Integrators + Linear Network Theory

Goal: Learn about a fundamental brain process - how we store short-term (~10's of seconds long) memories - while placing this problem in the larger context of linear network theory, which should be of use across a large number of topics in this course (and in neuroscience).

Powerpoints

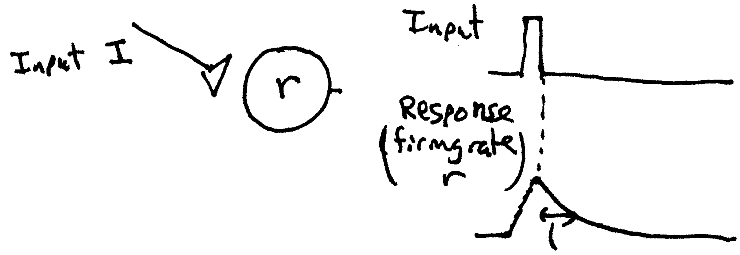
- Outline
- What is an integrator
- Neural correlate of short term memory: persistent neural activity
- Model system: goldfish oculomotor integrator
- Integration + memory storage by parametrically-encoded patterns of activity across a population of neurons

How can we explain this behavior?

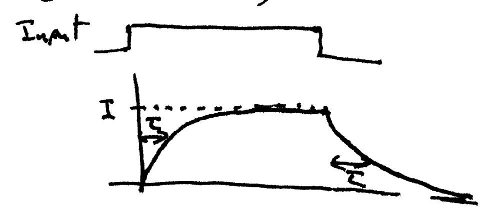
The traditional explanation, although often hidden in the gory details of cellular biophysics, is that such behavior is mediated by recurrently connected networks of neurons that provide positive feedback to one another. To see how this positive-feedback mechanism works, let's start with the simplest network model that can capture the essence of the behavior, a single neuron "network" with a synapse onto itself - an "autapse". We will see that this simple network can capture the essence of much of what happens in larger networks as well, - both integration and (for different parameters) amplification and changes in the speed of response.

I. Isolated neuron model

Typical neuron:



τ_{bio}
↳ biophysical decay time
(due to synapse + RC-filtering of membrane)



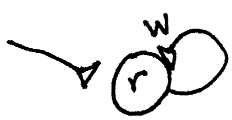
Model:

$$\tau_{bio}\frac{dr}{dt} = -r + I$$

for $I=0$: $r(t) = r(0)\,e^{-t/\tau}$

(+ for $I = \text{const}$, $r(t) \to I$ exponentially)

II. Autapse network



W = synaptic strength (or "weight")

$$\tau_{bio}\frac{dr}{dt} = \underbrace{-r + Wr}_{-(1-W)r} + I$$

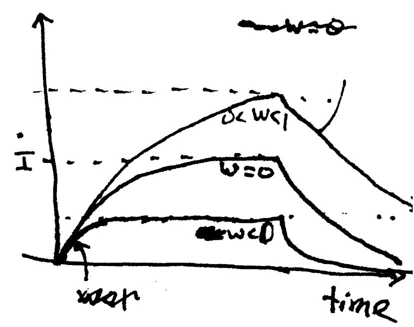
rearrange:

$$\underbrace{\frac{\tau_{bio}}{1-W}}_{\tau_{eff}}\frac{dr}{dt} = -r + \underbrace{\frac{I}{1-W}}_{r_\infty}$$

Behaves just like linear network, but with time constant + steady-state level amplified by the "amplification factor" $A \equiv \frac{1}{1-W}$

Cases:

w	A	$\tau_{eff} = A\tau_{w0}$ = response speed	$r_\infty = AI$ = amplification	Picture
$w<0$	$\frac{1}{1-(-)} < 1$	faster	attenuated	
$0<w<1$	$\frac{1}{1-(<1)} > 1$	slower	amplified	



Fundamental result in linear network theory:

SPEED-AMPLIFICATION TRADEOFF:

(aka "gain-bandwidth tradeoff" to engineers)

To speed up response, the cost is less amplification

To amplify, the cost is speed of response.

$w>1$: $A = \frac{1}{1-(>1)} < 0$ $\quad \underline{\tau < 0}$: exp'l growth

? → Return to equations:

$$\tau \frac{dr}{dt} = -\cancel{(1-w)}r + I$$
$$(w-1)r$$

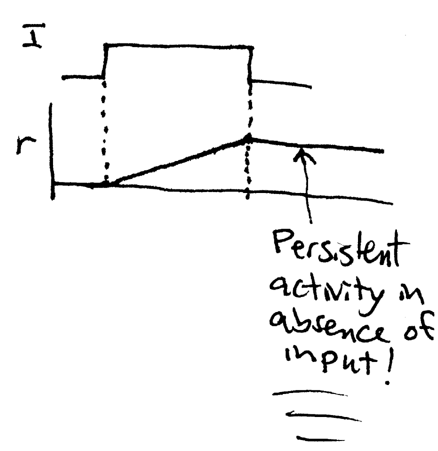
↳ exponential growth $r \sim e^{+t/|\tau_{eff}|}$

Finally, special case just on border of exp'l growth & decay

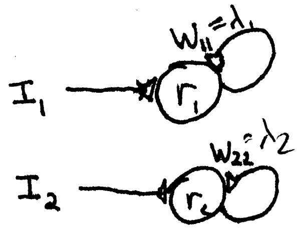
$w=1$:

$$\tau \frac{dr}{dt} = -\overbrace{\cancel{(1-w)}}^{=0} r + I$$

$$r = \frac{1}{\tau}\int I(t)\,dt \rightarrow \text{Integrator!}$$



III. Next most complicated netwk – 2 autapses



For a general network, we replace the single recurrent connection of weight w by a matrix of connection weights $\overleftrightarrow{W}$

where $W_{ij} \equiv$ strength of connection ~~from~~ from neuron j onto neuron i

Above example: $\overleftrightarrow{W} = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}$

$$\tau \frac{dr_1}{dt} = -r_1 + \lambda_1 r_1 + I_1$$

$$\tau \frac{dr_2}{dt} = -r_2 + \lambda_2 r_2 + I_2$$

$$\rightarrow \tau \frac{d}{dt}\begin{pmatrix} r_1 \\ r_2 \end{pmatrix} = -\begin{pmatrix} r_1 \\ r_2 \end{pmatrix} + \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}\begin{pmatrix} r_1 \\ r_2 \end{pmatrix} + \begin{pmatrix} I_1 \\ I_2 \end{pmatrix}$$

let $\vec{r} = \begin{pmatrix} r_1 \\ r_2 \end{pmatrix}$, $\vec{I} = \begin{pmatrix} I_1 \\ I_2 \end{pmatrix}$

$$\Rightarrow \tau \frac{d\vec{r}}{dt} = -\vec{r} + \overleftrightarrow{W} \cdot \vec{r} + \vec{I} \quad \rightarrow \text{general form}$$

In this case, $\overleftrightarrow{W}$ is diagonal, reflecting that neurons do not interact so we can solve immediately as 2 separate autapses

$$r_1 \rightarrow r_{1,\infty} = \frac{r_1}{1-\lambda_1} \qquad A_1 = \frac{1}{1-\lambda_1}$$

w/time const. $\tau_{1,eff} = \dfrac{\tau}{1-\lambda_1}$

$$r_2 \rightarrow r_{2,\infty} = \frac{r_2}{1-\lambda_2}$$

w/ $\tau_{2,eff} = \dfrac{\tau}{1-\lambda_2}$

e.g. if $\lambda_1 = \frac{1}{2} \rightarrow A_1 = \frac{1}{1-\frac{1}{2}} = 2 \rightarrow r_{1,\infty} = 2I_1$

$\tau_{1,eff} = 2\tau$

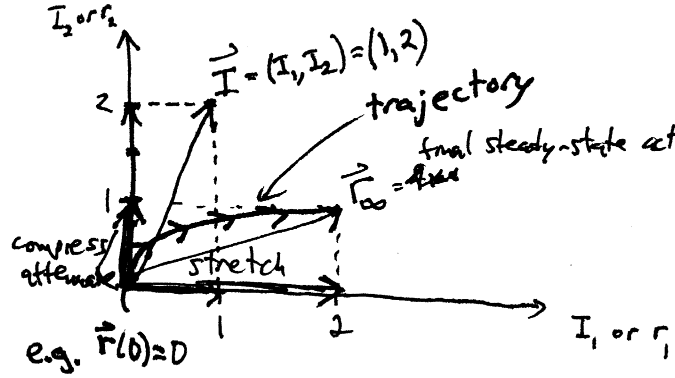
if $\lambda_2 = -1 \rightarrow A_2 = \frac{1}{1-(-1)} = \frac{1}{2}$ $\quad r_{2,\infty} = \frac{1}{2} I_2$

$\tau_{2,eff} = \frac{1}{2}\tau$

It's nice to picture this graphically, as this graphical description will generalize easily to more general connectivities:

Suppose $\vec{I} = \begin{pmatrix} 1 \\ 2 \end{pmatrix}$

A. ↳decompose: into indep. components $= \underbrace{\begin{pmatrix} 1 \\ 0 \end{pmatrix}}_{\text{1st component}} + 2\underbrace{\begin{pmatrix} 0 \\ 1 \end{pmatrix}}_{\text{2nd component}}$

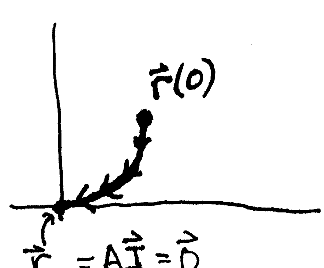


B. We have just seen that the effect of the network is to
$\boxed{\text{stretch}}$ the 1st component by a factor of 2
+ $\boxed{\text{compress}}$ the 2nd component to a factor ½
attenuate

C. Dynamics: although we'll end up at $\vec{r}_\infty$, the trajectory to get there won't generally be a straight line:

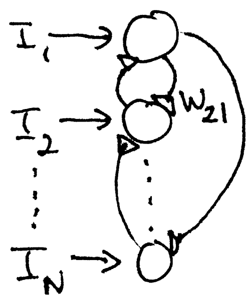
Rather: attenuation is fast (because $\tau_{eff} = A\tau$)
stretched component moves slowly " "

ASIDE:
[Likewise, if input $= \vec{0}$ fast 1st (r_1) component decays before slow 2nd (r_2) component



Note that always eventually decay to $\vec{0}$ if no input, unless network has a mode that blows up ($\lambda > 1$) or integrates ($\lambda = 1$)]

IV. General network



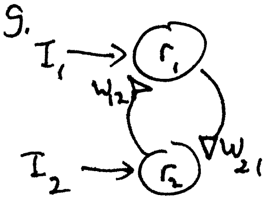
For the general network, we will see that we can again identify certain input components $\vec{\xi}^{(i)}$ that the network simply amplifies/stretches or attenuates (i.e. so that the output is simply a scaled version of the input). The goal, therefore, is to decompose the input into such components first, and then treat these components separately.

Again, equations are:

$$\tau \frac{d\vec{r}}{dt} = -\vec{r} + \overleftrightarrow{W}\cdot\vec{r} + \vec{I} \qquad (*)$$

but now $\overleftrightarrow{W}$ is not diagonal

e.g.



$$W = \begin{pmatrix} 0 & W_{12} \\ W_{21} & 0 \end{pmatrix}$$

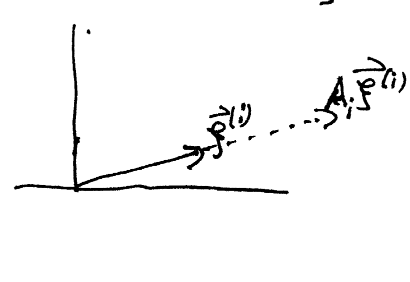
$$\tau \frac{dr_1}{dt} = -r_1 + W_{12} r_2 + I_1$$

$$\tau \frac{dr_2}{dt} = -r_2 + W_{21} r_1 + I_2$$

Notice: input patterns like $\vec{I} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$ will not simply be stretched into $c\begin{pmatrix} 1 \\ 0 \end{pmatrix}$ because neurons are now coupled.

$\Rightarrow$ Need to find new input patterns $\vec{\xi}$ that are simply stretched by $\overleftrightarrow{W}$,

i.e. for which $\overleftrightarrow{W}\cdot\vec{\xi}^{(i)} = \lambda_i \vec{\xi}^{(i)}$ $\Rightarrow$ eigenvectors of $\overleftrightarrow{W}$ with associated eigenvalue λ_i



Suppose we have found these eigenvectors:

Then decompose $\vec{I}$ and $\vec{r}$ into these eigenvector components:

$$\vec{I} = \sum_{i=1}^{N} b_i \vec{\xi}^{(i)}$$

$$\vec{r} = \sum_{i=1}^{N} c_i \vec{\xi}^{(i)}$$

Plug into (*)

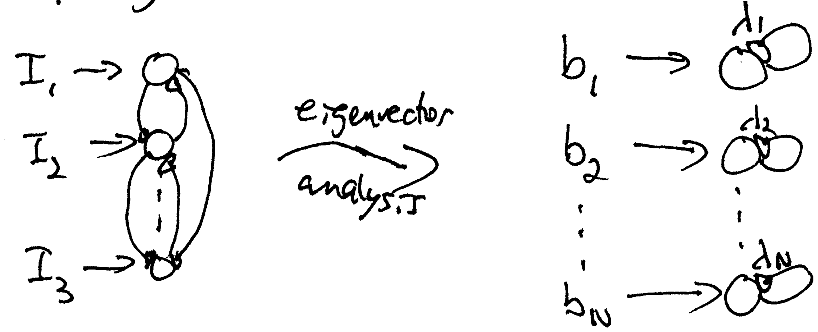
$$\tau \frac{d}{dt}\left(\sum c_i \vec{\xi}^{(i)}\right) = -\left(\sum c_i \vec{\xi}^{(i)}\right) + \overleftrightarrow{W} \cdot \sum c_i \vec{\xi}^{(i)} + \sum b_i \xi^{(i)}$$

$$\sum_i \left(\tau \frac{dc_i}{dt}\right) \vec{\xi}^{(i)} = \sum_i \left(-c_i + \lambda_i c_i + b_i\right) \vec{\xi}^{(i)}$$

For this to hold, coefficients of each component must be equal:

$$\Rightarrow \boxed{\tau \frac{dc_i}{dt} = -c_i + \lambda_i c_i + b_i} \rightarrow$$ Autapse equation for each component!

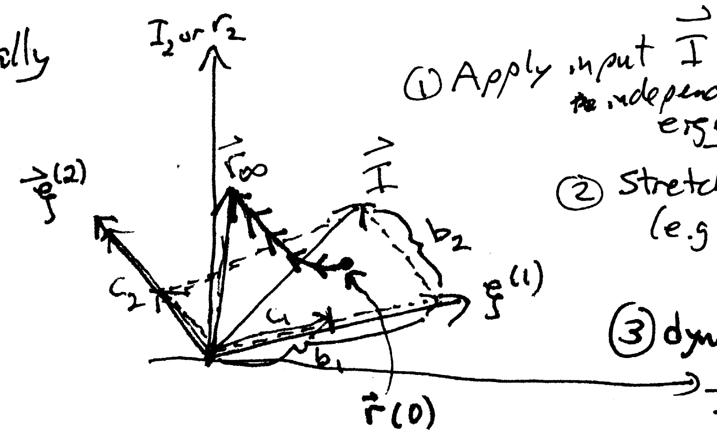
Conceptually:



where ○ now represents a pattern of neuronal firing $\vec{\xi}$.

[Idea: Graphically

SKIP

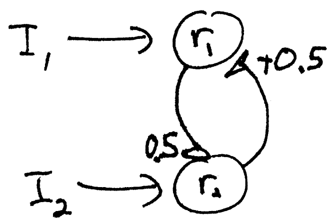


① Apply input $\vec{I}$ → decompose into independently behaving eigenvector components

② Stretch/compress components (e.g. suppose $\lambda_1 = 0.5$, $\lambda_2 = 1.5$)

③ dynamics: fast for c_1, slow for c_2]

Example 1:

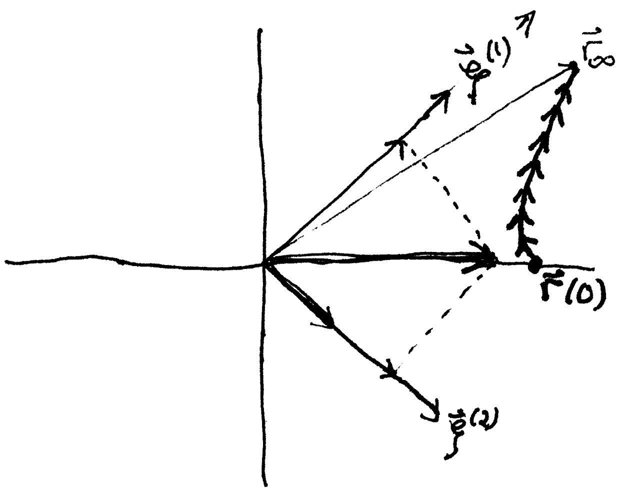


Can you guess the (eigenvectors) input patterns that will be amplified? attenuated?

By symmetry, eigenvectors must have same magnitude for each component

$\xi^{(1)} = \begin{pmatrix} 1 \\ 1 \end{pmatrix} \longrightarrow$ amplified common input (2 neurons help each other out) $\rightarrow \lambda_1 = \frac{1}{2} \rightarrow A_1 = \frac{1}{1-\frac{1}{2}} = 2$

$\xi^{(2)} = \begin{pmatrix} 1 \\ -1 \end{pmatrix} \longrightarrow$ attenuated differences between inputs (neurons fight each other) $\rightarrow \lambda_2 = -\frac{1}{2} \rightarrow A_2 = \frac{1}{\frac{3}{2}} = \frac{2}{3}$

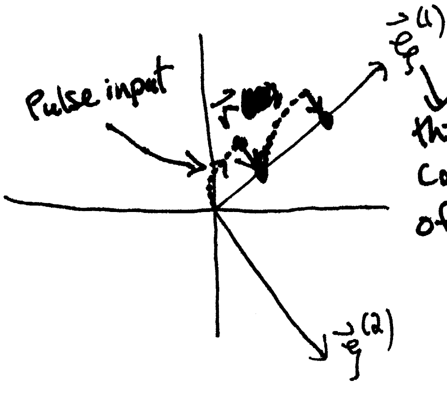


e.g. let $\vec{I} = \begin{pmatrix} 1 \\ 0 \end{pmatrix} = \frac{1}{2}\begin{pmatrix} 1 \\ 1 \end{pmatrix} + \frac{1}{2}\begin{pmatrix} 1 \\ -1 \end{pmatrix}$

Example 2: Change weights above to 1 and 1

$\Rightarrow$ integrator : $\lambda_1 = 1 \rightarrow A_2 = \infty \rightarrow$ no attenuation (+ same eigenvects.)

$\lambda_2 = -1 \rightarrow A_2 = \frac{1}{2}$



this is coding axis of integrator!

e.g. if input $\vec{I} = \vec{0}$, component along $\vec{\xi}^{(2)}$ decays with $\tau_{eff,2} = \frac{1}{2}\tau$

component along $\vec{\xi}^{(1)}$ doesn't decay