Mathematical models of spiking neurons

Mathematical models of spiking neural behavior vary in how many details of the neuron they explicitly model (Izhikevich, 2004). Models, which are used to simulate lots of neurons in a network, usually only explicitly model the membrane potential, and the strengths of the synapses to postsynaptic neurons.

In this case, the value of the membrane potential is the variable state of the neuron, and the evolution of the state is governed by a differential equation. An example of this is the integrate-and-fire model, which is one of the simplest neuron models, and which is very popular in SNNs. Spiking neuron models exist that explicitly models other variable states of the neuron in order to provide more biological detail to dynamics of the model of the neuron (Izhikevich, 2007). In these cases, the state of the neuron is described by a set of coupled differential equations. An example of this is the Hodgkin-Huxley model, which consists of four coupled differential equations (Gerstner et al., 2014).

Consisting of variable states, governed by differential equations, models of neurons can be thought of and analyzed as being dynamical systems (Izhikevich, 2007). A dynamical system consists of one or more variable states and one or more rules that determine how the state(s) evolve through time, including how the rate of change of the state depends on the previous state.

The neuron model, which is used in later experiments in this thesis is the Izhikevich model (Izhikevich, 2003). This model consist of two coupled differential equations, and is therefore said to be a two-dimensional model. The first differential equation describes the evolution of the membrane potential, the second differential equation models slow inner recovery dynamics of the neuron.

$$\Delta V = \frac{[k(V - V_{rest}))(V - V_{thres}) - u + I]}{C}$$

$$\Delta u = a[b(V - V_{rest}) - u]$$

then the threshold function

$$V = \begin{cases} c & V \geq V_{peak} \\ V & V < V_{peak} \end{cases}$$

$$u = \begin{cases} u + d & V \geq V_{peak} \\ u & V < V_{peak} \end{cases}$$

Here, V is the membrane potential, V_{rest} is the resting potential of the neuron, and V_{thres} is the value, that the membrane potential needs to reach in order to emit a spike. I is the sum of all incoming excitation and inhibition, whether that is from other neurons or from some external stimulus. k determines how quickly the neuron returns to its resting state, the larger k is, the faster this happens. A very small k will make the neuron a perfect integrator. A larger k will make the neuron behave more like a coincidence detector, as the influence of earlier inputs will fade quickly, and inputs will therefore need to reach the neuron in close temporal proximity to each other.

C is the membrane capacitance, affecting how large changes can be made to the membrane potential in a single update. a and b determines how much u can change in one update and how much that change depends on in the current state of the membrane potential. c is the value that the membrane potential is reset to after a spike and d determines the immediate after-spike behavior. The larger the value of d, the more input will be required for the neuron to be able to spike again immediately after having spiked.

Different parameter settings can result in a diverse range of behaviors, corresponding to many different types of neurons across all of the brain. It is thus a good compromise between biological realism, diverse computational capabilities and efficiency (Izhikevich, 2004). It is for these reasons that this is the type of neuron will be used in the experiments of this thesis.

The following parameters will make the model imitate a type of excitatory neuron called the 'regular spiking neuron':

$$\Delta V = \frac{[0.7(V - (-60))(V - (-40)) - u + I]}{100}$$

$$\Delta u = 0.03[-2(V - (-40)) - u]$$

then the threshold function

$$V = \begin{cases} -50 & V \geq 35 \\ V & V < 35 \end{cases}$$

$$u = \begin{cases} u + 100 & V \geq 35 \\ u & V < 35 \end{cases}$$

Figure 1 shows how the membrane potential of this model evolves over time, when a constant current is applied to it.
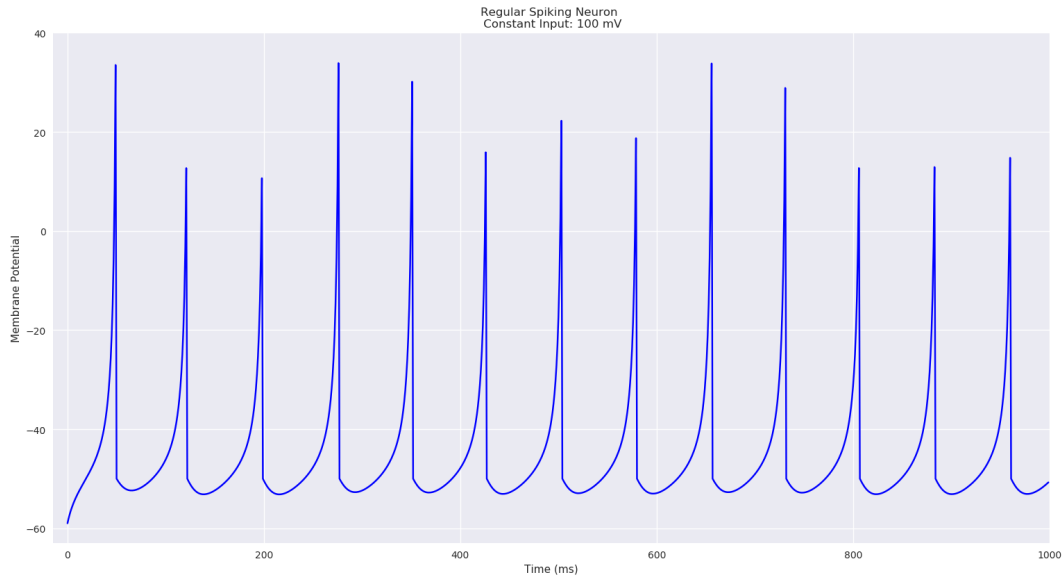

Figure 1: Simulation of a single regular spiking neuron receiving a constant input of 100 mV at every time step, where one time step corresponds to 1 ms.

Here the differential equation is approximated by a difference equation using the first-order Euler's method:

$$V_t = V_{t-1} + \frac{\Delta t [0.7(V_{t-1} - (-60))(V_{t-1} - (-40)) - u_{t-1} + I]}{100}$$

$$u_t = u_{t-1} + (\Delta t \cdot 0.03[-2(V_{t-1} - (-40)) - u_{t-1}])$$

then the threshold function

$$V_t = \begin{cases} -50 & V_t \geq 35 \\ V_t & V_t < 35 \end{cases}$$

$$u_t = \begin{cases} u_t + 100 & V_t \geq 35 \\ u_t & V_t < 35 \end{cases}$$

Where Δt is the size of each discrete time step, and thus determines the granularity of the simulation.

Of course, the input to a neuron is not always constant, and it might therefore be informative to see how the neuron model evolves, when faced with a varying input. Figure 2 shows just that.
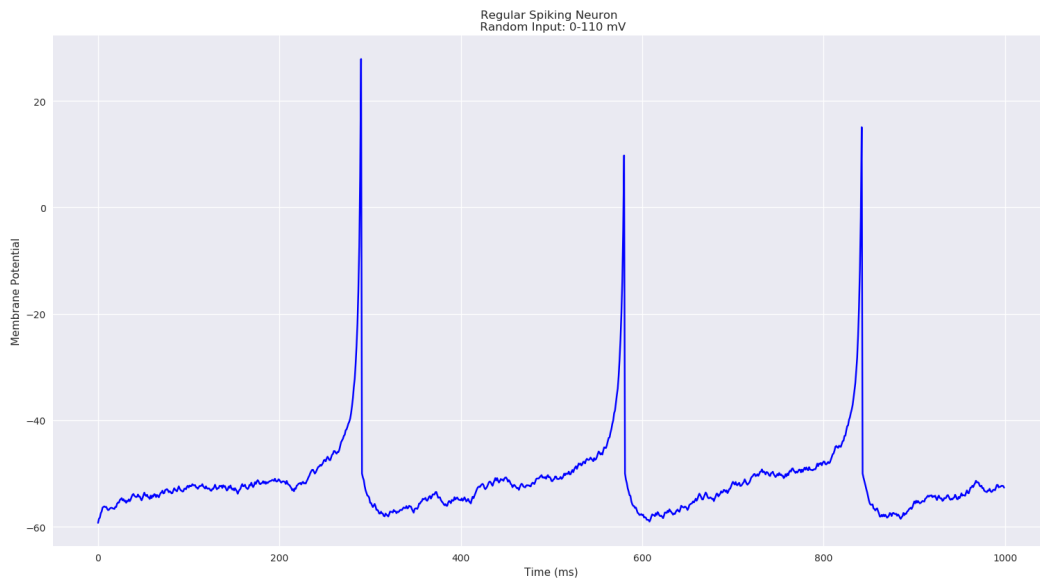

Figure 2: Simulation of a regular spiking neuron receiving random inputs between 0 and 110 mV at every time step. Compared to Figure 1, the neuron is in this situation much less likely to spike.

Whether the Izhikevich neuron spikes or not is determined by a threshold function on the membrane potential, but the rate of change of the membrane potential is affected by the recovery variable. This means that two neurons with the same membrane potential could react very differently to the same input strength, if they differ in the values of their recovery variables.

In order to gain some insight to the inner dynamics of this two-dimensional neuron model, a vector field with some representative trajectories can be useful. This is shown in Figure 3.
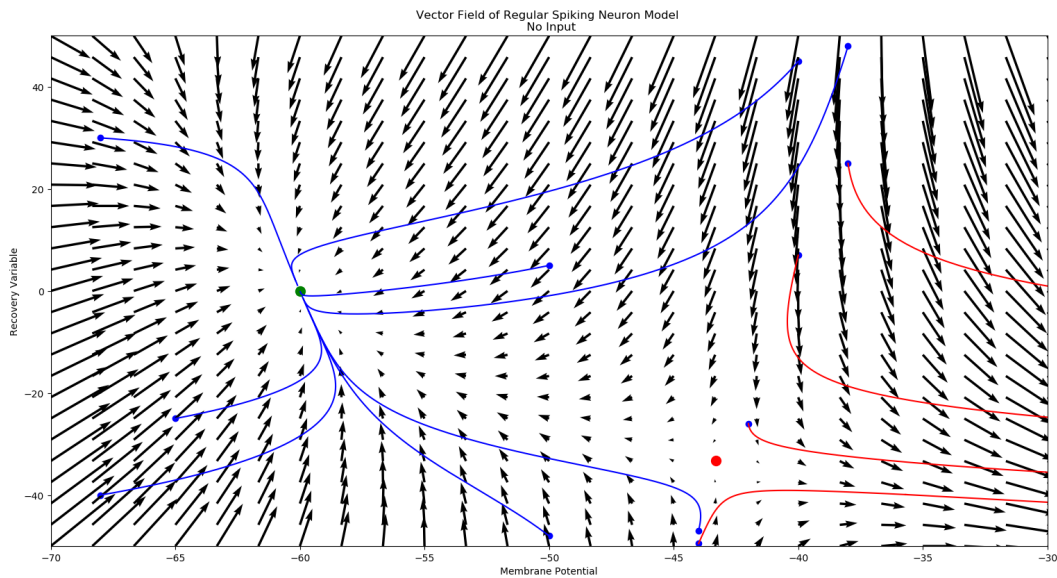

Figure 3: A vector field illustrating how the change of the state of the neuron depends on the neuron's current state. The green dot is a stable equilibrium. The red dot is an unstable equilibrium. The lines illustrate the trajectories from different starting points. Blue dots mark the initial state of a trajectory. Blue lines illustrate trajectories that settle into the stable equilibrium, red lines illustrate trajectories that do not.

This reveals how much the two states changes in the absence of inputs given their current states. In terms of dynamical systems theory, one can see that there are two equilibria points, i.e., points where the rate of change of both differential equations are zero (Izhikevich, 2007). One is stable and one is unstable (green and red dot, respectively). The stable equilibrium is when the value of the membrane potential is -60 and the recovery variable is zero. All initial states in the area around this point will in the absence of inputs have trajectories toward this resting point (blue lines). Once a trajectory has reached a stable equilibrium it will no longer change. On the contrary, an unstable equilibrium repels the state of the model away from it. It is only if the initial state is exactly at the unstable equilibrium, that the state can remain there. Even if the state of the model is very close to the equilibrium, it will have a trajectory away from it.

The unstable equilibrium divides the vector field into two areas: 1) if a state of the system is this area, its trajectory will lead to the stable equilibrium, and 2) in the other area all trajectories will lead to an increase of the membrane potential, until the point where a spike has been recorded and both variables of the system are reset. However, it is not easy to determine the exact boundary between these two areas.

When examining trajectories starting with a membrane potential close to -40, (which we have set to be the threshold value in the differential equation) we see that initial states with the same membrane potentials can have trajectories that end up en very different places, depending on the starting value of the recovery variable. More specifically, if the recovery variable is sufficiently negative, the membrane potential can – even in the absence of inputs – be pushed to become greater than -40 and then proceed to grow rapidly until it is reset. This means that even though the release of a spike is determined by a hard threshold function on the membrane potential, the "point-of-no-return" is much more blurred than it would be in a one-dimensional model. In other words, the two-dimensional Izhikevich model can be said to have threshold, which is sensitive to its history.
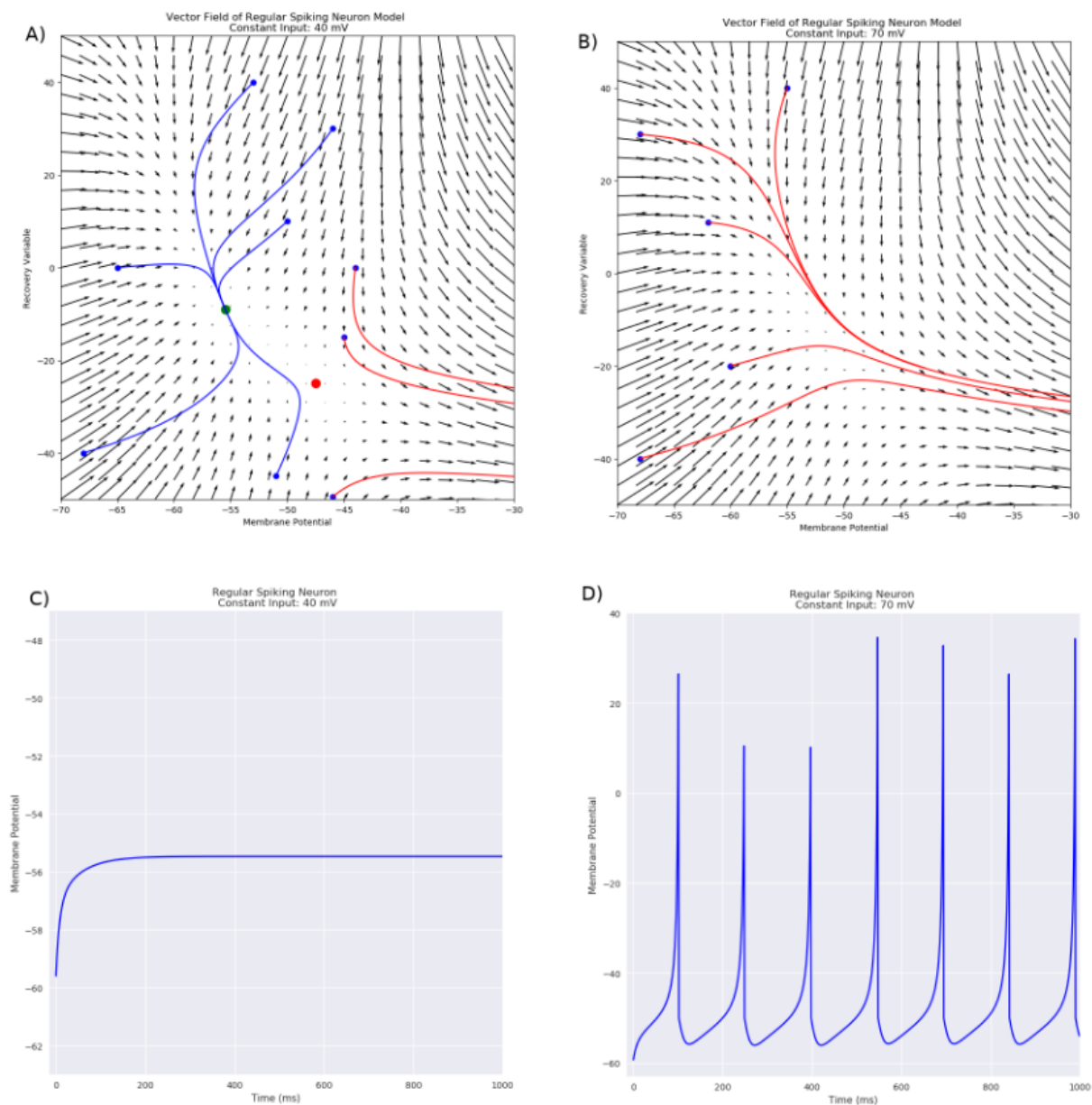
Figure 4: A) vector field and trajectories when the neuron receives a constant input of 40 mV. The two equilibria have been moved closer to each other. B) vector field and trajectories when the neuron receives a constant input of 70 mV. No equilibria exist here, so no trajectories settle. C) with the constant input of 40 mV, a resting neuron will not spike, but reach a stable state. D) the neuron is forced to spike by the input of 70 mV.

Figure 3 can tell us something about the information processing capabilities of the model of the neuron. If the membrane potential is very close to the threshold, but still below it, its rate of change is very close to zero. This means that if an input brings the neuron close to spiking, the neuron can stay in a near-threshold state for a while even in the absence of input. One could say that the neuron

"forgets" a subthreshold input at a non-linear rate depending on the strength of the input.One can also make a vector field of the neuron's behavior when a constant input is applied to it. The effect of this on the vector field is that the two equilibrium points move closer and closer together the stronger the constant input is. As long as these points are separated form each other, the neuron's membrane potential will settle to be a constant value above its resting potential, assuming that the neurons initial state its resting potential. In other words, the constant input is not strong enough to bring a resting neuron to spike. However, when the constant input is sufficiently strong, the two equilibria will collide and disappear. Now the neuron will be forced to emit a spike regardless of its starting position.

The sensitivity to the history does not mean that the neuron evolves erratically. As can be seen in Figure 4b, when the neuron is subjected to a constant input of 70mV, trajectories tends to converge to very similar ones, even when having a diverse range of initial states. Even though the stable point has disappeared, there is still an area in the vector field, where neither the membrane potential or the recovery variable changes very much, an the state of the neuron is attracted towards this area before moving on towards the action potential.

In sum, a spiking neuron is a type of models used to simulate biological neurons. To better understand the how the state of a neuron evolves in time it can be useful to describe the neuron as being a dynamical system. It is the subthreshold dynamics of a neuron, which determines how a neuron responds to incoming stimuli, and thus determines the information processing capabilities if the neuron. Above, we saw that the dynamics of a neuron depends on the its current state and therefore its history.

Referencer

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