Lecture 2: Connectionist approach
Elements and feedforward networks

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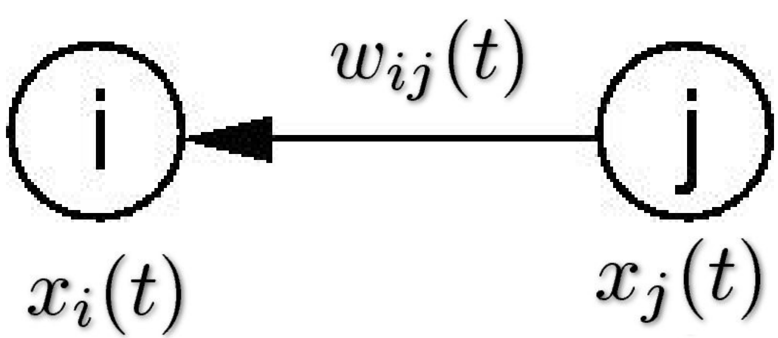
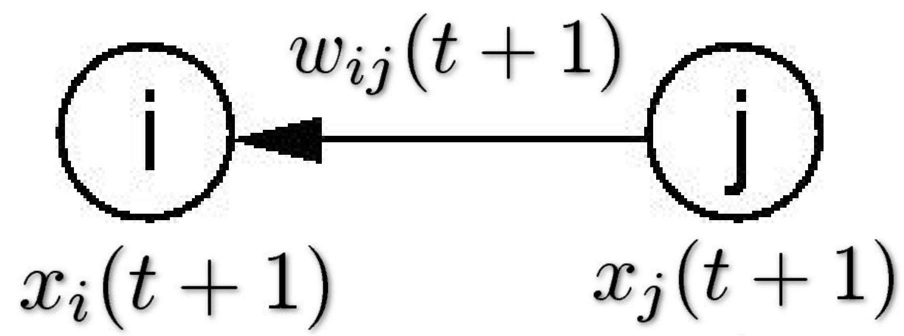
Connectionist approach

- The connectionist approach is an approach of minimal assuptions:
  - Neurons have two states “on” (1) or “off (0)
  - Time can be discretized in discrete steps
  - Neurons are either connected (1) or not (0)

At time t



At time $t+1$



McCulloch-Pitts neurons

In a connectionist approach, neurons are described by the McCulloch-Pitts neuron model:

$$x_i(t+1) = \Theta\left(\sum_{j=1}^{N} w_{ij}(t)x_j(t) - \theta\right)$$

$x_i(t) \in \{0,1\}$ - state of neuron i at time t

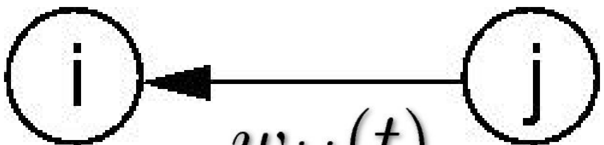
$w_{ij}(t) \in \{0,1\}$ - state of connection (synapse) from neuron j to neuron i at time t

$$\Theta(x) = \begin{cases} 1 & x > 0 \\ 0 & \text{otherwise} \end{cases}$$ - Heaviside function

$\theta \in \mathbb{N}$ - firing threshold

McCulloch-Pitts neurons

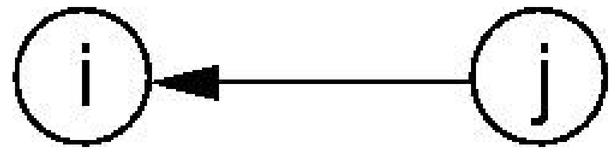
At time t



$w_{ij}(t)$

$x_i(t)$ $\qquad$ $x_j(t)$

At time $t+1$



$$x_i(t+1) = \Theta(w_{ij}(t)x_j(t) - \theta)$$

Note:

- Need to take values from previous time step
- The notation of $w_{ij}(t)$ may seem awkward at first:

$$w_{ij}(t) = w_{i \leftarrow j}(t)$$

Connectionist approach

- Advantages
  - Can be used even if details are not known
  - Remains valid if knowledge about details changes
  - Can often be applied to many systems, even if details differ

Connectionist approach

- Disadvantages
  - Some things are awkward to implement (e.g. mutual inhibition in layers)
  - Some things are almost impossible to include (e.g. sub-threshold oscillations)
  - Does not include intrinsically active neurons well
  - Intrinsic neuron dynamics not described (e.g. refractory period)
  - ...

McCulloch-Pitts neurons are hyperplanes

The equation $\sum_{j=1}^{N} w_{ij} x_j = \theta$ defines a plane in N dimensional space.

"McCulloch-Pitts neurons fire to the right of a hyper-plane and are silent on the left."

For example N=2:

$$w_{i1} x_1 + w_{i2} x_2 = \theta$$

$$\Leftrightarrow x_2 = -\frac{w_{i1}}{w_{i2}} x_1 + \frac{\theta}{w_{i2}}$$

$$\Leftrightarrow y = ax + b \qquad \left(a = -\frac{w_{i1}}{w_{i2}},\ b = \frac{\theta}{w_{i2}} \right)$$

Random connections

- In connectionist approaches connections are often chosen to be *random* ("generic"):

$$w_{ij} = \begin{cases} 1 & \text{with probability } p_c \\ 0 & \text{with probability } q_c = 1 - p_c \end{cases}$$

- Similarly input neurons are often assumed to fire with a fixed probability

$$x_j = \begin{cases} 1 & \text{with probability } p_{\text{in}} \\ 0 & \text{with probability } q_{\text{in}} = 1 - p_{\text{in}} \end{cases}$$

Propagation of probabilities

- With random connections and random input firing, other neurons i have a probability to fire

$$P\left(x_i = 1\right) = P\left(\sum_{j=1}^{N} w_{ij} x_j \geq \theta\right)$$

$$= \sum_{k=\theta}^{N} P\left(\sum_{j=1}^{N} w_{ij} x_j = k\right)$$

Statistical independence

Definition of **statistical independence**:

Event A is independent from event B if and only if

$$P(A \cap B) = P(A) \cdot P(B)$$

Conditional probabilities:

$$P(A|B) = \frac{P(A \cap B)}{P(B)}$$

Read: "P of A given B"

Bayes theorem

Why these definitions make sense: **If A and B independent**,

$$P(A \mid B) = \frac{P(A \cap B)}{P(B)} = \frac{P(A)P(B)}{P(B)} = P(A)$$

Bayes theorem:

$$P(A|B) = \frac{P(A \cap B)}{P(B)}$$

Total probability from conditional probability

If we have disjoint events X_i and $\sum_{i=1}^{N} P(X_i) = 1$

then $$P(Y) = \sum_{i=1}^{N} P(Y \mid X_i) P(X_i)$$

(Proof on the board)

Binomial distribution

If $x_i \in \{0,1\},\ i = 1,\ldots,N$ are independent random variables with distribution $\{p, 1-p\}$ then the probability distribution for the sum is

$$P\Big(\sum_{i=1}^{N} x_i = k\Big) = \binom{n}{k} p^k (1-p)^{N-k}$$

Quick proof: The sum is k if we put k "1" into the N x_i

x_i	1	0	0	1	0	1	0	1	1	0	0	1

$$P = \mathrm{p \cdot q \cdot q \cdot p \cdot q \cdot p \cdot q \cdot p \cdot p \cdot q \cdot q \cdot p} = p^k (1-p)^{N-k}$$

Proof of binomial distribution

There are $\binom{N}{k} = \frac{N!}{k!(N-k)!}$ ways to put the “1” and “0”,

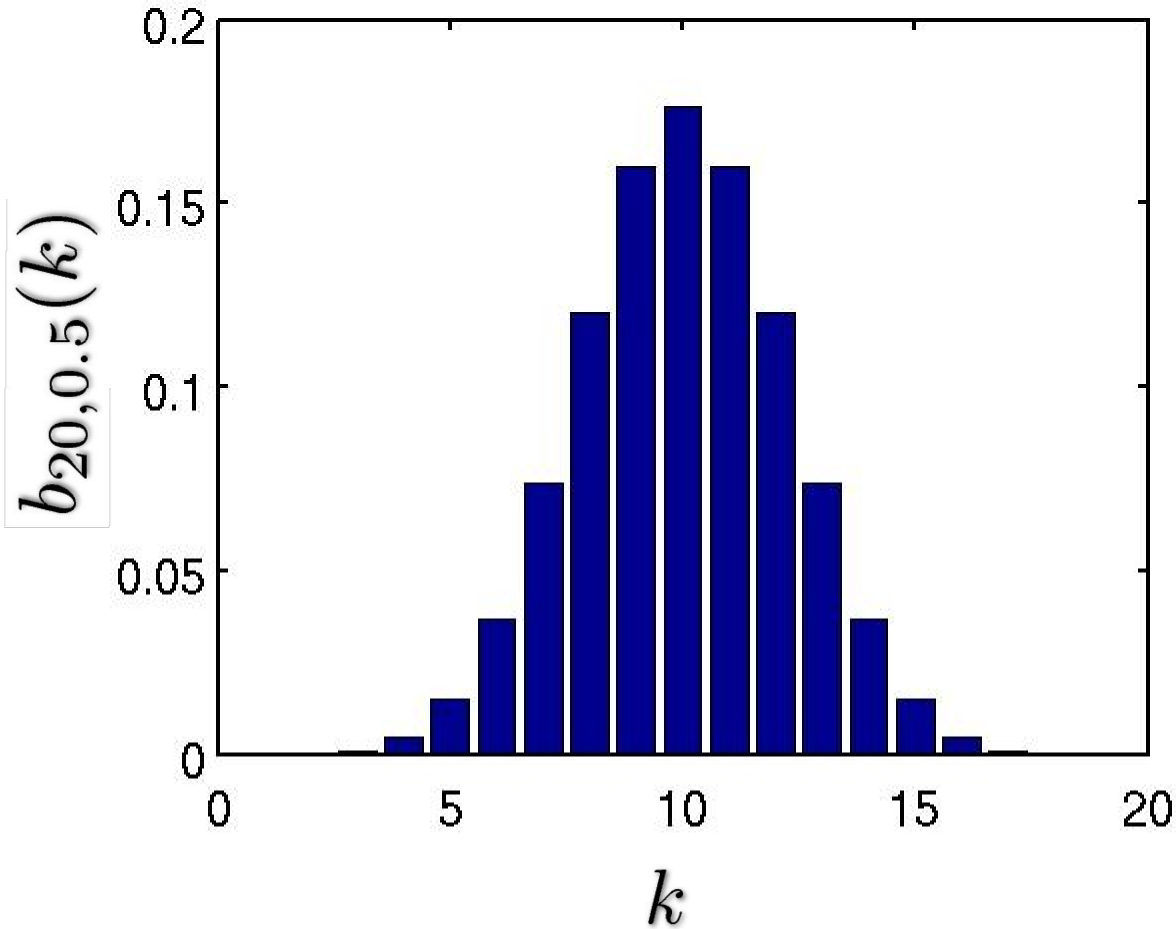
and all are mutually exclusive, therefore

$$P\Big(\sum_{i=1}^{N} x_i = k\Big) = \binom{N}{k} p^k (1-p)^{N-k}$$

The binomial distribution is often denoted as

$$P\Big(\sum_{i=1}^{N} x_i = k\Big) = b_{N,p}(k)$$

Binomial distribution properties



- Expectation value

$$\mathbb{E}\sum_{i=1}^{N} x_i = N \cdot p$$

- Standard deviation

$$\sigma_{\sum_{i=1}^{N} x_i} = \sqrt{Np(1-p)}$$

Expectation value and maximum are *not* the same

More on this: Lab session.

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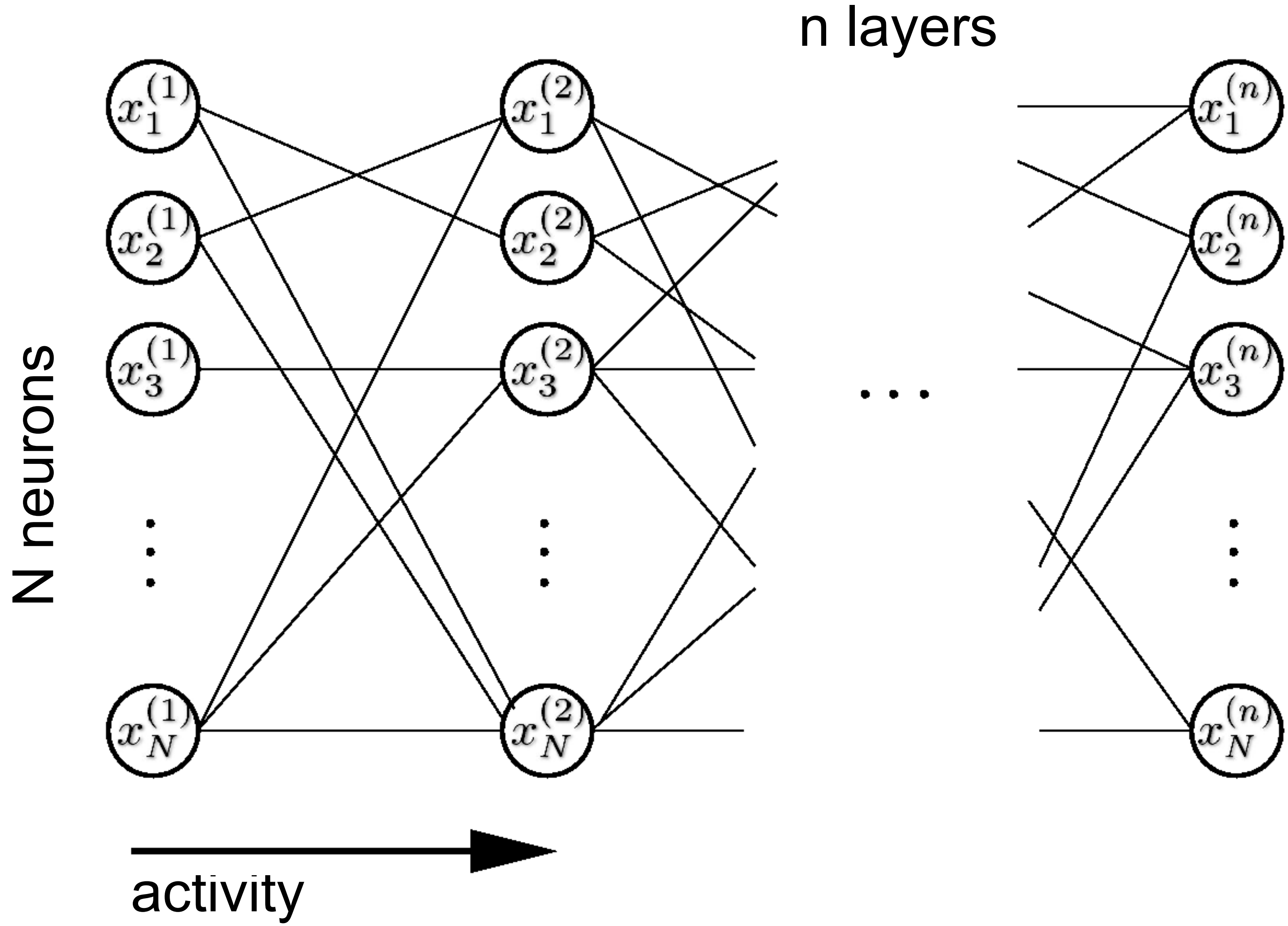
Feedforward networks



Feedforward networks

- Denote $X^{(j)} := \sum_{i=0}^{N} x_i^{(j)}$
- Assume that a_j neurons fire in Layer j
- Then the probability of a neuron in layer j+1 to fire is

$$p^{(j+1)}(a_j) := P(x_i^{(j+1)} = 1 \,|\, X^{(j)} = a_j) = \sum_{k=\theta}^{a_j} b_{a_j,p_c}(k)$$

Feedforward networks

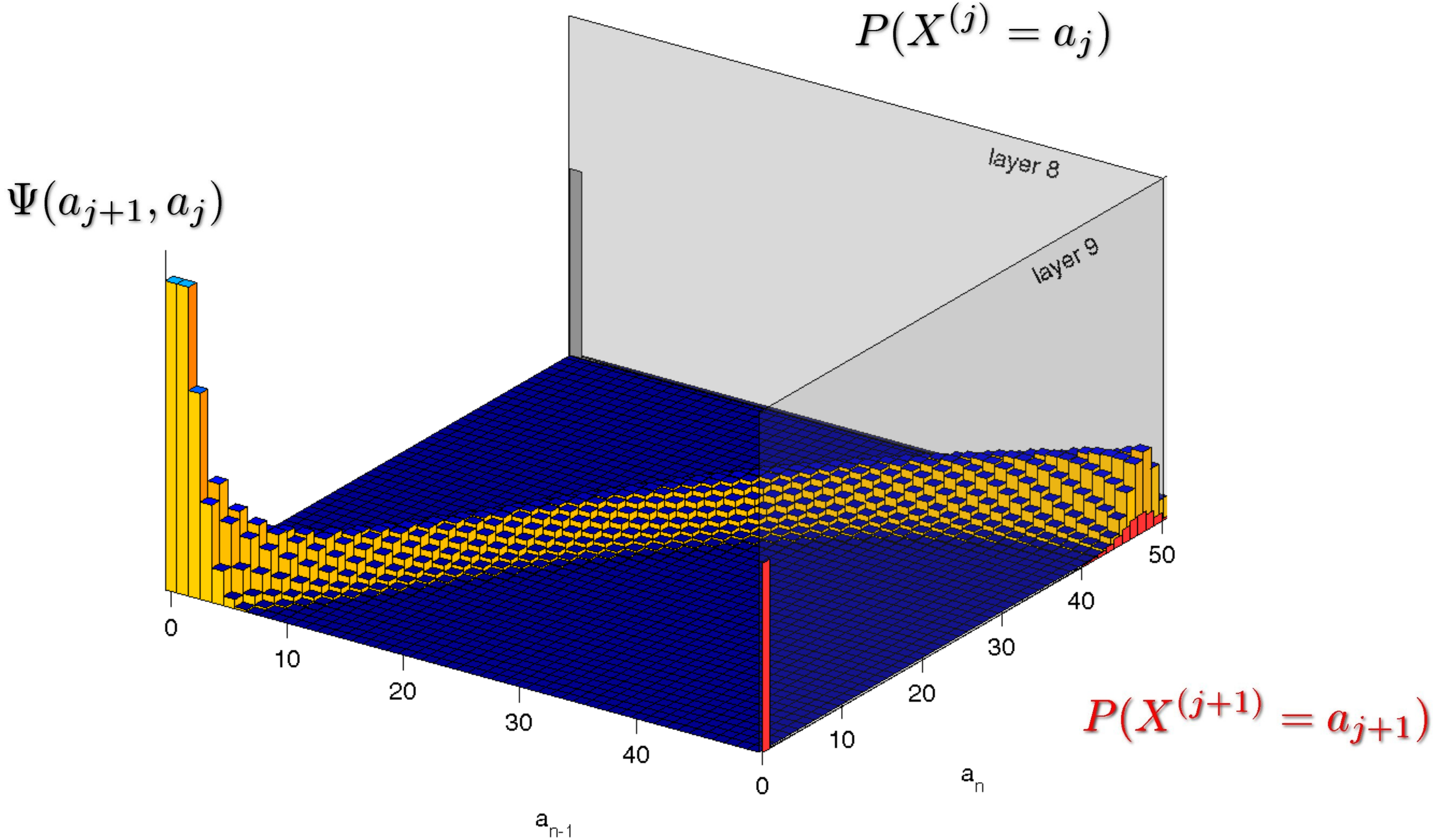
- Because the connections are chosen independently,

$$P(X^{(j+1)} = a_{j+1} \,|\, X^{(j)} = a_j) = \underbrace{b_{N,p^{(j+1)}(a_j)}(a_{j+1})}_{\Psi(a_{j+1},\, a_j)}$$

- Then, by definition of conditional probabilities

$$P(X^{(j+1)} = a_{j+1}) = \sum_{a_j=0}^{N} \Psi(a_{j+1}, a_j)\, P(X^{(j)} = a_j)$$

- We get an iteration equation!



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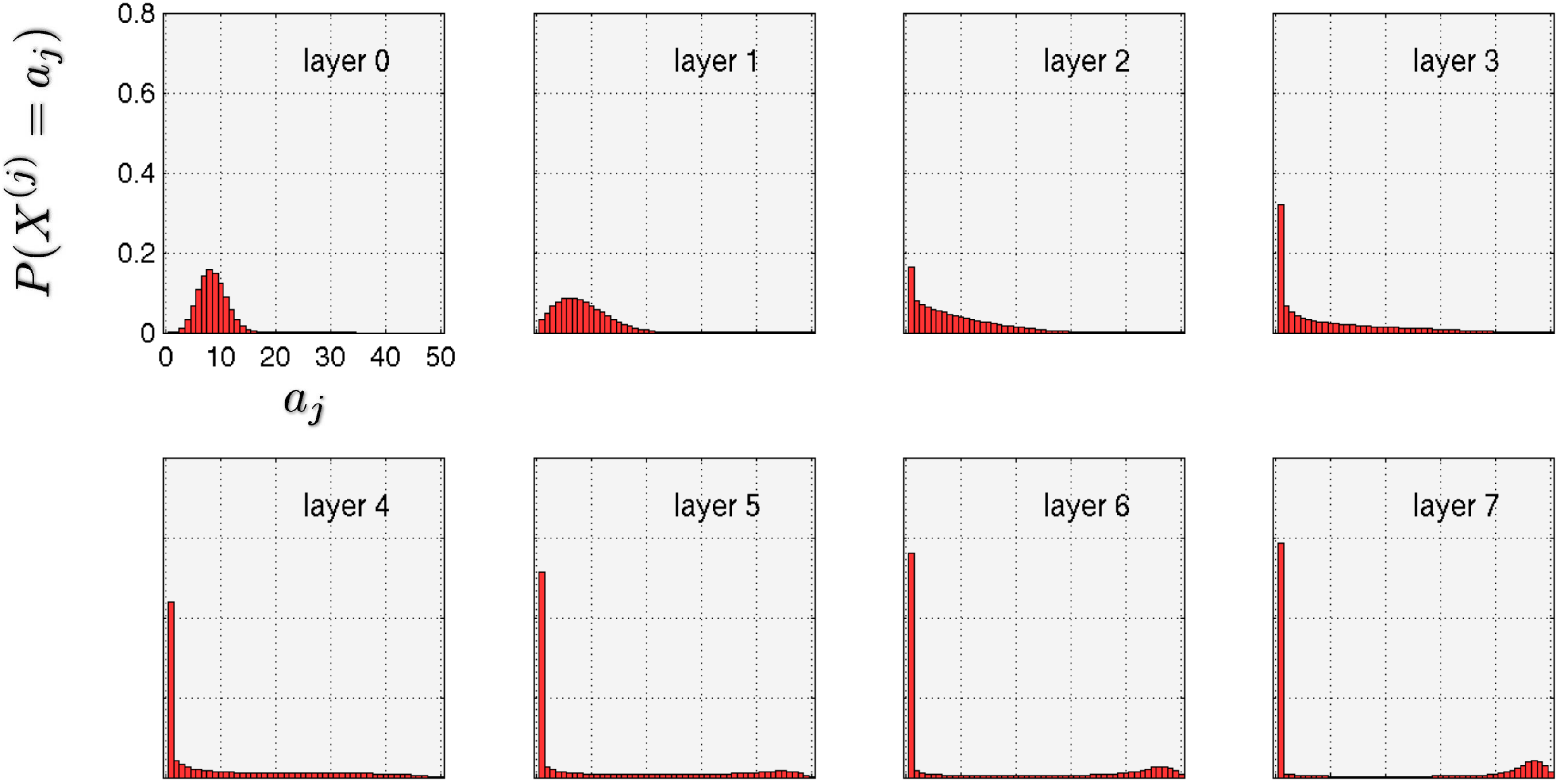
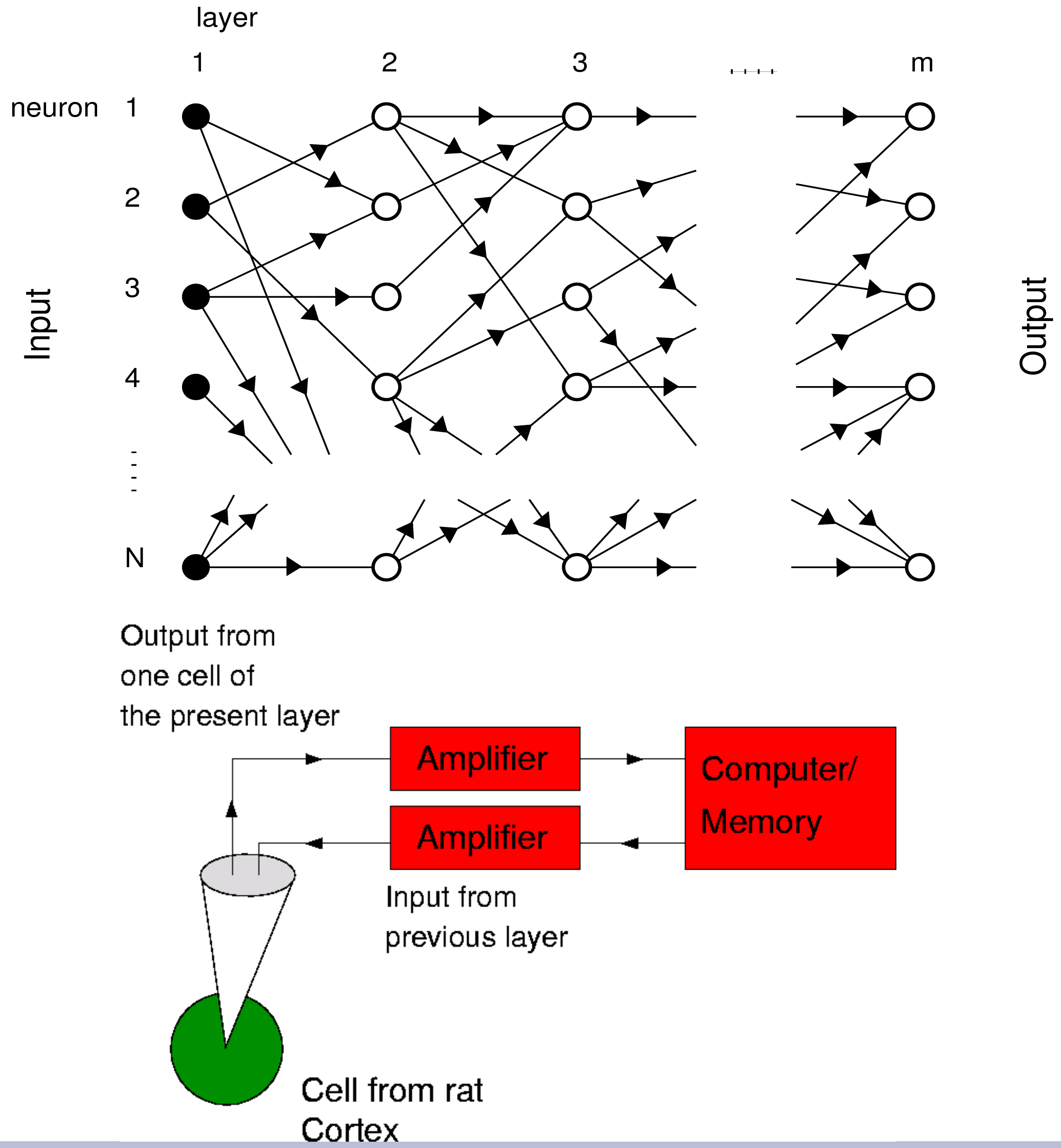
Iterated probability distribution



Neurons either all fire, or all are silent in deeper layers.

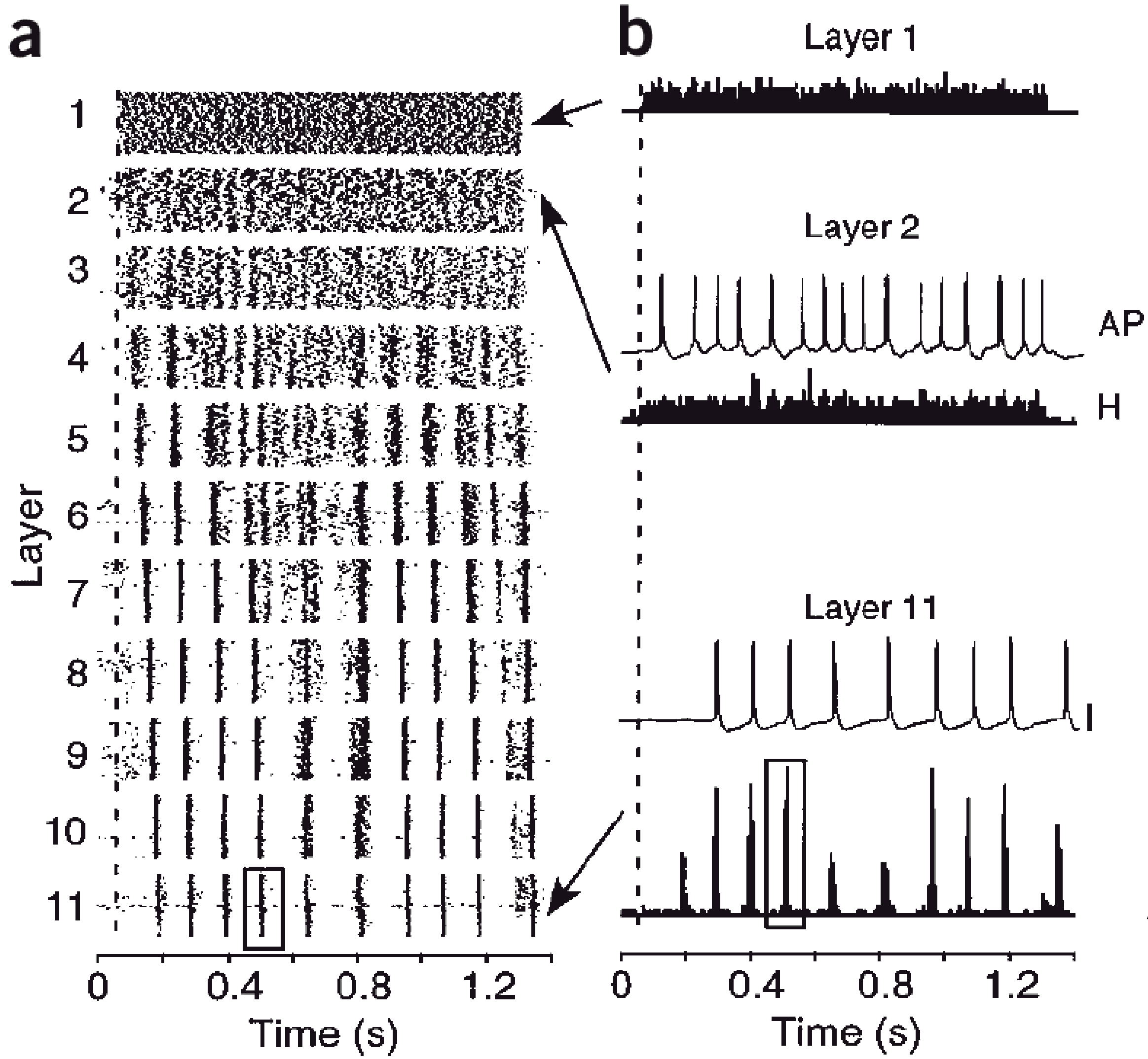
Iteratively constructed networks (ICNs)



- One or a few cortical neurons
- Dynamic clamp synapses
- Strictly feedforward networks
- Connectivity is randomly chosen by the computer

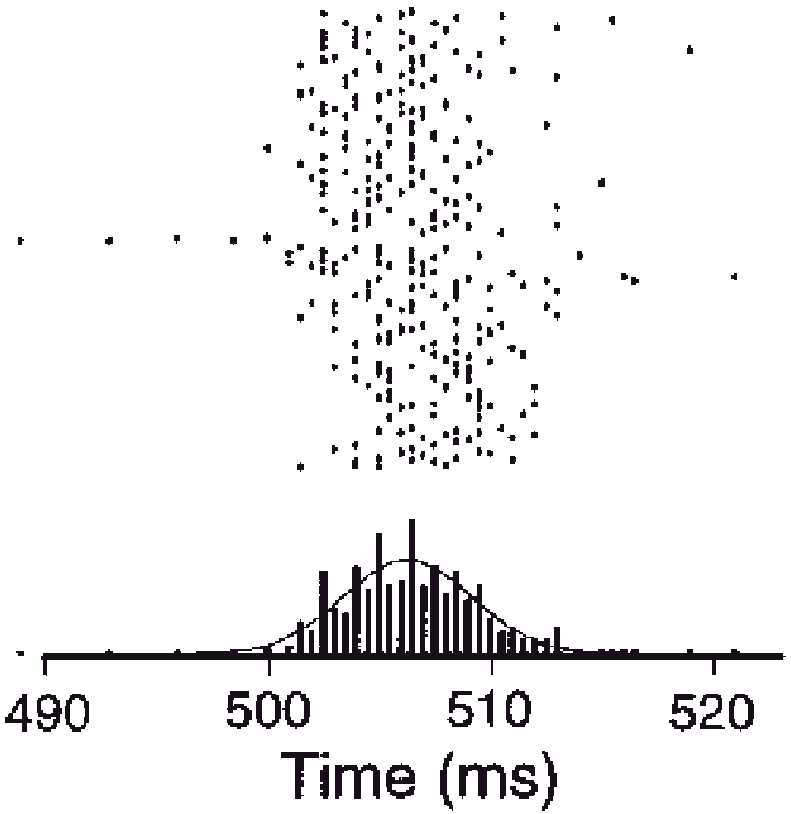
A. Reyes, Nat. Neurosci. **6**:593 (2003)

Reyes main results



A. Reyes, Nat. Neurosci. **6**:593 (2003)

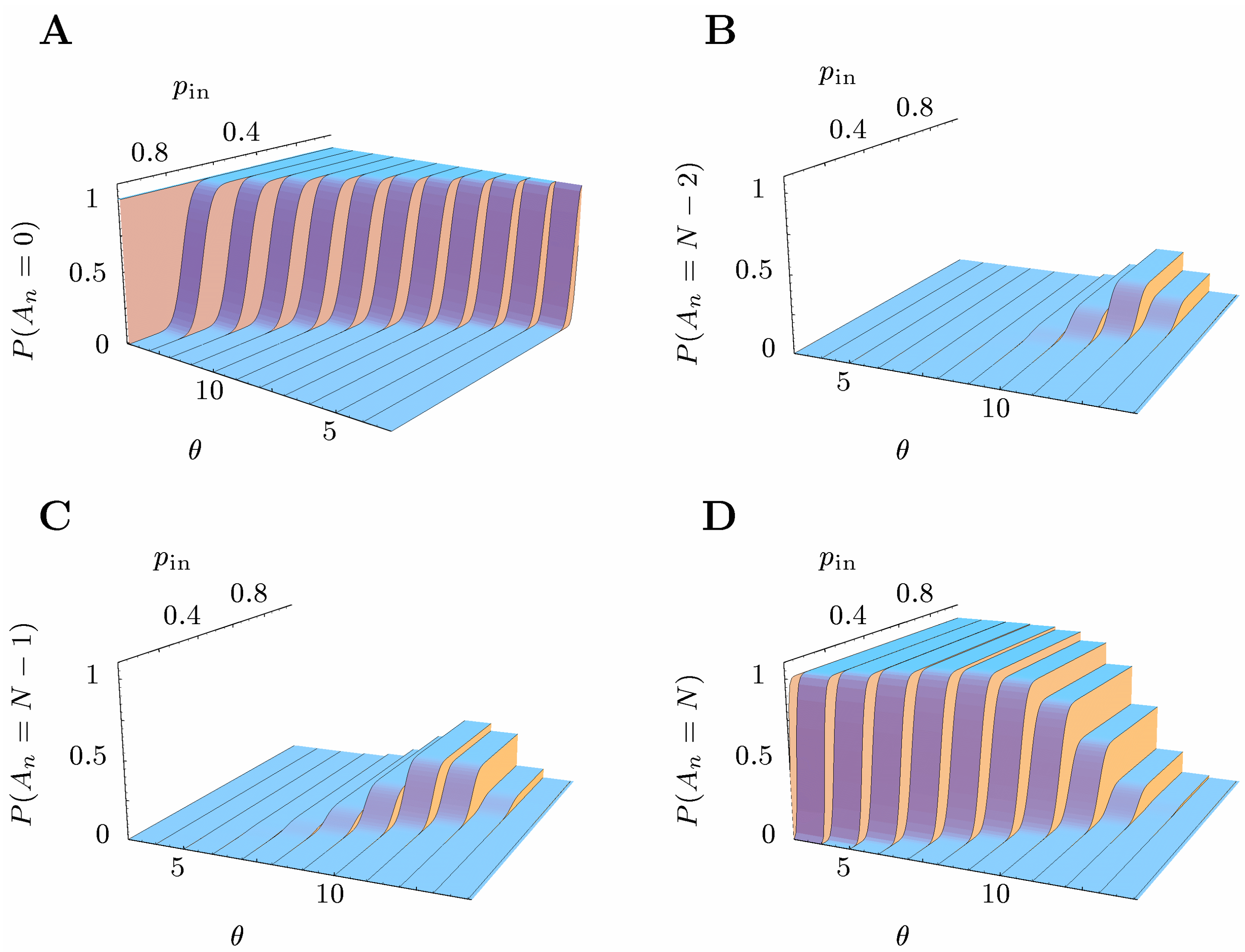
Interpretation of Δt



- McCulloch Pitts neurons: Δt is the integration time of the neurons
- Our analysis: Δt is the width of an isolated "synchronized event"

$\Delta t \approx$ 5-10 ms

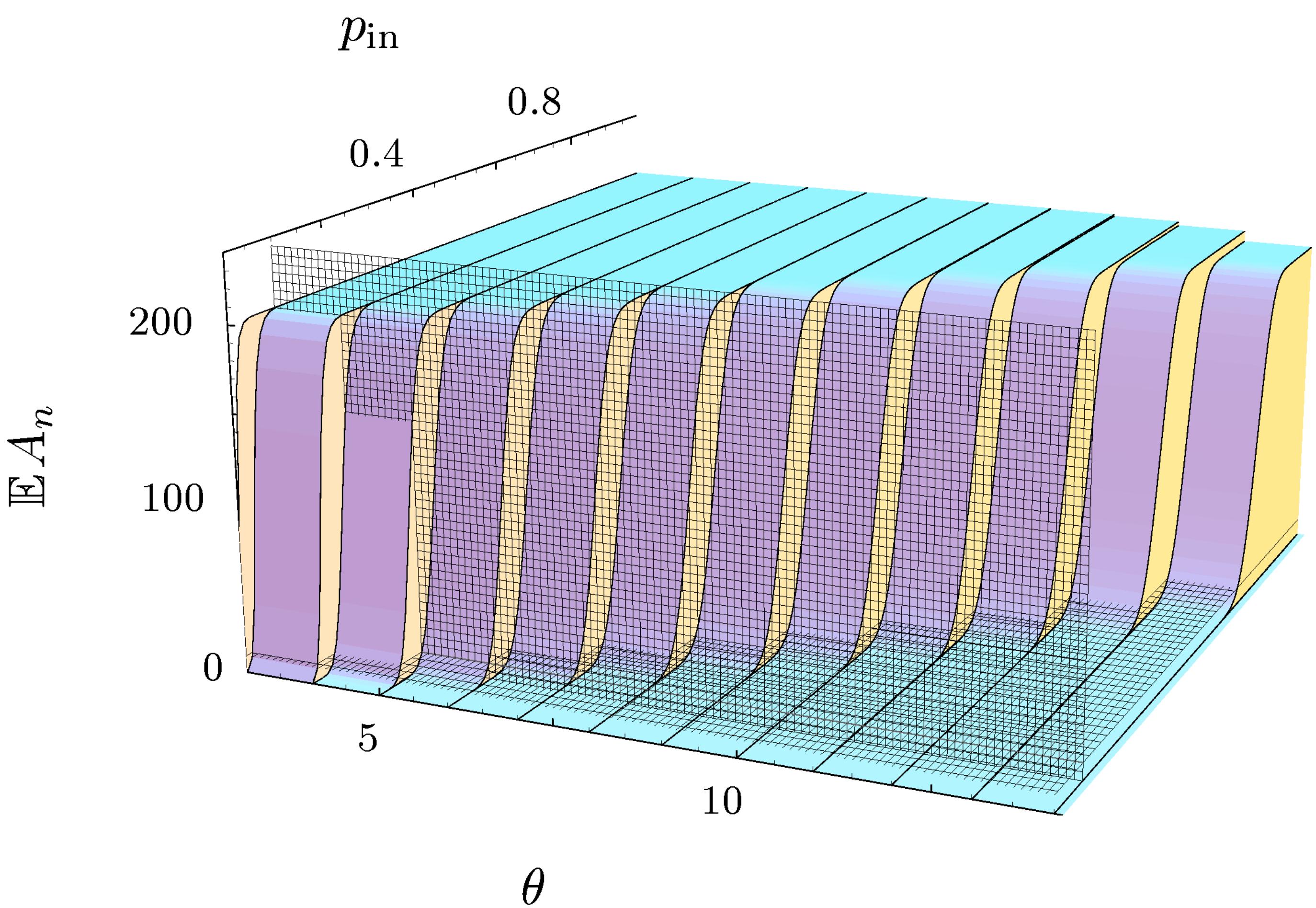
Properties of invariant measure



n=20

N=200

Threshold estimate for Reyes' neuron



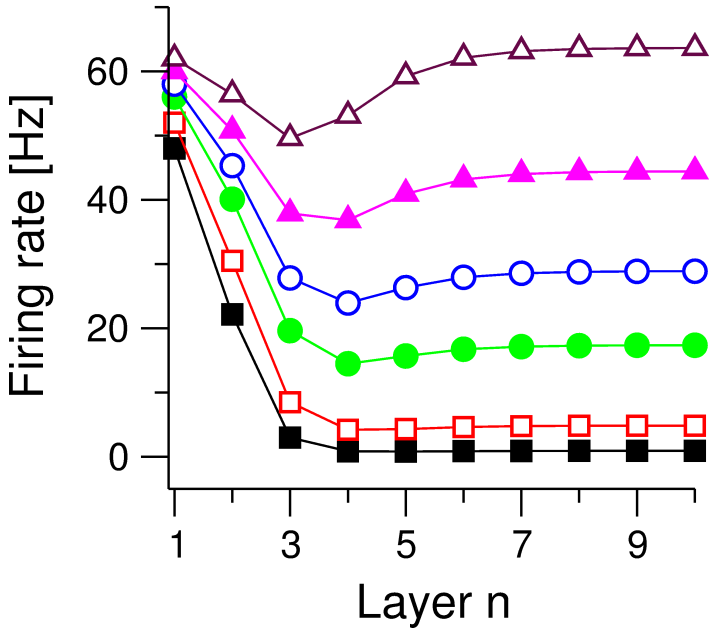
n=20

N=200

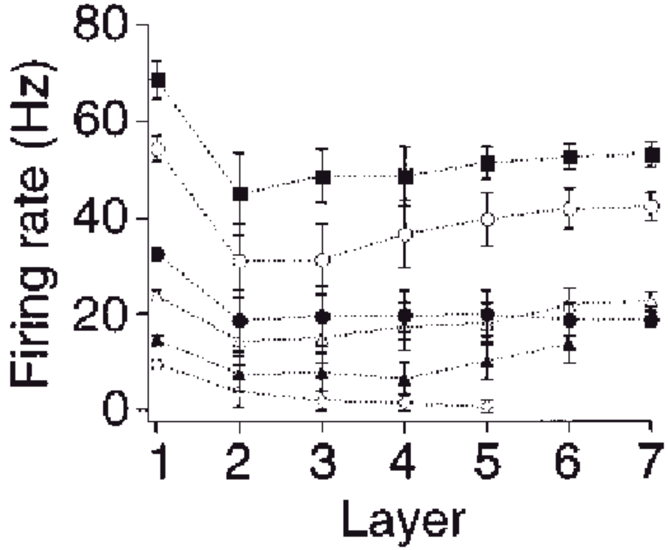
Estimated threshold is **θ**=5

Firing rate as a function of the layer

McCulloch-Pitts model



Reyes ICN



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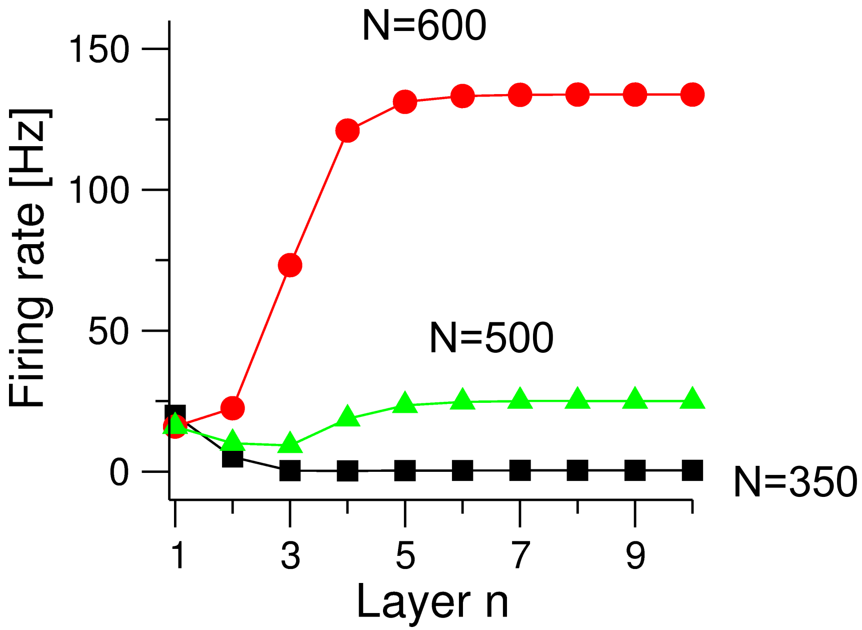
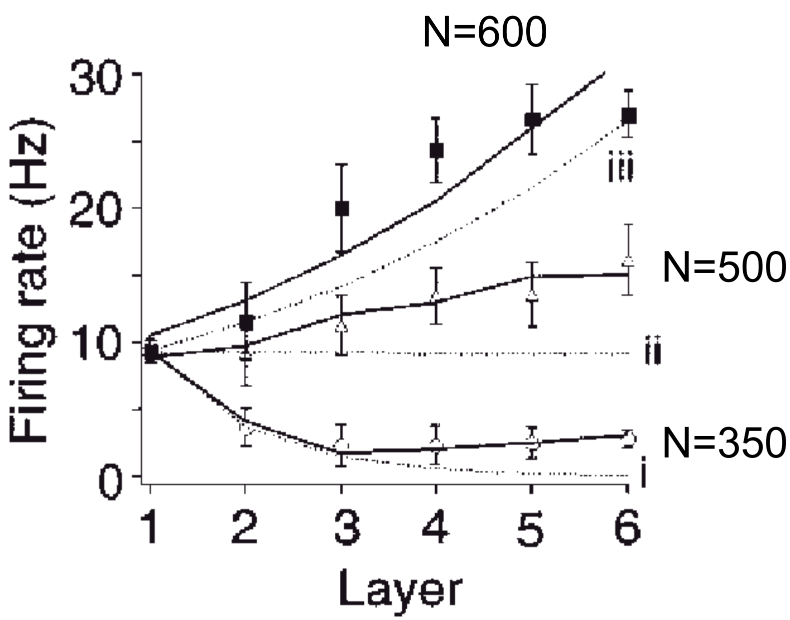
Firing rate as function of the layer

McCulloch-Pitts model



Reyes ICN



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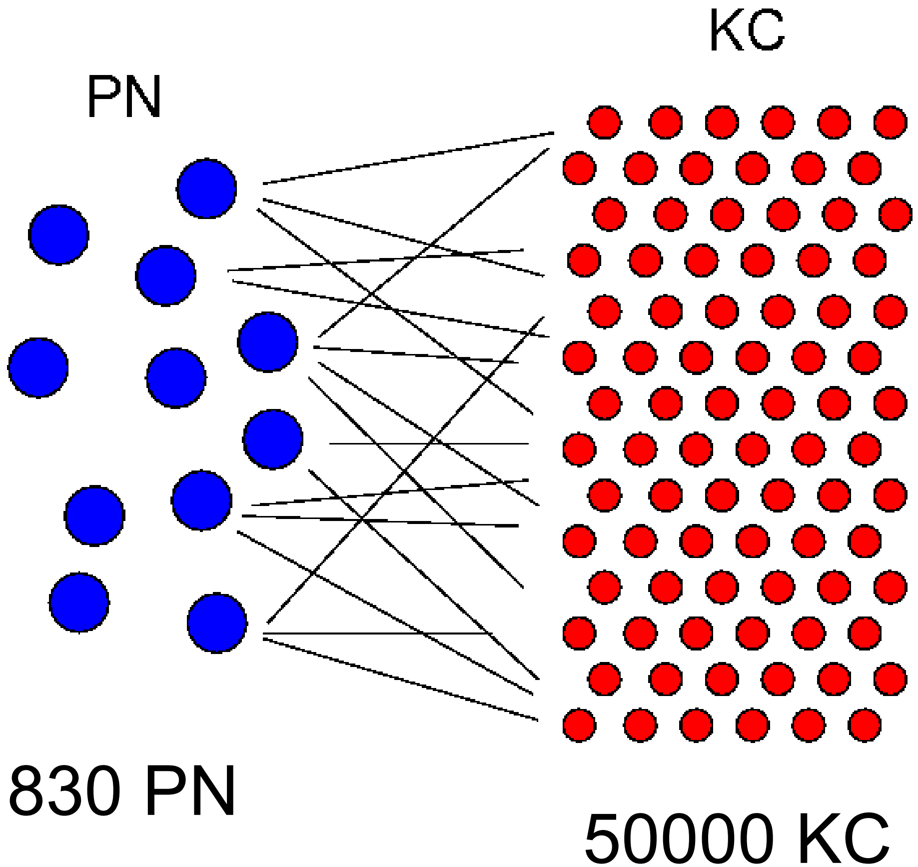
Application to the Insect olfactory system

AL-MB projections are ffwd



$$P(n_{\mathrm{PN}} = k) = b_{830,p_{\mathrm{PN}}}(k)$$

$$P(n_{\mathrm{KC}} = k) = ?$$

Example calculation: Probability distribution of the number of active KC

Probability for a Kenyon cell to be active, given n_x=k projection neurons fire:

$$P(y_i = 1 \,|\, n_x = k) = \sum_{l=\theta}^{k} \binom{k}{l} p_{y\leftarrow x}^{l} (p_{y\leftarrow x})^{k-l} \quad =: P_y$$

y_i - KC number i (a McCulloch-Pitts neuron)

n_x - number of active PNs in the AL

θ - firing threshold of the KCs

$p_{y\leftarrow x}$ - probability of a given KC to be connected to a given PN

Example calculation: Probability distribution of the number of active KC

Probability for the number of active Kenyon cells, given the number of active PN

$$P(n_y = r \,|\, n_x = k) = \binom{N_y}{r} P_y^r (1 - P_y)^{N_y - r}$$

Then the unconditioned probability is

$$P(n_y = r) = \sum_{k=0}^{N_x} P(n_y = r \,|\, n_x = k)\, P(n_x = k)$$

N_y - Total number of KC

N_x - Total number of PN

Aside: Why is this argument wrong?

$$\underbrace{P(y_i = 1)}_{:=p_y} = \sum_{j=0}^{N_x} \binom{N_x}{j} (p_{y\leftarrow x} p_x)^j (1 - p_{y\leftarrow x} p_x)^{N_x - j}$$

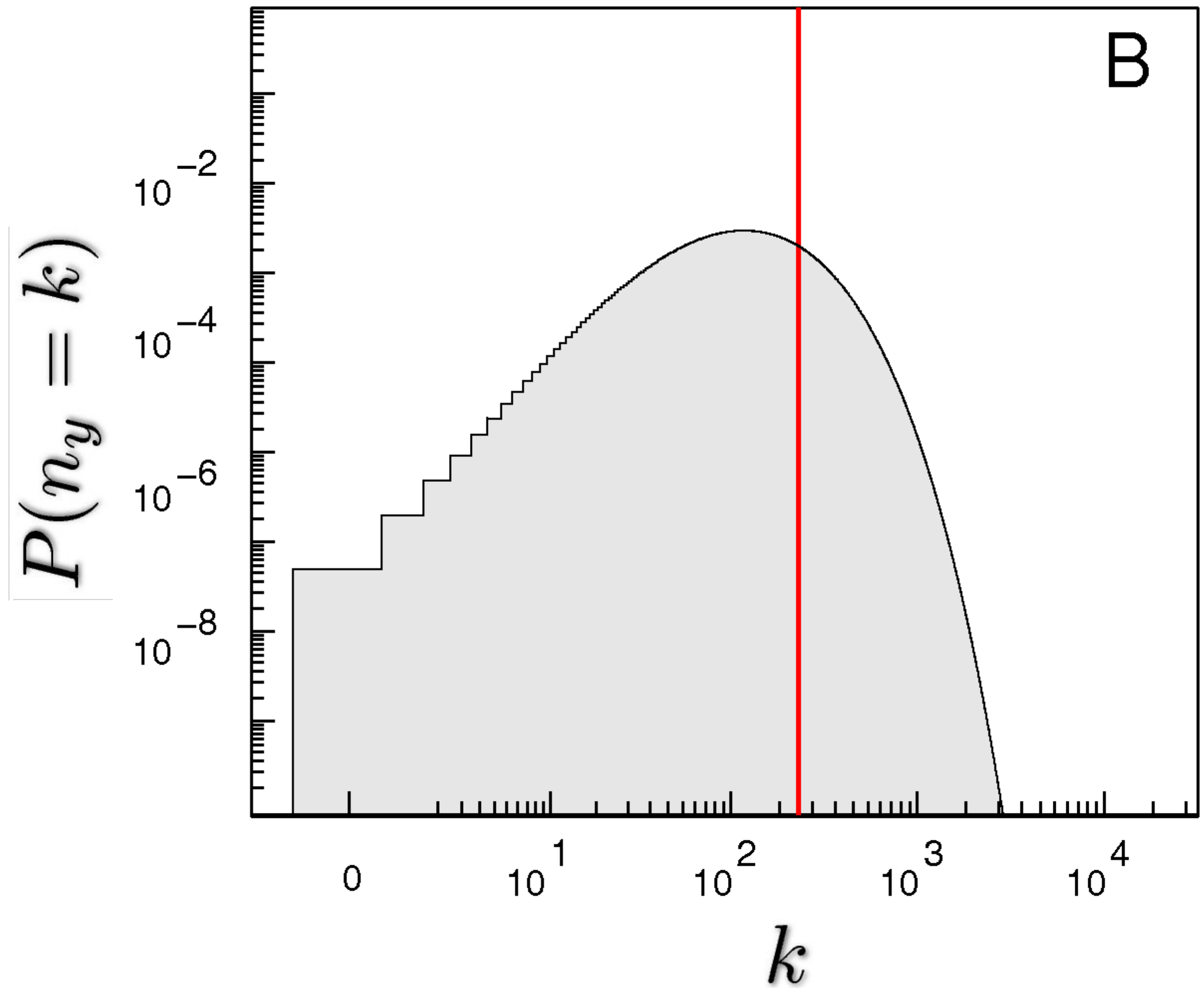
therefore

$$P(n_y = k) = \binom{N_y}{k} p_y^k (1 - p_y)^{N_y - k}$$

Warning: Wrong ... why?

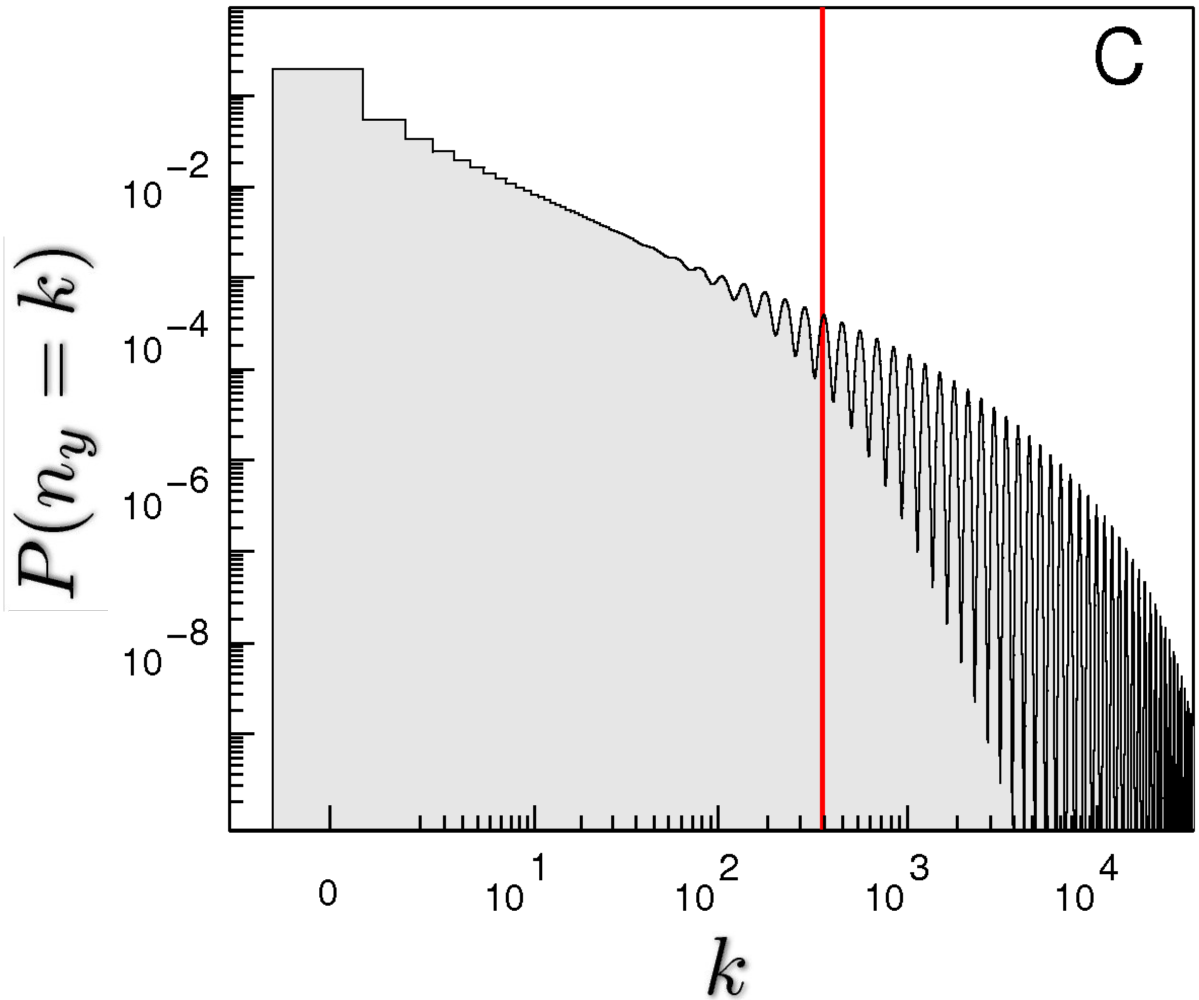
Activity in the MB: sparse connections

$$N_x = 830,\ N_y = 50000,\ \theta_{KC} = 17,\ p_{y\leftarrow x} = 0.05, p_x = 0.2$$



Activity in the MB: dense connections

$$N_x = 830,\ N_y = 50000,\ \theta_{KC} = 105,\ p_{y \leftarrow x} = 0.5, p_x = 0.2$$



Example calculation: Expectation value of the number of active KC

The expectation value for the number of active KC is

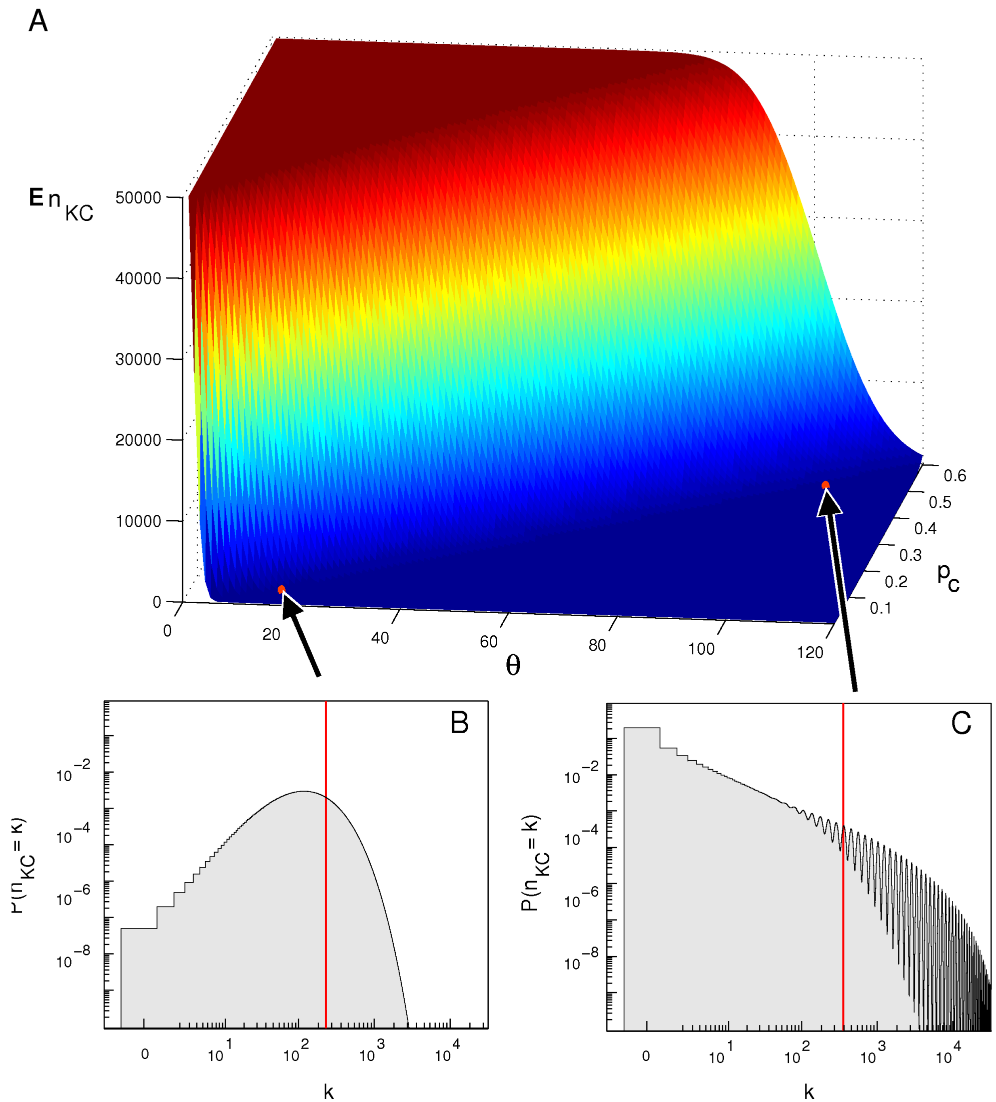
$$\mathbb{E}n_y = \sum_{l=0}^{N_y} l \cdot P(n_y = l)$$

Leading (after some simplification) to

$$\mathbb{E}n_y = \ldots = N_y p_x p_{y \leftarrow x}$$

(This is what we would naively expect; the naive expectation breaks down for $P(n_y = l)$ though ...)

MB activity



Expectation value for the number of active KC

Confusion and ground state

- Similarly one can calculate the “probability of confusion”

$$P(\text{confusion}) := P(\vec{y}_1 = \vec{y}_2 \mid \vec{x}_1 \neq \vec{x}_2)$$

- And the probability of quiescence at ground state

$$P(n_{\text{KC}} \geq N_0 \mid p_{\text{PN}} = p_{\text{baseline}})$$

Minimum conditions for successful operation

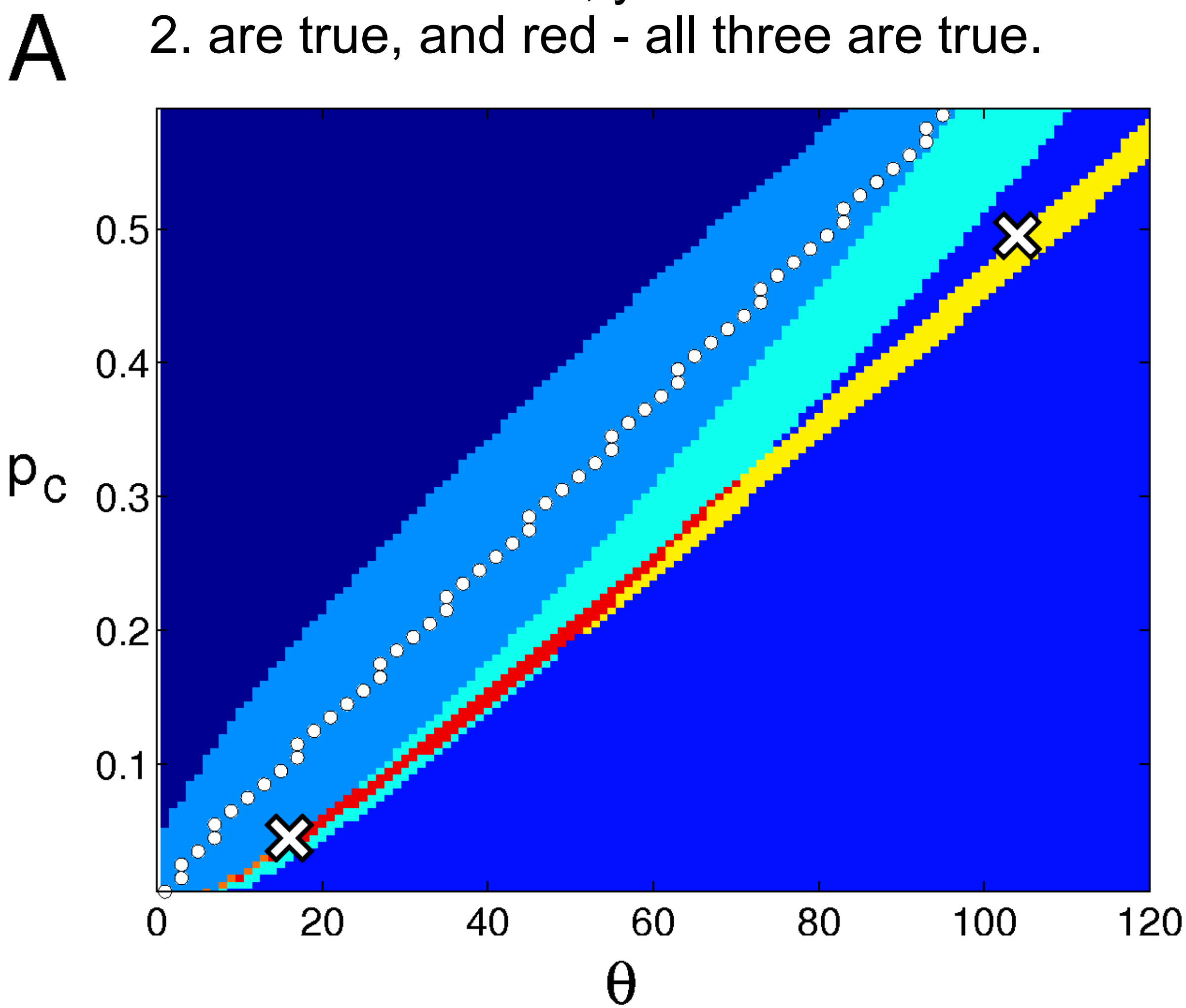
We can formulate minimal conditions for successful operation, e.g.:

1. $10 \leq \mathbb{E} n_{KC} \leq 500$
2. $p_{\text{confusion}} \leq 0.001$
3. $P(n_{KC} \geq 20 \,|\, p_{PN} = 0.13) \leq 0.01$

($p_{PN} = 0.13$ corresponds to baseline activity level)

Dense connections seem impossible!

Dark blue - none are fulfilled, blue - 3. is true, light blue - 2. is true, cyan - 2. and 3. are true, yellow - 1. and 3. are true, orange - 1. and 2. are true, and red - all three are true.



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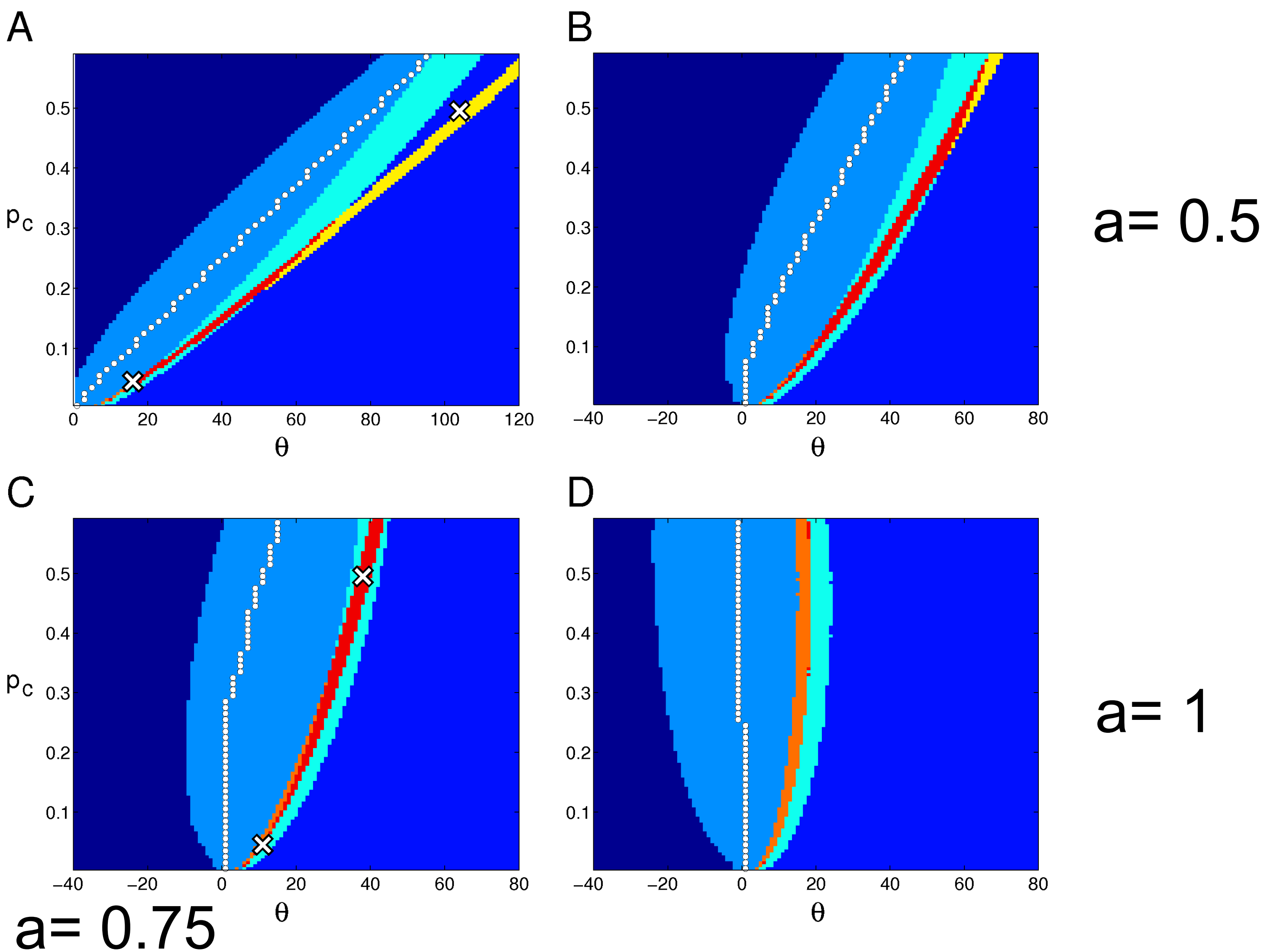
Fix: gain control

Substract the expected input from the input to each KC (feedforward inhibition)

$$y_i = \Theta\Big(\sum_{j=1}^{N_{\mathrm{PN}}} w_{ij} x_j - \theta - a\, p_c\, n_{\mathrm{PN}}\Big)$$

This can be fixed by gain control



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(Specific) Summary

- Synchrony in feedforward networks is a generic effect of connectivity
- McCulloch-Pitts approach is good enough to understand it
- For the AL-MB projections the analysis shows severe problems with dense connections
- Appropriate gain control may mediate those problems

(General) Discussion

- McCulloch-Pitts description can be quite powerful
- It might even give interesting results in unexpected areas (here synchronization)

- On the other hand, clearly it is not for everything
- Interpretation needs to be done carefully
- Quantitative agreement is rare

Further reading

- T. Nowotny and R. Huerta Explaining synchrony in feedforward networks: Are McCulloch-Pitts neurons good enough? Biol Cyber **89**(4): 237-241 (2003)
- A. Reyes, Synchrony-dependent propagation of firing rate in iteratively constructed networks in vitro, Nature Neurosci. **6**:593 (2003)
- T. Nowotny et al. How are stable sparse representations achieved in fan-out systems? (in preparation)

Next time

- Connectionist models of recognition and learning in the olfactory system of insects
- Spiking models of insect olfaction