Neural Networks

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1 Background

1.1 Neuronal Population Characteristics

To begin, consider some population of $N \in \mathbb{N}$ neurons ordered in the following way: $P_N = \{n_1, \ldots, n_N\}$.

Definition 1.1 (P = **neuron population**). Consider a population of N neurons for some $N \in \mathbb{N}$. Call the indexed collection of neurons $P_N = \{n_1, \ldots, n_N\}$.

Then define a potential vector $V = (V_1, \ldots, V_N)$, where for any $i \in \{1, \ldots, N\}$, V_i is the electric potential difference across the membrane to ground of the i^{th} neuron.

Definition 1.2 ($\mathbf{v}(t)$ = **neuron potential vector**). Given a population of neurons P_N, for any $i \in \{1, \ldots, N\}$, let $V_i(t) \in \mathbb{R}$ be the electric potential difference (in volts, V) across the membrane of neuron n_i, with respect to its local surroundings, at time $t \in \mathbb{R}$.

Call the neurons' potential difference, or voltage, vector $\mathbf{v}(t) \in \mathbb{R}^N \times \mathbb{R}$

$$\mathbf{v}(t) = \begin{bmatrix} V_1(t) \\ \vdots \\ V_N(t) \end{bmatrix}$$

In a normal resting state, each neuron sits at a particular equilibrium voltage given the neuron's characteristics. So define a corresponding equilibrium voltage vector to account for these.

Definition 1.3 ($\mathbf{e}(t)$ = **neuron equilibrium potential vector**). Given a population of neurons P_N, for any $i \in \{1, \ldots, N\}$, let $E_i \in \mathbb{R}$ be the equilibrium, or resting, potential difference (in volts, V) across the membrane of neuron n_i, with respect to its local surroundings, at time $t \in \mathbb{R}$.

Call the neurons' equilibrium potential difference, or voltage, vector $\mathbf{e}(t) \in \mathbb{R}^N \times \mathbb{R}$

$$\mathbf{e}(t) = \begin{bmatrix} E_1(t) \\ \vdots \\ E_N(t) \end{bmatrix}$$

Now, with N total neurons, there are a possibility of $N(N-1)$ inter-neural connections, or synapses (not counting self connections). Each of these synapses in an open state has an associated maximum conductance, which we idealize as constant. So set these conductances within a $N \times N$ matrix, where the columns index the sending neurons, and the rows index the receivers.

Because the connections are directional in nature (that is to say that incoming and outgoing signals pass through separate channels) this matrix will not normally be symmetric.

Definition 1.4 (G = **synapse maximum conductance matrix**). Given a population of neurons P_N, let $G(t) \in \mathbb{R}^N \times \mathbb{R}^N$ where $G = [g_{ij}]_{i,j=1}^n$.

Then for any $i, j \in \{1, \ldots, N\}$ such that $i \neq j$, let $g_{ij} \in \mathbb{R}$ be the maximum conductance of the collective synapse (in siemens, S) passing from neuron n_j to neuron n_i in an open state, and in the case that $i = j$, let $g_{ii}(t) = 0$ so that

$$G = \begin{bmatrix} 0 & g_{12} & \cdots & g_{1N} \\ g_{21} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & g_{(N-1)N} \\ g_{N1} & \cdots & g_{N(N-1)} & 0 \end{bmatrix}$$

1.2 Electrical Considerations

Now we consider some properties of electrical circuits to gain the beginnings of a dynamic system. To start, imagine the membrane of each neuron as a capacitor that holds charged ions separated on either side of its surface. The capacitance of the membrane is the ratio of the separated charge over the corresponding potential difference:

$$C(t) = \frac{q(t)}{V(t)} \implies q(t) = C(t)V(t)$$

If we idealize the capacitance as a fixed physical constant for each neuron ($\forall t$, $C(t) = C$), then the resulting derivative collapses:

$$\dot{q}(t) = V(t)\dot{C}(t) + C(t)\dot{V}(t) = C\dot{V}(t)$$

And since current is defined as the change in charge over time, $I(t) = \dot{q}(t)$, then

$$C\dot{V}(t) = I(t)$$

We can track the current in and out of a neuron very well conceptually, so this is a convenient way to correlate synaptic activity to the potential in each cell. Let us formalize these definitions before we move on:

Definition 1.5 ($\mathbf{c}$ = **membrane capacitance vector**). Given a population of neurons P_N, for any $i \in \{1, \ldots, N\}$, let $C_i \in \mathbb{R}$ be neuron n_i's membrane capacitance (in farads, F).

Call the neurons' membrane capacitance vector $\mathbf{c} \in \mathbb{R}^N$

$$\mathbf{c} = \begin{bmatrix} C_1 \\ \vdots \\ C_N \end{bmatrix}$$

Now to correlate the derivative and create a system of ODEs, we define the total incoming current for each neuron as follows:

Definition 1.6 ($\mathbf{i}(t)$ = **incoming current vector**)**.** Given a population of neurons P_N, for any $i \in \{1, \ldots, N\}$, let $I_i(t) \in \mathbb{R}$ be the net current entering the neuron n_i's membrane (in amperes, A) at time $t \in \mathbb{R}$.

Define the current vector $\mathbf{i}(t) \in \mathbb{R}^N \times \mathbb{R}$ to be

$$\mathbf{i}(t) = \begin{bmatrix} I_1(t) \\ \vdots \\ I_N(t) \end{bmatrix}$$

If we apply Ohm's law ($V = IR \implies I = V/R = gV$) across each synapse, then since the current is coming out of each neuron,

$$\mathbf{i}(t) = -G\mathbf{v}(t)$$

So along with the equation derived above, we

$$\mathbf{i}(t) = \mathbf{c} \cdot \dot{\mathbf{v}}(t)$$

gives us the differential equation of a passive, or unregulating, population of neurons with all synapses in a completely open state:

$$\boxed{\mathbf{c} \cdot \dot{\mathbf{v}}(t) = -G\mathbf{v}(t)}$$

If we imagine there is some perfect way to put an electrode on each individual neuron, we can also define the associated input current vector

Definition 1.7 ($\mathbf{u}(t)$ = **applied current vector**)**.** Given a population of neurons P_N, for any $i \in \{1, \ldots, N\}$, let $u_i(t) \in \mathbb{R}$ be the electrical current (in amps, A) applied to neuron $n_i \in P_N$ at time $t \in \mathbb{R}$.

Call the neurons' applied current vector $\mathbf{u}(t) \in \mathbb{R}^N \times \mathbb{R}$

$$\mathbf{u}(t) = \begin{bmatrix} u_1(t) \\ \vdots \\ u_N(t) \end{bmatrix}$$

Definition 1.8 ($\mathbf{x}(t)$ = **natural current vector**)**.** Given a population of neurons P_N, with a net current vector $\mathbf{i}(t)$, and an applied current vector $\mathbf{u}(t)$, then for any $i \in \{1, \ldots, N\}$, call $x_i(t) \in \mathbb{R}$ the "natural current" for neuron n_i where $x_i(t) = I_i(t) - u_i(t)$

Then call the neurons' natural current vector

$$\mathbf{x}(t) = \begin{bmatrix} x_1(t) \\ \vdots \\ x_N(t) \end{bmatrix} = \begin{bmatrix} I_1(t) - u_1(t) \\ \vdots \\ I_N(t) - u_N(t) \end{bmatrix} = \mathbf{i}(t) - \mathbf{u}(t)$$

Since the natural current is the only thing depending on the conductance of the synapses,

$$\mathbf{x}(t) = G\mathbf{v}(t)$$

and thus, we can add in the incoming current from $\mathbf{u}(t)$,

$$\boxed{\mathbf{c} \cdot \dot{\mathbf{v}}(t) = -G\mathbf{v}(t) + \mathbf{u}(t)}$$

which is the system of differential equations for an unregulating population of neurons, with an input, and with all synapses open.

2 Equilibrium Dynamics

Now we must account for the properties of a neuron to settle a particular voltage. This activity is due to the active and passive ion pumps embedded in each neuron's membrane. We must also model the gating activity at each synapse, as well as the different synapses' connection weights.

2.1 Self Regulation

So consider the previous equation:

$$\mathbf{c} \cdot \dot{\mathbf{v}}(t) = -G\mathbf{v}(t) + \mathbf{u}(t)$$

If the input electrodes were perfect conductors and G were invertible, then this would lead to an ideal case where we could regulate the neurons ourself:

$$\begin{aligned} \mathbf{c} \cdot \dot{\mathbf{v}}(t) &= -G\mathbf{v}(t) + \mathbf{u}(t) \\ &= -G\mathbf{v}(t) + GG^{-1}\mathbf{u}(t) \\ \mathbf{c} \cdot \dot{\mathbf{v}}(t) &= -G\left[\mathbf{v}(t) - G^{-1}\mathbf{u}(t)\right] \end{aligned}$$

This would progressively move the voltage vector $\mathbf{v}(t) \to G^{-1}\mathbf{u}(t)$ for our choice of said input.

Now G may not be invertible, but in the same way, we know that the protein pumps embedded in each neuron produce a net current across their membranes. This somehow regulates them to an equilibrium voltage for each neuron, as previously defined on pg.1.

If we ignore the mechanism and simply model the self regulation to the defined equilibrium vector as above, then we can model the system using the conductance across each membrane locally.

Definition 2.1 (G_{L} = **local membrane conductance matrix**). Given a population of neurons P_N, for any $i \in \{1, \ldots, N\}$, let $(g_{\mathrm{L}})_i \in \mathbb{R}$ be neuron n_i's local membrane conductance (in siemens, S).

Call the neurons' membrane conductance vector $\mathbf{g}_{\mathrm{L}} \in \mathbb{R}^N$

$$\mathbf{g}_{\mathrm{L}} = \begin{bmatrix} (g_{\mathrm{L}})_1 \\ \vdots \\ (g_{\mathrm{L}})_N \end{bmatrix}$$

and call the neurons' membrane conductance matrix $G_{\mathrm{L}} \in \mathbb{R}^{N \times N}$

$$G_{\mathrm{L}} = \mathrm{diag}\{\mathbf{g}_{\mathrm{L}}\} = \begin{bmatrix} (g_{\mathrm{L}})_1 & 0 & \cdots & 0 \\ 0 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & 0 \\ 0 & \cdots & 0 & (g_{\mathrm{L}})_N \end{bmatrix}$$

With all this in place, since G has no diagonal entries, and G_{L} is a purely diagonal matrix, then using the formula above to set the equilibrium,

$$\begin{aligned} \mathbf{c} \cdot \dot{\mathbf{v}}(t) &= -G\mathbf{v}(t) + G_{\mathrm{L}}\mathbf{e} + \mathbf{u}(t) \\ \mathbf{c} \cdot \dot{\mathbf{v}}(t) &= -\left(G + G_{\mathrm{L}}\right)\left[\mathbf{v}(t) - \mathbf{e}\right] + \mathbf{u}(t) \end{aligned}$$

So call

$$\boxed{G^\star = G + G_{\mathrm{L}}}$$

so that

$$\boxed{\mathbf{c} \cdot \dot{\mathbf{v}}(t) = -G^\star\left[\mathbf{v}(t) - \mathbf{e}\right] + \mathbf{u}(t)}$$

This is the system of differential equations for an actively regulating population of neurons with all synapses open.

2.2 Coupling Strength and Gating

So with the given system, each synapse has an equal "weight," but we know that synapses are not all the same. They slowly change the strength of their connections to account for frequency of use, as well as a variety of other factors. So ignore the slow change, and instead look at small time scales where the connections can be considered constant. The corresponding weights of each will be as well, and we account for them with another matrix that augments the maximum conductance matrix.

Definition 2.2 (W = **coupling strength matrix**). Given a population of neurons P_N, let $W \in \mathbb{R}^N \times \mathbb{R}^N$ where $W = [w_{ij}]_{i,j=1}^n$.

Then for any $i, j \in \{1, \ldots, N\}$ such that $i \neq j$, let $w_{ij}(t) \in \mathbb{R}$ represent the relative weight of the synapses passing from neuron n_i to n_j at time $t \in \mathbb{R}$. In the case that $i = j$, let $w_{ii}(t) = 1$ so that

$$W = \begin{bmatrix} 1 & w_{12} & \cdots & w_{1N} \\ w_{21} & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & w_{(N-1)N} \\ w_{N1} & \cdots & w_{N(N-1)} & 1 \end{bmatrix}$$

In a similar way