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Excitatory and Inhibitory Interactions in Localized Populations of Model Neurons

Gosse Overal

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Overview

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- Response Functions
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 - Saddle-node bifurcation
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Introduction	Model	Time Coarse Graining	Phase Plane Analysis
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Context

Model Neurons

Populations Higher functions of neurons \Rightarrow Complex patterns that require shift of focus, from single cell to cell populations.

Excitatory When excited, will fire increasing excitation.

Inhibitory When excited, will fire decreasing excitation.

Localized Close spatial proximity, interconnections random \Rightarrow neglect spatial interactions.

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Variables



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Equations

Discrete derivation: what happens at $t + \tau$, given E(t), I(t)?

$$E(t+\tau) = \left(1 - \int_{t-\tau}^{t} E(t') dt'\right)$$
$$\cdot S_e \left(\int_{-\infty}^{t} \alpha(t-t') \left(c_1 E(t') - c_2 I(t') + P(t')\right) dt'\right)$$
$$I(t+\tau') = \left(1 - \int_{t-\tau}^{t} I(t') dt'\right)$$
$$\cdot S_i \left(\int_{-\infty}^{t} \alpha(t-t') \left(c_3 E(t') - c_4 I(t') + Q(t')\right) dt'\right)$$

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Refractory Period			

Refractory Period

After firing, refractory period r, assumed constant.

 Sensitive proportion

 Refractory cells:

 $\int_{t-r}^{t} E(t') dt'$

 Hence sensitive cells:

$$\left(1-\int_{t-r}^{t}E(t')\mathrm{d}t'\right)$$

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Response Functions			

Response Functions

Given excitation x(t) at the instant t:



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Response Functions			

Response Functions

Given excitation x(t) at the instant t:

S(x(t)) Proportion of sensitive cells that are excited at instant t

Excited cell A cell must receive at least threshold excitation

Example

 S_e and S_e

Assume x(t) is equal for all cells, $D(\theta)$ the threshold distribution function of the population. $S(x) = \int_0^{x(t)} D(\theta) d\theta$ 'All cells which have threshold θ , such that $\theta \le x(t)$, will start firing'

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Response Functions			

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Sigmoid functions

Definition

A function f(x) has sigmoid form if

1 f(x) is monotonically increasing on $(-\infty, \infty)$

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$$\lim_{x\to-\infty} f(x) = 0$$
, $\lim_{x\to\infty} f(x) = 1$

3 f has only one inflection point.

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Excitation			

New Excitation

New excitation at instant t'

E(t') = cells that start firing.

$$c_1 E(t') - c_2 I(t') + P(t')$$

- c1 average number excitatory synapses connected to excitatory cell
- c₂ average number inhibitory synapses connected to excitatory cell

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P(t') External input to excitatory subpopulation

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Excitation			

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Decay and Total

$\alpha(t)$, the synaptic response function

After excitation, the rate of firing decays, $\alpha(t)$ $\alpha(0) = 1$, $\alpha(t) \rightarrow 0$ as $t \rightarrow \infty$

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Excitation			

Decay and Total

$\alpha(t)$, the synaptic response function

After excitation, the rate of firing decays, $\alpha(t)$ $\alpha(0) = 1$, $\alpha(t) \rightarrow 0$ as $t \rightarrow \infty$

Total excitation at instant t

$$\int_{-\infty}^{t} \alpha(t-t') \left(c_1 E(t') - c_2 I(t') + P(t') \right) \mathrm{d}t'$$

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Motivation			

Motivation

Clear physiological interpretation, Math. complexity

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Motivation			

Motivation

Clear physiological	
interpretation,	\rightarrow
Math. complexity	

New biological assumptions, Removal of temporal integrals (Phase Plane Analysis)

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Motivation			

Motivation

Clear physiological		New biological assumptions,
nterpretation,	\rightarrow	Removal of temporal integrals
Math. complexity		(Phase Plane Analysis)

"Replace by average over appropriate interval"

Definition

Replace f(t) by

$$\bar{f}(t) := \frac{1}{s} \int_{t-s}^{t} f(t') \mathrm{d}t'$$

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Motivation			

Biological Assumptions

- Rapid behaviour which is lost is not significant for the problem at hand
- $\alpha(t) \sim 1$ for $0 \leq t \leq r$, $\alpha(t)$ drops fairly rapidly to 0 for t > r

Coarse Grained variables

$$\int_{t-r}^{t} E(t') dt' \to r\bar{E}(t)$$
$$\int_{-\infty}^{t} \alpha(t-t') E(t') dt' \to k\bar{E}(t)$$

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Equations			

Equations

Note: smoothing effect
$$\rightarrow$$
 use Taylor expansions.
 $E(t + \tau) \rightarrow \overline{E}(t) + \tau \frac{d\overline{E}}{dt} \qquad I(t + \tau') \rightarrow \overline{I}(t) + \tau' \frac{d\overline{I}}{dt}$

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

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

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Transform, specify and clean up

Definition $\mathcal{S}(x(t)) := rac{1}{1 + \exp\left(-a(x(t) - \theta) ight)} - rac{1}{1 + \exp\left(a\theta\right)}$

Note: Maximum slope $S'(\theta) = \frac{a}{4}$ Total amount of cells has to be corrected.

Correct for transformation and rename variables and parameters

$$\tau_e \frac{\mathrm{d}E}{\mathrm{d}t} = -E + (k_e - r_e E) \mathcal{S}_e(c_1 E - c_2 I + P)$$

$$\tau_i \frac{\mathrm{d}I}{\mathrm{d}t} = -I + (k_i - r_i I) \mathcal{S}_i(c_3 E - c_4 I + Q)$$

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Isoclines			

Isoclines

$$\frac{\mathrm{d}E}{\mathrm{d}t} = 0 \ c_2 I = c_1 E - \mathcal{S}_e^{-1} \left(\frac{E}{k_e - r_e E}\right) + P$$
$$\frac{\mathrm{d}I}{\mathrm{d}t} = 0 \ c_3 E = c_4 I + \mathcal{S}_i^{-1} \left(\frac{I}{k_i - r_i I}\right) - Q$$



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Isoclines			

Note that:

$$S_e^{-1} : [k_e - 1, k_e] \to (\infty, \infty)$$
$$S_i^{-1} : [k_i - 1, k_i] \to (\infty, \infty)$$

 These functions are monotonically increasing with one inflection point.

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Isoclines			

Note that:

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These functions are monotonically increasing with one inflection point.

So we conclude

- I-isocline: E as a monotonically increasing function of I
- E-isocline: I as a generally decreasing function of I, except over a short range where it may temporarily increase.

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Saddle-node bifurcation			

c₁ large



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Saddle-node bifurcation			

c_1 at bifurcation



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Saddle-node bifurcation			

c_1 small



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Saddle-node bifurcation			

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When do we have a kink in $\frac{dE}{dt} = 0$?



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Saddle-node bifurcation			

When do we have a kink in $\frac{dE}{dt} = 0$?

- No kink \Rightarrow only trivial solution.
- We have a kink \Leftrightarrow The maximum slope of the *E*-isocline (*I* as function of *E*) is greater that 0.

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Saddle-node bifurcation			

When do we have a kink in $\frac{dE}{dt} = 0$?

- No kink \Rightarrow only trivial solution.
- We have a kink ⇔ The maximum slope of the E-isocline (I as function of E) is greater that 0.

Tedious to compute, consider the slope of the E-isocline at the inflection point of \mathcal{S}_e^{-1} :This slope is

$$\left(\frac{c_1}{c_2}-\frac{9}{a_ec_2}\right)$$

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Theorem			

Theorem

If $c_1 > \frac{9}{a_e}$, then there is a class of constant values P and Q such that there are three equilibria.

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Theorem			

Theorem

If $c_1 > \frac{9}{a_e}$, then there is a class of constant values P and Q such that there are three equilibria.

Proof.

- Sufficient condition for kink.
- *I*-isocline approaches vertical line as asymptote.
- Transforming along the axes using P and Q can transform the I-isocline to just the right position.

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Theorem			

Recall: small c_1



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Theorem			
Note:	Actually $c_1 < rac{9}{a_e}$. Zooming out yield	was satisfied (barely) ds:	
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Theorem			

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Transforming the isoclines using P = 0.5, Q = -5, we get



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