What can we learn from synaptic weight distributions?

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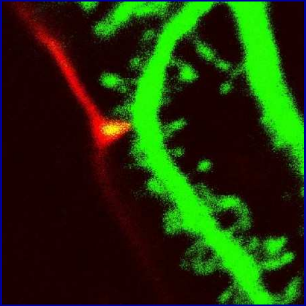


Outline

- Experimental distributions of synaptic weights.

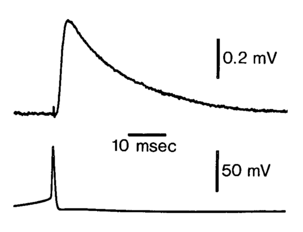
- Different types of theories

i) based on a plasticity rule

ii) based on a learning task

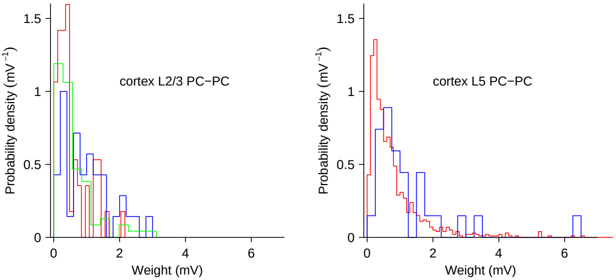
Synaptic weight

- Available measurements obtained from somatic recordings : Synaptic weight defined as peak somatic depolarisation.



A. Mason et al, J Neurosci 11, 72-84 (1991)

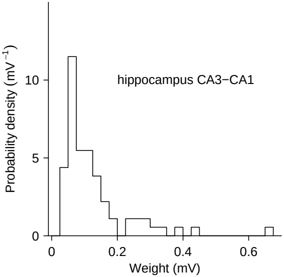
Connections between cortical pyramidal cells



- **L2/3: Mason et al, J Neurosci (1991), Holmgren et al, J Physiol (2003), Feldmeyer et al, J Physiol (2006).**
- **L5: Sjoström et al, Neuron (2001), Plos. Biol. (2006); Frick et al, Cereb Cortex (2008).**

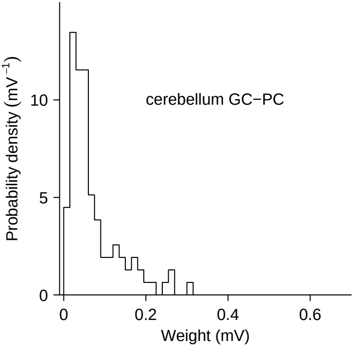
- **connection probability $\sim 10\%$; comparison with anatomy: potential synapses.**

Connections between hippocampal pyramidal cells



- **connection probability ~ 6%**
- **CA3-CA1: Sayer et al, J Neurosci (1990).**
- **"Silent" synapses with NMDA receptors but no AMPA receptors; immunochemistry: 20% Schaffer collaterals-CA1 pyramidal cell synapses no detectable AMPAR (Nusser et al, 1998).**

Cerebellar Parallel fiber-Purkinje cell synapses



- **PF-PC: Isope and Barbour, J Neurosci (2002).**
- **connection probability $\sim 7\%$**
- **Comparison with anatomical data (Harvey and Napper, 1991) suggests $\sim 80\%$ of anatomical synapses have undetectable weights i.e are silent.**

Summary of experimental data

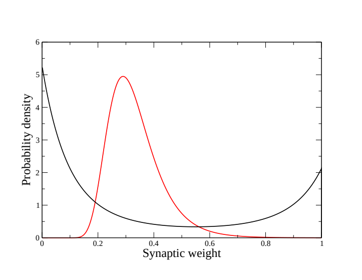
• Similar distribution shapes (but different scales) in different areas : monotonic decay from a peak close to zero weight.

• Large fraction of "potential" synapses (cortex) or "silent" synapses (cerebellum).

• Explanations?

Distributions from STDP plasticity rules

(Song et al 2000, van Rossum et al 2000, Rubin et al 2001,...)
• prescribed pre and post synaptic activities (e.g. poisson spike trains with imposed correlations)
• simple additive rule generally lead to bimodal shapes.
• multiplicative rule can lead to unimodal distribution (depression increases with synaptic strength)



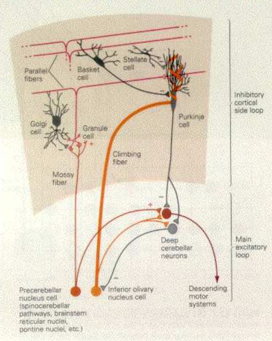
van Rossum et al, J Neurosci 20 (2000)

Distributions from optimal learning

- weights are modified to perform a task.
- deduce the weight distribution from the task itself.
- bypass the details of the learning rule if the task is optimally performed.
- example for the cerebellar PF-PC synaptic weight distribution.

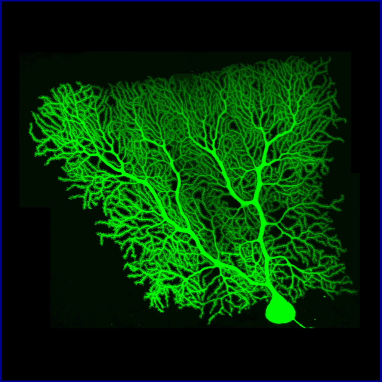
The logic of the cerebellar circuitry

An influential theoretical proposal (Marr (1969), Albus (1971)):
•**Learning**: change of the parallel fibers/Purkinje cells synapse
•**Teacher**: **error signal** coming from the climbing fibers (one for each Purkinje cell)



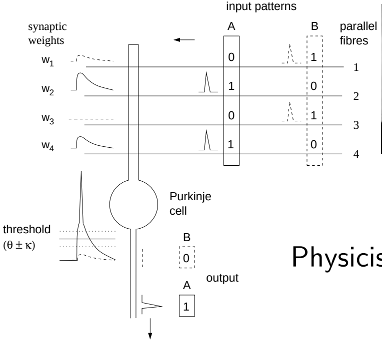
Experiments: Ito,...

The Purkinje cell



B. Barbour

The simplest model: the Purkinje cell as a perceptron





Physicist (spike) or Biologist (no spike)?

Input: a set $(N \sim 150000)$ active $(G_i = 1)$ or inactive $(G_i = 0)$ granule cells

Rule: spike emission $(P = 1)$ or silence $(P = 0)$ depending on whether the depolarization created by the inputs is larger or smaller than a threshold θ with a security margin κ.

$$P = 1 \text{ if } \sum_i w_i G_i > \theta + \kappa, \quad P = 0 \text{ if } \sum_i w_i G_i < \theta - \kappa$$

• **Classic learning problem**: can one choose (and how) the synaptic weights $\{w_i\}$ so as to satisfy desired associations between input patterns $(\{G_i^\mu\}, \mu = 1, \cdots, p)$ and outputs P^μ

(Rosenblatt, Minsky et Papert, Cover,...)

Statistical physics techniques are powerful for this kind of problem ("spin glasses": Sherrington-Kirkpatrick,...,**Parisi**,...)

• Main idea (**E. Gardner**) : compute the **typical volume of solutions** in the space of synaptic weights

many contributions $\sim 85 - 95$.

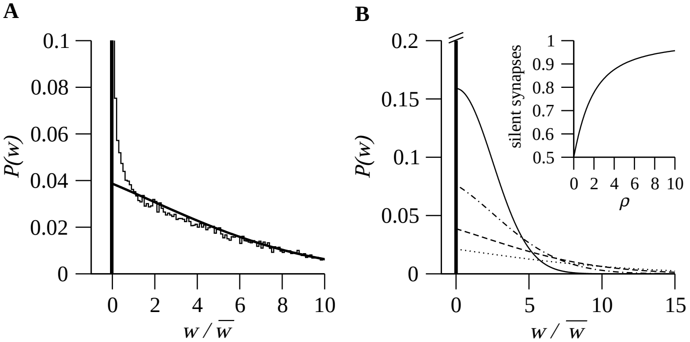
• **Particularities here**: **positive synapses**, fraction of active input f, fraction of active outputs f', threshold θ (analogous to Gutfreund-Stein (1990) + correction for threshold).

• Essential composite **parameter** : $\rho = \frac{\kappa}{\theta}\sqrt{\frac{fN}{1-f}}$

Distribution of synaptic weights

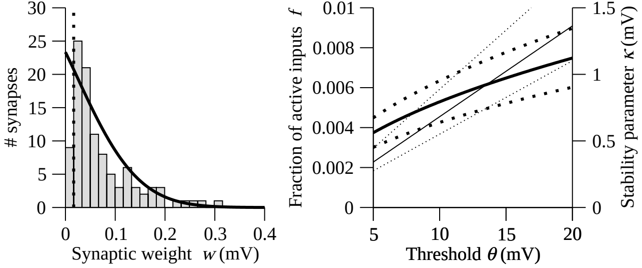
$$P(w) = \frac{1}{V}\int \delta(w - w_1)\prod_j d\rho(w_j)\prod_\mu \Theta\left[(2P^\mu - 1)\left(\sum_j w_j G_j^\mu - \theta\right) - \kappa\right]$$

Analytical solution using replicas ($1/V = \lim_{n->0} V^{n-1}$)
When learning is maximal (critical capacity) a finite fraction of synapses have zero weights!



Comparison with experimental data

data + 80% of undetected synapses $\Rightarrow \rho = 2.1, \overline{w} = 0.015mV$.



Two relations between f, θ et κ

(e.g. $\theta = 10mV, f = .0045, \kappa = .81mV$).

What has this theoretical analysis told us?

- **Silent synapses : synapses of given sign (excitatory synapses) + hypothesized maximal learning or maximal robustness.**

- **Why are they kept? learning of a new set of associations.**

- **Estimate of a difficult quantity to assess otherwise : each Purkinje cell can store up to** 40000 **associations.**

N. Brunel, V. Hakim, P. Isope, J.-P. Nadal et B. Barbour,
Neuron **43**, 745-757 (2004).

What about cortical synaptic weight distributions?

• prescribing attractor states (a cell is either active or inactive) in a recurrent network is equivalent to independently solving a perceptron problem for each cell.

• When a maximal number of attractors is stored (or when maximal robustness is desired for a given number of attractors), the synaptic weight distribution is identical to the optimal perceptron distribution.

• Is attractor dynamics a main feature of cortex dynamics? it is at least a main model for many experimental observations (persistent activity, tuning curves,....).

• Another optimality criterion? Mitya Chklovskii's talk.

B. Barbour, N. Brunel, V. Hakim and J.P. Nadal,
TINS **30**, 622-629 (2007).

Some conclusions and open issues

- Direct experimental tests of theories: immature vs mature animals, animals raised in different environments, genetic manipulation of some parameters (activity, noise,...)?

- Analog or discrete synapses?

- Learning rules : error signal and supervision, optimal learning with graceful forgetting,...?

- Synaptic weight distributions are interesting quantities that deserve more analysis.

- New experimental techniques will hopefully make easier the measure of synaptic weight distributions (Ed Gallaway's talk).

The End.

Thank you!