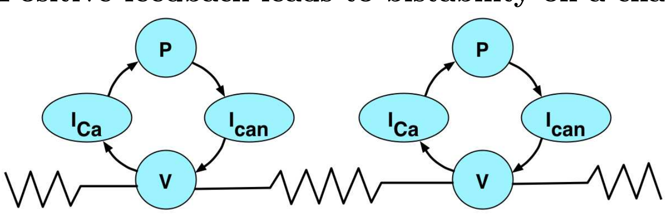
In practice: to make a discrete integrator from bistable pools of neurons with recurrent excitation, each group of neurons would show large jumps in firing rate (not seen in the data). More likely: discrete states arise within a single neuron.

Single Cell Multistability



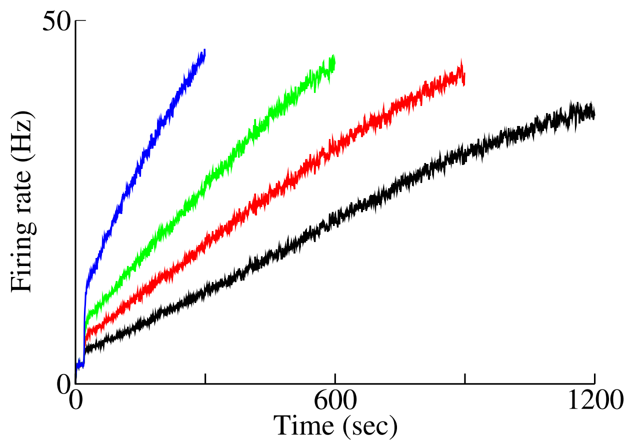
Section of dendrite with bistable I_{can} channels.
Ca-activated non-specific cation channels and Ca-channels in dendrites.
Ca-dependent phosphorylation increases the conductance of cation channels.
Phosphorylated channels (green) have greater conductance.

Positive feedback leads to bistability on a channel-by-channel basis.



Random phosphorylation (P) of I_{can} channel increases I_{can}, which increases the membrane potential (V), increasing Ca^{2+} influx, which sustains phosphorylation. Coupling to nearby channels through increase of V and $[Ca^{2+}]$, raises their phosphorylation probability.

Trial-averaged firing rates appear as a continous ramp.



Different colors represent different applied currents to the neuron, increasing by a factor of 2 from black (lowest current = slowest ramping) through red and green to blue (highest current = fastest ramping). Data from average across 100 trials.