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INFORMATION STORAGE CAPACITY OF SYNAPTIC CONNECTIVITY PATTERNS

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How much information can be encoded in synaptic connectivity patterns through formation and elimination of dendritic spines? To answer this question, we perform geometrical analysis and derive an expression for the number of potential synapses, i.e. the number of axons that pass within a spine length of a given dendrite. We evaluate this expression by using our measurements and existing anatomical data, and find that the ratio of actual to potential synapses is 0.21 in mouse neocortex, 0.12 in rat hippocampus, and 0.16-0.23 in macaque visual cortex. Consequently, mammalian synaptic connectivity patterns may encode up to 3-5 bits per synapse.

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Introduction

Learning and memory relies on plasticity of neuronal circuits. Synaptic contributions to plasticity fall into two categories[1]: changes in pre-existing synapses without alterations of inter-neuronal connectivity and changes in inter-neuronal connectivity due to formation and elimination of synapses. The second category includes contributions from formation and elimination of dendritic spines and major remodeling of dendritic and axonal branches. These three contributions occur on distinct time scales. Synaptic strength changes are the fastest, then dendritic spine contribution, and, finally, branch remodeling[2]. Therefore, we can consider these contributions separately.

To quantitatively characterize plasticity potential due to formation and elimination of dendritic spines we estimate the information capacity associated with this contribution. First, we perform geometrical analysis to express the number of potential synapses (i.e. the number of axons that pass within a spine length of a dendrite) in terms of measurable anatomical parameters. Second, we evaluate this expression by using our measurements and existing anatomical data and find the ratio of actual to potential synapses in different species and brain areas. Third, we use this ratio to calculate the information capacity associated with dendritic spines.

Number of potential synapses

To estimate the number of potential synapses on a dendrite, imagine a virtual cylinder centered on dendritic axis, with the radius equal to the spine length (as measured from the dendritic axis), Fig.1. Only those axons, which intersect the cylinder, form potential synapses with the dendrite and need to be counted.

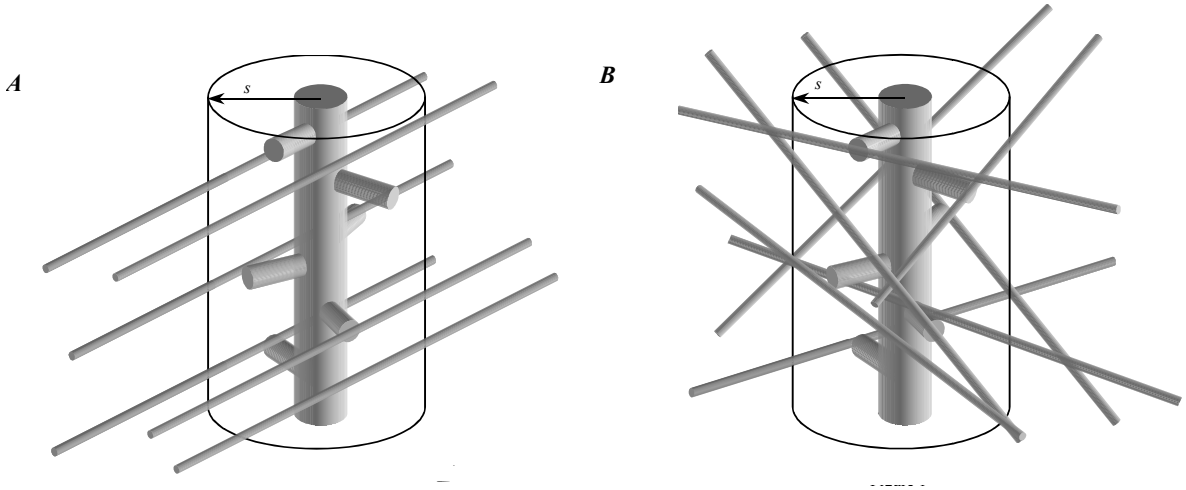

Fig.1: Geometry of synaptic connectivity. **A.** All axons are perpendicular to the dendrite. **B.** Axons are randomly oriented.

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First, consider a simplified situation where all axons pass in the same direction, perpendicular to dendritic axis, Fig.1A. Draw a rectangular box with dimensions of axonal length, L_a (parallel to the axons), dendritic length, L_d, (parallel to the dendrite), and two spine lengths, $2s$. Only those axons, whose cell bodies belong to the box, hit the cylinder. The number of these axons and, hence, the number of potential synapses, N_p, is given by the product of the box volume and neuronal density, *n*:

$$N_p = 2sL_aL_dn\,. \tag{1}$$

Second, consider a more realistic situation where axons pass in different directions, Fig.1B. Assuming that the distribution of axons is isotropic relative to the dendrite, we average over possible directions and find:

$$N_p = \frac{\pi}{2} sL_aL_dn\,. \tag{2}$$

The number of actual synapses, *N*, is expressed through the ratio of actual to potential synapses, *f*:

$$N = fN_p = \frac{\pi}{2} fsL_aL_dn\,. \tag{3}$$

Eq.(3) is rather general. Its derivation relies only on a few realistic assumptions. Volume exclusion by axons is ignored because axonal diameters are much less than spine lengths. Branch points of axons and dendrites are ignored because their segment lengths are greater than spine lengths. Axons and dendrites are assumed straight because their curvature radii are greater than spine lengths.

No assumptions are made about arbor shapes or branch densities as a function of the distance to the cell body. We do assume an isotropic distribution of intersection angles between axons and dendrites, which is already true for isotropic distribution of *either* axonal or dendritic brandhes. If the distribution of intersection angles is anisotropic, the numerical coefficient could be different. However, comparison of Eqs. (1) and (2) shows that the coefficient does not vary much in realistic situations.

Anatomical estimates

The utility of Eq.(3) is in relating the ratio of actual to potential synapses, f, which would normally require laborious EM reconstructions, to the anatomical parameters measurable mostly by optical microscopy.

We estimate f by using existing and our own (asterisks) data, Table 1. Since it is difficult to measure axonal length reliably, we take advantage of the fact that the

expression for f following from Eq.(3) depends only on the average inter-synaptic distance along the axon, L_a/N. For neuronal density in hippocampus CA3 we use the ratio of the total number of neurons and volume of the entire CA3.

Table 1

	$n\,[10^5 mm^{-3}]$	$L_d\,[mm]$	$L_a/N\,[\mu m]$	$s\,[\mu m]$	f
Mouse areas: MOs, VISp	7.8[3]	3-4[3]	4-5[3]	2.5[3, 4]	0.21
Rat CA3	33[5]/18[6]=1.8	16.1[7]	7[8]	2.5[9]	0.12
Monkey areas: V1	1.3*	1.4[10]	6.4[11]	3.5*	0.16
V2	0.77*	1.6[10, 12]	6.4[11]	3.5*	0.23
V4	0.65*	2.1[12]	6.4[11]	3.5*	0.21
7a	0.47*	2.6[10]	6.4[11]	3.5*	0.23

Information storage capacity

Knowledge of the ratio of actual to potential synapses allows us to find the information storage capacity. The number of synaptic patterns equals to the number of ways to choose N actual synapses out of N_P potential synapses, which, in the limit of large N is:

$$C_{N_P}^{N} = [(1-f)^{1-f} f^{f}]^{-N_P}. \tag{4}$$

The information storage capacity is the base two logarithm of the number of synaptic patterns:

$$I = -N_P[(1-f)\log_2(1-f) + f\log_2 f]. \tag{5}$$

Information storage capacity per synapse:

$$\frac{I}{N} = -\log_2 f - \frac{1-f}{f}\log_2(1-f). \tag{6}$$

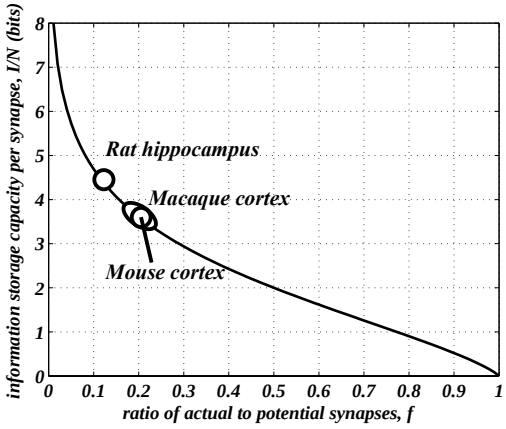

Fig.2: Information storage capacity per synapse vs. ratio of actual to potential synapses, Eq.(6).

Using our estimates for f from Table 1 we find that the information storage capacity per synapse is 3.5 bits in mouse neocortex, 4.4 bits in rat hippocampus and 3.4-4.0 bits in macaque visual cortex.

Two comments on Eq.(6) are in order. Equating the number of different inter-neuronal connections to the number of synapses is appropriate because the fraction of multiply connected neurons is small[3]. Inclusion of the variability, ΔN, in the number of synapses per neuron, N, leads only to a small correction of order $\Delta N / N$.

Conclusion

We quantitatively characterized the contribution to structural plasticity coming from the formation and elimination of dendritic spines by estimating associated information capacity. Our approach can be used to analyze plasticity potential in various experiments, such as those in sensory deprivation paradigms.

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