Neurons and Neuroscience

1. Introduction
2. Neurobiology
3. Simple models of a single neuron
4. Systems with a few neurons
5. Silicon neurons
6. Event based control
7. Summary

Introduction

- A major challenge
- Golgi staining 1885
- Cajal 1911 Mapping of the neurons using Golgi staining
- McCulloch and Pitts 1943
- Wiener 1948 Cybernetics - Control and Communication in the Animal and the Machine
- Rosenblatt perceptron artificial neural networks 1957
- Detailed studies of animal behavior
- The Hodkin-Huxley Equations 1952
- Carver Mead 1989 neurons in silicon

A Major Challenge!

Explain some key functions such as

- Perception, how do we see and hear?
- Motor control, how to swim walk and fly?
- Short term memory
- Long term memory
- Emerging group behavior.

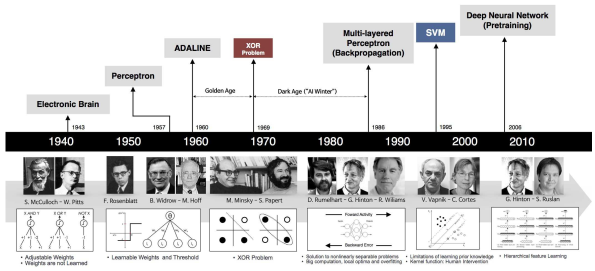
Technical and Biological Systems

- A recurrent theme
- Two driving forces: understand and imitate
- Cybernetics: Wiener 1948 and Ashby 1956
- Neural Systems: McCulloch Pitts 1943 and Rosenblatt 1957
- Adaptation and Learning: Early experiments 1955, theory, industrial use 1980
- Artificial Intelligence:
  - Dartmouth Conference 1956
  - Artificial neural networks
  - Deep learning
- Mind and Matter (Symbols versus Hardware)

Artificial Neural Networks

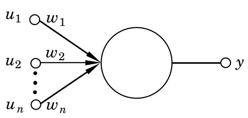
- The beginning: McCulloch and Pitts 1943, Hebb 1949
- First successes: Rosenblatt 1958 (The Perceptron), Widrow-Hoff 1961 (Adaline), the XOR problem
- Into the Doldrums
  - Minsky and Papert 1969
  - Survivors Andersson, Grossberg, Kohonen
- A Revival
  - Hopfield 1982
  - The Parallel Distributed Process Group
  - The Snowbird Conference
- Cult Status
  - Deep Learning - Image processing

Pictorial History of Neural Networks

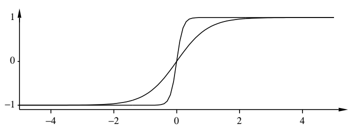


Artificial Neural Networks

$$y(t) = f\Big(\sum a_i u_i(t)\Big)$$



The sigmoid function



- A nonlinear function of several variables with learning
- Sorting, classification and optimization

Kolmogorov's Theorem 1957

Theorem: Any continuous real-valued functions $f(x_1, x_2, ..., x_n)$ defined for x_i in the range $[0, 1]$ can be represented in the form

$$f(x_1, x_2, ..., x_n) = \Sigma_{j=1}^{n} g_j \Big(\Sigma_{i=1}^{n} \phi_{ij}(x_j) \Big)$$

where g_j are properly chosen continuous functions of one variable, and ϕ_{ij} are continuous monotonically increasing functions.

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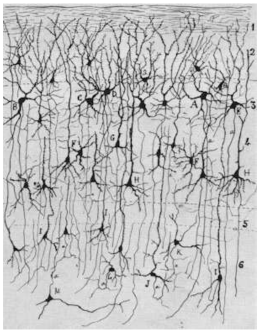
Golgi Staining

Golgi 1885 developed a model for selective staining which was a key to see the microstructure of the nervous system. Cajal made extensive use of Golgis technique in a book on the histology of the nervous system 1904

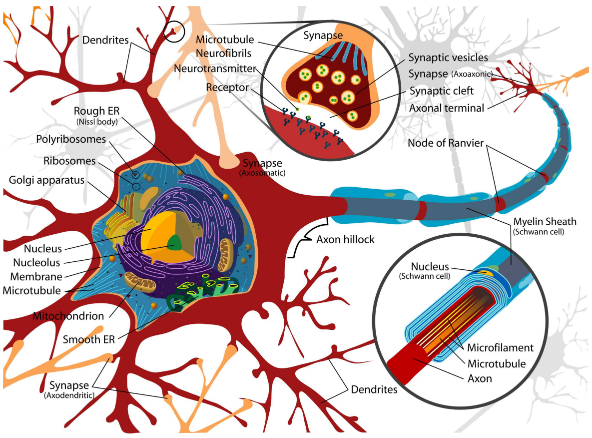


Neurobiology

- How many neurons are there?
  - 10^4 to 10^5 in simple nonvertebrates
  - 10^{11} in the human
- What do neuron look like?
  - Cell body (soma) 5-100 μ m
  - Dendrites 0.001 m
  - Axons 0.001-1 m
  - Synapse (contact point between neurons)
- Are neurons very different?
- How are neurons connected?
  - Synapses
- What goes on in a neuron?

Picture of a Neuron

Another Picture of a Neuron



A Family of Models

- Electro-chemistry of cell and membrane
- Electrical spike activity
- Simplified models for average spike rate
- Complexity (number of neurons)

Level	Number of Neurons	Describes
Molecular	Part of a neuron	Electro Chemistry
Ion Channel	Part of a neuron	Synapses
Action potential	1-10	Spike trains
Spike rate	1-100	Interaction
PET, NMR	$10^5 - 10^9$	Activated brain regions

Modeling a Neuron

- What happens at a synapse
  - Excitation by a spike
  - Opens ion channels (two types excitory or inhibitory)
  - Changes in post-synaptic potential
- Activity from several dendrites added in the cell body
- A pulse is generated when the potential exceeds a threshold
- The pulse travels along the axon and makes contact with other neurons at other synapses

An Ion Channel

The current is governed by Ohms law $I = g(V - E)$ where I is the ionic current across the nerve membrane, g is the conductance, V voltage difference across the membrane and E the equilibrium potential given by

$$E = \frac{RT}{zF} \log \frac{C_{out}}{C_{in}}$$

The post-synaptic voltage is given by

$$C\frac{dV}{dt} = g_l(E_l - V) + g_e(E_e - V) + g_i(E_i - V)$$

Leakage (l), exitatori (e) and inhibitory (i)

Modeling Post-synaptic Potential

$$C\frac{dV}{dt} = g_l(E_l - V) + g_e(E_e - V) + g_i(E_i - V)$$

where g_l and E_l are conductance and equilibrium potential for the leakage current, g_e and E_e refer to excitory ion channel and g_i and E_i refer to inhibitory ion channel. Typical values are $C = 12.5 \times 10^{-12}$, $g_l = 1$ nS, (nano Siemens) $E_l = E_i = -75mV$ and $E_e = 0$. This gives $g_l/C = 12500$. Using ms as the time unit and mV as the unit for voltages the equation can be written as

$$12.5\frac{dV}{dt} = -75 - V - \frac{g_e}{g_l}V + \frac{g_i}{g_l}(75 - V)$$

The Post-synaptic Potential

$$12.5\frac{dV}{dt} = -75 - V - \frac{g_e}{g_l}V + \frac{g_i}{g_l}(75 - V)$$

What happens if there is an excitory pulse $g_e = 2$ nS for 1 ms? When nothing happens $g_e = g_i = 0$ the equilibrium voltage is $V = -75$ mV. When excitation occurs ($g_e/g_l = 2$) the system is described by

$$12.5\frac{dV}{dt} = -75 - V - 2V = -75 - 3V, \quad \frac{dV}{dt} = -0.24V - 6$$

This equation has the solution

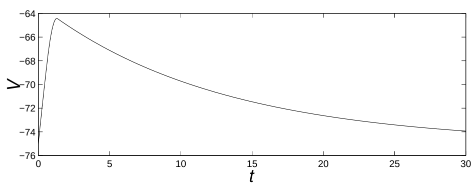
$$V(t) = -75e^{-0.24t} - 6\int_0^t e^{t-\tau}d\tau = -75e^{-0.24t} - \frac{6}{0.24}(1 - e^{-0.24t}$$
$$= -75e^{-0.24t} - 25(1 - e^{-0.24t}) = -50e^{-0.24t} - 25$$

The Post-synaptic Potential ...

For $t = 1$ we get $V = -64.3$. For $t \geq 1$ we have $g_e = 0$ and the voltage is given by

$$12.5\frac{dV}{dt} = -75 - V, \quad \frac{dV}{dt} = -0.08V - 6$$

$$V(t) = -64.3e^{-0.24(t1)} - 75(1 - e^{-0.08(t-1)})$$



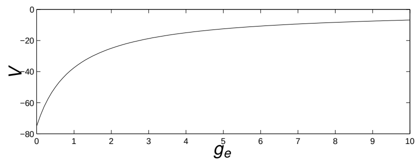
Notice Nonlinear Behavior

Consider the effect of an excitory input

$$C\frac{dV}{dt} = g_l(E_l - V) + g_e(E_e - V) + g_i(E_i - V)$$

Steady state response ($g_i = 0$)

$$V = \frac{g_l E_l + g_e E_e}{g_l + g_e} = -\frac{75}{1 + g_e}$$



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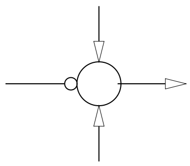
A Simple Neuron Model

As a first attempt at modeling neuron as a system with several inputs and one output. The input is the excitation which is the post-synaptic potential at the site for spike generation.

Inputs may be excitory, indicated by an arrow in the figure, or inhibitory, indicated by a circle in the figure. The output can be either excitory or inhibitory. The output is either spikes or the average spike rate.



A Static Model

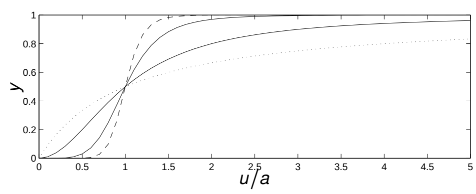
The static relation between input and output has a sigmoid shape which can be approximated by

$$y(u) = \begin{cases} \frac{ku^n}{a^n + u^n} & \text{if } u \geq 0 \\ 0 & \text{if } u < 0 \end{cases}$$

where k is a constant which gives the maximum spike rate and a a parameter that gives the input where the spike rate is half of the maximum value.
This function $y(u)$ is called the Nake-Rushton function. The same function has also been used in chemical kinetics and in population dynamics where it is called the Michaelis-Menton function.

Nake-Rushton Function

Normalized spike rate y/b as a function of normalized potential u/a, for $n = 1$ (dotted), n=2, n=5, and n=10 (dashed)



A Dynamic Model

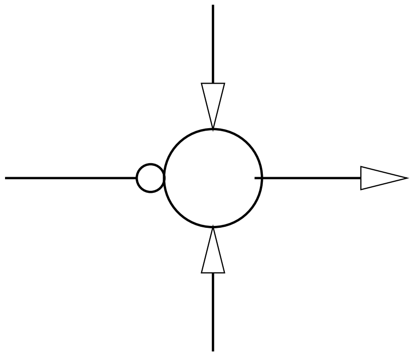
To obtain a dynamic model we must take into account that a change of the post-synaptic potential does not give an instantaneous change in spike rate. A simple model that captures this is

$$\frac{dy}{dt} = \frac{1}{T}(-y + f(u))$$

where f is the Naka-Rushton function. This model gives the steady state behavior $y = f(u)$ and dynamics is characterized by the time constant T which is in the range of ms.
This model can be considered as a static nonlinearity followed by a first order dynamics with time constant T. If we consider several inputs the model becomes

$$\frac{dy}{dt} = \frac{1}{T}(-y + f(\sum_k u_k))$$

Graphical Representation



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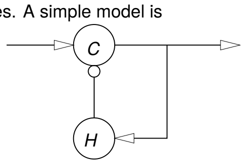
Simple Neural Systems

- Investigate simple systems obtained by combining neurons in different ways
- Negative feedback in the retina - a second order linear system
- Short term memory - a nonlinear second order system

Negative Feedback In the Retina

Cell structure: cones and horizontal cells. The cones are excited by light. The horizontal cells are excited by the cones. There is inhibitory feedback from the horizontal cells to the cones. A simple model is

$$T_c\frac{dC}{dt} = -C - kH + u$$
$$T_h\frac{dH}{dt} = -H + Ch$$

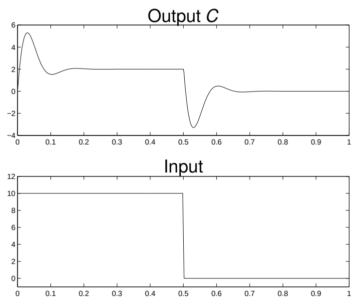


This model is in standard form with

$$\frac{dx}{dt} = \begin{pmatrix} -1/T_c & -k/T_c \\ 1/T_h & -1/T_h \end{pmatrix} x + \begin{pmatrix} 1/T_c \\ 0 \end{pmatrix}$$

Simulation

Using the values $T_c = 0.025$ $T_h = 0.08$, $k = 4$ we find



An Improved Model for Inhibition

Physiological evidence indicate that the nonlinear model model

$$T_1\frac{dx_1}{dt} = -x_1 + \frac{1}{1 + bx_2}u$$
$$T_2\frac{dx_2}{dt} = 2x_1 - x_2$$

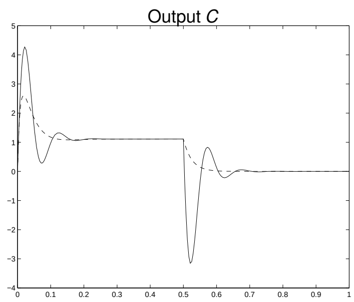
is better than the linear model

$$T_1\frac{dx_1}{dt} = -x_1 - kx_2 + u$$
$$T_h\frac{dC}{dt} = 2x_1 - x_2$$

Steady state

$$x_1 = \frac{u}{1 + 2k}, \quad x_1 = -\frac{1}{4b} + \sqrt{\frac{1}{16b^2} + \frac{u}{2b}}$$

An Improved Model for Inhibition



Models matched to give the same steady state for $u = 10$, linear model (full), nonlinear model (dashed).

Pattern Generators and Muscle Control

Periodic phenomena are used much in biological systems

- Walking, running, swimming
- Breathing, heartbeat
- Sleeping
- Motor neurons

Control of Respiration

The following 4 neuron system can generate an oscillation for $k = 3$

$$\frac{dx}{dt} = \begin{pmatrix} -3 & 0 & -k & -5 \\ -5 & -3 & 0 & -k \\ -k & -5 & -3 & 0 \\ 0 & -k & -5 & -3 \end{pmatrix} x$$

Since the system is linear the oscillation will however not be asymptotically stable.

Short Term Memory Circuit

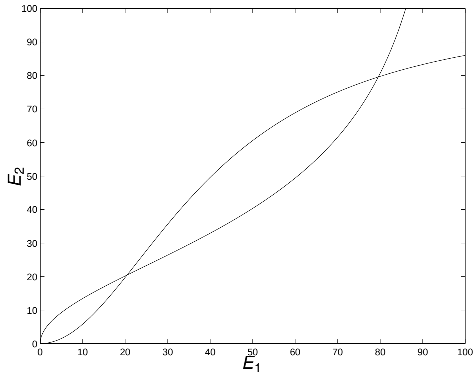
$$\frac{df}{dx} = \frac{1}{T} f(x) = \frac{1}{T} \begin{pmatrix} -x_1 + \dfrac{100x_2^2}{40^2 + x_2^2} \\ -x_2 + \dfrac{100x_1^2}{40^2 + x_1^2} \end{pmatrix}$$

Equilibria

$$x_1 = x_2$$
$$x_1 = \frac{100x_1^2}{40^2 + x_1^2}$$

Three equilibria $x_1 = x_2 = 0$, $x_1 = x_2 = 20$ and $x_1 = x_2 = 80$

Equilibria



Local Behavior Close to Equilibria

The Jacobian is given by

$$J = \frac{1}{T}\frac{\partial f(x)}{\partial x} = \begin{pmatrix} -1 & \dfrac{320000x_2}{(40^2 + x_2^2)^2} \\ \dfrac{320000x_1}{(40^2 + x_1^2)^2} & -1 \end{pmatrix}$$

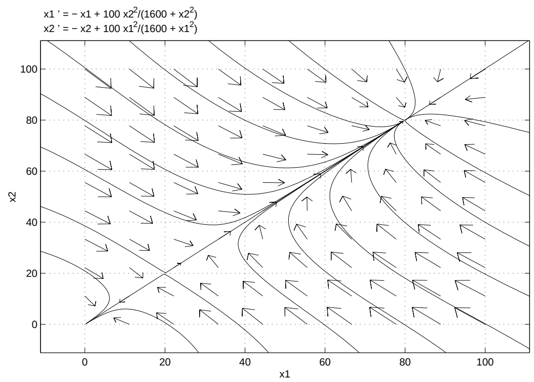
Evaluating the Jacobian for the different equilibria we get

$$J_0 = \frac{1}{T}\begin{pmatrix} -1 & 0 \\ 0 & -1 \end{pmatrix}, \; J_{20} = \frac{1}{T}\begin{pmatrix} -1 & 1.6 \\ 1.6 & -1 \end{pmatrix}, \; J_{80} = \frac{1}{T}\begin{pmatrix} -1 & 0.4 \\ 0.4 & -1 \end{pmatrix}$$

Eigenvalues

$$T\lambda_1 = -1, \qquad T\lambda_1 = -2.6, \qquad T\lambda_1 = -1.4$$
$$T\lambda_2 = -1, \qquad T\lambda_2 = 0.6, \qquad T\lambda_2 = -0.6$$

Phase Plane



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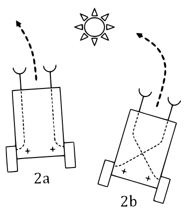
Braitenbergs Vehicle

The Italian-Austrian cyberneticist Valentino Braitenberg (now director of the Max Planck Institute of Biological Cybernetics) proposed a vehicle as an agent that can autonomously move around based on its sensor inputs. It has primitive sensors that measure some stimulus at a point, and wheels (each driven by its own motor) that function as actuators or effectors. In the simplest configuration, a sensor is directly connected to an effector, so that a sensed signal immediately produces a movement of the wheel. Braitenberg, V. (1984). Vehicles: Experiments in synthetic psychology. Cambridge, MA: MIT Press.

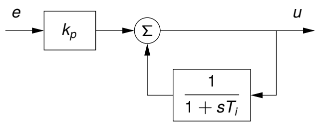


A Neural Servo - with Carver Mead

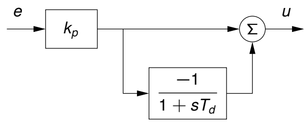
- Visual sensor: C. A. Mead Analog VLSI and Neural Systems. Addison-Wesley 1989
- Demonstrator
  - Optical sensor for encoder
  - Integrated all neural drive system
  - Pulses all the way from sensors to drive motor
  - Dual channels: exhibitory and inhibitory
  - Implementation of control systems with silicon neurons
- High parallelism by having multiple circuits and adding the pulses
- Extreme robustness part of the chip could be cut off
- Design theory for implementing neural controllers?

Implementation of Neural Controllers

- Inhibitory and exhibitory channels permit simple adding of signals
- Integral action



- Derivative action



PD Control using Silicon Neurons

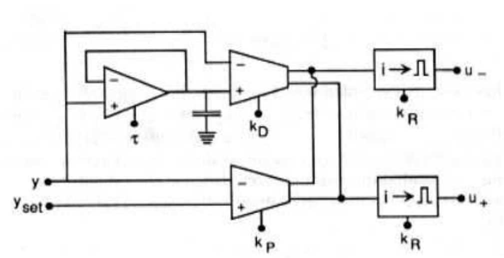
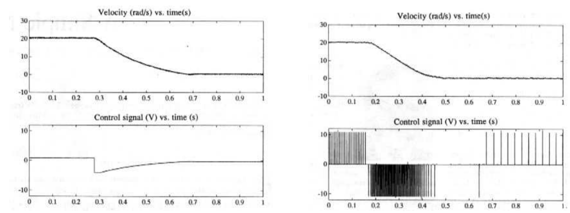


Fig. 2. P-D controller implemented using the circuit in Fig. 1 with a wide-range dual-output differentiator as one of its two elements.

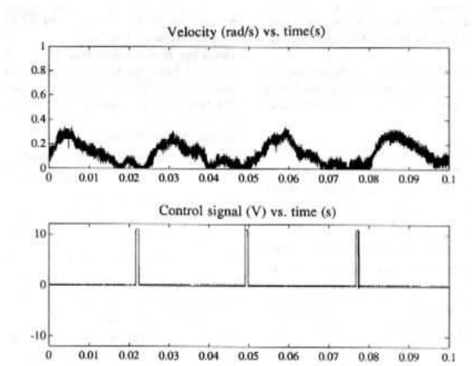
DeWeerth, Nielsen, Mead, Astrom A simple neuron servo. IEEE Trans. Neural Networks 1991(2),248-251

Analog and Neural Motor Control



Neurons implemented as asynchronous systems in analog VLSI, processing of the encoder signals were made on the same chip. Many parallel systems implemented pulses were added to give high reliability!

Neural Motor Control - Details



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A Simple Example - with Bo Bernhardsson 1999

Process model

$$dx = udt + dv,$$

where $v(t)$ is a Wiener process,

$$E(v(t+s) - v(t))^2 = |s|$$

Compare strategies based on periodic and event based control

- Sample equidistantly
- Sample when output exceeds given limits
- First order hold or impulse control
- Compare performances

Sampled Data Control - Minimum Variance Control

Sample system and loss function with period h (alternative to lifting)

$$hV_{PFOH} = \int_0^h Ex^2(t)\,dt = E\left(x^TQ_1x + 2x^TQ_{12}u + u^TQ_2u + J_e\right)$$

$$Q_1(h) = h,\ \ Q_{12}(h) = \frac{h^2}{2},\ \ Q_2(h) = \frac{h^3}{3},\ \ R_1(h) = h,\ \ J_e = \frac{h^2}{2}$$

The minimal loss function is

$$V_{PFOH} = \frac{1}{h}(R_1S + J_e) = \frac{3+\sqrt{3}}{6}h$$

The optimal control law is

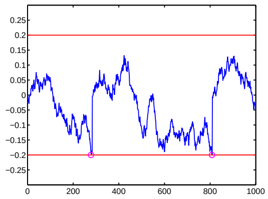
$$u = -\frac{1}{h}\frac{3+\sqrt{3}}{2+\sqrt{3}}x$$

Comparison of periodic and event based sampling for first-order stochastic systems KJ Åström, B Bernhardsson - IFAC Proceedings, 1999 - Elsevier

Event Based Control

A very simple control law: Apply a restoring impulse that brings the state to zero whenever the output reaches the boundary $|x| = d$.(Impulse sampling)

Let $T_{\pm d}$ be the exit time from 0 i.e. first time t_k when the boundary $|x(t_k)| = d$ is reached



The random variable $t - x_t^2$ is a martingale, hence

$$\bar{h}_L := E(T_{\pm d}) = E(x_{T_{\pm d}}^2) = d^2.$$

Crude control requires very slow sampling!
Sampling rate increases quadratically with precision

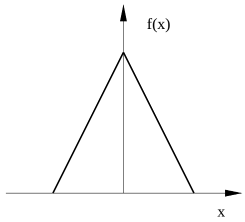
Stationary Distribution

Kolmogorov forward equation gives probability density for x

$$\frac{\partial f}{\partial t}(x) = \frac{1}{2}\frac{\partial^2 f}{\partial x^2}(x) - \frac{1}{2}\frac{\partial f}{\partial x}(d)\delta_x + \frac{1}{2}\frac{\partial f}{\partial x}(-d)\delta_x.$$

Stationary distribution

$$f(x) = \frac{1}{d^2}(d - |x|)$$



Mean

The mean variance is

$$V_{EIH} = \frac{d^2}{6}.$$

sampling rate $\bar{h}_E = d^2$

Comparison

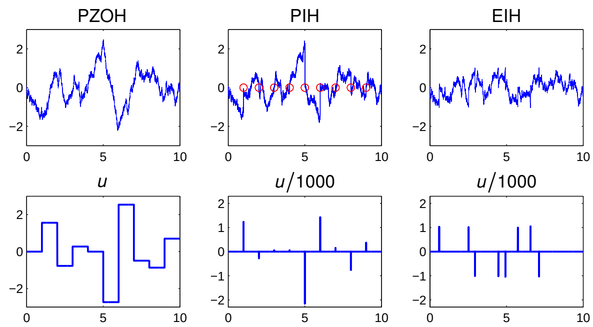
Choose $\bar{h}_E = h$, to obtain the same average sampling rate for the control laws.

$$V_{PZOH} = \frac{3+\sqrt{3}}{6}h = 0.79h, \quad V_{PIH} = \frac{h}{2}, \quad V_{EIH} = \frac{h}{6} = 0.17h$$

Traditional sample-data control requires 4.7 times faster sampling than event based control to give the same error variance! What are the reasons for the difference?

Faster detection (2/3) faster action (1/3)!

Simulation



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Summary

- Neural systems are very interesting
- Simple dynamic models give a lot of insight
- The standard tools are very useful
  - Modeling
  - Equilibria
  - Local behavior
  - Numerical solutions
  - Phase plane
- Much remains to be done
- We have barely touched the surface
  - Pulse behavior
  - Silicon neurons
  - Event based control

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