Cerebral Cortex: A network theoretical approach

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ABSTRACT

Network theoretical analysis have mainly studied unweighted and bidirectional networks in contrast to properties of real networks. Previous studies of cortical networks have focused on global average properties. In our study, we make a closer, localized, study of cortical networks looking for the effects of non-reciprocal connections and connection strengths. We find cortical networks to lie between Watts-Strogatz type and scale-free networks. A new cluster that may play important role on integration of information is detected. Connection strengths may have functionally been adjusted to help synchronization. Structural organization is uncorrelated from vertex degree and clustering, so organization must have developed from pure functional necessities. We do this work with the hope that innovative network theoretical analysis in a detailed scale, in combination with modelling and dynamical simulations will help bridging the gap between structure and functionality.

CORTICAL NETWORKS

Macaque and cat cortico-cortical networks have been found to have ***Small-World*** [1] network properties and ***modular organization*** [2]. Thus, hierarchical processing of sensory information becomes in the cortex into a processing based on the inter-relation of different clusters [3].

The cat cortico-cortical connectivity data was first published by Scannell [4] as a collation of existing single connection reports and later re-analyzed using Optimal Cluster Analysis [3].

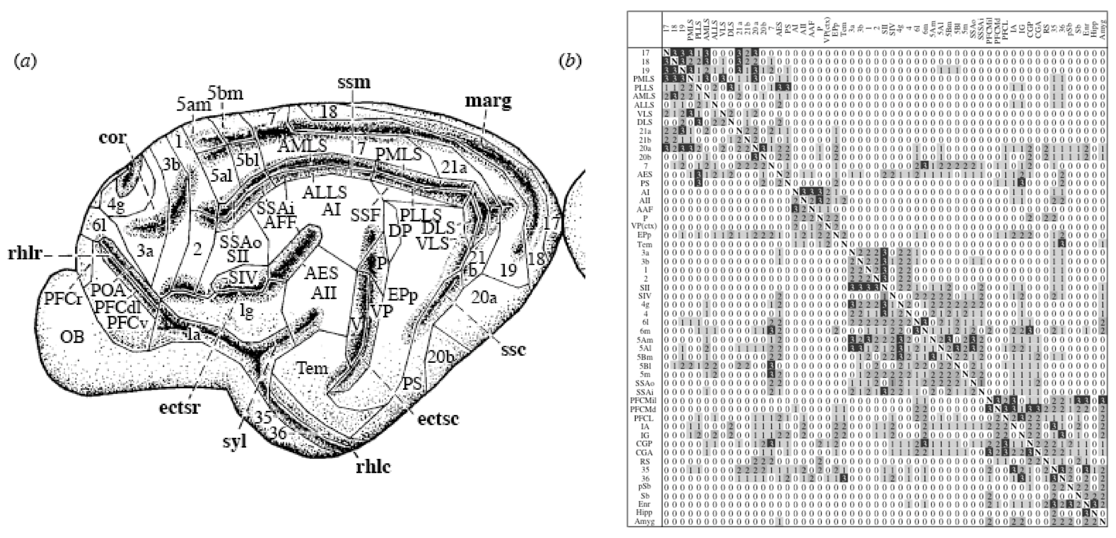


Figure-1: CAT CORTEX
a) Map of cat cortex as divided by [4]. b) Cat cortico-cortical adjacency matrix as given by [3]

RANDOM NETWORKS

No work on real networks can be published nowadays without refering to Small World (SW), Scale-Free (SF) networks and the models by Watts-Strogatz (W-S model) and Barabási-Albert (B-A model). Besides, Scale-Free networks are a special class of Small World networks and both lie within the frame of random networks. Average, whole net measures, can not distinguish SF nets from other SW nets.

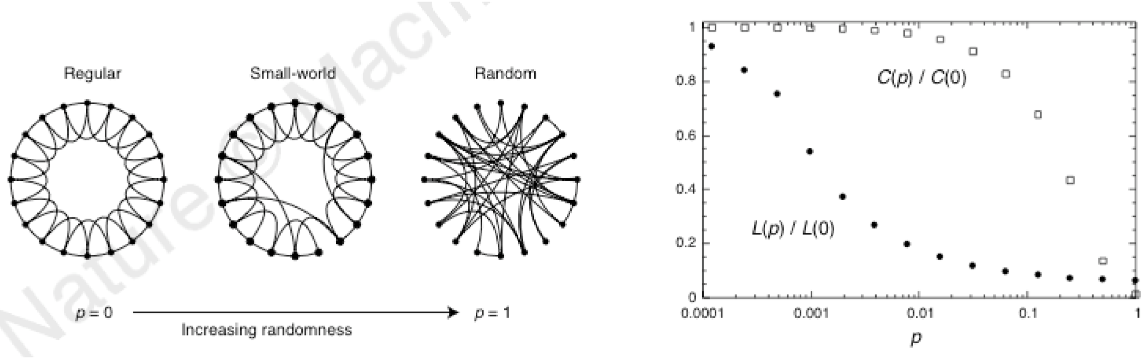


Figure-2: WATTS-STROGATZ MODEL
Transition from lattice to Erdos-Renyí type of random networks.

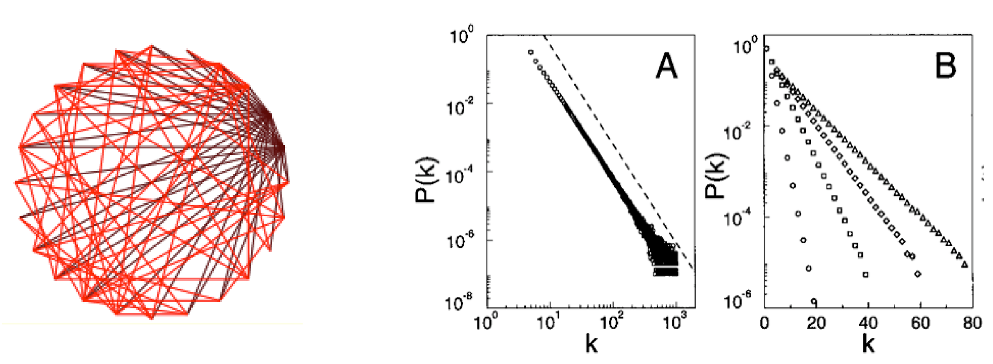


Figure-3: BARABASI-ALBERT MODEL
Scale-Free networks can be generated using: Growing and Preferential Attachment.

CLASSIFICATION

Cortical networks are small world networks. Further classification is limited by their small size. Even if degree distribution show no power low, two properties support the idea of ***SF cortical networks***:

1. Some high degree vertices are present.
2. Robustness studies [5] suggest similar behaviour to SF network under random vertex or edge removal

We compare different properties of the cat cortical network to random networks of the W-S type and complete random (E-R type).

Properties supporting ***cortical networks of the W-S type***:

1. Modularity of the network into few large clusters.
2. Average properties resemble those of W-S type networks with a rewiring parameter around p = 0.1 - 0.2

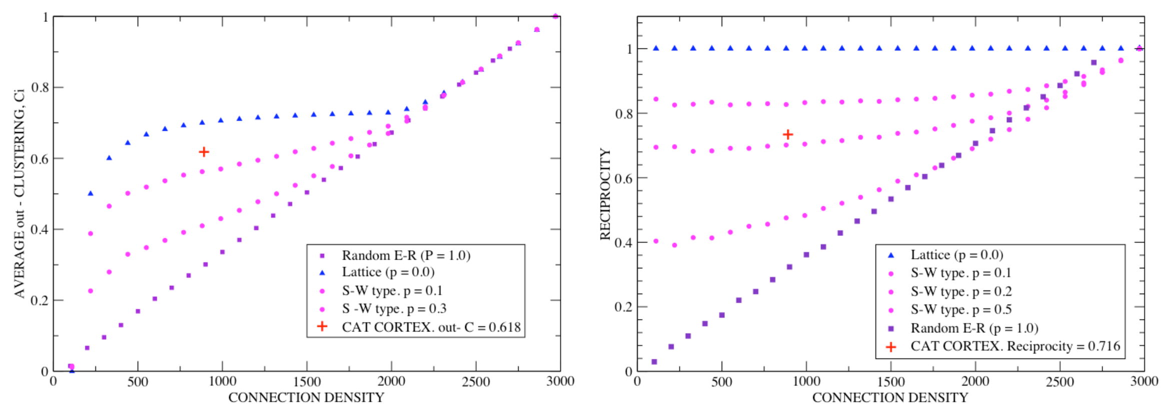


Figure-5: CLASSIFICATION OF CAT CORTEX
Comparison of cat cortex properties to randomly generated networks of same size. a) Out-Clustering coeficient b) Reciprocity of directed connections.

We conclude that, even if cat cortical network is a SW network, further classification to known models is not possible. **Cat cortex seem to lie somewhere in between SF networks and W-S model networks**.

CORTICAL STRUCTURE

The clustering of a vertex v quantifies how close are neighbours of v connected together. Detailed analysis of clustering shows that high degree vertices do have lowest clustering coeficients. This happens because these vertices play important role linking clusters together. Besides, we found that these vertices form another highly connected cluster which does not appear in previous studies. Thus we believe that this new cluster is involved in the integration and synchronization of information coming from different modalities.

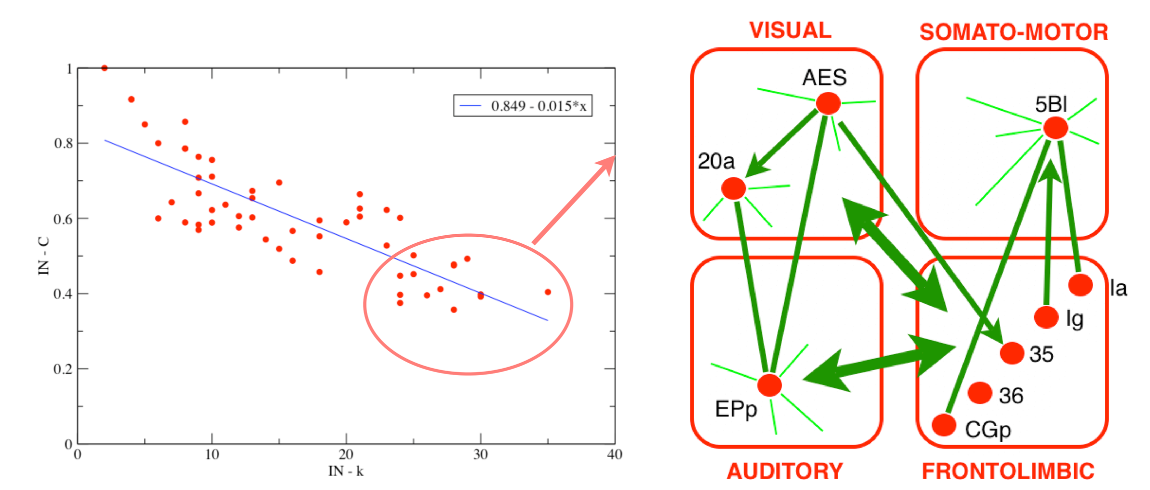


Figure-6: THE 5TH CLUSTER:
The cluster formed by high-k / low-C vertices might be involved into highest level of information integration and synchronization.

FUNCTIONAL ORGANIZATION

We do observe that both degree and clustering coeficient of a vertex are uncorrelated to the degree and clustering of its neighbours. Thus, connections are not organized due to local structural information. **Cortical structure should have exclusively been shaped due to functional requirements of the system**.

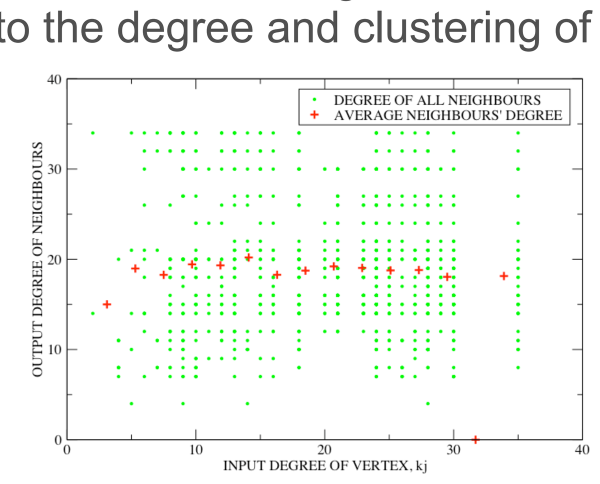


Figure-7: UNCORRELATED DEGREE AND CLUSTERING
Connectivity is found to be independent of local structural information. Thus, structural organization is *exclusively* due to functional requirements.

WEIGTHS AND DYNAMICS

Connection weights can play an important role shaping the structural properties. Recently, specific distributions of weights have been shown to modulate dynamical properties of the network and even enhance synchronization [5]. In cat cortex, the redefinition of structural measurements to include connections weight, did not significantly affect structural properties from those non-weighted definitions. But the specific distribution of weights may be helping to enhance the syncronization.

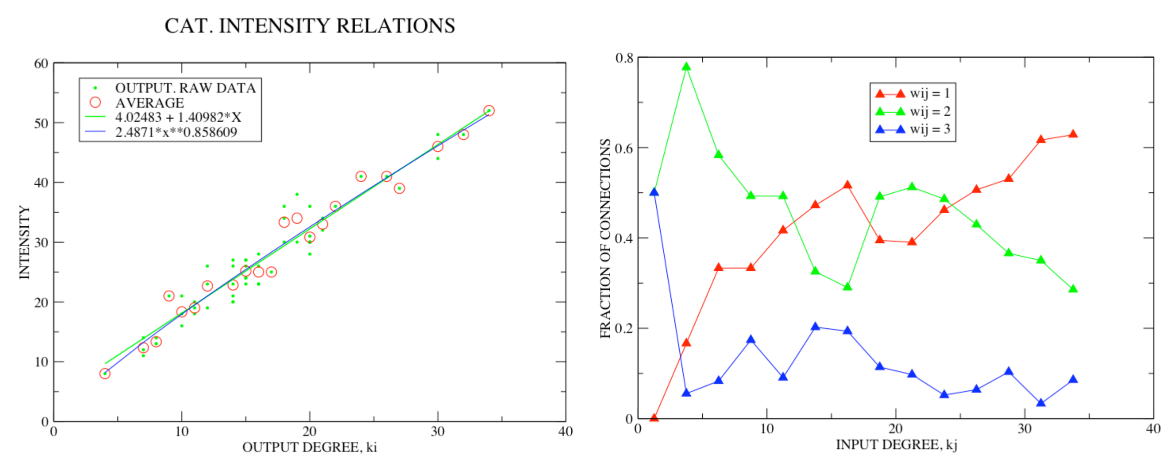
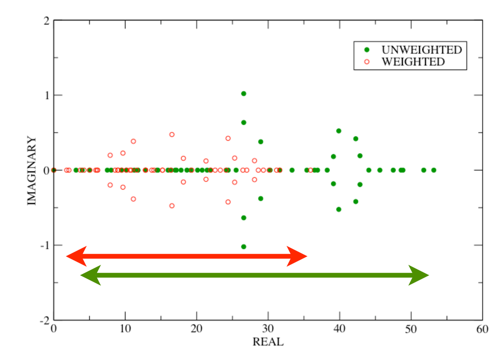


Figure-8: CONNECTION WEIGHTS
a) Nonlinear vertex intensity due to b) inhomogeneous weight distributions may be a sign for enhancement of synchronization [5].



	unweight	weighted
Cat Cortex	19.8144	17.0377
Visual	4.2739	4.0377
Auditory	1.7500	2.6354
Frontolimb.	2.8624	3-3303
Sens-Motor	6.0094	5.7229

Figure-9: SYNCHRONIZATION
a) Eigenvalues for weighted and unweighted Laplacian of Cat Cortex. b) Eigenratios for whole cortex and subclusters. Smaller eigenratios are meaningful of enhancement of synchronization.

RECIPROCAL CONNECTIONS

Around 30% of connections in cat cortex are non–reciprocal and its effects on synchronization are still unclear. As we observe reciprocality to be independent of |out-k – in-k|, we define a new measure of reciprocality to study this effect; ***ratio of excess (output or input) connections*** as

$$r^{\pm} \equiv \frac{\#\,\text{of non–reciprocal out(in)put connections}}{\text{out–k} + \text{in–k}}$$

For further information and preliminary work, please do not hesitate to ask.

CENTRALITY

To overcome uncertainties on the classical centrality measures (reviewed in [6]) we re-define the concept of network center as:

$$\mathcal{C}(G) \equiv \{v \in V : d(v) < \delta\}$$

where d(v) is the average distance from v to all other vertices and delta is some arbitrary threshold. We find different cortical areas playing the role of centers if definition is applied to output or input connections.

FUTURE WORK

1. Effects of non-reciprocal connections on the synchronizability of the network. Use reciprocal measures to detect areas performing specific tasks.
2. Biological interpretation of centers and combine with analysis of Betweenness Centrality and path multiplicity.
3. Generate evolutionary models to explain observed properties.

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G. Zamora is supported by the Helmholtz Institute for Supercomputational Physics. C. Zhou is supported by the Humboldt Stiftung.

All computations have been programmed using: python