

# Dissertation: Background and Literature

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## 1 Brain Formation and structure

### 1.1 Parsimonious (wiring) principles

These reach back very far to as Ramon y Cajal (1899).

### 1.1.1 Network wiring cost

There is overwhelming evidence in favor of this hypothesis (Bullmore and Sporns 2012):

- Cost of building and maintaining axonal connections and speed of transmission increase in wiring volume which is proportional to length (D)
- White matter grows faster than grey-matter as function of brain size, driven by increase in axonal diameter and number synapses per neuron
- Fraction of grey matter neurons that send myelinated axons into white matter slowly reduces with brain size
- The probability distribution of connection distances is skewed towards short distances that will be relatively parsimonious in wiring cost

Factors which potentially explain the deviations from this simple wiring principle (Bullmore and Sporns 2012):

- Volume exclusions = Due to the limited size of the brain, axonal projections must perturbate from the straight line connection
- Functional properties = Example: Monosynaptic vs. Polysynaptic nerves, when you need low latency you would build a high cost long axonal connection

### 1.1.2 Network running cost

Not part of Cajal's initial principal's, but metabolic cost of running the brain has become an increasingly important principle for network formation.

- Bigger brains are metabolically more expensive, with a rate increasing faster than overall body oxygen increase as function of weight
- The cost attributable to maintenance of electrochemical gradients across membranes
- Cost increases in overall neuronal membrane size as well as axonal length and diameter, this controlling length also limits energy requirements
- Limitation: Networks often functionally configured to be less expensive than possible within the anatomical constraints (network formation), e.g., through sparse coding

## 1.2 Network topology - Small-world architecture

- Watts and Strogatz analyses nervous system of C. Elegans as binary graph and found both high clustering and short path-length
- Brains possess the small-world properties of high clustering and global efficiency, a modular community structure and a heavy tailed degree distribution, that indicate high connected nodes or hubs
- High clustering and efficiency is attractive to allow for segregation of process (e.g., visual analysis) and integration (distributed process, executive functions)
- IQ negatively correlated with path lengths, which supports workspace theory, that effortful tasks depend on oscillations in ensembles of anatomically distributed regions
- Topological modularity might also be helpful to evolution, making it more robust to rewiring

## 1.3 Combining Parsimonious principle and Topological characteristics

This is to investigate how the physical embedding is constraint or constraints network topologies. How do the two concepts relate.

- Molecular gradients of attractive and repulsive guidance cues determine the trajectories of growing nerve fibres
- The spatial distribution of molecules that are involved neural development and physical constraints limit range of many connections, which could result in a bias towards high clustering
- Topological characteristics that favour segregation are also parsimonious in wiring cost
- Long distance connections preferentially link to hub regions, and they are costly but reduce path length for information transfer
- Evidence: In *C. Elegans*, wiring cost is not strictly minimized but the networks show similarities to networks that achieve cost constrained spatial embeddings of topologically complex networks
- Issue in MEG networks: Usually stationary picture of networks, but when studied under stimuli, MEG networks with high efficiency emerge under high effort tasks and vice versa

## 2 Generative network models

These models were first developed and applied to connectome data by Betzel et al. (2016). Can be considered as an extension to the economic trade-off principle, which states that configuration of the brain can be accounted for by economic balancing of wiring cost minimization and topological efficiency maximization.

### 2.1 Evaluation

$$E = \max(KS_k, KS_c, KS_b, KS_e)$$

to quantify the difference between the synthetic and observed data using the Kolmogorov-Smirnov statistic. The corresponding statistic is computed for every vertex, and then the distributions are compared.

- $KS_K$  Nodal degree = Number of edges that are incident to a vertex
- $KS_C$  Clustering (coefficient) = Measure of the degree to which nodes in a graph tend to cluster together, proportion of possible connections realized among the neighbors of a vertex (Where the neighbor of a vertex are all the other connected vertices)
- $KS_b$  Betweenness centrality = Measures the centrality of a vertex by investigating the number of shortest paths that pass through the vertex (For every pair of vertices there exists a shortest path between them minimizing either the number of edges or the summed weights of the edges)
- $KS_e$  Edge length = Sum of all the edge length that are incident to a vertex

### 2.2 Optimization

### 2.3 Rules

#### 2.3.1 Geometric

- Promotion of low cost connections is promoted, but forming only the shortest connections, produces lack of long distance connections, which increases path length, and reduces efficiency
- Problems in reproducing clustering and edge length distributions simultaneously ( $KS_c, KS_e$ ), this is because strong distance penalty required to make high clustering but then lacking long distance connections

### 2.3.2 Degree

### 2.3.3 Clustering

### 2.3.4 Homophilic

Prioritize wiring of nodes with with overlapping connectivity patterns. These principles are often interpreted as manifestation of Hebbian learning, when two unconnected nodes share multiple neighbors, they will likely showcase similar firing behavior. Consequently, they are also more likely to connect with each other in the future.

#### 2.3.4.1 Neighbors

For any combination of nodes get the number of common neighbors

$$\sum_l A_{il}A_{jl} \quad (1)$$

#### 2.3.4.2 Matching index

Intersection of i's and j's neighbors except each other over the union of i's and j's neighbors.

$$\frac{|N_{i/j} \cap N_{j/i}|}{|N_{i/j} \cup N_{j/i}|} \quad (2)$$

- Normalized measure of the overlap in two vertexes neighborhoods
- that eta and gamma seem to trade offer with each other, such that a connectome is either shaped by geometry or non-geometric constraints

## 3 Computational developmental models

Computational developmental models can generally be divided into those focusing on **cognitive development**, that is they try to perform tasks inspired by neurobiological principles, vs. those that focus on **neurobiological development**, which are models that try to capture neurobiological development. Cognitive models are fit to cognitive data with learning inspired by neurobiology, thereby trying to capture trajectories of change (Astle, Johnson, and Akarca 2023). These include:

- Cascade correlation models
- Knowledge-based cascade correlations
- Neuroconstructivist representation learning
- Spatially embedded recurrent neural networks

On the other hand, neurobiological development models are fit to neurobiological data and try to capture trajectories in physiological development. The models include:

- Generative network models
- Synaptic pruning in development
- Growth cone chemotaxis

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### 3.1 Cascade correlation neural network (CC)

- Classical input output networks are trained to solve a supervised problem
- At some point, the model will struggle to improve performance given the limited computational capacity (restricted number of neurons / layers)
- A new unit is then added as hidden layers (?) which has been trained independently as to maximize the correlation with the error (a pool of candidates are trained)
- This arguably reassembles neurogenesis as it can solve a particular computation which could not have been solved previously (this is done iteratively)
- Different to regular neuronal networks, the architecture of this network does not require an a priori guess
- Criticism: Will fail to use prior knowledge to learn because they do not have any

### 3.2 Knowledge based cascade correlations (KNCC)

- An extension to the CCs, models that can recruit an entire sub-network based on a previously learned task

### 3.3 Spatially embedded recurrent neural networks (seRNNs)

- One of the only models, that merges biophysical principles with task-solving
- Exist in a 3D space, where connection weights are penalized as a function of their lengths
- seRNNs are limited in their communication via direct and indirect connections
- These constraints are placed into a single optimization problem
- The networks embody modularity and small-worldness, both of which are crucial development principles
- As they are trained, neurons within the seRNNs become increasingly specialized to distinct aspects, so we can observe a functional specialization that is spatially patterned

## 4 Graphs

### 4.1 Rich clubs

- Measure the extent by which well connected nodes are connected to each other
- Networks of high rich-club coefficients have many connections between nodes of high degree

## 5 Automatic differentiation

## 6 Random dictionary

- Gray matter = Composed of the neurons (appears darker due to higher levels of melanin)
- White matter = Mainly made up of myelinated axons also called tracts (light appearance through the lipid content of myelin)
- Monosynaptic reflex = There is only one synapse between the afferent nerve and the efferent nerve (slow latency)
- Polysynaptic reflex = There are more than one synapse between the nerves, such that there is higher latency

- Sparse coding = Neural coding that represents the information by activation of small subset of the available neurons
- Small-world = Combine random and regular topological properties, i.e., high efficiency (short path length) and high clustering
- Community structure = Sub-global organization of a complex network, an example is modular organization
- Heavy-tailed degree distributions = Proportion of high degree nodes is larger than in random graphs (so that they can be hubs)
- Computational neuroconstructivism = Computationally formalize neuroconstructivist principles by parameterized interactions between populations over time

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