Model networks

Basic principles

Suggested reading:

- Burgi, PY (1992) Analysis and understanding of neuronal structures. Neurocomputing 4:137-166.
- Grossberg, S (1988) Nonlinear Neural Networks: Principles, Mechanisms, and Architectures. Neural Networks, 1:17-61.
- Salinas E, Abbott LF (1996) A model of multiplicative neural responses in parietal cortex. Proc Natl Acad Sci U S A, 93:11956-61.

Model networks: Basic principles

Contents:

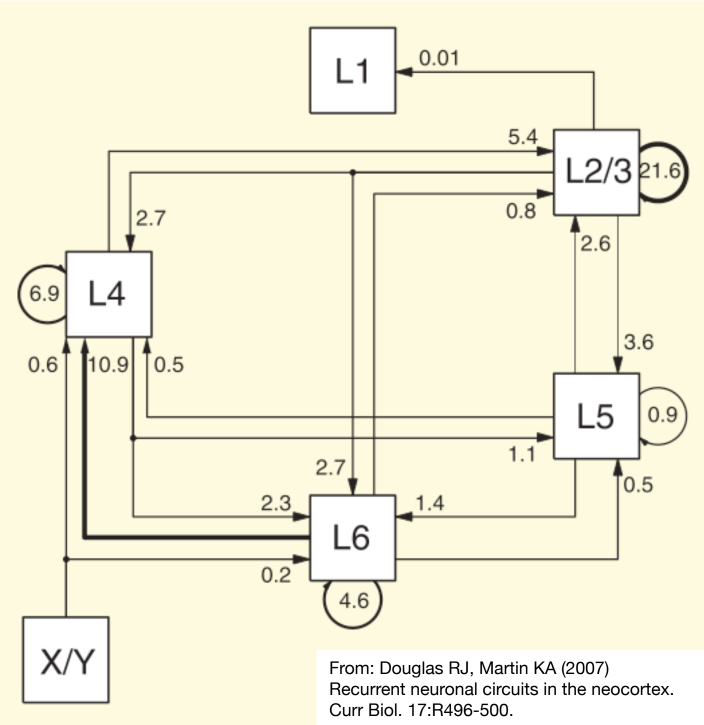
Microcircuits

Brain areas are organized in multiple layers.

The communication within a brain area is usually higher than between areas (e.g. the figure shows the connections between excitatory neurons in area 17 of the cat).

These recurrent processing could potentially account for phenomena such as

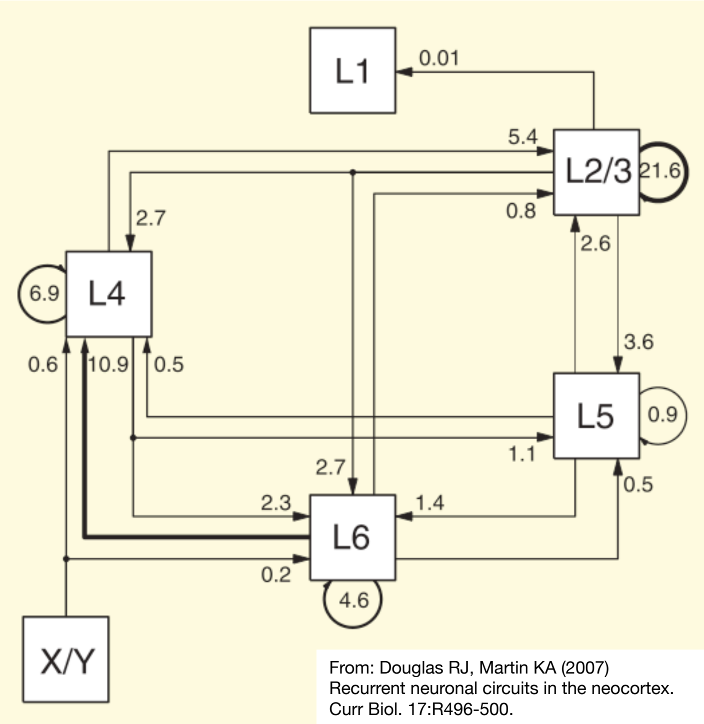
- Gain normalization
- Soft winner-takes all
- Dynamic gain control



From: Douglas RJ, Martin KA (2007)
Recurrent neuronal circuits in the neocortex.
Curr Biol. 17:R496-500.

Microcircuits

Since the exact functions of such laminar processing is not fully understood, most models of cortical processing do not aim to implement such cortical microcircuits, but rather account for the observed phenomena in more abstract models.



From: Douglas RJ, Martin KA (2007)
Recurrent neuronal circuits in the neocortex.
Curr Biol. 17:R496-500.

The additive model

In this model the effects of excitatory and inhibitory inputs is assumed to add linearly. It was used by Cohen & Grossberg, 1984; Amari 1977, Amari and Arbib 1977, Hopfield 1984.

The effect of a spike train *u(t)* on the input current of a cell can be described by

$$I_i(t) = \sum_{j=1}^{n} w_{ij} u_j(t) * g(t)$$

g(*t*) is the synaptic transfer function and is here simplified as compared to the alpha-function:

$$g(t) = \frac{e^{-\frac{t}{\tau}}}{\tau}$$

Such a choice of *g*(*t*) allows us to receive a simple differential equation for the potential:

$$\tau \frac{d}{dt} I_i(t) = -I_i(t) + \sum_{j=1}^{n} w_{ij} u_j(t)$$

Does not refer to any particular cell time constant

The additive model

The relation *f* between the output rate and the input current is called the gain function of the neuron.

Instead of a spike train, the output firing rate of the presynaptic neuron is used. In order to account for threshold and saturation effects it is often assumed to be non-linear in formal neuron models

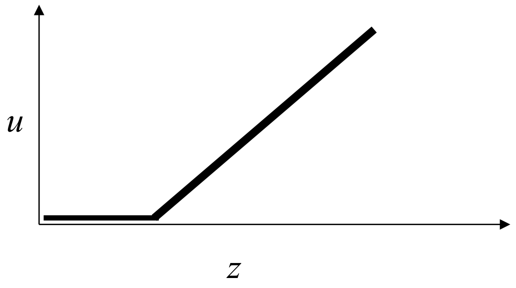
$$\tau \frac{d}{dt} I_i(t) = -I_i(t) + I_i^0 + \sum_{j=1}^{n} w_{ij} f(I_j(t))$$

The dynamic equation continuously decreases the energy function (Hopfield, 1984) until reaches an equilibrium point - attractor of the system.

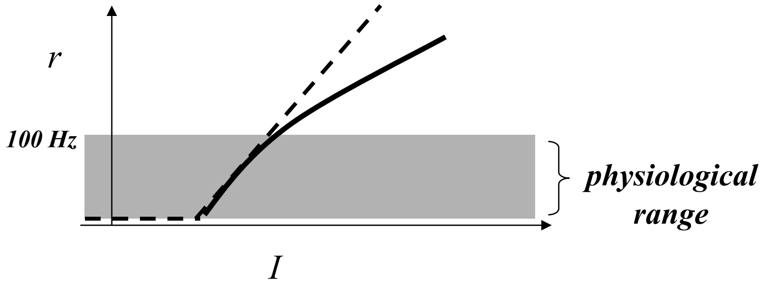
Gain function

- Linear-Gain:

$$f(z)=\begin{cases}0 & \text{if } z<z_{th}\\ a(z-z_{th}),a>0 & \text{if } z\geq z_{th}\end{cases}$$

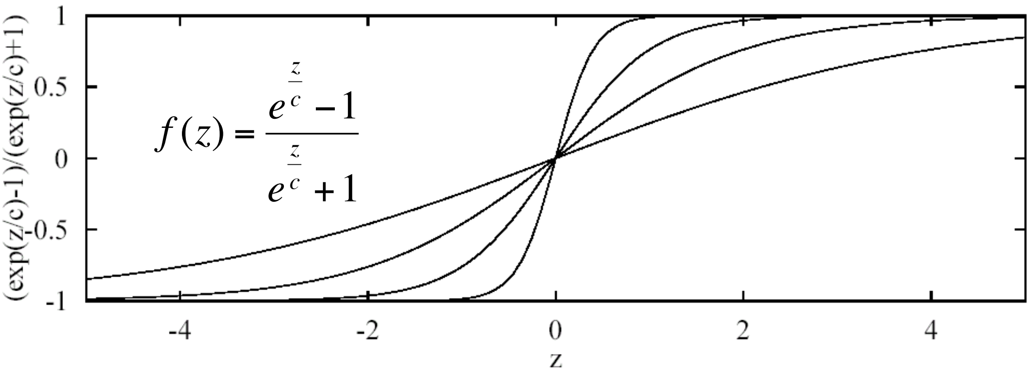


Based on physiological properties of real cells:



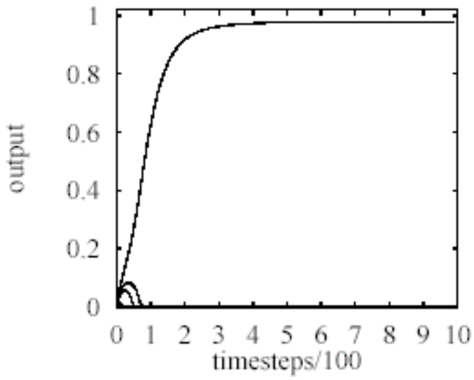
Gain function

- Non-linear-Gain:

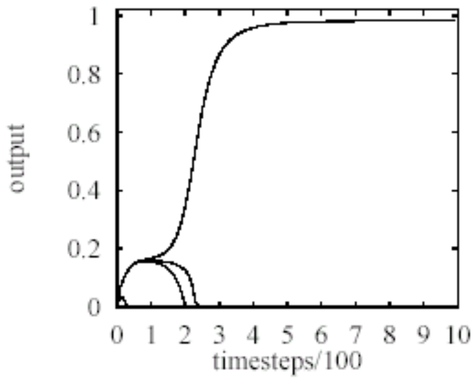


Non-linear gain functions such as the one above, lead to a strong competition among cells, since a small change in the input current leads to a strong change in the output rate.

Winner-takes all competition



Neuron	Input
1	0.4
2	0.6
3	0.65
4	0.8



Neuron	Input
1	0.887
2	0.8865
3	0.65
4	0.888

$$\tau \frac{\partial z_i}{\partial t} = -z_i + I_i^{ext} + p \cdot f(z_i) - q \sum_{j=1}^{n} f(z_i)$$

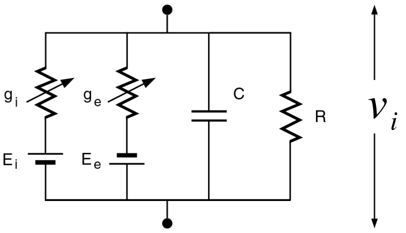
p=4.5 and q=3

The shunting model

General assumptions

- an excitatory input produces, with a constant proportionality, a conductance increase
- the activation of an inhibitory input results, with a constant proportionality, in a conductance decrease
- through this conductance a portion of the excitation-produced current is shunted

We recall:



The current flowing within the circuit is:

$$i_{C_i}(t) = i_{e_i}(t) - i_{i_i}(t) - i_{leak_i}(t)$$

The potential can be written as:

$$\tau \frac{dv_i}{dt} = g_e(E_e - v_i) - g_i(E_i + v_i) - v_i g_{leak}$$

The conductances are determined separately by summing all presynaptic signals expressed by the rate u modulated by the weight before multiplied by a constant.

$$g_e = \beta \sum_j^m a_{ij} u_j^e \qquad\qquad g_i = \alpha \sum_j^n b_{ij} u_j^i$$

$$\tau \frac{dv_i}{dt} = (E_e - v_i)\beta \sum_j^m a_{ij} u_j^e - (E_i + v_i)\alpha \sum_j^n b_{ij} u_j^i - v_i g_{leak}$$

By separating between feedforward input and recurrent or feedback influences we can write:

$$\tau \frac{dv_i}{dt} = (E_e - v_i)\beta \left(v_i^e + \sum_j^m a_{ij} f(v_j^e) \right) \\ - (E_i + v_i)\alpha \left(v_i^i + \sum_j^n b_{ij} f(v_j^i) \right) - v_i g_{leak}$$

Differences between the additive and the shunting model

Additive model:

$$\tau \frac{d}{dt} I_i = -I_i + \sum_{j=1}^n w_{ij} f(I_j) + I_i^e$$

Shunting model:

$$\tau \frac{dv_i}{dt} = -Av_i + (B - v_i)\left(v_i^e + \sum_j^m C_{ij} f(v_j^e) \right) - x_i \left(v_i^i + \sum_j^n E_{ij} f(v_j^i) \right)$$

Shunting networks possesses automatic gain control properties capable of generating an infinite dynamic range within each input patterns.

Steady-state of the additive model

In the steady state, the system reached its fixed point and no changes in the rate occur:

$$f(I_i(t)) = I_i(t) = r_i(t)$$

$$\tau \frac{d}{dt} r_i = -r_i + \sum_{j=1}^{n} w_{ji} r_j + I_i^e = 0$$

$$r_i = w_{ii} r_i + \sum_{j \neq i} w_{ji} r_j + I_i^e$$

$$r_i = \frac{\sum_{j \neq i} w_{ji} r_j + I_i^e}{1 - w_{ii}}$$

The firing rate does not directly represent the external input. It depends heavily on the chosen weights.

Automatic gain control in the shunting model

Simplified shunting model:

$$\tau \frac{dv_i}{dt} = -Av_i + (B - v_i)I_i - v_i \sum_{k \neq i} I_k$$

$$v_i^e = I_i$$

$$v_i^i = 0$$

Steady state:

$$v_i = \frac{BI_i}{A + I_i + \sum_{k \neq i} I_k}$$

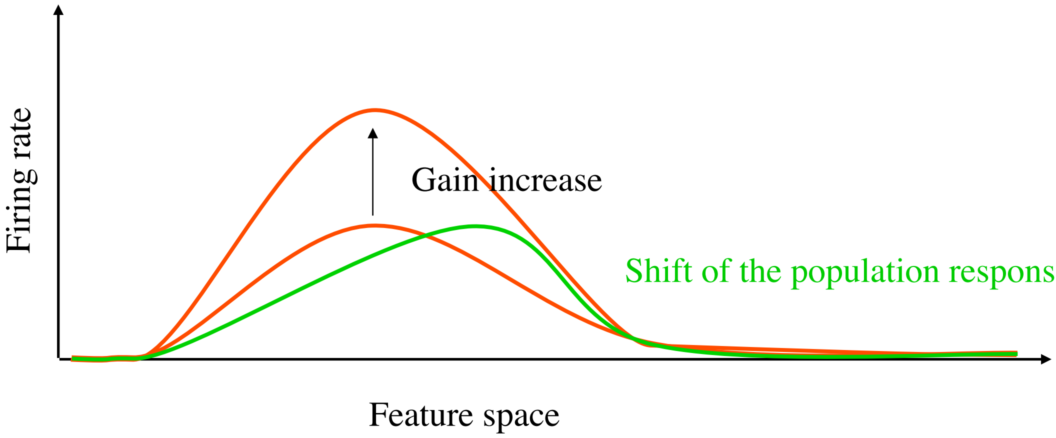
Summary

The firing of a neuron is affected by a large number of variables such as the state of activation and inactivation of numerous ion channels and the concentration of calcium and other second messenger molecules inside the cell, that cannot be described purely in terms of the firing rate itself. However, fits with measured data can be incorporated into firing rate models phenomenologically.

Firing rate models still remain greatly simplified but perhaps sufficient complex to describe the essential dynamics.

Population Code

The population coding principle does not encode a stimulus attribute by the firing rate of one particular neuron in a cortical map, but by a distribution of activity in a population of neurons.
Each neuron is tuned to a specific value of the attribute, and the activity landscape in the whole population is an implicit representation of this attribute.



Neural fields

Neural field equation:

Amari and Arbib, 1972
Amari, 1977

$$\tau \frac{\partial z(x,t)}{\partial t} = -z + \int w(x - x') f(z(x',t)) dx' + h + I^{ext}(x)$$

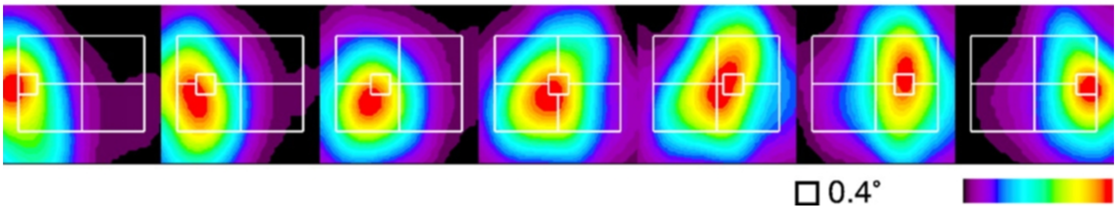
since *w* depends only on (*x*-*x*‘) the field is homogeneous. Typically, a lateral inhibition type kernel is used.

$$\tau \frac{\partial z(x,t)}{\partial t} = -z + \int w(x - x') f(z(x',t)) dx' + h + I^{ext}(x)$$

Alternatively, a Gaussian kernel together with a global inhibition is used.

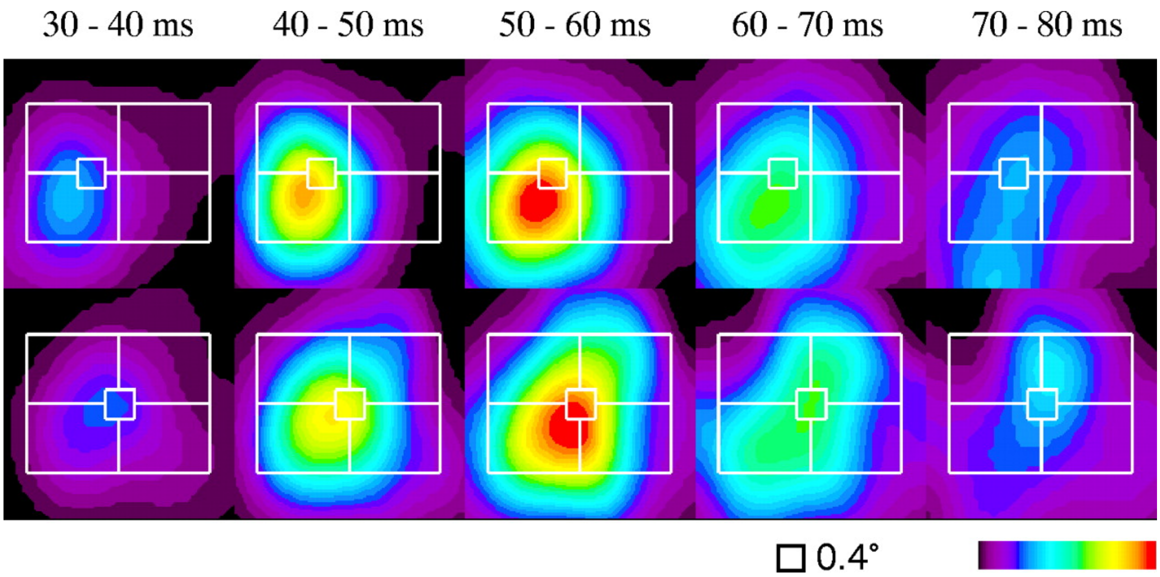
$$\tau \frac{\partial z(x,t)}{\partial t} = -z + \int w(x - x') f(z(x',t)) dx' - q \int f(z(x',t)) dx' + I^{ext}(x)$$

Application: Representation of small visual stimuli by the joint activation of a population of neurons



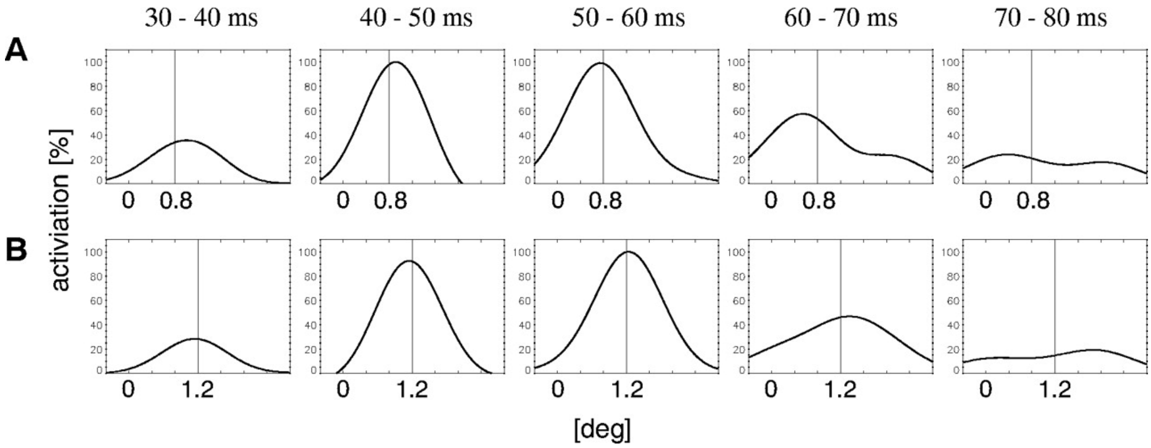
Population representations of the elementary stimuli computed as two-dimensional distributions of population activations over visual space after Gaussian interpolation. The construction was based on the activity of 178 neurons. Distributions of population activations were computed in the time interval between 40 and 65 msec after stimulus onset.

Temporal evolution of the distributions of population activations of elementary stimuli



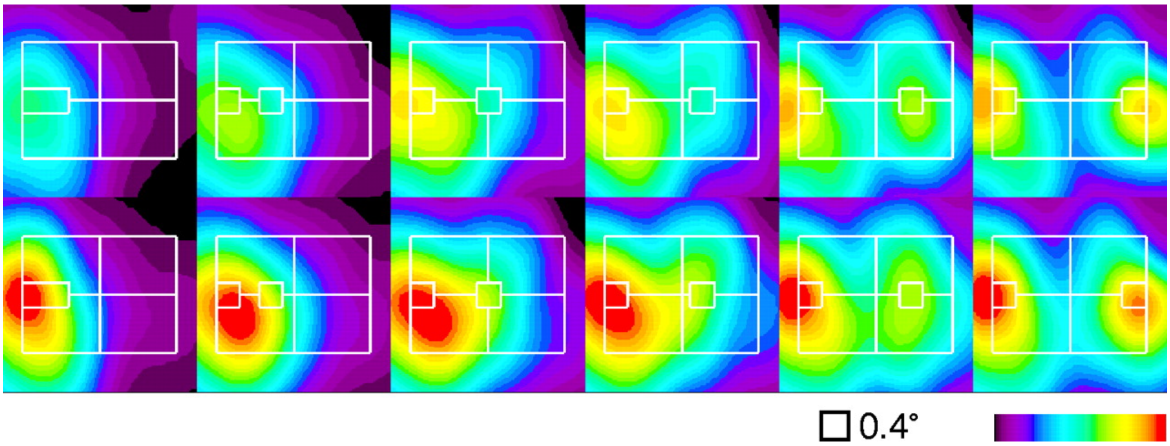
Two-dimensional distributions of population activity of adjacent elementary stimuli (top and bottom) derived by Gaussian interpolation. The DPAs were obtained for consecutive intervals of 10 msec duration covering the period from 30 to 80 msec after stimulus onset.

Temporal evolution of the distributions of population activations of elementary stimuli



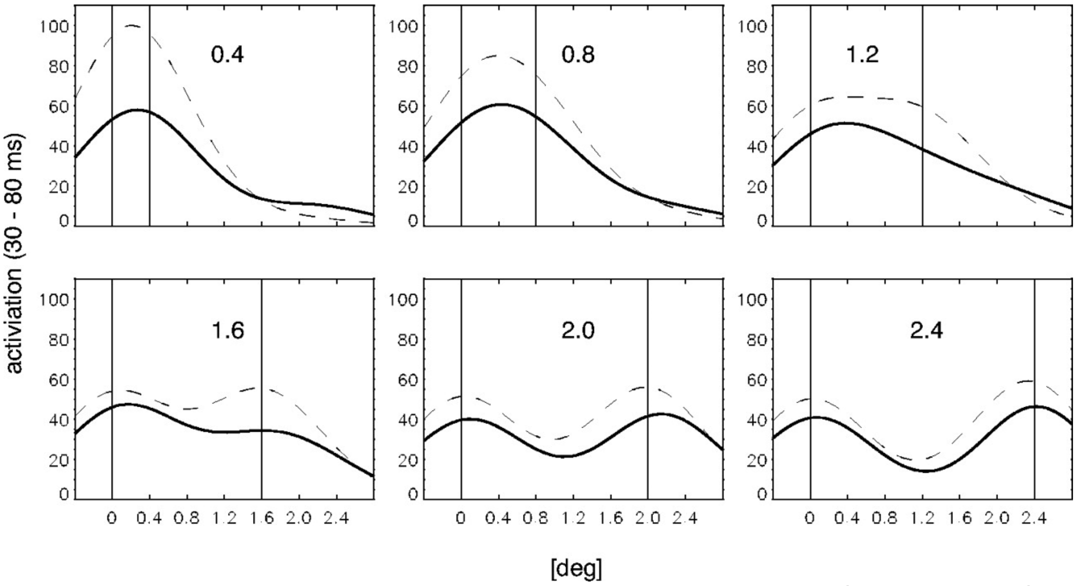
The temporal evolution of two DPAs after optimal linear estimation. The position of the maximum of each distribution closely approximates the stimulus position of the elementary stimulus throughout the time course of the neural population response, yet less accurately in the late time epoch.

Distributions of population activations of composite stimuli



The measured two-dimensional DPAs (*top*) of composite stimuli (from left to right, 0.4-2.4° separation) were compared to the superpositions of the representations of their component elementary stimuli (*bottom*). The DPAs were based on spike activity of 178 cells averaged over the time interval from 30 to 80 msec after stimulus onset.

Superposition vs. measured responses of composite stimuli



The most striking deviation from the linear superposition (dashed line) was a reduction of activity compared to the measured responses (solid line), which is particularly strong for small stimulus separations. This reduction is not caused by a saturation of population activity because it is also observed for composite stimuli of larger separations where the distributions are bimodal and have little overlap.

Dynamic field model

At each position, x, an activation variable, *u*(*x*), is introduced that defines a field of neural activation along the horizontal dimension of visual space.

$$\tau \frac{\partial u(x,t)}{\partial t} = -u(x,t) + h + S(x,t) + f\big(u(x,t)\big)\Big[\int w_u(x-x')f\big(u(x',t)\big)dx' - v(x,t)\Big]$$

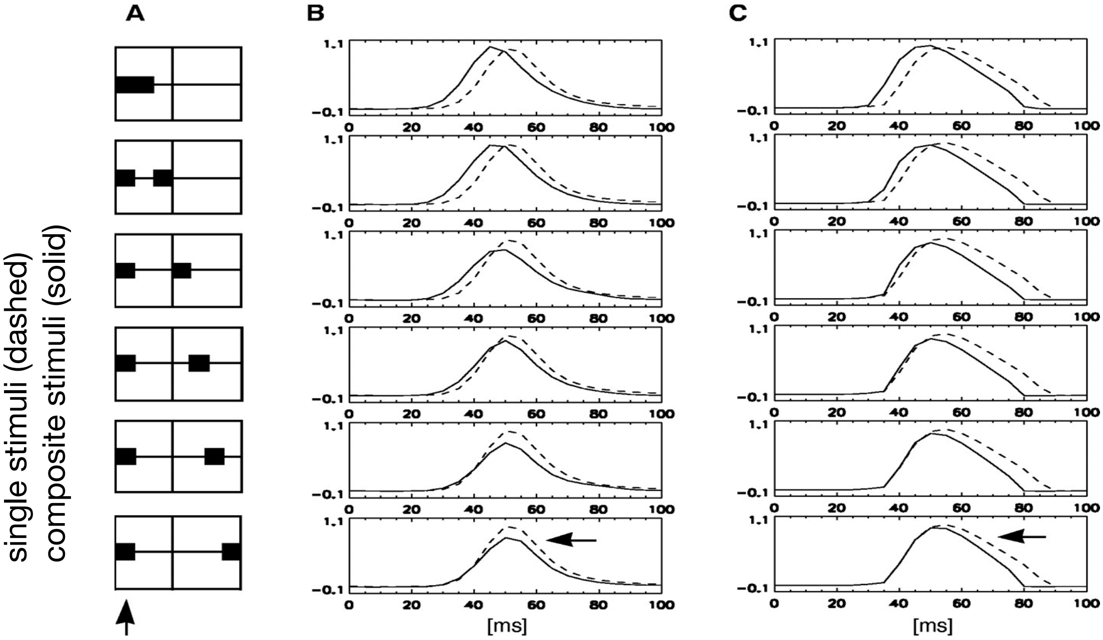
$$\tau \frac{\partial v(x,t)}{\partial t} = -v(x,t) + \int w_v(x-x')f\big(u(x',t)\big)dx'$$

$$w_u(x-x') = A_u \exp\left[-\frac{(x-x')^2}{2\sigma_u^2}\right]$$

$$w_v(x-x') = A_v \exp\left[-\frac{(x-x')^2}{2\sigma_v^2}\right]$$

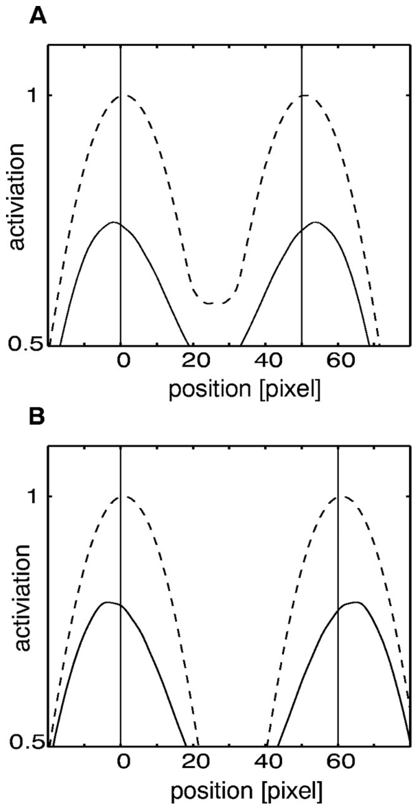
This neural field is assumed to evolve continuously in time under two different types of inputs: (1) afferent input from sensory stimulation activates those regions of the field that represent the specified values of the parameter space; and (2) inputs from interaction processes within the field exert excitatory or inhibitory effects onto the field. What locations excite or inhibit each other is determined by interaction kernels $w_u(x)$ and $w_v(x)$, respectively.

Measured responses (left) vs. model (right)



At small distances, the activation to composite stimuli had a significantly smaller latency accompanied by an earlier onset of the decay of the population activity as compared to the elementary stimuli. The late part of the responses to the composite stimuli was characterized by an overall inhibition.
Parameter values used for this simulation are: A_u = 5.2, A_v = 4, s_u = 15, s_v = 25, A_s = 4, B_s = 10, b = 1, h = -3, t= 15.

Repulsion effect



In the model, the two excited regions attract each other to unite into one excited region when they interact directly through the excitatory connections. Conversely, when two peaks of activation are induced at somewhat larger distances, they interact primarily through the longer range inhibitory interactions, and this leads to the documented repulsion of the two peaks.

Simulation of the repulsion effect. Shown are the simulated DPAs in response to the composite stimuli of 2.0° (A) and 2.4° (B) separation (solid lines). These are compared to the superpositions (dashed lines). The two vertical lines mark the position of the elementary stimuli. Repulsion is manifested by an outward shift of the maxima.

A model of multiplicative neural responses

Gainmodulated responses can be achieved by a recurrent network, even when the individual cells sum their synaptic inputs linearly and are not intrinsically capable of computing a product (Salinas, Abbott, 1996).

The multiplicative neuronal responses seen in the model are thus an emergent property of the network, not of its individual elements.

The model has two inputs, one that depends only on the retinal location of the visual stimulus (*V*) and describes the receptive field, and another that depends only on gaze direction (*G*) and accounts for the gain field.

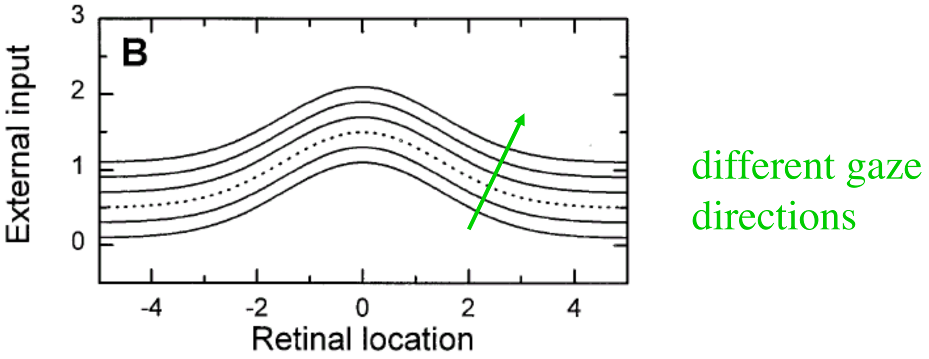
$$h_i = h_i^V(x) + h_i^G(y).$$

The visual input to neuron *i* is a Gaussian function of the difference between the stimulus location on the retina *x* and its preferred location x_i.

$$h_i^V(x) = h_{max}^V \exp\left(-\frac{(x - x_i)^2}{2\sigma_V^2}\right)$$

The input representing gaze direction is the same for all cells and it increases or decreases linearly as the gaze direction changes.

$$h_i^G(y) = m y_i + b_i.$$



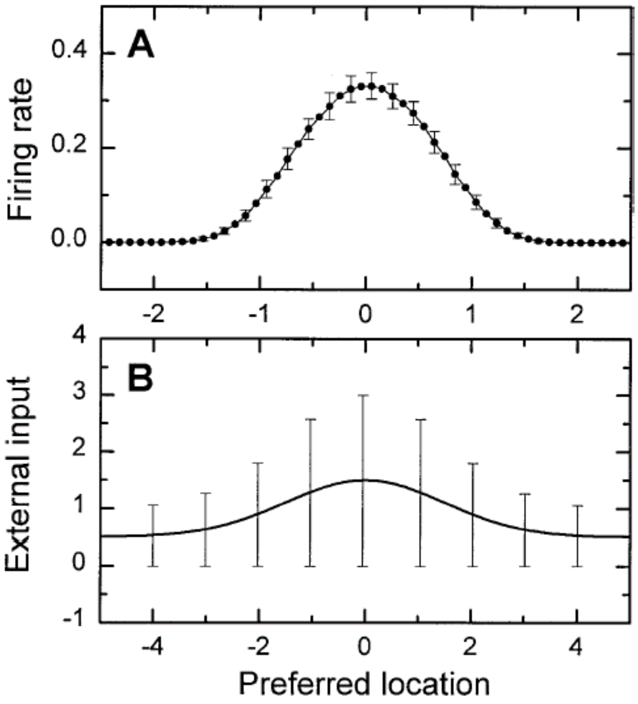
When the sum of the external input and the recurrent contribution to a neuron is less than a threshold value h_{th}, the neuron is silent. For larger inputs, the firing rate increases linearly. The firing rate of neuron *i* is given by

$$r_i = s\left[h_i + \sum_j W_{ij} r_j - h_{th} \right]_+$$

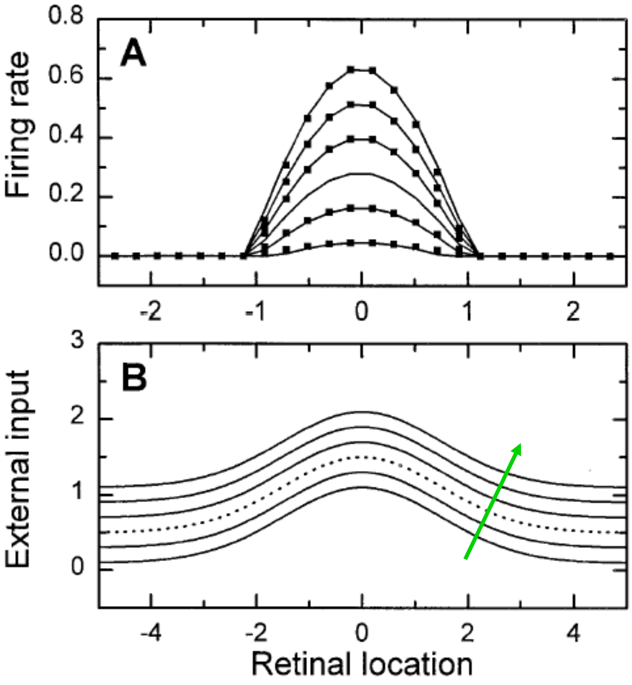
The recurrent synaptic connections between neurons depend on the distance between their preferred retinal locations. The synaptic weight W_{ij} from presynaptic neuron *j* to postsynaptic neuron *i* is given by a difference of two Gaussians

$$W_{ij} = A_E \exp\left(-\frac{(x_i - x_j)^2}{2\sigma_E^2} \right) - A_I \exp\left(-\frac{(x_i - x_j)^2}{2\sigma_I^2} \right)$$

As all recurrent neworks with inhibition the network shows noise suppression

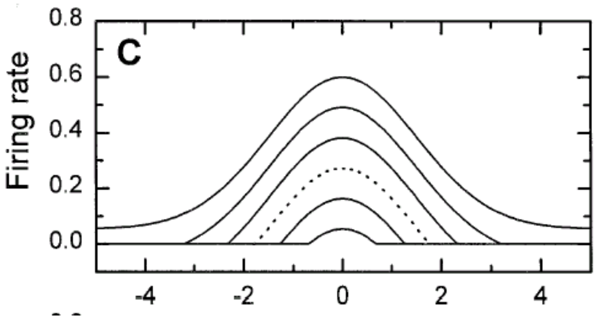


Gain modulated response through a change in gaze

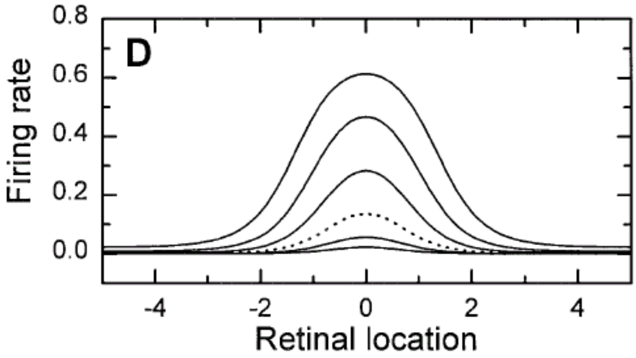


different gaze
directions

Tuning curve without recurrent interactions (feedforward)



Tunig curve of a feedforward network with a sigmoid activation function



Where is the magic of multiplicative neural responses

An important factor determining whether or not a multiplicative interaction is generated is the width of the input signal relative to the range of the excitatory connections. A multiplicative behavior is produced robustly whenever $\sigma_V \geq \sigma_E$, but fails when narrower inputs are used.

The key feature that produced multiplicative responses was the fact that one input (the visual one) was distinct for each neuron, whereas the other (the gaze-direction input) was similar for each neuron.

References:

- Cohen, M.A. and Grossberg, S. (1984). Neural dynamics of brightness perception: Features, boundaries, diffusion, and resonance. Perception & Psychophysics, 36:428-456.
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- Amari, S., Arbib, M.A. (1977) Competition and cooperation in neural nets. In: J. Metzler (ed), Systems Neuroscience, Academic Press, 119-165.
- Hopfield, J. J. (1984) Neurons with graded response have collective computational properties like those of two-state neurons. PNAS, 81:3088-3092.