Excitatory and Inhibitory Interactions in Localized Populations of Model Neurons

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Overview

Context

Model Neurons

Populations	Higher functions of neurons ⇒ 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 ⇒ neglect spatial interactions.

Variables

$E(t)$: Proportion of excitatory cells firing per unit of time at the instant t

Continuous,
value in $[0, 1]$.

$I(t)$: Proportion of Inhibitory cells firing per unit of time at the instant t

Continuous,
value in $[0, 1]$.

t: Time

Continuous

Equations

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

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

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

Refractory Period

After firing, refractory period r, assumed constant.

Sensitive proportion

Refractory cells:

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

Hence sensitive cells:

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

Response Functions

Given excitation $x(t)$ at the instant t:

$\mathcal{S}_e$ and $\mathcal{S}_e$

$\mathcal{S}(x(t))$ Proportion of sensitive cells that are excited at instant t

Excited cell A cell must receive at least threshold excitation

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Example

Assume $x(t)$ is equal for all cells, $D(\theta)$ the threshold distribution function of the population.

$\mathcal{S}(x) = \int_0^{x(t)} D(\theta)\mathrm{d}\theta$

'All cells which have threshold θ,
such that $\theta \leq x(t)$, will start firing'

Sigmoid functions

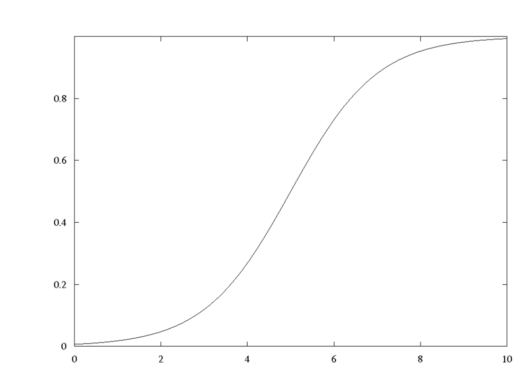
Definition

A function $f(x)$ has sigmoid form if

1. $f(x)$ is monotonically increasing on $(-\infty, \infty)$
2. $\lim_{x\to-\infty} f(x) = 0$, $\lim_{x\to\infty} f(x) = 1$
3. f has only one inflection point.

Example

$$f(x) = \frac{1}{1 + e^{-a(x-\theta)}}$$



New Excitation

New excitation at instant t'

$E(t')$ = cells that *start* firing.

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

- c_1 average number excitatory synapses connected to excitatory cell
- c_2 average number inhibitory synapses connected to excitatory cell
- $P(t')$ External input to excitatory subpopulation

Decay and Total

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

After excitation, the rate of firing decays, $\alpha(t)$
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Total excitation at instant t

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

Motivation

Clear physiological
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"Replace by average over appropriate interval"

Definition

Replace $f(t)$ by

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

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

$$\int_{t-r}^{t} E(t')\mathrm{d}t' \rightarrow r\bar{E}(t)$$

$$\int_{-\infty}^{t} \alpha(t-t')E(t')\mathrm{d}t' \rightarrow k\bar{E}(t)$$

Equations

Note: smoothing effect → use Taylor expansions.

$E(t+\tau) \rightarrow \bar{E}(t) + \tau \frac{\mathrm{d}\bar{E}}{\mathrm{d}t} \qquad I(t+\tau') \rightarrow \bar{I}(t) + \tau' \frac{\mathrm{d}\bar{I}}{\mathrm{d}t}$

$$\tau \frac{\mathrm{d}\bar{E}}{\mathrm{d}t} = -\bar{E} + (1 - r\bar{E})\mathcal{S}_e\left(kc_1\bar{E} - kc_2\bar{I} + kP\right)$$
$$\tau' \frac{\mathrm{d}\bar{I}}{\mathrm{d}t} = -\bar{I} + (1 - r\bar{I})\mathcal{S}_i\left(k'c_3\bar{E} - k'c_4\bar{I} + k'Q\right)$$

Transform, specify and clean up

Definition

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

Note: Maximum slope $\mathcal{S}'(\theta) = \frac{a}{4}$

Total amount of cells has to be corrected.

Correct for transformation and rename variables and parameters

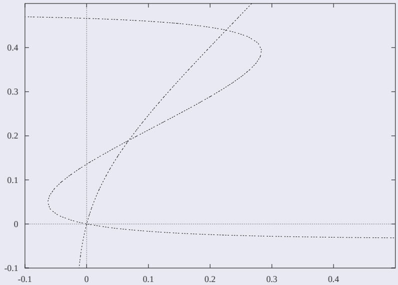
$$\tau_e \frac{\mathrm{d}E}{\mathrm{d}t} = -E + (k_e - r_e E)\mathcal{S}_e(c_1 E - c_2 I + P)$$

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

Isoclines

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

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



Note that:

- $\mathcal{S}_e^{-1} : [k_e - 1, k_e] \rightarrow (\infty, \infty)$
- $\mathcal{S}_i^{-1} : [k_i - 1, k_i] \rightarrow (\infty, \infty)$
- These functions are monotonically increasing with one inflection point.

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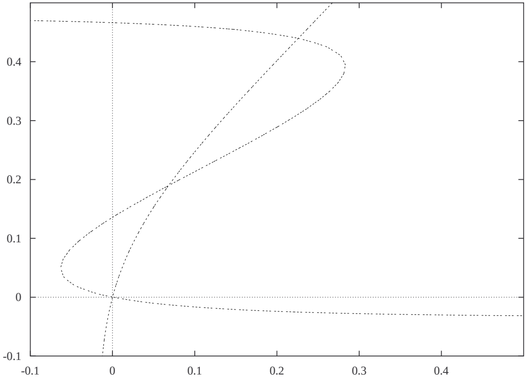
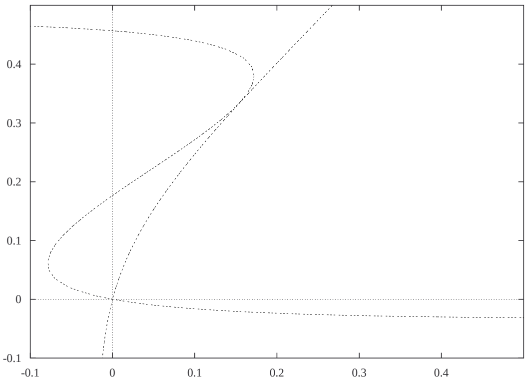
So we conclude

- 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.

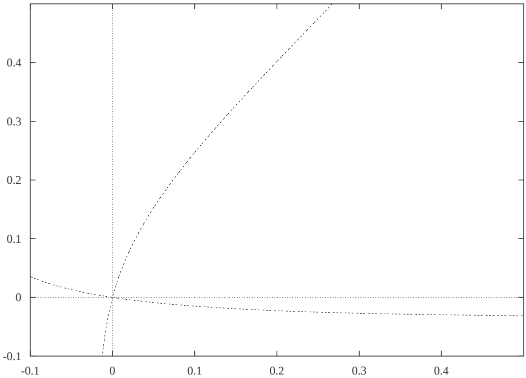
c_1 large



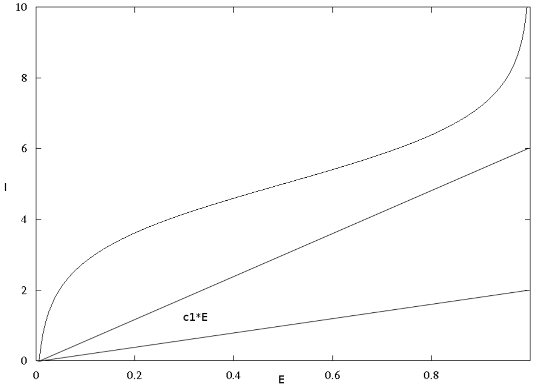
c_1 at bifurcation



c_1 small



When do we have a kink in $\frac{\mathrm{d}E}{\mathrm{d}t} = 0$?



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

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

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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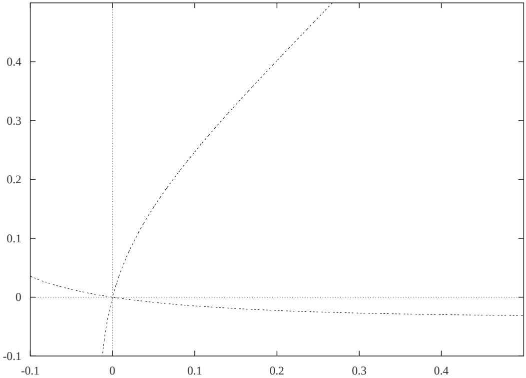
Proof.

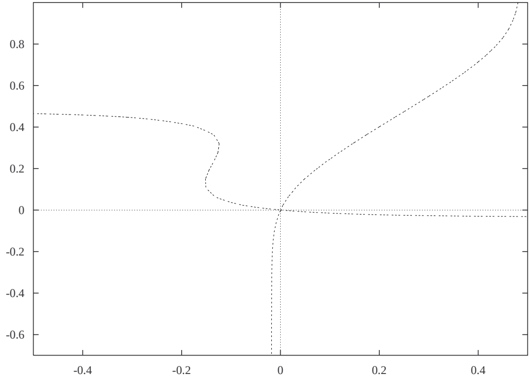
- Sufficient condition for kink.
- I-isocline approaches vertical line as asymptote.
- Transforming along the axes using P and Q can transform the I-isocline to just the right position.

□

Recall: small c_1



Note: Actually $c_1 < \frac{9}{a_e}$ was satisfied (barely)
Zooming out yields:



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