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HAS THE BRAIN MAXIMIZED ITS INFORMATION STORAGE CAPACITY?

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Learning and memory may rely on the reorganization of neuronal circuits by spine remodeling. We look for geometrical parameters of cortical circuits, which maximize information storage capacity associated with this mechanism. In particular we calculate the volume fractions of various neuropil components, which maximize information storage capacity. The optimal values of axonal and dendritic volume fractions are not significantly different form anatomical measurements in mouse and rat neocortex and rat hippocampus. This leads us to suggest that maximizing information storage capacity associated with spine remodeling may have been an important driving force in the evolution of the cortex.

Introduction

Many important brain functions such as learning and memory rely on the plasticity of neuronal circuits. Traditionally, plasticity is thought to rely on the following biological mechanisms: changes in the strengths of existing synaptic connections, formation and elimination of synapses without remodeling of neuronal arbors, and remodeling of dendritic and axonal branches. In order to unravel the respective roles of these mechanisms we began to evaluate their plasticity potential, i.e. the number of available yet different circuits. In particular, we calculated the plasticity potential associated with reorganization of neuronal circuits by formation and elimination of synapses. We expressed our results in terms of the logarithm of the number of available circuits, or the information capacity.

In this paper we look for geometrical parameters of cortical circuits which maximize information storage capacity due to formation and elimination of synapses. In particular, we find axonal, and dendritic volume fractions, which maximize synaptic information capacity as functions of dendritic and axonal length densities, average spine length, and density of synapses. Then we compare these optimal geometrical parameters with the anatomical data and find a reasonable agreement.

Based on this observation, we suggest that maximizing information storage capacity due to formation and elimination of synapses may have been and important driving force in the evolution of the neocortex.

Information storage capacity

We start by briefly reviewing the framework behind the calculation of the information storage capacity due to formation and elimination of synapses, which has been done previously [4].

Because the majority of excitatory synapses are located on spines [1] the reorganization of neuronal circuits can be implemented by a dendritic spine retracting from a current pre-synaptic axon and extending towards another axon. Such switching of pre-synaptic partners is only possible if within a spine length of a dendrite there are available axons, which do not have synapses with the dendrite. The availability of such adjacent axons relies on their abundance relative to the number of spines on a given dendrite, Fig.1. If the number of axons within a spine length of a dendrite is equal to the number of spines, Fig.1B, then there are no available pre-synaptic partners and spine remodeling cannot contribute to circuit reorganization. If the number of adjacent axons is greater than the number of spines, Fig.1C, then spine remodeling can contribute to circuit reorganization, Fig.1D.

To determine which scenario (Fig. 1B or Fig. 1C) better reflects the real brain, we have derived a mathematical expression (making no assumptions about neuronal arbor shapes) for the ratio of actual synapses to adjacent axons, which we call the filling fraction, *f*:

$$f = \frac{n_s}{\overline{\sin(\theta)} 2 s \rho_a \rho_d} \qquad (1)$$

Here s is the spine length (measured from the tip of the spine to the midline of dendritic branch), ρ_a and ρ_d are axonal and dendritic length densities, and $\overline{\sin(\theta)}$ is the mean sine of the intersection angle between axonal and dendritic branches inside considered unit volume. The

sine is equal to $\pi/4$ for uniformly distributed axonal or dendritic branches (cortex, hippocampus), and to 1 for axons and dendrites intersecting at the right angle (parallel fibers of granular cells and dendrites of Purkinje neurons in cerebellum).

The filling fraction f is a measure of plasticity potential associated with spine remodeling, as it reflects the number of different circuits that can be realized in given neuropil volume through spine reorganization. For example, high filling fraction implies small plasticity potential due to small number of available potential synapses (potential synapses with no actual synaptic connection).

The information storage capacity of unit volume of neuropil due to spine remodeling is defined as base two logarithm of the number of different synaptic connectivity patterns. We have shown that the information storage capacity depends on the filling fraction as (Stepanyants et al., 2002):

$$i = n_s \left(1.25 - \log_2 f\right). \qquad (2)$$

Eq. (2) is an approximation of a more general expression for information storage capacity see [4], made for small values of filling fraction, $f < 0.4$.

Optimal neuropil

Considered unit volume of neuropil can be broken down into several components,

$$\kappa_a + \kappa_d + \kappa_{syn} + \kappa_{rest} = 1, \qquad (3)$$

where κ_a and κ_d are the axonal (not including boutons) and dendritic (without spines) volume fractions, κ_{syn} is the synaptic volume fraction, including dendritic spines, axonal boutons, and

the part of glia dedicated to synapse maintenance, κ_{rest} is the remaining part of the neuropil, including the rest of glia and the extracellular space.

One way of providing a large structural synaptic information storage capacity per unit volume of neuropil is, according to Eq.(2), by increasing the axonal and/or dendritic length densities $\rho_{a,d}$. This change results in decrease in filling fraction f, Eq. (1), and, consequently, increase in the information capacity i. However, due to the constraint on the volume of neuropil, Eq. (3), the increase in $\rho_{a,d}$ has to be accompanied by a reduction in the synaptic density n_s. This reduction for biologically relevant values of filling fraction $f < 0.4$ has an opposite effect on information capacity. The three considered components, i.e. axonal, dendritic and synaptic have to be perfectly balanced in order to achieve the maximum information capacity. This balance is realized when axons and dendrites occupy equal fractions of neuropil given by the following function of filling fraction only (see Methods for details):

$$\kappa_a = \kappa_d = \frac{1-\kappa_{rest}}{1.87 - \ln f}. \qquad (4)$$

This function is illustrated in Fig. 1 for a special case of $\kappa_{rest} = 0$.

Anatomical data

Volume fractions of neuropil components and corresponding filling fractions f are presented in Table 1. The filling fractions for the mouse neocortex and CA1 field of the rat hippocampus (based on CA3 → CA1 projection only) have been previously estimated in [4]. Axonal and dendritic volume fractions are taken from [1,2,3].

In comparing these volume fractions with the optimal fractions, Eq. (4) we set $\kappa_{rest} = 0$. This is justified by the fact that κ_{rest} which consists mainly of extracellular space is significantly reduced in serial section electron microscopy preparation. The anatomical fractions from Table 1 contain a large spread, and are within 20% of theoretically predicted value, Fig. 2. A more consistent study, which would measure volume fractions and filling fraction from the same brain, is needed in order to farther justify the hypotheses that neuropil is optimally designed to store information in patterns of synaptic connectivity.

Conclusion

We calculated volume fractions occupied by axons, dendrites and synapses in a volume of neuropil optimally designed to maximize information storage capacity due to spine remodeling. These optimal volume fractions are not significantly different from those measured anatomically. This leads us to suggest that maximizing information storage capacity due to spine remodeling may have been an important driving force in the evolution of the cerebral cortex.

Methods

In this section we derive the expression for the optimal values of axonal and dendritic volume fractions (Eq. (4) in the main text). This optimization problem, constrained by the fact that neuropil consists of several particular components, Eq. (3), is equivalent to the problem of finding the maximum of the following function,

$$I = i - \lambda(\kappa_a + \kappa_d + \kappa_{syn} + \kappa_{rest}), \qquad (5)$$

where λ is a positive parameter.

We search for the maximum of the function I by varying axonal and dendritic length densities $\rho_{a,d}$ and density of synapses n_s, while keeping basic neuropil properties, i.e. basic geometry of axonal and dendritic arbors, geometrical factor $\overline{\sin(\theta)}$ and the average spine length s unchanged. Since, axonal and dendritic volume fractions $\kappa_{a,d}$ and their length densities $\rho_{a,d}$ scale with total length of axons and dendrites per neuron respectively, and the synaptic volume fraction κ_{syn} is proportional to the density of synapses n_s, we have,

$$\frac{\partial \kappa_{a,d}}{\partial \rho_{a,d}} = \frac{\kappa_{a,d}}{\rho_{a,d}}, \quad \frac{\partial \kappa_{syn}}{\partial n_s} = \frac{\kappa_{syn}}{n_s}. \tag{6}$$

To find the optimal volume fractions of neuropil components we first set the partial derivatives of the function I with respect to $\rho_{a,d}$ and n_s, to zero,

$$\begin{aligned} \frac{\partial I}{\partial \rho_{a,d}} &= \frac{n_s}{\rho_{a,d} \ln 2} - \lambda \frac{\kappa_{a,d}}{\rho_{a,d}} = 0 \\ \frac{\partial I}{\partial n_s} &= 1.25 - \log_2 f - \frac{1}{\ln 2} - \lambda \frac{\kappa_{syn}}{n_s} = 0 \end{aligned} \tag{7}$$

Next, we exclude parameter λ from these equations and receive the relations among synaptic axonal and dendritic volume fractions,

$$\kappa_{syn} = -\kappa_{a,d}(0.13 + \ln f). \tag{8}$$

Finally, by substituting synaptic volume fraction κ_{syn} from Eq. (3) into Eq. (8) we arrive at:

$$\kappa_a = \kappa_d = \frac{1 - \kappa_{rest}}{1.87 - \ln f}. \tag{9}$$

This is Eq. (4) of the main text.

References

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[3] Ikari, K., and Hayashi, M. (1981). Aging in the neuropil of cerebral cortex--a quantitative ultrastructural study. Folia Psychiatr Neurol Jpn *35*, 477-486.

[4] Stepanyants, A., Hof, P. R., and Chklovskii, D. B. (2002). Geometry and structural plasticity of synaptic connectivity. Neuron 33, in press.

Table 1. Axonal and dendritic volume fractions, and corresponding filling fractions for the mouse neocortx and the rat hippocampus

	Axonal volume fraction κ_a	Dendritic volume fraction κ_d	Filling fraction f
Mouse and rat neocortex	0.31 ± 0.09 [3] 0.36 ± 0.03 [2] 0.34 (Braitenberg and Schüz, 1998)	0.24 ± 0.07 [3] 0.23 ± 0.02 [2] 0.35 (Braitenberg and Schüz, 1998)	0.26 [4]
Rat hippocampus CA1 (CA3→CA1projection)	0.29 ± 0.03 [2]	0.26 ± 0.03 [2]	0.22 [4]

Figure Captions

Figure 1. Spine remodeling as a mechanism of circuit reorganization [4]. **A.** Spiny dendrite in macaque neocortex visualized by light microscopy. **B**. If the number of adjacent axons is equal to the number of spines (filling fraction is one) spine remodeling cannot contribute to circuit re-organization. **C**. If the number of adjacent axons is much greater than the number of spines (low filling fraction) spine remodeling can contribute to circuit re-organization. Dashed contours show possible spine locations **D**. Reorganized circuit obtained from **C** through spine remodeling.

Figure2. Optimal volume fractions of axons and dendrites as a function of the filling fraction f, solid line. Circles represent anatomical data from Table 1.

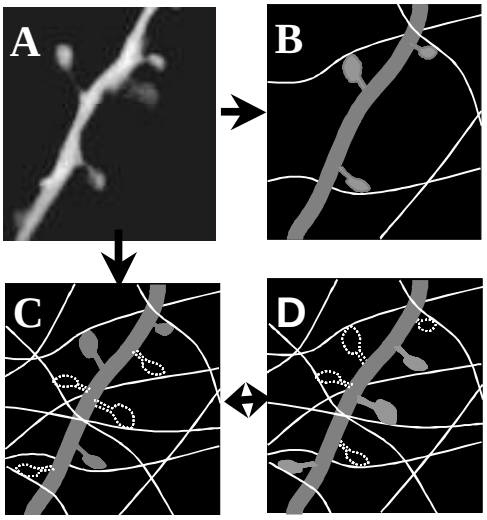

Figure 1

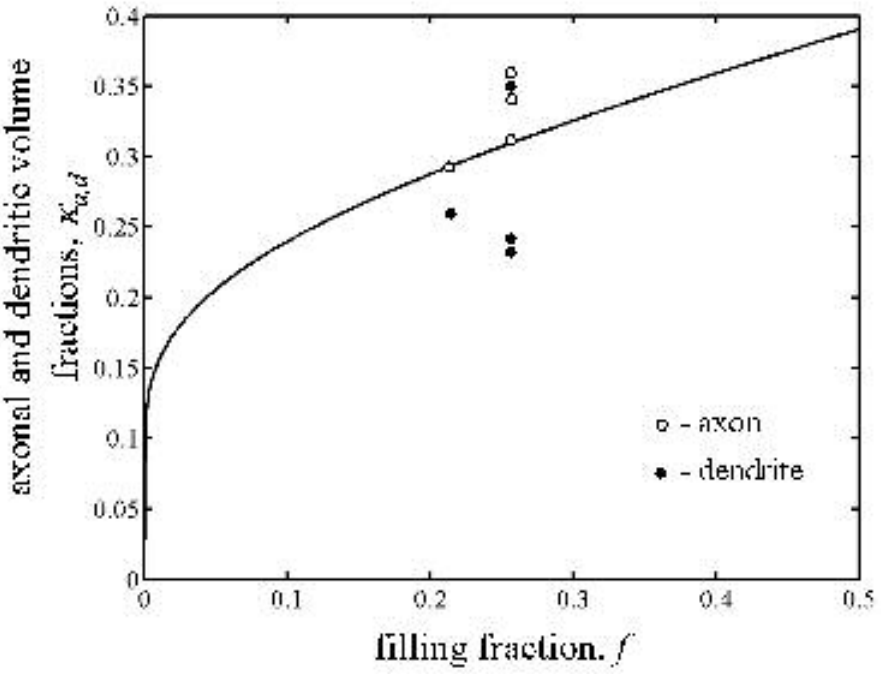
axonal and dendritic volume fractions, $\kappa_{a,d}$
filling fraction, f
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0
0.1
0.2
0.3
0.4
0.5
- axon
- dendrite

Figure 2