General information

Lecture Topic:
Introduction to Network models

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Some research papers related to the lectures are available on my webpage.

Supplementary teaching material: a chapter "Network Models" from a textbook "Theoretical Neuroscience" by P. Dayan and L. F. Abbott (MIT Press, 2001). It is freely available as a sample chapter
`http://people.brandeis.edu/~abbott/book/toc.html`

A neuron

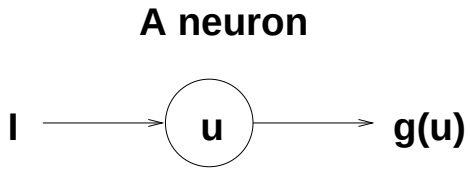
u: neuron's membrane potential.
τ: membrane time constant
I: input current to this neuron.

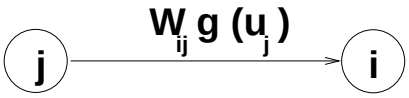
$\dot{u} = -u/\tau + I$ (like a capacitor)

Interaction between neurons

$g(u)$: Output value from a neuron, monotonic (with saturation and thresholds).
W_{ij}: synaptic weight from neuron j to i.
I_{ext}: the external input.

$I_i = I_{ext} + \sum_j W_{ij} g_j(u_j)$



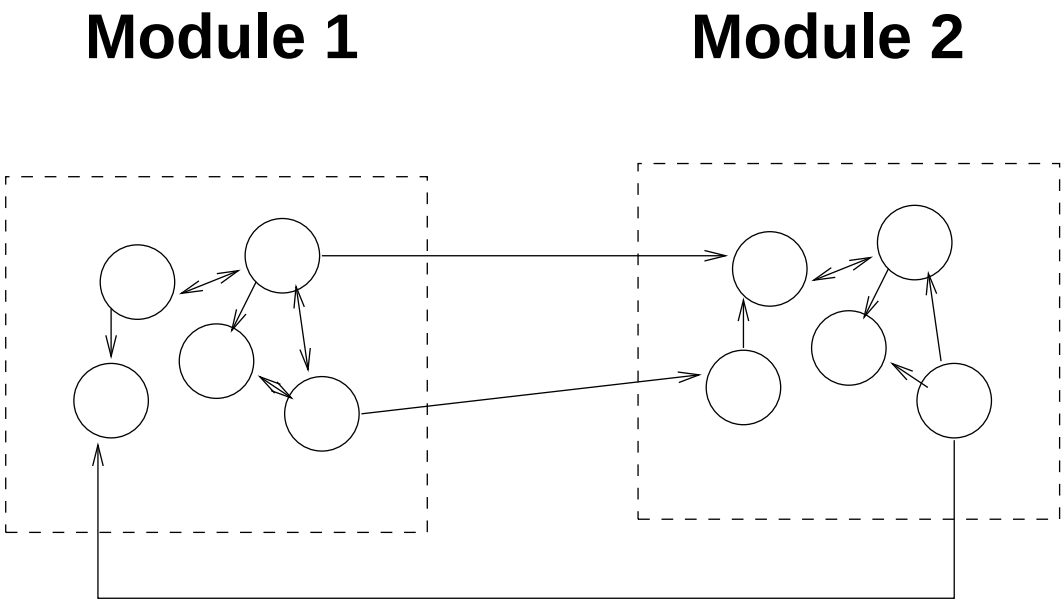


Excitatory and Inhibitory Neurons

Excitatory neuron j: $\rightarrow W_{ij} \geq 0$ for all i.
Inhibitory neuron j: $\rightarrow W_{ij} \leq 0$ for all i.

Organizations of the neural network in the brain

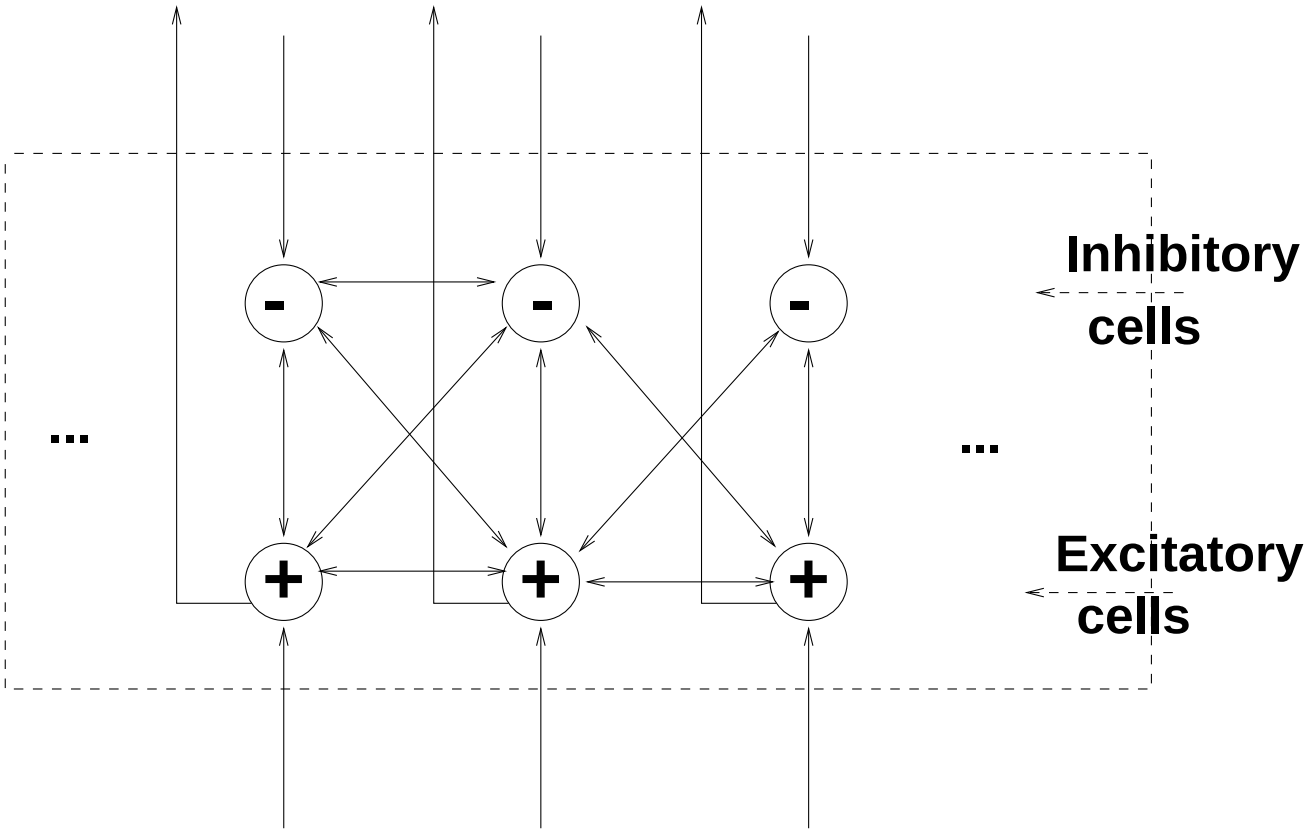
(1) The cortex is composed of different cortical **modules**.



(2) Different cortical modules **interact** with each other, often **reciprocally**.

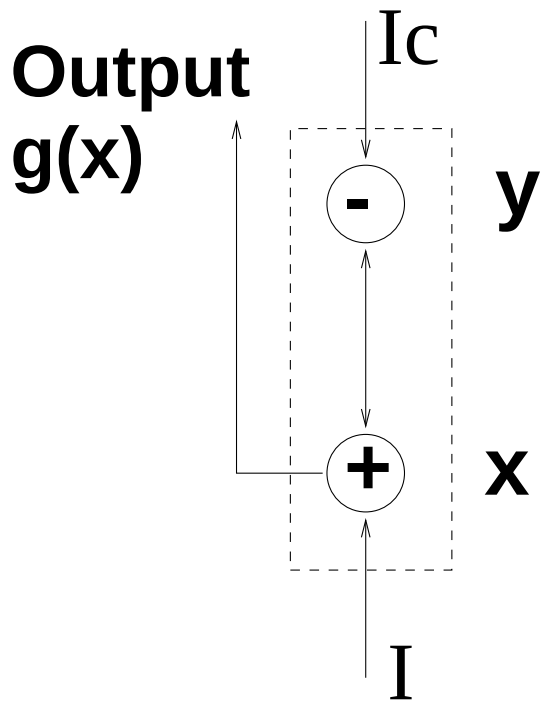
(3) Only the **excitatory** neurons output to other modules. Neurons that do not output to other modules are called **interneurons**.

The basic cortical circuit within a cortical area (module)



Neurons are often only connected to their **neighbors**, neuron groups are often located in distinctive **layers**. In this example, the excitatory neurons receive external inputs and send outputs from this cortical area.

A simple model of the basic circuit element



$$\dot{x} = -h \cdot g_y(y) - \alpha_x x + I, \quad (1)$$

$$\dot{y} = w \cdot g_x(x) - \alpha_y y + I_c. \quad (2)$$

x:	excitatory cell's membrane potential.
y:	inhibitory cell's membrane potential.
I:	external input to the excitatory cell
I_c:	external input to the inhibitory cell
h, w:	the synaptic weights between cells
$1/\alpha_x$,	$1/\alpha_y$: cells' membrane time constants

The input-output of this basic element

$(I, I_c) \to g_x(x)$.

Find the fixed point $(\bar{x}, \bar{y})$ where $\dot{x} = \dot{y} = 0$:

$$-h \cdot g_y(\bar{y}) - \alpha_x \bar{x} + I = 0$$
$$w \cdot g_x(\bar{x}) - \alpha_x \bar{y} + I_c = 0.$$

See how $g_x(\bar{x})$ depends on I and I_c

$$\begin{aligned} \delta g_x(\bar{x})/\delta I &= \frac{\alpha_y g'_x(\bar{x})}{\alpha_x \alpha_y + hw g'_y(\bar{y}) g'_x(\bar{x})} \\ \delta g_x(\bar{x})/\delta I_c &= \frac{-h g'_y(\bar{y}) g'_x(\bar{x})}{\alpha_x \alpha_y + hw g'_y(\bar{y}) g'_x(\bar{x})} \\ &= \frac{-h g'_y(\bar{y})}{\alpha_y} \cdot [\delta g_x(\bar{x})/\delta I] \end{aligned}$$

Compare with: $\delta g_x(\bar{x})/\delta I = g'_x(\bar{x})/\alpha_x$ — when the inhibitory interneuron (and external input I_c) is absent.

The basic element as a neural oscillator

$$\begin{aligned}\dot{x} &= -h \cdot g_y(y) - \alpha_x x + I,\\ \dot{y} &= w \cdot g_x(x) - \alpha_y y + I_c.\end{aligned}$$

Shift origin of the coordinates:
$x - \bar{x} \to x$, $y - \bar{y} \to y$, hence

$$\begin{aligned}\dot{x} &= -h \cdot (g_y(y + \bar{y}) - g_y(\bar{y})) - \alpha_x x,\\ \dot{y} &= w \cdot (g_x(x + \bar{x}) - g_x(\bar{x})) - \alpha_y y\end{aligned}$$

Linearize:

$$\begin{aligned}\dot{x} &= -h \cdot g_y'(\bar{y}) y - \alpha_x x,\\ \dot{y} &= w \cdot g_x'(\bar{x}) x - \alpha_y y\end{aligned}$$

Compare with:

$$\begin{aligned}\dot{x} &= -\omega y - \alpha x\\ \dot{y} &= \omega x - \alpha y\end{aligned}$$

or

$$\ddot{x} + 2\alpha\dot{x} + (\omega^2 + \alpha^2)x = 0$$

Hence: $hwg_x'(\bar{x})g_y'(\bar{y}) \to \omega^2$, frequency, $2\alpha\dot{x}$ is the damping term.

y could be seen as the momentum for x.

Oscillation trajectory

When $\alpha_x = \alpha_y = 0$, x and y oscillate around $(\bar{x}, \bar{y})$ in a closed curve

Lyapunov Function:

$$R \equiv \int_{\bar{x}}^{\bar{x}+x'} w(g_x(s) - g_x(\bar{x}))ds + \int_{\bar{y}}^{\bar{y}+y'} h(g_y(s) - g_y(y_o))ds = \text{constant} \geq 0$$

When $\alpha_x, \alpha_y > 0$, the oscillation is damped,

$$\begin{aligned} dR/dt &= -\alpha w(g_x(x) - g_x(x_o))(x - x_o) \\ &\quad -\alpha h(g_y(y) - g_y(y_o))(y - y_o) \leq 0 \end{aligned}$$

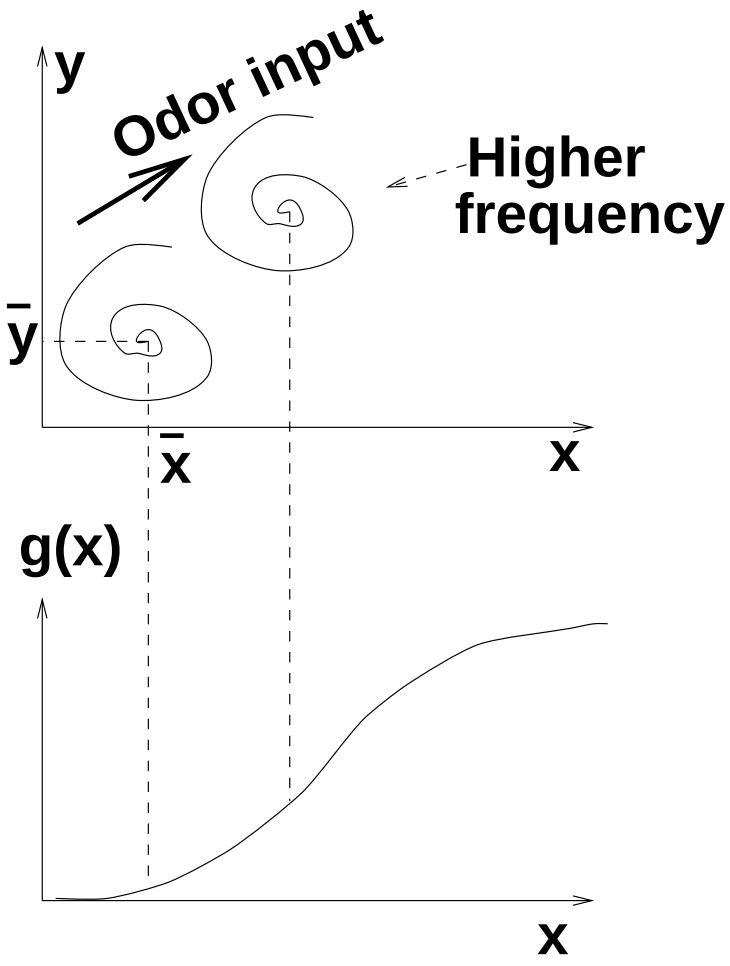
A non-linear damped oscillator.

Example: Olfactory bulb

Odor Input: I, Higher center feedback I_c. x: the excitatory mitral cells. y : the inhibitory granule cells.

(Reference reading for oscillation analysis and olfactory computation: Zhaoping Li (1995) Modeling the Sensory Computations of the Olfactory Bulb Published in Models of Neural Networks Vol. 2, Eds. E. Domany, J. L. van Hemmen, and K. Schulten, page 221-251. Springer-Verlag New York. Available on line at `http://www.gatsby.ucl.ac.uk/~zhaoping/olfaction.html`.)

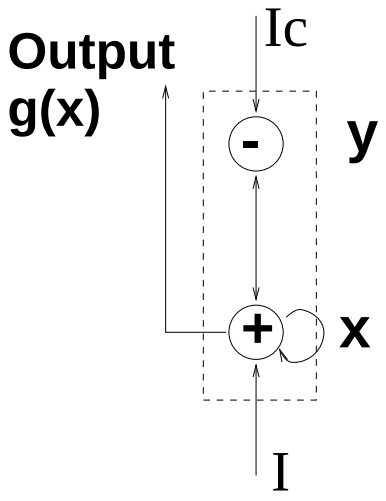
The mean field solution $\bar{x}$ and oscillation frequency $hwg'_x(\bar{x})g'_y(\bar{y})$ are input (odor) dependent.



Prediction: The inhibitory cells oscillate with a quarter cycle phase lag behind the neighboring excitatory cells — observed by Frank Eeckman and W. Freeman, 1989.

To think about now: This oscillator is damped, i.e., does not spontaneously oscillate. However, the olfactory bulb exhibit spontaneous oscillation (40 Hz) under odor inputs which does not oscillate. Why?

A slight modification — including self-excitation



$$\begin{aligned} \dot{x} &= -h \cdot g_y(y) - \alpha_x x + J_o g_x(x) + I, \\ \dot{y} &= w \cdot g_x(x) - \alpha_y y + I_c. \end{aligned}$$

$J_o g'_x(\bar{x})$ can be seen as negative dissipation to overcome the dissipation caused by α_x.

Consequences: (1) Input-output $I \to g(x)$ has a larger gain (slope).

(2) Non-damping oscillation possible when J_o is strong enough,

Example: Response of a visual cortical cell, say, tuned to an oriented bar or edge, to external or contextual inputs I and I_c.

$$\dot{x} = -x - g_y(y) + J_o g_x(x) + I \quad (3)$$

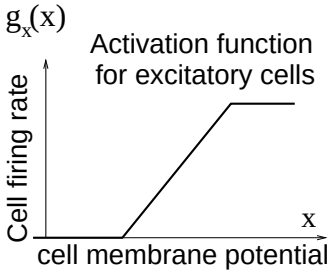
$$\dot{y} = -y + g_x(x) + I_c \quad (4)$$

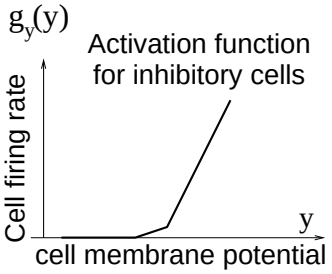
At equilibrium:

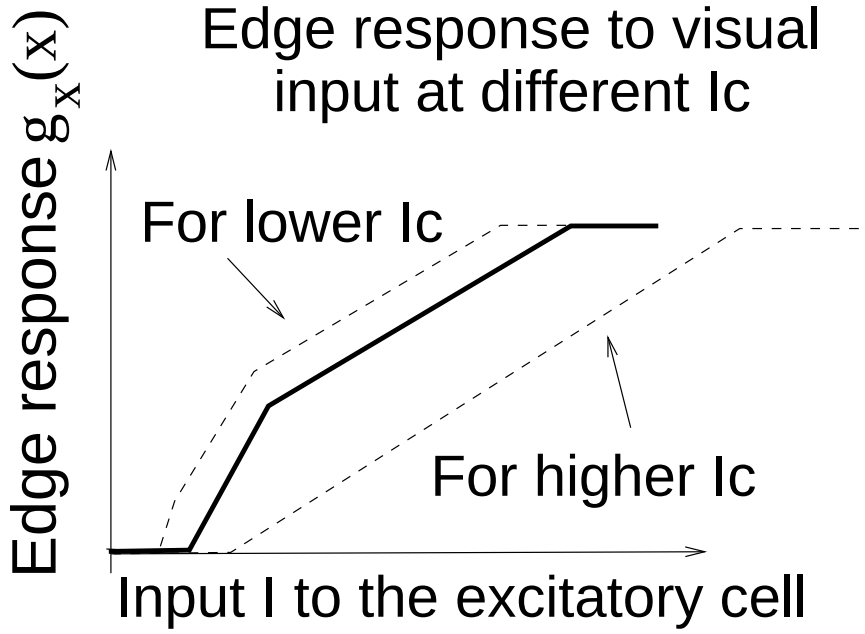
$$\frac{\delta g_x(\bar{x})}{\delta I} = \frac{g'_x(\bar{x})}{1 + g'_x(\bar{x}) g'_y(\bar{y}) - J_o g'_x(\bar{x})},$$

$$\frac{\delta g_x(\bar{x})}{\delta I_c} = -g'_y(\bar{y}) \frac{\delta g_x(\bar{x})}{\delta I}$$

Gain Control: $\frac{\delta g_x(\bar{x})}{\delta I} = \frac{g'_x(\bar{x})}{1+g'_x(\bar{x})g'_y(\bar{y})-J_o g'_x(\bar{x})}$,





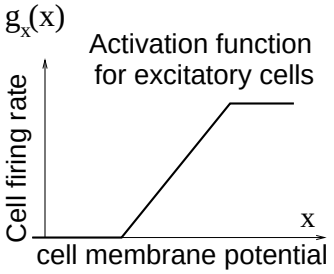


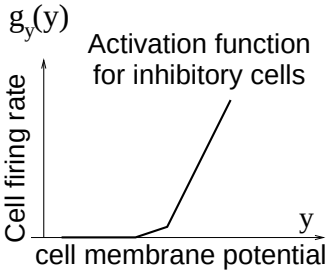
Facilitatory and suppressing modulations

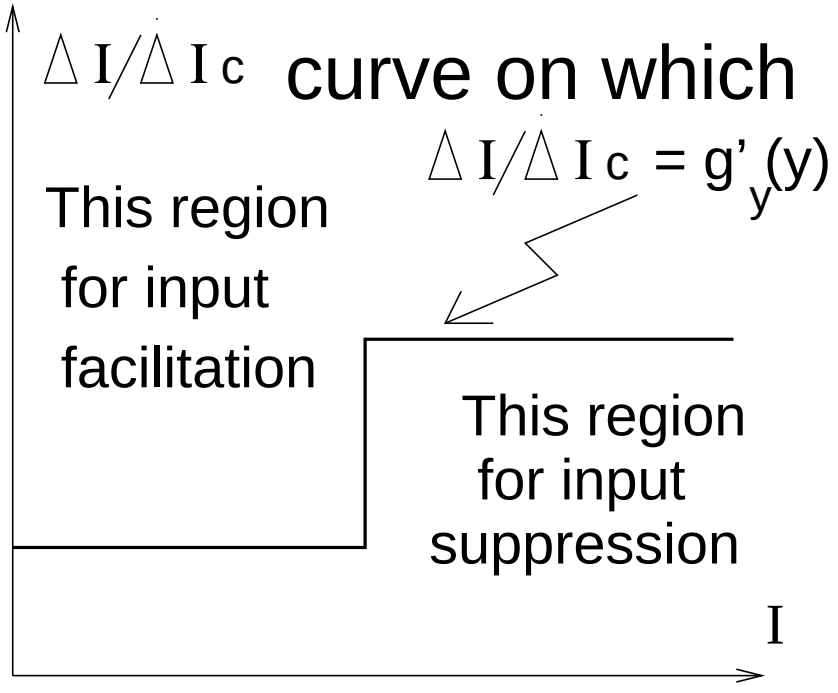
Shifting (I, I_c) to $(I + \Delta I, I_c + \Delta I_c) \rightarrow$

$\Delta g_x(\bar{x}) \approx (\delta g_x(\bar{x})/\delta I)(\Delta I - g'_y(\bar{y})\Delta I_c)$,

$\Delta g_x(\bar{x}) > 0$ if $\Delta I/\Delta I_c > g'_y(\bar{y})$.







Increased tendency to oscillation

$$\begin{aligned} \dot{x} &= -h \cdot g_y(y) - \alpha_x x + J_o g_x(x) + I, \\ \dot{y} &= w \cdot g_x(x) - \alpha_y y + I_c. \end{aligned}$$

Linearize around the fixed point $\bar{x}, \bar{y}$, shifting origin to $\bar{x}, \bar{y}$:

$$\begin{aligned} \dot{x} &= -h \cdot g'_y(\bar{y}) y - (\alpha_x - J_o g'_x(\bar{x})) x, \\ \dot{y} &= w \cdot g'_x(\bar{x}) x - \alpha_y y \end{aligned}$$

Arriving at

$$\ddot{x} + (2\alpha - J_o g'_x(\bar{x}))\dot{x} + (hw g'_y(\bar{y}) g'_x(\bar{x}) + \alpha^2 - \alpha J_o g'_x(\bar{x}))x = 0$$

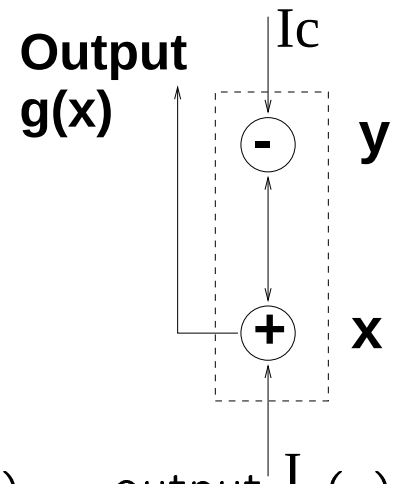
The damping $2\alpha \to 2\alpha - J_o g'_x(\bar{x})$, when J_o is large enough, the damping becomes negative, giving growing oscillatory solution

$x(t) \propto e^{-(\alpha - J_o g'_x(\bar{x})/2)t - i\omega t}$, where
$\omega = \sqrt{hw g'_y(\bar{y}) g'_x(\bar{x}) - (J_o g'_x(\bar{x}))^2/4}$.

There is no excitatory-to-excitatory connections in the olfactory bulb, which nevertheless exhibits oscillation — it is a network property, discussed later.

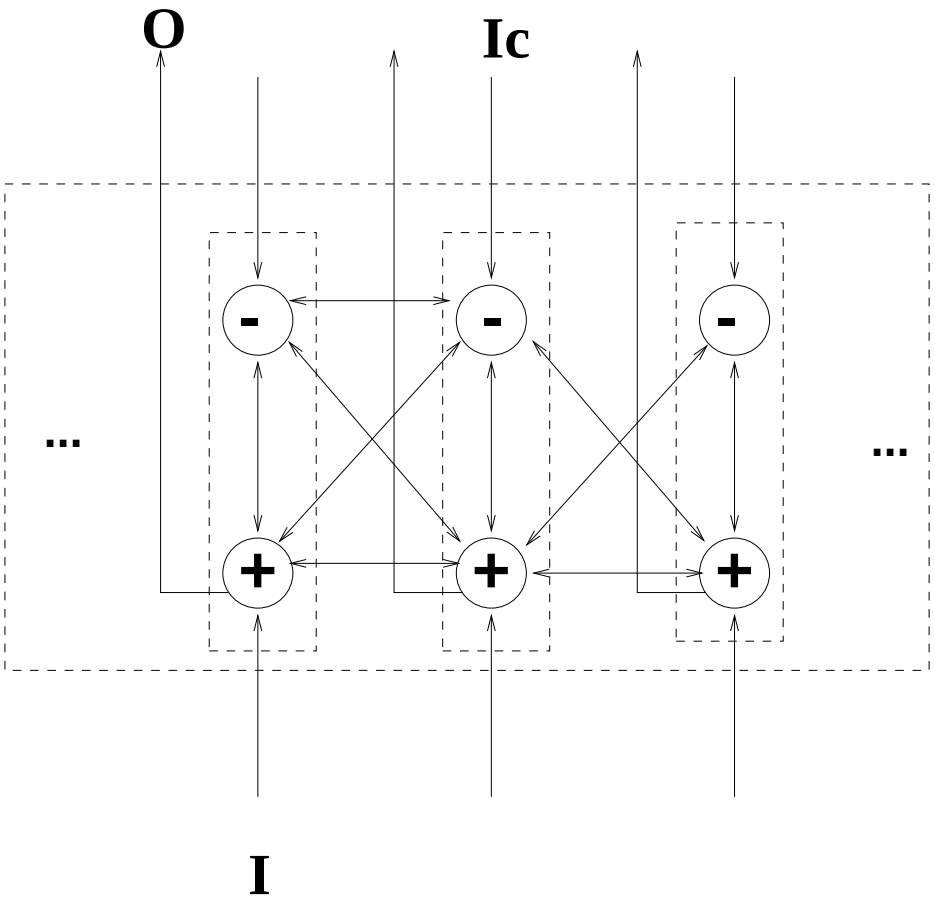
For visual cortical cells, local circuit is such that J_o is not strong enough to give oscillations normally, unless larger network behaviors are evoked, discussed later.

Summary on the basic neural element:



- Input (I, I_c) — output $g_x(x)$.
- The output $g(x)$ has both a DC and a AC component.
- The DC component $g_x(\bar{x})$ increases with I and decreases with I_c.
- The AC component is generated by a damped neural oscillator. The oscillation frequency is controlled by I and I_c, and is proportional to the connnection weights h and w.

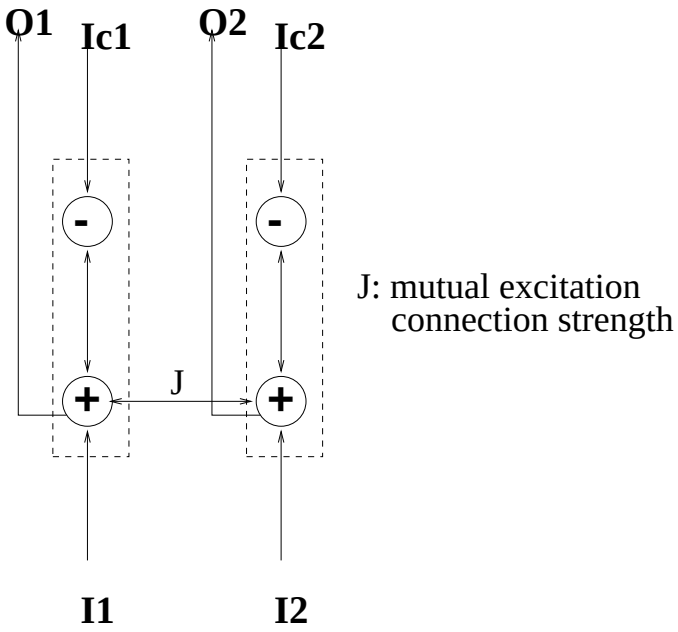
Computation by interactions between the basic elements



Input: $I = (I_1, I_2, ...),\ I_c = (I_{c,1}, I_{c,2}, ...),$
Output: $O \equiv (O_1, O_2, ...) \equiv (g_x(x_1), g_x(x_2), ...)$

O_i depends on $I_i, I_{c,i}$ as well as $I_j, I_{c,j}$

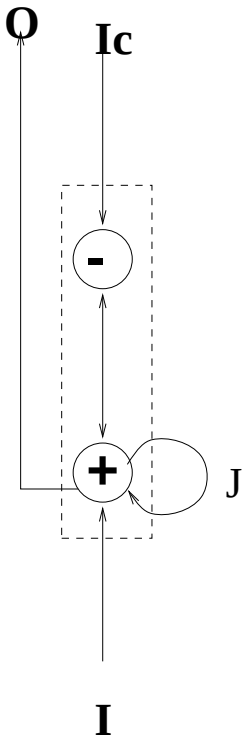
Toy example I — two mutually exciting elements.



$$
\begin{aligned}
\dot{x}_1 &= -h \cdot g_y(y_1) - \alpha_x x_1 + J_o g_x(x_2) + I_1, \\
\dot{y}_1 &= w \cdot g_x(x_1) - \alpha_y y_1 + I_{c,1}. \\
\dot{x}_2 &= -h \cdot g_y(y_2) - \alpha_x x_2 + J_o g_x(x_1) + I_2, \\
\dot{y}_2 &= w \cdot g_x(x_2) - \alpha_y y_2 + I_{c,2}.
\end{aligned}
$$

Assume $I_1 = I_2$, $I_{c1} = I_{c2}$, by symmetry, $O_1 = O_2$ at the fixed point — the mean field solution.

The equivalent system — toy I.



Like an original single element with its damping reduced $\alpha_x \to \alpha_x - J_o g'_x(\bar{x})$ — this leads to a higher input-output gain (when $\alpha_x = 1$) $\frac{\delta g_x(\bar{x})}{\delta I} = \frac{g'_x(\bar{x})}{1+g'_x(\bar{x})g'_y(\bar{y})-(J_o+J)g'_x(\bar{x})}$. and stronger outputs, determined by the fixed point equations.

Dynamics around the mean field solution — toy I

$$
\begin{aligned}
\dot{x}_1 &= -h \cdot g_y(y_1) - \alpha_x x_1 + J_o g_x(x_2) + I_1, \\
\dot{y}_1 &= w \cdot g_x(x_1) - \alpha_y y_1 + I_{c,1}. \\
\dot{x}_2 &= -h \cdot g_y(y_2) - \alpha_x x_2 + J_o g_x(x_1) + I_2, \\
\dot{y}_2 &= w \cdot g_x(x_2) - \alpha_y y_2 + I_{c,2}.
\end{aligned}
$$

$(\bar{x}, \bar{y})$: the mean field solution, linearize around it.

Take $x_+ = x_1 + x_2,\ x_- = x_1 - x_2,$
$y_+ = y_1 + y_2,\ y_- = y_1 - y_2,$

then

$$
\begin{aligned}
\dot{x}_+ &= -h \cdot g_y(y_+) - \alpha_x x_+ + J_o g_x(x_+) \\
\dot{y}_+ &= w \cdot g_x(x_+) - \alpha_y y_+
\end{aligned}
$$

$$
\begin{aligned}
\dot{x}_- &= -h \cdot g_y(y_-) - \alpha_x x_- - J_o g_x(x_-) \\
\dot{y}_- &= w \cdot g_x(x_-) - \alpha_y y_-.
\end{aligned}
$$

Two normal modes: + and -. The + mode is stronger, under-damped, when the two oscillators oscillate in phase. The - mode is weaker, over-damped, when the two oscillate out of phase.

Stimulus dependent oscillations in visual cortex There has been controversies as to whether the visual cortical neurons exhibit oscillatory behavior, different experimental data from different labs do not agree. One possible explanation is that different experiments used different visual stimulus.

Stimulus 1: $I_1 > 0$ and $I_2 = 0$ — input only to one cell being recorded and not other cells near by. This effectively de-coupled 2 from the system.

Stimulus 2: $I_1 > 0$ and $I_2 > 0$ — inputs to both cells.

Stimulus 2 recruits the mutual excitation J_o, stimulus 1 does not. Stimulus 2 tends to evoke oscillation more than stimulus 1.

(Reference reading on the network interactions for visual processing and grouping: Zhaoping Li (2001) Computational design and nonlinear dynamics of a recurrent network model of the primary visual cortex, published in Neural Computation 13/8, p.1749-1780, 2001, available at `http://www.gatsby.ucl.ac.uk/~zhaoping/preattentivevision.html`)

Example: A long horizontal line as the visual input — contour integration

sampled by many cells i tuned to horizontal orientation, lateral connections J_{ij} (colinear excitation) tend to link between them:

$$\begin{aligned} \dot{x}_i &= -x_i - g_y(y_i) + J_o g_x(x_i) + \sum_{j \neq i} J_{ij} g_x(x_j) + I_i \\ \dot{y}_i &= -y_i + g_x(x_i) + I_c \end{aligned}$$

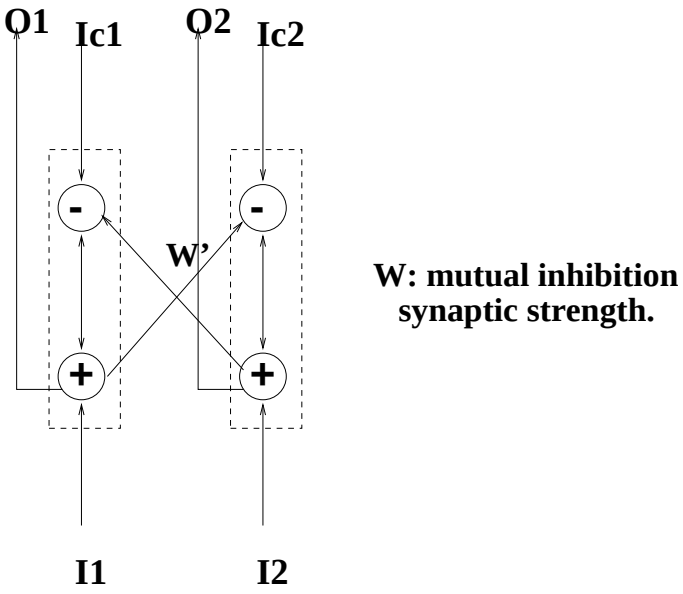
Translation symmetry, $I_i = I_j = I$ for all i, j and J_{ij} only depends on $|i - j|$, implies that $x_i = x_j = x$, $y_i = y_j = y$, and hence:

$$\begin{aligned} \dot{x} &= -x - g_y(y) + (J_o + \sum_{i \neq j} J_{ij}) g_x(x) + I \\ \dot{y} &= -y + g_x(x) + I_c \end{aligned}$$

This is equivalent to a single neural pair with the substitution $J_o \rightarrow J_o + \sum_j J_{ij}$. The response to bars in the array is thus higher than that to an isolated bar. It also has a stronger tendency to oscilllate.

The longer the line, the stronger is $(J_o + \sum_{i \neq j} J_{ij})$ and thus the tendency to oscillate. In fact, a homogeneous extended input texture also has large $(J_o + \sum_{i \neq j} J_{ij})$ and thus a strong tendency to evoke oscillation. Indeed, physiologically, grating stimuli are more likely to induce oscillations than (short) bar stimuli (Molotchnikoff, Shumikhina, and Moisan, 1996).

Toy example II — two mutually inhibiting elements.



Assume $I_1 = I_2$, $I_{c1} = I_{c2}$, by symmetry, $O_1 = O_2$ at the fixed point — the mean field solution.

This solution has a weaker gain ($\alpha_x = \alpha_y = 1$):
$\frac{\delta g_x(\bar{x})}{\delta I} = \frac{g'_x(\bar{x})}{1+h(w+w')g'_x(\bar{x})g'_y(\bar{y})-J_o g'_x(\bar{x})}$. Thus a weaker output given input $I_1 = I_2$.

Around the mean field solution — toy II

$$
\begin{aligned}
\dot{x}_1 &= -h \cdot g_y(y_1) - \alpha_x x_1 + I_1, \\
\dot{y}_1 &= w \cdot g_x(x_1) + w' \cdot g_x(x_2) - \alpha_y y_1 + I_{c,1}. \\
\dot{x}_2 &= -h \cdot g_y(y_2) - \alpha_x x_2) + I_2, \\
\dot{y}_2 &= w \cdot g_x(x_2) + w' \cdot g_x(x_1) - \alpha_y y_2 + I_{c,2}.
\end{aligned}
$$

$(\bar{x}, \bar{y})$: the mean field solution, linearize around it.

Take $x_+ = x_1 + x_2$, $x_- = x_1 - x_2$,
$y_+ = y_1 + y_2$, $y_- = y_1 - y_2$,

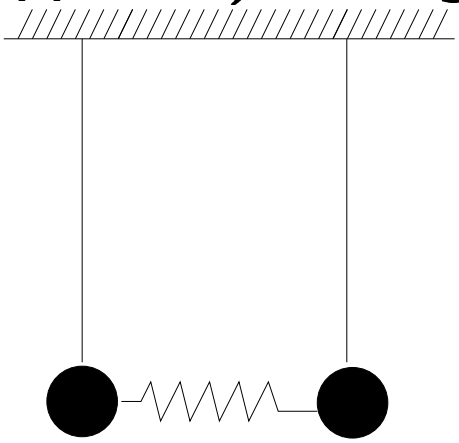
then

$$
\begin{aligned}
\dot{x}_+ &= -h \cdot g_y(y_+) - \alpha_x x_+ \\
\dot{y}_+ &= (w + w') \cdot g_x(x_+) - \alpha_y y_+
\end{aligned}
$$

$$
\begin{aligned}
\dot{x}_- &= -h \cdot g_y(y_-) - \alpha_x x_- \\
\dot{y}_- &= (w - w') \cdot g_x(x_-) - \alpha_y y_-.
\end{aligned}
$$

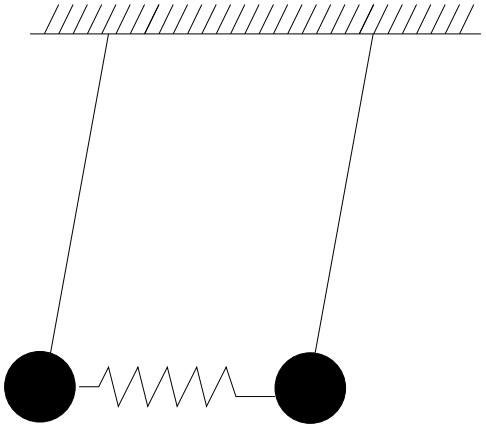
Two normal modes: + and -. Both equally damped (if $w' < w$), oscillating with different frequencies $\propto \sqrt{h(w \pm w')}$.

A coarse (opposite) analogy

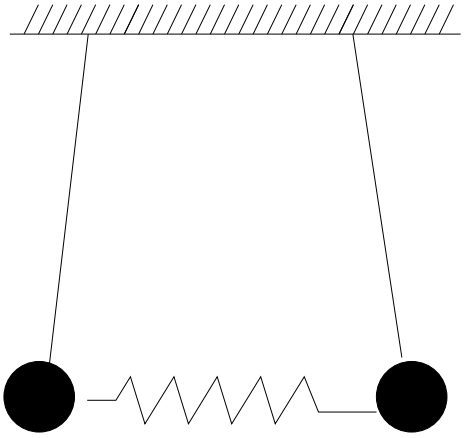


Two coupled oscillators

Mode +



Mode -



Example: Visual Response suppression to a homogeneous texture A texture may be a regular array of short bars, each gives direct input to an excitatory pyramidal cell (coupled reciprocally with a local inhibitory interneuron). Each pyramidal cell is to receive di-synaptic inhibition (omitting excitation) from the neighboring cells responding to neighboring parts of the texture.

$$\begin{aligned} \dot{x}_i &= -x_i - g_y(y_i) + J_o g_x(x_i) + I_i \\ \dot{y}_i &= -y_i + g_x(x_i) + \sum_{j \neq i} W_{ij} g_x(x_j) + I_c \end{aligned}$$

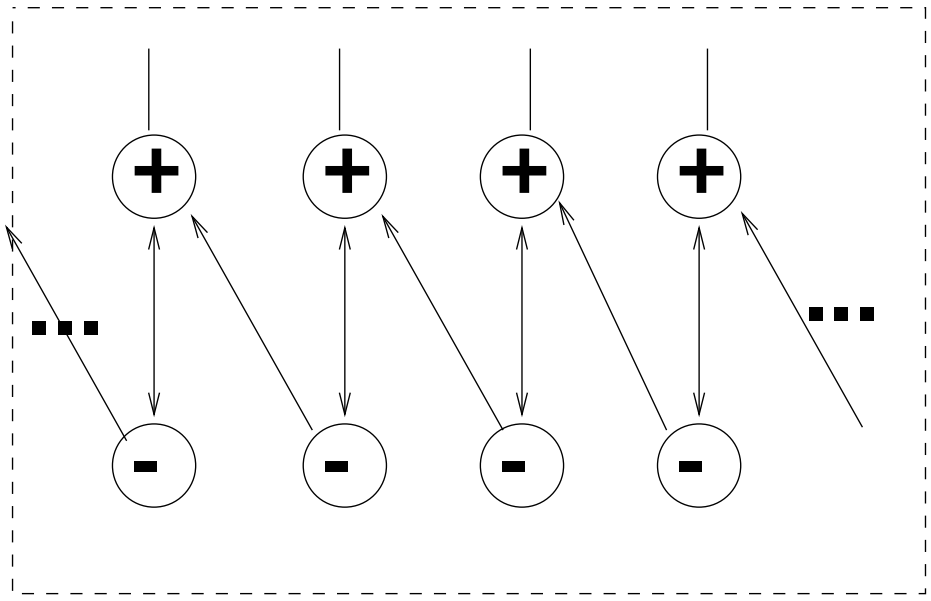
Translation invariance ($I_i = I_j = I$ and W_{ij} depends only on $i - j$) again gives the mean field solution, the whole texture is equivalent to a single E-I (excitatory-inhibitory) pair, with a stronger inhibition

$$\begin{aligned} \dot{x} &= -x - g_y(y) + J_o + I \\ \dot{y} &= -y + g_x(x)(1 + \sum_j W_{ij}) + I_c \end{aligned}$$

Input-output gain: $\frac{\delta g_x(\bar{x})}{\delta I} = \frac{g'_x(\bar{x})}{1+(1+\sum_j W_{ij}) g'_x(\bar{x}) g'_y(\bar{y}) - J_o g'_x(\bar{x})}$.

Example: asymmetrically coupled damped oscillators

$$\begin{aligned} \dot{x}_i &= -H_{ij} \cdot g_y(y_j) - \alpha_x x_i + I_i, \\ \dot{y}_i &= g_x(x_i) - \alpha_y y_i + I_c. \end{aligned}$$



Each inhibitory cell only connects to its left neighbor.

Simplification: Assume translation invariance, $I_i = I_j = I$, H_{ij} depends only on $i - j$. Fixed point $\bar{x}_i = \bar{x}_j = \bar{x}$, and $\bar{y}_i = \bar{y}_j = \bar{y}$.

Small amplitude approximation around the mean field solution. (Take $\alpha_x = \alpha_y$ for simplicity).

$$\begin{aligned} \dot{x}_i &= -H_{ij} g'_y(\bar{y}) y_j - \alpha x_i \\ \dot{y}_i &= g'_x(\bar{x}) x_i - \alpha y_i. \end{aligned}$$

Take Fourier transform, then each Fourier mode will be decoupled from each other, and each is like a single oscillator. The N Fourier modes are:

$$\begin{pmatrix} \sin(k1) \\ \sin(k2) \\ \vdots \\ \sin(ki) \\ \vdots \\ \sin(kN) \end{pmatrix} e^{-\alpha t \pm i\sqrt{\lambda_k} t}$$

$$\begin{pmatrix} \cos(k1) \\ \cos(k2) \\ \vdots \\ \cos(ki) \\ \vdots \\ \cos(kN) \end{pmatrix} e^{-\alpha t \pm i\sqrt{\lambda_k} t}$$

where $k = 2\pi \frac{K}{N}$, K is an integer, $0 \leq K < \frac{N}{2}$

Let mode k has amplitude x^k and y^k, then

$$\begin{aligned} \dot{x}^k &= -H^k g'_y(\bar{y}) y^k - \alpha x^k \\ \dot{y}^k &= g'_x(\bar{x}) x^k - \alpha y^k. \end{aligned}$$

where H^k is the Fourier transform of spatial function H_{i-j}. Fourier modes are eigenvectors of matrix H. This has solution $x^k(t) \propto e^{-\alpha t \pm i\sqrt{H^k g'_x(\bar{x}) g'_y(\bar{y})}t}$. For asymmetric matrix H, H^k is not real, hence it is possible that x^k will have growing or non-decaying oscillation amplitude. The strongest mode k will dominate the network behavior.

This is an example where a group of damping oscillators, coupled together without any excitatory-to-excitatory connections, can generate oscillations. Olfactory bulb is a complicated version of such a system.

Are interneurons simply biological hardware constraints?

If we ignore oscillations, can we model cortical networks by a simplified version: delete the interneurons, each principal neuron can arbitrarily excite or inhibit another neuron?

The simplified network model:

$\dot{x}_i = -x_i + \sum_j T_{ij} g(x_j) + I_i$

T_{ij} connection strength that can be positive or negative.

Example: Hopfield network, when $T_{ij} = T_{ji}$. This kind of symmetry may be seen as quite suitable for visual cortical networks where there is reflection symmetry in connections.

To be continued ...