Algebraic tests for a model for emergent order in neuronal networks through selective neuronal and synaptic death

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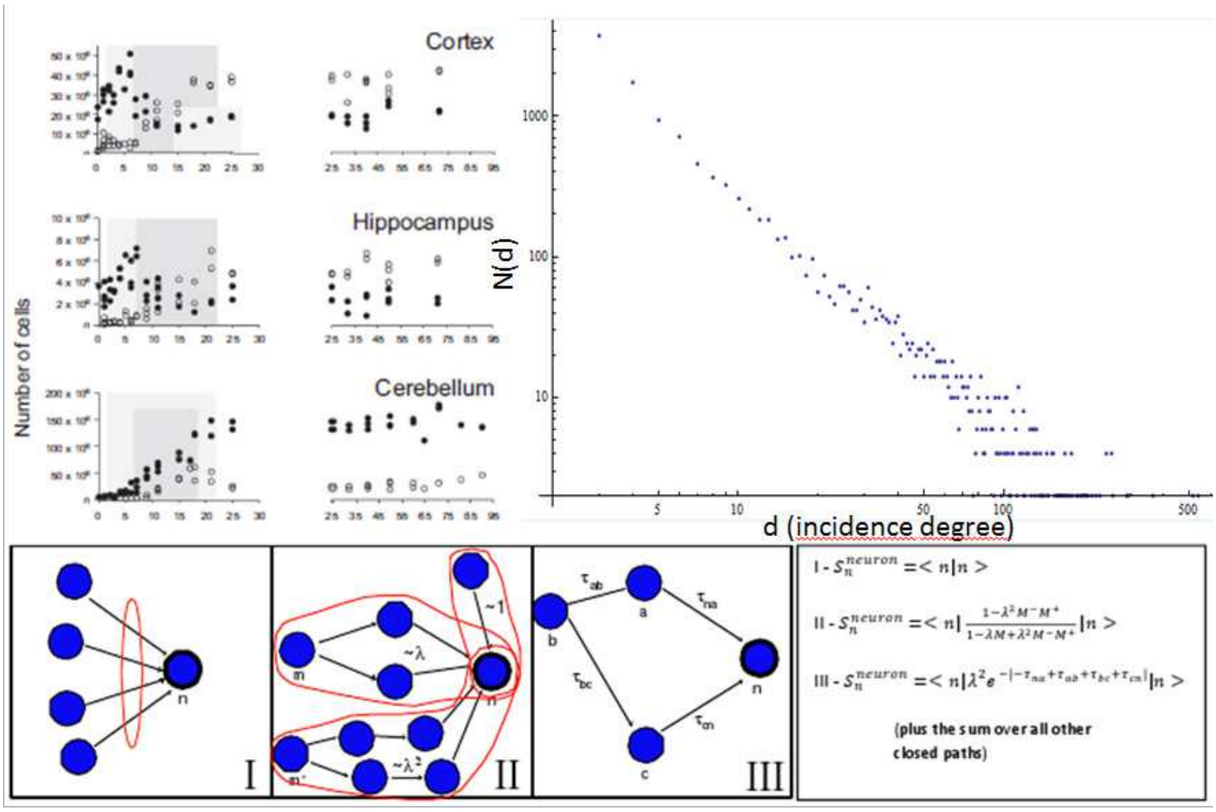
When one compares the complexity of neuronal networks to the estimated number of genes that control their development, it becomes clear that their generating mechanisms should be emergent, and preserved in their broad strokes across phyla. Such mechanisms presumably act on individual synapses and neurons in a relatively simple but uniform way to produce a complex, well-adapted network that is ordered but non-regular, and are neither entirely random nor deterministic. The large span (4-5) of orders of magnitude in structure size and component (neuron) numbers suggest such mechanisms must operate on a scale-invariant manner. This is indeed what has been consistently found in quantitative comparative neuroanatomical studies, in our lab and elsewhere, in which power law scaling across species suggests the presence of scale invariance in the way cerebral structures are built. There are a number of known ways of generating networks that display scale invariance and other characteristics also present in neuronal networks, such as robustness and short path lengths; a particular popular class of models of growing networks rely on the attachment of new nodes to preexisting nodes that are more well-connected. Preferential attachment is not, however, a plausible mechanism for the emergence of neuronal networks, as it assumes that neurons are somehow able to detect, or at any rate be affected by, the (highly non-local) connectivity properties of its neighbours. What could a more biologically plausible mechanism look like?

It has been shown that at least 60% of all cerebral neurons with which the animal is born die before or shortly after gliogenesis. Since we can only measure the difference between the rates of neuronal differentiation and death, the fraction of neurons that don't survive into adulthood is likely much higher. This seems to be a very wasteful way of producing a network. Perhaps there is some crucial adaptive value to this peak of early neuronal mortality, and to the closely related synaptic pruning that is known to occur shortly thereafter? On the other hand, it is well known that the brain operates on a policy of use it or lose it: Underutilized synapses, neurons and networks are eventually eliminated. We thus postulate that the selective deletion of nodes and edges plays a crucial part in generating the fine-grained structure of the networks in the brain.

We have modelled growing neuronal networks as directed graphs, where edges/synapses are formed randomly as nodes/neurons are added to the network; and at the same time nodes and edges are removed with a probability that is given by the element associated with the relevant nodes of a function of the connectivity matrix; or a modification thereof that counts the number of synchronous loops. We devise a number of algebraic tests (such as a generalized clustering coefficient) to quantify the networks thus obtained. We show that this simple model is sufficient to generate a robust network with a scale-free incidence degree distribution, with a pruning mechanism that is self-limiting.



Clockwise: Number of neuronal and non-neuronal cells in mice brains as a function of days after birth; incidence degree of a neuronal network with selective neuronal and synaptic deletion; outline of different connectivity functions S: Indegree, number of loops, number of synchronous loops.