

VS 265 Lecture notes

Linear neuron models

Definition of a linear system

- A linear system is one in which the input-output behavior may be described in terms of a linear function.
- A linear function obeys the rules of *superposition*: $f(x + y) = f(x) + f(y)$ and *scaling*: $f(ax) = af(x)$
- Example: $f(x) = kx$.
- *Linear algebra* provides a powerful tool for the analysis of complex, multivariate systems.
- Although most systems in nature are non-linear, our understanding of them can still be aided by the intuitions and insights gained from linear systems analysis.

Neurons

- The brain contains approximately 10^{10} neurons. Each neuron can essentially be thought of as a *device* having a number of inputs and a single output. The inputs consist of the currents generated by the approximately 1000 axons of other neurons that form synapses on the dendritic tree. The output consists of the action potentials carried by the axon. The axon branches so as to send many copies of the output to other neurons.
- The overall input-output characteristic of a neuron is very complicated and still not fully understood. What we do know is that the input currents are generated by ion-specific channels in the membrane which change their *conductance* in response to chemicals (neurotransmitters) released by other neurons. These currents are (roughly) summed together into the soma, whose voltage rises and decays with the fluctuations in current. When the soma voltage exceeds a certain threshold, an action potential is generated, which then propagates down the axon.
- A conventional way of attempting to understand a neuron is to break it up into many small elements, or *compartments*. The membrane potential of a given compartment is determined by the conductances of the various ion channels within it. For the Na, K, and Cl ion channels, we have

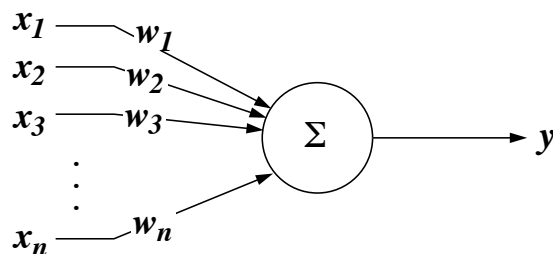
$$V_m = \frac{V_{Na}G_{Na} + V_KG_K + V_{Cl}G_{Cl}}{G_{Na} + G_K + G_{Cl}}$$

where V_m is the membrane voltage, G_x denotes the conductance of the ion channel selective to ion x , and V_x denotes the reversal potential (or so-called Nernst potential) of ion x .

- Note that V_m is *not* a linear function of the conductances. In addition, the action-potential is a highly non-linear function of V_m .

Linear neuron model

- Despite the non-linearities mentioned above, it is still possible to build a simplified, linear model of a neuron that provides a starting point for understanding the computations performed by neurons in the brain.
- A schematic of a linear neuron model is shown below:



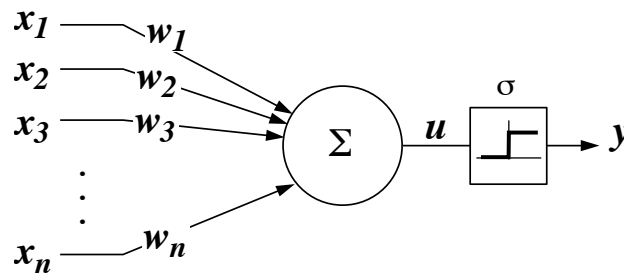
- Each input x_i is multiplied by a corresponding weight w_i and these values are summed together to form the output y . Thus, the output is given as a function of the inputs and weights by the equation

$$y = \sum_i^n w_i x_i$$

or, in vector form, $y = \mathbf{w} \cdot \mathbf{x}$, or $y = \mathbf{w}^T \mathbf{x}$.

- The inputs x_i in a linear neuron model can be thought of as the action potentials from other neurons that are impinging upon this neuron's synapses. The weights w_i can be thought of as the *efficacies* of the synapses. The larger w_i , the the more input x_i affects the neuron's output. The biophysical properties of a real neuron that determine the value of w_i include the number of synaptic vesicles in the presynaptic terminal, and the number of ligand-gated channels in the post-synaptic membrane. The sign of w_i reflects whether it is an excitatory or inhibitory synapse.

- A useful modification to the linear neuron above is to add a non-linear threshold function at the output, which is a crude model of the all-or-nothing action potential generated by a neuron:



In this case, the output is given by $y = 1$ if $u > \theta$ and $y = 0$ otherwise, where θ is the threshold voltage of the neuron, and $u = \sum_i^n w_i x_i$.