Simple Models of Point Neurons
Mathematical and Computational Methods

Lecture 4

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Quadratic Integrate-and-Fire

Leaky IaF

\[ \varepsilon \frac{dy_j}{dt} = -Ay_j + I \]

Does not really matter how fast you cross the threshold, there is no delay in the spike generation

Reset happens at the moment of threshold crossing

QIaF is designed to mimic suprathreshold dynamics

\[ \varepsilon \frac{dy_j}{dt} = Ay_j^2 - B + I \]

Reset happens at the peak of the action potential

As a result slow threshold crossing leads to a delayed spike
Critical Points of L and Q Integrate-and-Fire

Leaky

\[ 0 = -Ay_j + I \]
\[ y_j = \frac{I}{A} \]

Single critical point if
\[ y_j > \frac{I}{A} \]
the derivative is negative

\[ y_j < \frac{I}{A} \]
the derivative is positive

Quadratic

\[ 0 = Ay_j^2 - B + I \]
\[ y_j^2 = \frac{B - I}{A} \]

Can have 0, 1, or 2 critical points depending on whether
\[ B > I \]
Phase Portraits of L and Q Integrate-and-Fire

Representing geometrically:
- Plot derivative as a function of $y_j$
- See if it is positive or negative
- Mark the areas
- Determine the stability
QIaF Phase Portrait

![Diagram of QIaF Phase Portrait](image-url)
Systems of Equations

Let’s have two neurons:

\[ \frac{dy}{dt} = -A_y y + w_{xy} x \]

\[ \frac{dx}{dt} = -A_x x + w_{yx} y \]

Equilibrium solution gives us

\[ y = \frac{w_{xy}}{A_y} x \]

\[ x = \frac{w_{yx}}{A_x} y \]

If we plot these two lines they will represent where the derivatives are zero – nullclines

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Phase Portrait of the System

Above nullcline

\[ y > \frac{w_{xy}}{A_y} x \]

and the derivative is negative closer to nullcline it is smaller
Similarly for $x$, except the derivative is negative to the right of a nullcline.
Phase Portrait of the System

Combining the two fields shows
For my parameter choice the system is unstable
The critical point exists (intersection of nullclines), but it is a saddle
Now, I guessed my lines from biological parameters, so it seems that two excitatory coupled neurons are unstable
Too broad of a conclusion
Systems of Equations

Let’s have two neurons:

\[
\frac{dy}{dt} = -A_y y + w_{xy} x \\
\frac{dx}{dt} = -A_x x + w_{yx} y
\]

Here the general solution is

\[
y(t) = a \exp(\lambda_1 t) + b \exp(\lambda_2 t) \\
x(t) = c \exp(\lambda_1 t) + d \exp(\lambda_2 t)
\]

where \( a, b, c, d \) are constants (possibly complex) depending on parameters and initial conditions \( \lambda_1 \) and \( \lambda_2 \) are eigenvalues of the matrix

\[
M = \begin{pmatrix}
-A_y & w_{xy} \\
w_{yx} & -A_x
\end{pmatrix}
\]
Eigenvalues

If the real parts of eigenvalues are positive the activations will grow without bounds.
If they are negative the activations will die out.
The only meaningful behavior (without other inputs) will be if they are zero, then the network will oscillate indefinitely.
The intersections of eigenvectors define critical points.
The signs of real eigenvalues mean:
  – Opposite – intersection of corresponding eigenvectors is a saddle.
  – Both positive – critical point is an unstable source.
  – Both negative – critical point is a stable sink.
Complex eigenvalues lead to orbits and oscillations.
Stability of a Critical Point

A critical point is stable if all the trajectories that start near the critical point stay near this point as time evolves.

The system in the middle displays stable oscillations.
If the trajectories converge to critical point, it is called asymptotically stable (point on the left).
If the starting point does not matter than the critical point is globally asymptotically stable (right).
Stability of a Critical Point

The critical point is unstable if the trajectories starting near critical point move away as time progresses.
Stability of a System

When talking about system of equations stability is different: even a system with only stable critical points can be unstable

System of equations is called stable if all variables converge to some critical points as the time progresses

Here oscillation is usually not considered as stability
Stability of a Linear System

Considering the system

\[ \dot{x}_1 = A_{10} + A_{11} x_1 + \ldots + A_{1n} x_n \]

\[ \vdots \]

\[ \dot{x}_n = A_{1n} + A_{n1} x_1 + \ldots + A_{nn} x_n \]

with constant coefficients \( A_{ij} \)

The stability will be determined by the coefficient matrix

\[
\begin{pmatrix}
A_{11} & \ldots & A_{1n} \\
\vdots & \ddots & \vdots \\
A_{n1} & \ldots & A_{nn}
\end{pmatrix}
\]
Stability of a Linear System

Setting to equilibrium

\[ 0 = A_{10} + A_{11}x_1 + \ldots + A_{1n}x_n \]

\[ \ldots \]

\[ 0 = A_{ln} + A_{n1}x_1 + \ldots + A_{nn}x_n \]

we can see that we have \( n \) equations with \( n \) variables, so given linear independency it has one and only one solution, thus a single critical point

To consider the stability of this point we need to look at eigenvalues of the matrix \( A \)

If all eigenvalues have negative real part then the point is globally asymptotically stable, and the system will be stable too
Stability of a Linear System

If any eigenvalue has a positive real part the point is unstable and so is the system.

If real parts are negative or zero then things get complicated:
- If imaginary eigenvalues are non-repeating the point will show stable oscillations, but we will not consider the system stable.

The bigger issue is that most of the neural models are nonlinear due to nonlinear signal functions.
Stability of a Non-linear System

General approach is:

– determine all critical points
– approximate the system with a linear one through Jacobian in the neighborhood of each point
– analyze the local stability around each point
– if possible build a phase plane for a global picture

There are also theorems that prove stability of different specific systems of non-linear ODEs

Unfortunately, these theorems usually handle very limited cases rarely applicable to functional neural models
Do We Need Stability in Neural Models?

It is nice to have it from analytical point of view
But it is hard to prove for most non-trivial cases
Given a delicate nature of the brain activity, abundance of oscillations in the brain, and how relatively easy is to disturb proper neuronal functioning, the brain does not appear as a stable system

Some self-regulatory mechanisms for stabilizing the model are necessary,
but don’t sweat too much trying to build a model with proven absolute stability, you might be diverging from reality…
Shunting Equation with Constant Input

\[ \frac{dy_j}{dt} = -Ay_j + (B - y_j)I = -(A + I)y_j + BI \]

Given that input is constant we can rearrange the terms and arrive at the similar exact solution as for leaky integrator

If someone wants to play with

\[ \frac{dy}{dt} = -A_y y + (B_y - y)w_{xy} x \]

\[ \frac{dx}{dt} = -A_x x + (B_x - x)w_{yx} y \]

I will give extra credit for a general form solution
What is a Neural Network?

A neural network is simply a collection of abstracted neurons connected to each other through weighted connections ("synapses")

The computations performed by these interconnected neurons are represented by mathematical equations or computer algorithms.

The adaptation of the weights are also represented by mathematical equations or computer algorithms.
A Breakdown of Some Classic Neural Networks

**LINEAR**
- WIDROW (1962)
- ANDERSON (1968)
- KOHONEN (1971)

**NONLINEAR**

**CONTINUOUS**
- HARTLINE-RATLIFF-MILLER (1963)
- GROSSBERG (1967, 1968)

**BINARY**
- MCCULLOCH-PITTS (1943)
- CAIANNIELLO (1961)
- ROSENBLATT (1962)

**ADDITIVE**
- SPERLING & SONDHI (1968)
- WILSON-COWAN (1972)
- GROSSBERG (1973)

**SHUNTING**
Additive Network

Adding parameters $B$ and $C$ to designate relative strength of excitation and inhibition:

$$
\varepsilon \frac{dy_k}{dt} = -Ay_k + B \sum_i f(x_i)w_{ik} - C \sum_j f(x_j)w_{jk}
$$

Because the inputs are simply “added up” in this equation, it is referred to as an additive network.
Additive Network

Finally, consider many “second layer” cells $y_k$, and assume that the set $E$ denotes all excitatory connections and $I$ denotes all inhibitory connections:

Our additive network equation becomes:

$$\varepsilon \frac{d y_k}{d t} = -A y_k + B \sum_{i \in E} f(x_i) w_{ik} - C \sum_{i \in I} f(x_i) w_{ik}$$
Shunting Network

Here parameters $B$ and $C$ designate saturation levels of excitation and inhibition:

$$
\varepsilon \frac{dy_k}{dt} = -Ay_k + (B - y_k) \sum_i f(x_i)w_{ik} - (C + y_k) \sum_j f(x_j)w_{jk}
$$

Because the input effects are bound by the shunts, it is referred to as a shunting network.
Shunting Network

Again, consider second layer cells $y_k$, and assume that the set $E$ denotes all excitatory connections and $I$ denotes all inhibitory connections:

Our shunting network equation becomes:

$$
\epsilon \frac{dy_k}{dt} = -Ay_k + (B - y_k) \sum_{i \in E} f(x_i)w_{ik} - (C + y_k) \sum_{i \in I} f(x_i)w_{ik}
$$
What is the “Right” Equation?

We will see later that the shunting equation for a neuron is a better approximation than the additive equation to the neuron’s membrane potential as measured in physiological experiments.

Still a rough approximation (cf. compartmental model of a neuron)

Depending on how important biological plausibility is to our model, we may want to use:

- Algebraic equations (low accuracy, very simple)
- Additive differential equations (slightly higher accuracy, slightly more complicated)
- Shunting differential equations (higher accuracy, more complex)
- Even more complex approximations (e.g., compartmental models)
Next Time

Biophysics of cell membrane and equivalent electrical circuits used to derive classical Hodgkin-Huxley membrane equations

D&A Chapters 5 (sections 1-4) and 6 (sections 3-4)