SIMPLIFIED MODELS OF INDIVIDUAL NEURONS

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Introduction

- Goal of the chapter: to develop a single cell model to ask functional questions, such as:
    - What time scale does the cell operate?
    - What operations can it carry out?
    - How good is it at encoding information?
- How do you develop this model cell?
    (1) completely neglect the dendritic tree.
    (2) replace conductance based description of spiking process (single ODE rather than coupled, nonlinear PDEs)
- What level of description allows us to retain the key properties of the system while removing nonessential elements from the problem?
- Types of whole cell models:
    - *Spike/pulse model*: generate discrete, all-or-none impulses. No information in spike width or height (series of delta functions).
    - *Firing rate model*: output is a continuous firing rate.

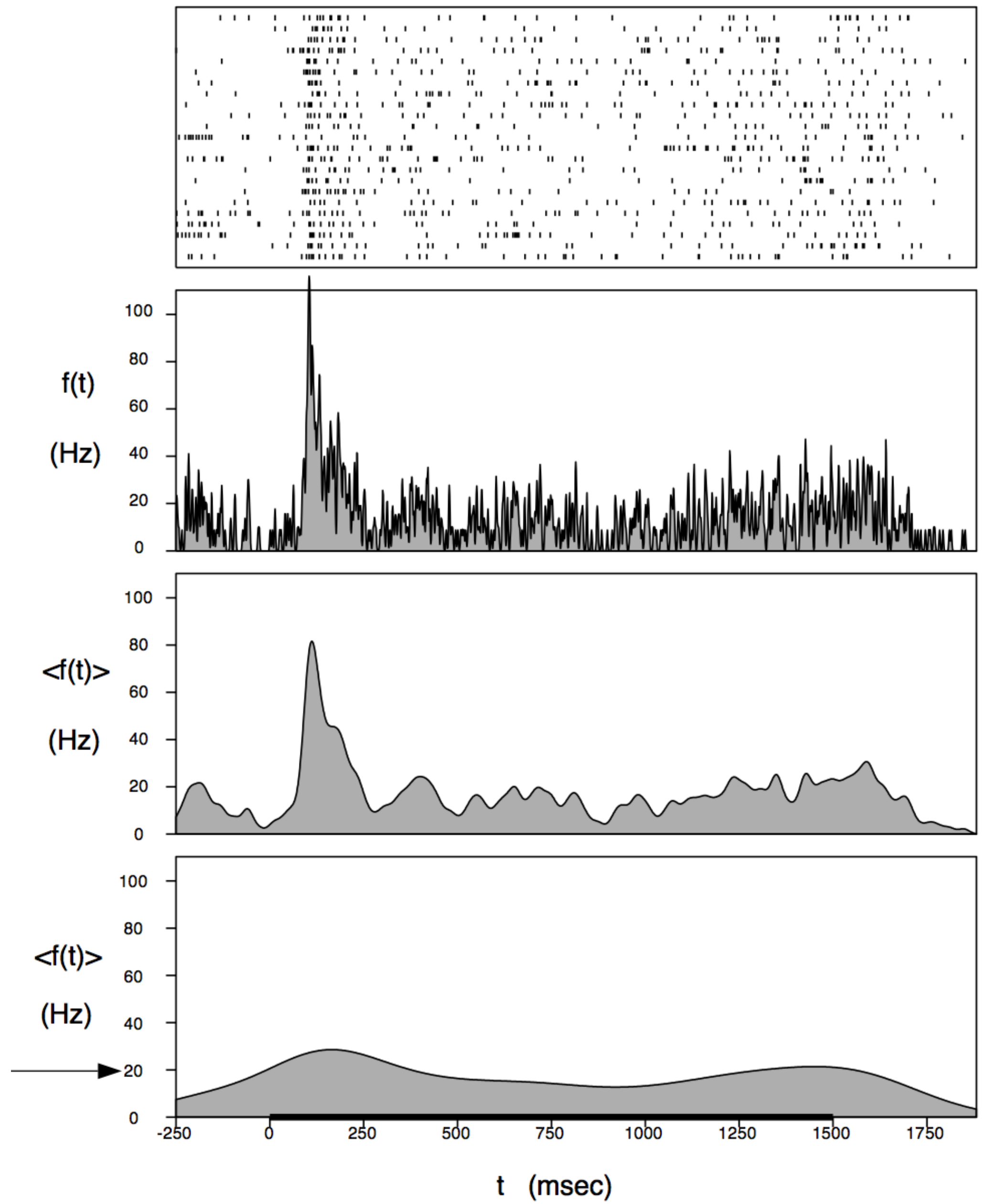
What is the firing rate?

Instantaneous firing rate *f(t)* – obtained by averaging the spiking response of a single neuron to multiple presentations of the same stimulus.

Usually the temporal average firing rate, $\langle f(t) \rangle$ is used due to the stochastic nature of neuronal response.

Claim: in many instances $\langle f(t) \rangle$ - averaged over a 5 to 10 msec time frame – appears to be a relevant code to transmit information.

→ mean rate is relevant code and detailed time course of spikes is not.



Integrate-and-fire models

Captures two key aspects of neuronal excitability:
(1) passive, integrating subthreshold domain.
(2) generation of stereotypical impulses once a threshold has been exceeded.

Retains timing information of individual action potentials.

Three types:
(1) The perfect or non-leaky integrate-and-fire unit (only capacitance)
(2) The leaky or forgetful integrate-and-fire unit (capacitance and resistance)
(3) The adapting integrate-and-fire unit

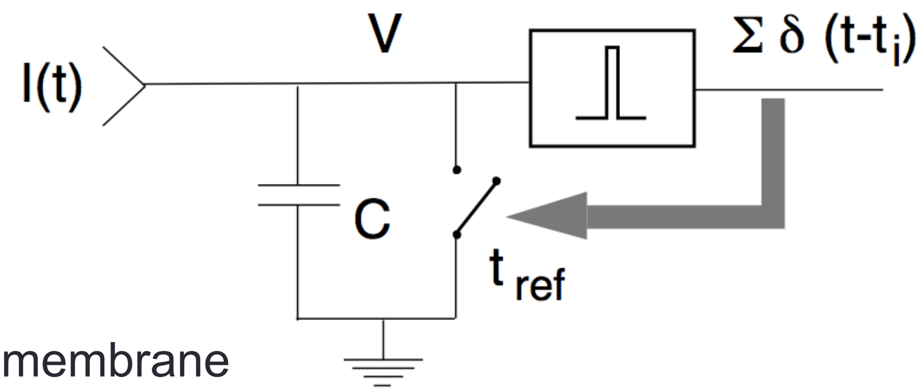
All three types accomplish spike generation with a voltage threshold V_{th}.

Whenever the membrane potential $V(t)$ reaches V_{th} a pulse is generated and the unit is short circuited.

For a duration t_{ref} following spike generation, any input $I(t)$ is shunted to ground (absolute refractory period).

The perfect integrate-and-fire unit

Voltage trajectory governed by first-order ODE:



$$C\frac{dV(t)}{dt} = I(t)$$

In response to a maintained current, membrane potential will charge up the capacitance until V_{th} is reached and V is reset to zero.

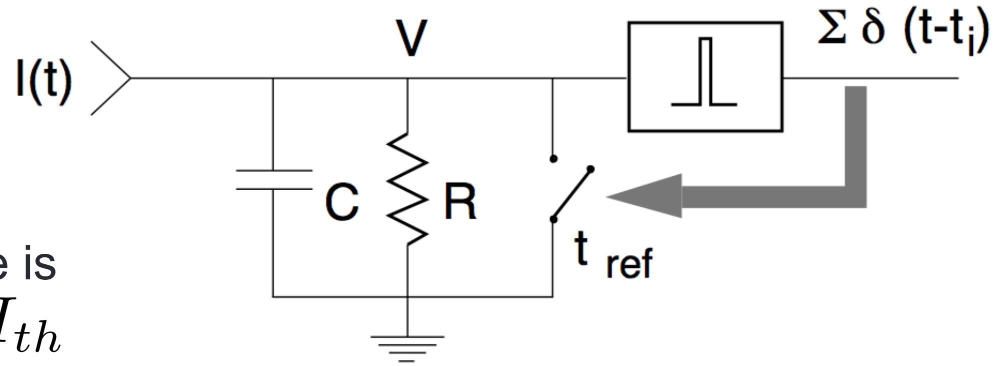
The relationship between the injected current step and average firing frequency is computed as the inverse of the interspike interval.

$$\langle f \rangle = \frac{I}{CV_{th} + t_{ref}I}$$

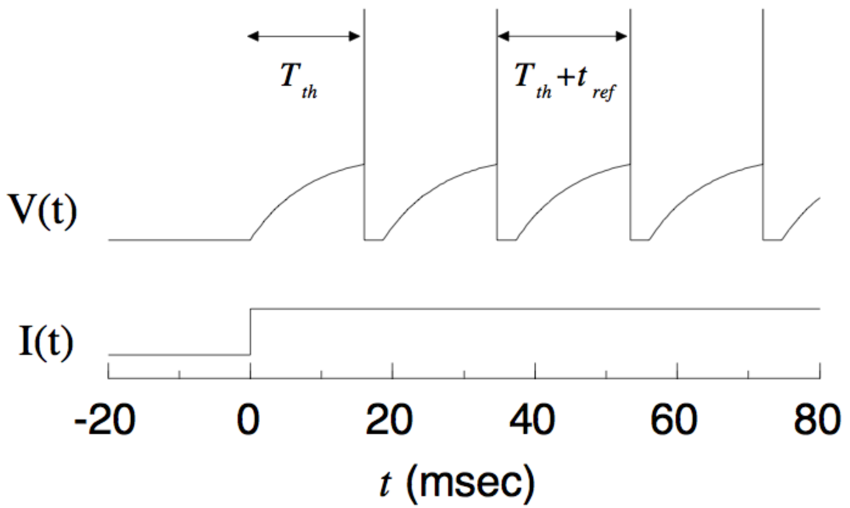
The output consists of a series of impulses, all of which are spaced at least t_{ref} apart.

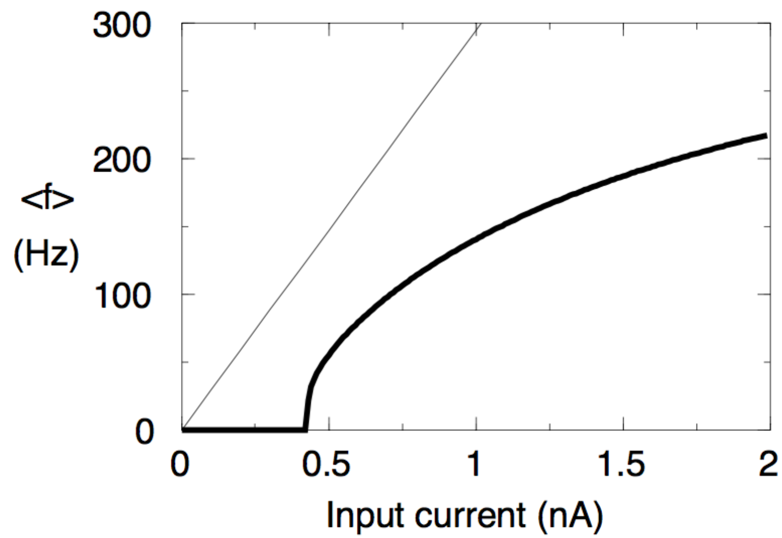
The leaky integrate-and-fire unit

$$\langle f \rangle = \frac{1}{T_{th} + t_{ref}} = \frac{1}{t_{ref} - \tau \log(1 - \frac{\mathrm{V_{th}}}{\mathrm{IR}})}$$

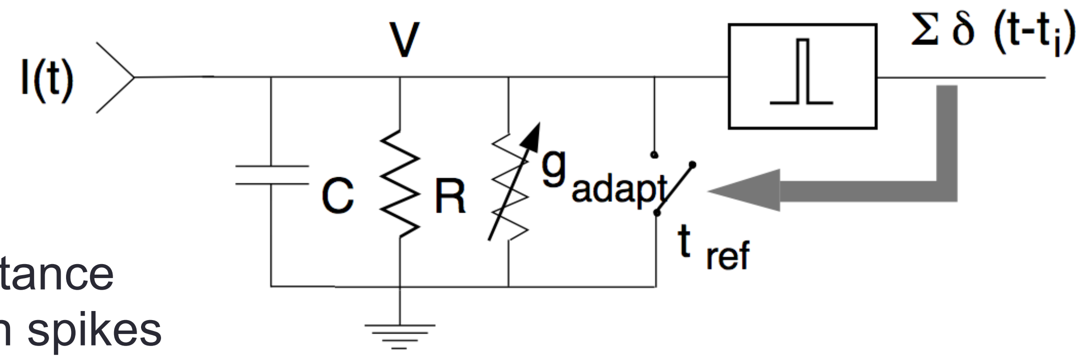


Where T_{th} is the time an output impulse is generated for any current I larger than I_{th}





Other variants

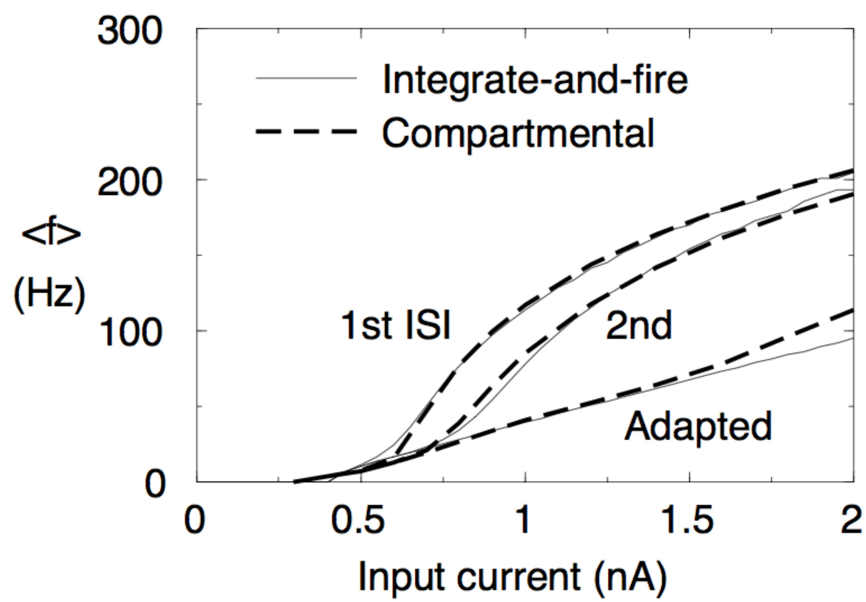


Introduction of time-dependent shunting conductance g_{adapt}. Each spike increases this conductance by a fixed amount G_{inc} . Between spikes g_{adapt} decreases exponentially with a time constant τ_{adapt} to zero.

In the subthreshold domain, this unit is described by

$$C\frac{dV}{dt} = -\frac{V(1 + Rg_{adapt})}{R} + I$$

$$\tau_{adapt}\frac{dg_{adapt}}{dt} = -g_{adapt}$$

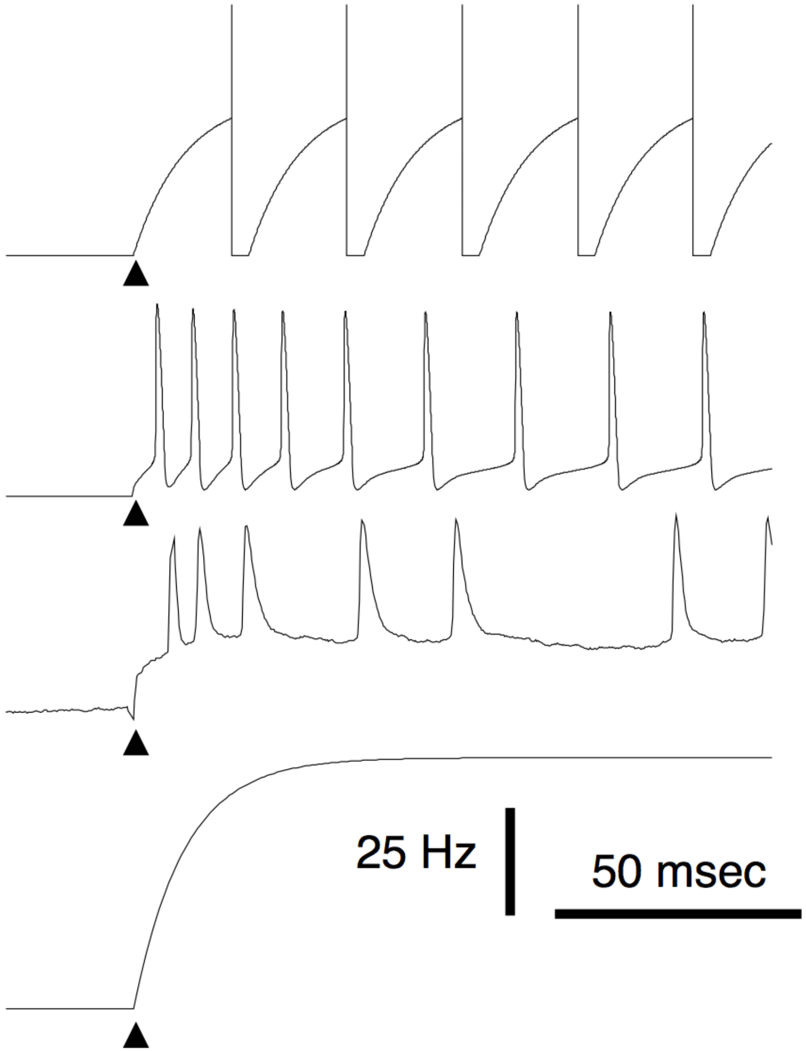


Response time of integrate-and-fire units

When a spiking, non-adapting membrane receives a sustained suprathreshold current, membrane potential never reaches equilibrium but moves along a limit cycle.

A step change in current requires *integrate-and-fire* neurons to converge to its limit cycle by the end of the first interspike interval after change.

Adaptation – still reach maximum firing rate by the first interspike interval.

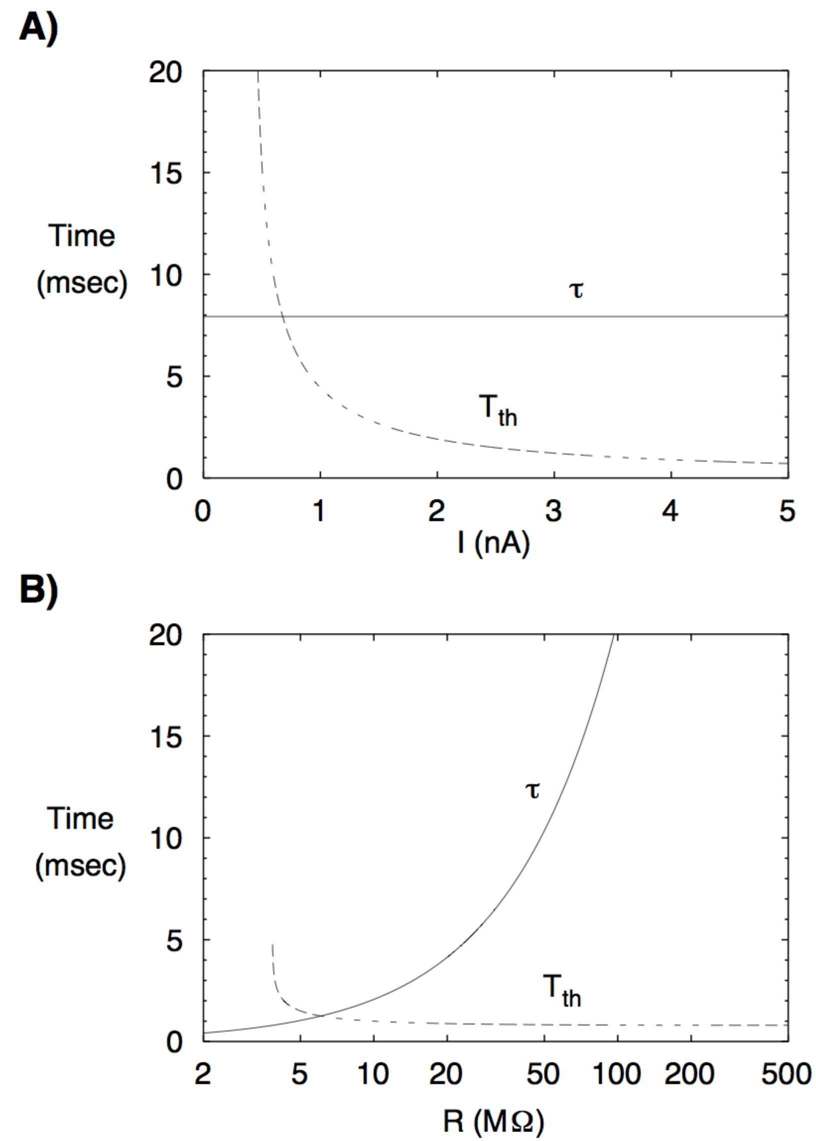


Integrate-and-fire units can respond much faster than τ

As amplitude of injected current increases, the unit can spike very rapidly.

As τ diverges, T_{th} converges to CV_{th}/I, the time it takes the voltage across a capacitance to reach V_{th}.

Dynamics of subthreshold domain do not carry over into the suprathreshold domain.

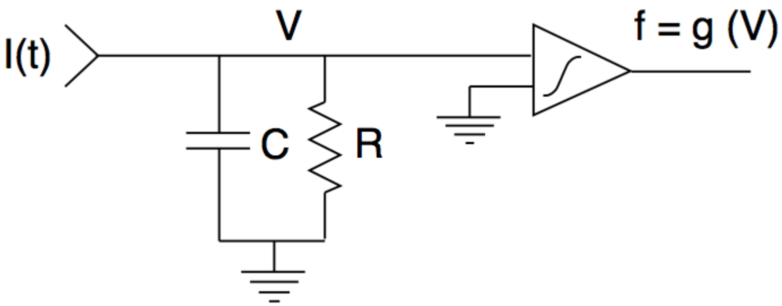


Firing rate models

Assume that it is only the average, or mean firing rate of a neuron that matters to postsynaptic targets.

Same dynamics as in leaky integrate-and-fire units

$$C\frac{dV(t)}{dt} = -\frac{V(t)}{R} + I(t)$$

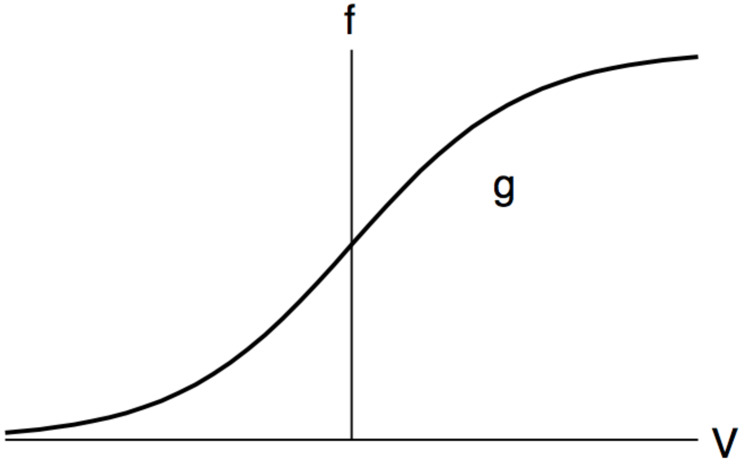


Instantaneous output is a continuous, non-linear function of $V(t)$,

$$f = g(V)$$

Monotonic increasing, positive, saturating function,

$$f = \frac{1}{1+e^{-2\beta V}}$$

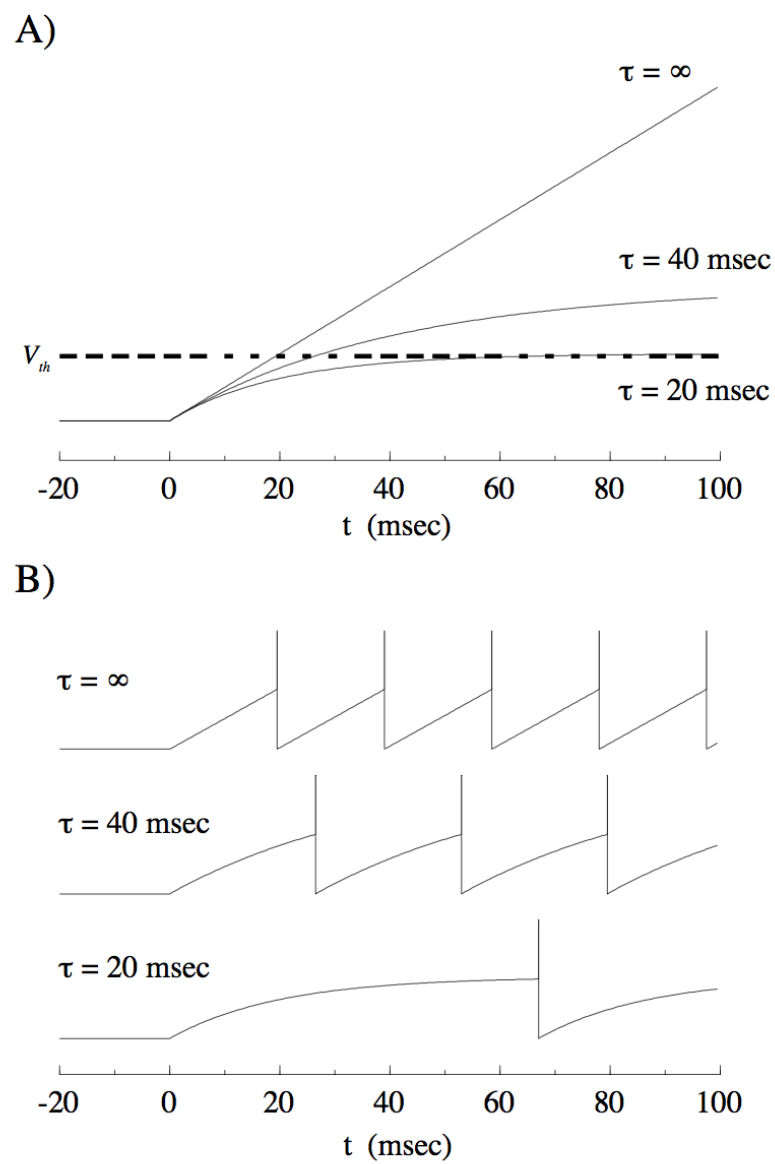


Response time in spiking and firing rate models

Effect of changing the membrane time-constant on (A) a non-spiking neuron and (B) an integrate-and-fire neuron.

Non-spiking neurons converge more slowly as the time constant increases.

In the extreme case of $\tau \to \infty$, the integrate-and-fire model converges to integrator model, while firing rate model does not approach an equilibrium.



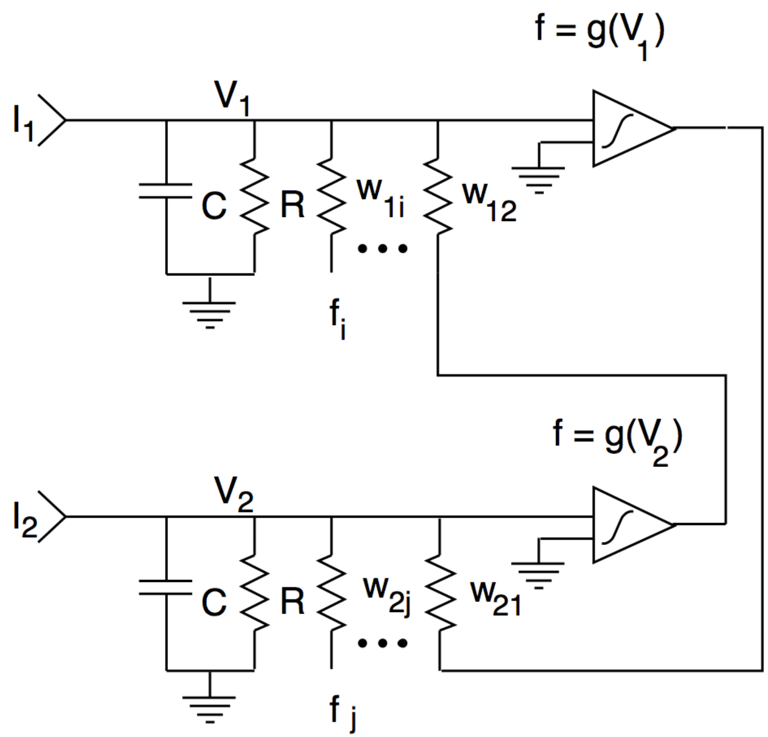
Neural Networks

Neurodynamics of a network is governed by a coupled system of single cell equations (mean rate model). For any cell *I* (out of *n* cells), it takes the form,

$$C\frac{dV_i(t)}{dt} = -\frac{V_i(t)}{R} + I_i + \sum_{j=1}^{n} w_{ij} f_j(t)$$

A change of δf_j in the firing activity of the *j*-th presynaptic neuron leads to a change $w_{ij}\delta f_j$ in the current delivered to the operational amplifier.

Synaptic inputs act as current sources.



What I didn’t cover . . .

Correlation coding (able to exploit exact temporal relationships among streams of action potentials).

- favor of coupling among pairs, triplets, or higher-order groupings of spikes.

Population coding → multiplicative interactions and neural networks

- previous section assumes neural networks are built on linearity of synaptic interactions.
- functions such as *sigma-pi* account for higher-order interactions.