

Optimal wiring principle and plateaus in the degree of separation for cortical neurons

Jan Karbowski

Department of Mathematics, University of Pittsburgh, PA 15260, USA

email: jkarb@euler.math.pitt.edu

Abstract

Available experimental scaling laws for cortical neurons, synapses and axons are used to study theoretically an optimal wiring of the cortex. It is argued that the optimal wiring principle should take into account minimization of both axonal length and energy cost required in the long distance communication between areas. The latter quantity is proportional to an average degree of separation between neurons. Using scaling arguments, it is shown that this principle leads naturally to a trade-off between saving axons and saving energy used in the communication. The distinction between convoluted and smooth cortices is discussed too.

Preference: ORAL PRESENTATION.

There exist a strongly held belief in the neuroscience community that the architecture of the cerebral cortex is designed in such a way as to save available resources [1], which include axons and dendrites. Since axons are very important in long distance communication between cortical areas, they have been a prime target of saving. As a consequence, several authors [2,3,4,5] have explored the principle of minimal axon length as a candidate for an optimal wiring. In this type of wiring, one assumes that the cortex has a volume or geometry that minimizes the average length of long-range axons. However, this principle, and similar to it [6], do not take into account energetic constraints involved in the transfer of information over long distances.

In this paper, we address this additional aspect by studying a quantity characterizing the degree of separation between neurons. This quantity is a good measure of how fast information can be conveyed in a network. It is also proportional to the overall energy cost required in this communication, since it is directly related to the number of spikes fired by neurons. For efficient communication, one would expect that the degree of separation should be as small as possible. We show that, in fact, there is a trade-off between minimizing the energy cost and minimizing the biochemical resources, i.e. axonal length and number of synapses. This is because shorter axons require more steps in connecting remote cortical areas, and vice versa.

We study a network of volume V_g with a geometry that mimics that of the gray matter of the cortex, i.e. with a surface area $W = R_{\parallel}^2$ and thickness R_{\perp} ($V_g = WR_{\perp}$), with a condition $R_{\perp}/R_{\parallel} \ll 1$. We assume that neurons are sparsely connected in a stochastic manner, i.e. each neuron is directly connected to M_0 others of the total number of neurons M , where $M_0/M \ll 1$. We also assume that despite many classes of neurons, there can be defined some global average probability of a direct connection $p(r)$ that is distance r dependent. The part of $p(r)$ with small r corresponds to local connections involving intracortical axons. For large r , $p(r)$ describes a possible connection mediated by long-range axons through the white matter.

There are three basic densities in the cerebral cortex which are roughly constant across cortical regions and different species [7]: (i) surface density of neurons $\rho = M/W$, (ii) volume density of synapses MM_0/V_g , and (iii) total length of short-range (intracortical) axons per volume ML_1/V_g , where

L_1 is the total length of short-range axons per neuron. It is not clear experimentally how the total length of long-range (cortico-cortical) axons scales with the gray matter volume. However, if we assume that the cortical white matter is composed primarily of long-range axons and that average axonal width does not change with a brain size [7], then we have $ML_2 \sim V_w$, where L_2 is the total length of long-range axons per neuron and V_w is volume of white matter. Since the latter scales with the volume of the gray matter as $V_w \sim V_g^\gamma$, where exponent $\gamma = 1.22 - 1.33$ [8,9,10], we obtain for long-range axons that density ML_2/V_g^γ should be roughly constant (brain size independent).

Based on the above experimental facts, we can introduce the following new scale transformations (s is a new scale): $M \mapsto Ms$, $M_0 \mapsto M_0sf(s)$, $R_\parallel \mapsto R_\parallel s^{1/2}$, $R_\perp \mapsto R_\perp sf(s)$, $L_1 \mapsto L_1sf(s)$, $L_2 \mapsto L_2s^{2\gamma-1}(f(s))^\gamma$, which leave the above four densities invariant. Guided by experimental data [8,9,11-13], we choose scaling function $f(s) \sim s^{\alpha-1}$ for $s \gg 1$, where α is a scaling exponent. This limit, of large brains, is of our prime interest.

The total axonal length L per neuron can be defined as $L = \kappa L_1 + (1 - \kappa)L_2$, where κ is a fraction of neurons with short-range axons only. In the limit of large brains, L_1 and L_2 scale like $L_1 \sim s^\alpha$ and $L_2 \sim s^{\gamma(\alpha+1)-1}$, which indicates that L is the exponentially growing function of the exponent α . The same is true for the number of synapses M_0 per neuron, which scales like $\sim s^\alpha$. Thus, the cost of biochemical resources increases very quickly with α .

From the above scaling transformations we can infer the scaling law for the probability of a direct connection $p(r)$. It is given by $p(r(s), s) = f(s)p(r, 1)$. This relation is crucial for determining the degree of separation between neurons in the network. In order to achieve this, we have to find a probability representing a possible connection between two neurons, along at least one of the shortest paths that use k steps (k synapses). This, in turn, enables us to find the average degree of separation $\langle N \rangle_s$ at arbitrary scale s by calculating the expected number of minimal steps, which are necessary to connect two neurons. In the interval $0 < \alpha < 1$, and in the limit $s \mapsto \infty$, $\langle N \rangle_{s \mapsto \infty}$ takes a simple form [14]:

$$\langle N \rangle_{s \mapsto \infty} \approx \text{int} \left[\frac{1}{\alpha} + 1 \right], \quad (1)$$

where $\text{int}[x]$ denotes an integer part of x . This equation shows that the average degree of separation between neurons displays a decaying trend and numerous plateaus as a function of α .

The average degree of separation $\langle N \rangle_{s \rightarrow \infty}$ and the total axonal length L per neuron depend differently on the exponent α (the former decreases, while the latter increases with α). These two quantities are related respectively to the energy consumption during communication and to the use of biochemical resources in a wiring design. In the case of an optimal wiring, one wants to have both $\langle N \rangle_{s \rightarrow \infty}$ and L as small as possible, which turns out to be impossible to satisfy simultaneously. Thus, there is a trade-off between minimizing energetic and biochemical costs suggesting that an optimal situation should arise somewhere for intermediate values of the exponent α . Experimentally, for larger cortices of different species with sizes spanning few orders of magnitude [8,9,11-13], we have $\alpha_{ex} \approx 0.10$. For smaller non-convoluted cortices [9,12] $\alpha_{ex} \approx 0.25$. These values yield the following estimates of the average degree of separation: $\langle N \rangle_{\infty} = 10 - 11$ for $\alpha_{ex} \approx 0.10$, and $\langle N \rangle_{\infty} = 5$ for $\alpha_{ex} \approx 0.25$. The fact that α_{ex} is closer to zero than to one may suggest that for the cortices, especially bigger, it is more advantageous to save axons than to save energy. Also the appearance of the plateaus in the degree of separation may be an advantageous feature in the cortex design, because it allows to save axonal fibers at the same energetic cost required in the communication.

References

- [1] S. Ramon y Cajal, *Histology of the Nervous System of Man and Vertebrates*. (Oxford Univ. Press, New York, 1995), vol.1.
- [2] G. Mitchison, Proc. R. Soc. Lond. B, **245**, 151 (1991); Trends Neurosci., **15**, 122 (1992).
- [3] J. M. J. Murre and D. P. F. Sturdy, Biol. Cybern., **73**, 529 (1995).
- [4] D. C. Van Essen, Nature (London) **385**, 313 (1997).
- [5] D. Chklovski and C. F. Stevens, in *Advances in Neural Information Processing Systems*, vol.12, (MIT Press, Cambridge, MA), in press.
- [6] C. Cherniak, Trends Neurosci., **18**, 522 (1995).
- [7] V. Braitenberg and A. Schuz, *Cortex: Statistics and Geometry of Neuronal Connectivity*. (Springer, Berlin, 1998).

- [8] G. Schlenska, J. Hirnforsch. **15**, 401 (1974).
- [9] M. A. Hofman, Brain Behav. Evol. **27**, 28 (1985); Prog. Neurobiol. **32**, 137 (1989).
- [10] K. Zhang and T.J. Sejnowski, Proc. Natl. Acad. Sci. USA **97**, 5621 (2000).
- [11] J. W. Prothero and J. W. Sundsten, Brain Behav. Evol. **24**, 152 (1984).
- [12] H. J. Jerison, in *Primate Brain Evolution: Methods and Concepts*, eds. E. Armstrong and D. Falk. (Plenum, New York, 1982), pp. 77-84.
- [13] C. F. Stevens, Neural Comput. **1**, 473 (1989).
- [14] J. Karbowski, Phys. Rev. Lett. **86**, 3674 (2001).