A Mathematical Theory of the Functional Dynamics of Cortical and Thalamic Nervous Tissue

H. R. Wilson and J. D. Cowan

1973

Gosse Overal

Overview

Recall:

Localized model neurons

Earlier work of Wilson and Cowan (1972). Excitatory (E) and inhibitory (I) neurons.

$$E(t+\tau) = \left(1 - \int_{t-r}^{t} E(t')\mathrm{d}t'\right) \cdot \mathcal{S}_e\left(\int_{-\infty}^{t} \alpha(t-t')\left(c_1 E(t') - c_2 I(t') + P(t')\right)\mathrm{d}t'\right)$$

$$I(t+\tau') = \left(1 - \int_{t-r}^{t} I(t')\mathrm{d}t'\right) \cdot \mathcal{S}_i\left(\int_{-\infty}^{t} \alpha(t-t')\left(c_3 E(t') - c_4 I(t') + Q(t')\right)\mathrm{d}t'\right)$$

Recall:

Coarse Grained forms

$$\tau \frac{\mathrm{d}\bar{E}}{\mathrm{d}t} = -\bar{E} + (1 - r\bar{E})\mathcal{S}_e \left(kc_1\bar{E} - kc_2\bar{I} + kP\right)$$

$$\tau' \frac{\mathrm{d}\bar{I}}{\mathrm{d}t} = -\bar{I} + (1 - r\bar{I})\mathcal{S}_i \left(k'c_3\bar{E} - k'c_4\bar{I} + k'Q\right)$$

Biological Context

- The authors compare the neural tissue of 3 species:
  Edible frog, Rabbit and Man.
- The higher vertibrates have more neurons and cortical surface.
- The thickness of cortex layers increases,
  but packing density decreases

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- The authors compare the neural tissue of 3 species: Edible frog, Rabbit and Man.
- The higher vertibrates have more neurons and cortical surface.
- The thickness of cortex layers increases, but packing density decreases
- The number of neurons contained within a cylinder of cross sectional area of $1mm^2$ is roughly constant
- The authors postulate that: "individual anatomical regions of cerebral cortex are functinally organised as two-dimensional surfaces"
- and "One reason for the distribution of neurons in depth might be to provide the local redundancy necessary for reliable operation"

Goal: To model a very generalised cortex-like tissue

Assumptions:

- The cortical tissue is represented as a 2-D sheet.
- The cortical tissue consists of 2 types of neurons only, excitatory and inhibitory.
- The sheet is homogenous and isotropic
  i.e.
  - both types of neurons are uniformly distributed and
  - the lateral connectivity is dependent of distance only.
- Individual neurons summate incoming excitation both spatially and temporally, in a linear time-invariant fashion.
- Neurons have excitation thresholds θ and absolute refractory periods of duration r.
- There is a synaptic delay τ, i.e. the time between excitation reaching threshold and

1-D or 2-D?

The authors assume a 2-D sheet of cortical tissue.

Simplifying assumption

"Only stimuli that vary in one spatial dimension are considered"
Homogeneity and isotropy imply patterns will only vary in the same dimension.
Assumption: Space is one dimensional.

Equations

Dependent variables: $E(x,t)$, $I(x,t)$
Independent variables: $t, x \in \mathbb{R}$

Mean rates of arrival of impulses at excitatory neurons

$$\text{exc.:} \int_{-\infty}^{\infty} \varrho_e E\left(X, t - \frac{|x-X|}{v_e}\right) \beta_{ee}(x-X)\mathrm{d}X$$

$$\text{inh.:} \int_{-\infty}^{\infty} \varrho_e I\left(X, t - \frac{|x-X|}{v_i}\right) \beta_{ie}(x-X)\mathrm{d}X$$

And likewise for inhibitory neurons

Combine with external input and the post-synaptic membrane potential behaviour.

Mean value of excitation for excitable neuron at t, x:

$$N_e(x,t) = \int_{-\infty}^{t} \left(\int_{-\infty}^{\infty} \varrho_e E\left(X, T - \frac{|x-X|}{v_e}\right) \beta_{ee}(x-X)\mathrm{d}X - \int_{-\infty}^{\infty} \varrho_e I\left(X, T - \frac{|x-X|}{v_i}\right) \beta_{ie}(x-X)\mathrm{d}X \pm P(x,T) \right) \alpha(t-T)\mathrm{d}T$$

And likewise for inhibitory neurons

Finishing touches

Sensitive neurons

i.e. not refractory $R_e(x, t) = \left(1 - \int_{t-r_e}^{\infty} E(x, T)\mathrm{d}T\right) \varrho_e \delta x$

Finishing touches

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Expected number of activated neurons in interval δt

$$E(x, t+\tau)\varrho_e \delta x \delta t = R_e(x,t) \cdot \mathcal{S}_e(N_e)\delta t$$

where $\mathcal{S}$ is the response function.

Hence we get

$$
\begin{aligned}
& E(x, t+\tau)\varrho_e \delta x \delta t \\
&= \left(1 - \int_{t-r_e}^{\infty} E(x,T)\mathrm{d}T\right) \varrho_e \delta x \cdot \mathcal{S}_e \Bigg[\\
& \int_{-\infty}^{t} \left(\int_{-\infty}^{\infty} \varrho_e E\left(X, T - \frac{|x-X|}{v_e}\right) \beta_{ee}(x-X)\mathrm{d}X \right. \\
& - \int_{-\infty}^{\infty} \varrho_e I\left(X, T - \frac{|x-X|}{v_i}\right) \beta_{ie}(x-X)\mathrm{d}X \\
& \left. \pm P(x,T) \right) \alpha(t-T)\mathrm{d}T \Bigg] \delta t
\end{aligned}
$$

And likewise for inhibitory neurons.

ϱ_e cancels and we let $\delta t, \delta x \to 0$.

We assume $\alpha(t) = \alpha e^{-\frac{t}{\mu}}$, where μ is the membrane time constant.

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Further assumptions concerning simplification:

- Velocity of impulse propagation is very large compared to domain size.
- Use time coarse graining:

$$\langle E(x,t)\rangle = \frac{1}{\mu}\int_{-\infty}^{t} E(x,T)e^{-\frac{t-T}{\mu}}\,\mathrm{d}T$$

  and likewise for I, P and Q.
- $r_e \ll \mu$ and $\tau \ll \mu$

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Let $\otimes$ denote the convolution operation

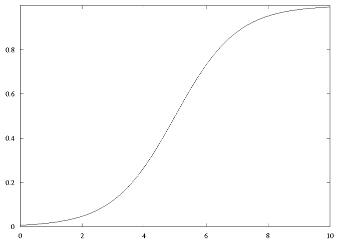
Simplified equations

$$\mu\frac{\partial}{\partial t}\langle E(x,t)\rangle = -\langle E(x,t)\rangle + (1 - r_e\langle E(x,t)\rangle) \cdot \mathcal{S}_e[\alpha\mu(\varrho_e\langle E(x,t)\rangle \otimes \beta_{ee}(x) - \varrho_i\langle I(x,t)\rangle \otimes \beta_{ie}(x) \pm \langle P(x,t)\rangle)]$$

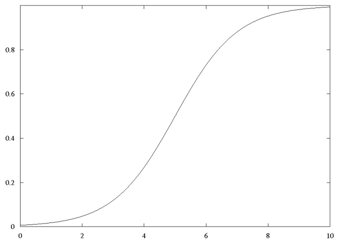
$$\mu\frac{\partial}{\partial t}\langle I(x,t)\rangle = -\langle I(x,t)\rangle + (1 - r_i\langle I(x,t)\rangle) \cdot \mathcal{S}_i[\alpha\mu(\varrho_e\langle E(x,t)\rangle \otimes \beta_{ei}(x) - \varrho_i\langle I(x,t)\rangle \otimes \beta_{ii}(x) \pm \langle Q(x,t)\rangle)]$$

Recall:

Sigmoid function



Recall:
Sigmoid function



Response function choice

$$\mathcal{S}_e(N_e) = \left(1 + e^{-\nu(N_e - \theta_e)}\right)^{-1} - \left(1 + e^{\nu\theta_e}\right)^{-1}$$

Exponentials are chosen for the connectivity function.
The argument here is distance between two points $(X - x)$

$$\beta_{jj'}(x) = b_{jj'}\, e^{-|x|/\sigma_{jj'}}$$

Notes

Localized

Set the β functions constant (homogenous) over space.
This localized model exactly follows the model discussed last time for homogenous solutions.

non-linearity

The Partial differential integro formulae are very complex still.
Analysis of behaviour and pattern formation is therefore done numerically by the authors.

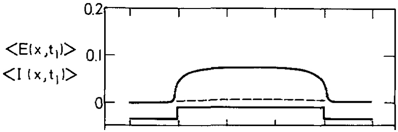
To account for patterns, some parameters are chosen and three distinct types of patterns can arise.

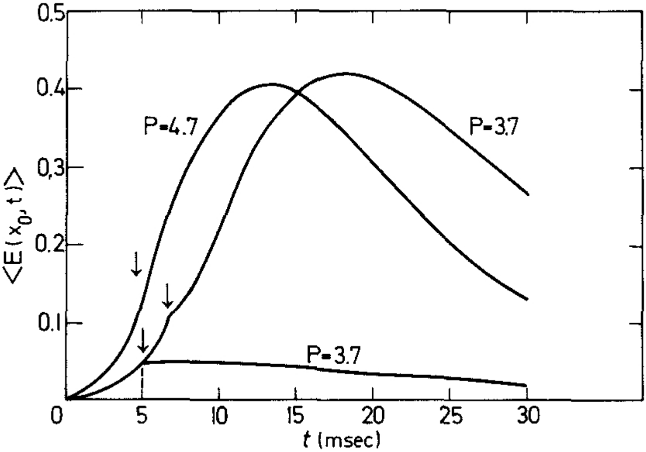
Apply stimulus in a block wave fashion

We apply the following:

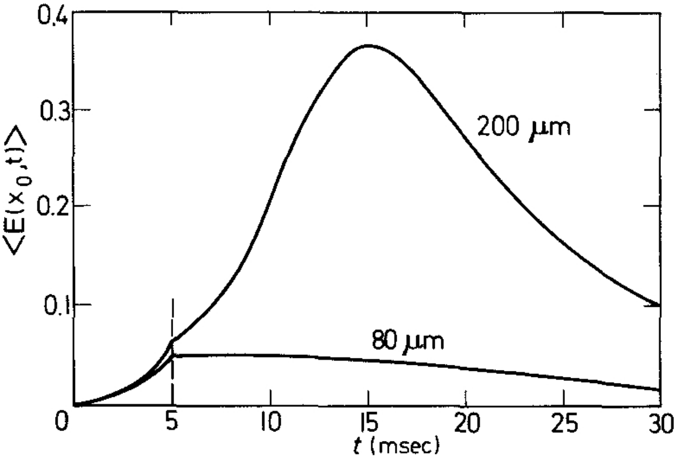
$$\langle P(x,t)\rangle = \begin{cases} 0 & \text{for} \quad x < L_1 \\ P & \text{for} \quad L_1 \leq x \leq L_2 \\ 0 & \text{for} \quad x > L_2 \end{cases}$$

Length L, period Δt and signal strength P



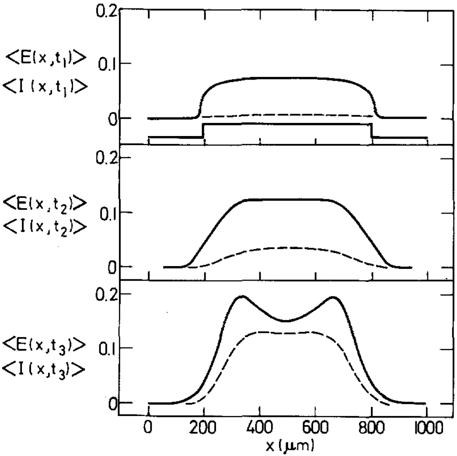

0.5
0.4
0.3
0.2
0.1
0
5
10
15
20
25
30
P=4.7
P=3.7
P=3.7
<E(x0, t)>
t (msec)

Active Transients

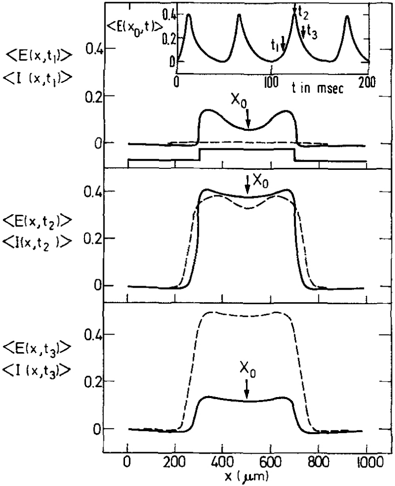


Active Transients

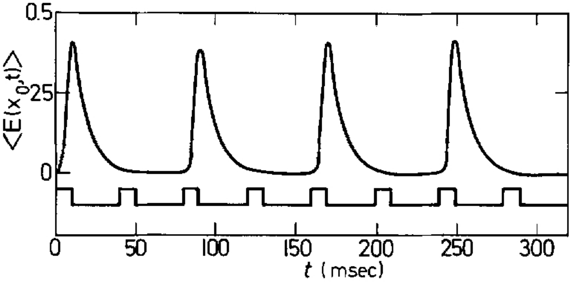
For even wider $L_2 - L_1$ we get edge inhancement:



Apply sustained stimulus:



Thalamic Oscilators



Summary of results

We conclude:

- Active transients can occur, but have a noise filter.
- Localised limit cycles can occur under sustained stimulus. The frequency increases monotonely with the stimulus.
- Thalamic Oscilators can also be modeled using this model. Frequency demultiplication can occur.