Structural and Functional Integration in the Cat Cerebral Cortex

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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 intensities. We find cortical networks to lie between Watts-Strogatz type and SF networks and their modularity to be independent of degree distribution. We have detected a new cortical cluster that may play important role on integration of information and higher level processing. Our hypothesis is possitively tested for functional integration after different rewiring and attack procedures. Besides, connection strengths may have functionally been adjusted to help synchronization. We do this work with the hope that local network analysis rather than global average measurements, in combination with modelling and dynamical simulations will help understand 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 [2].

The cat cortico-cortical connectivity data was first published by Scannell [3] as a collation of existing single connection reports and later re-analyzed using Optimal Cluster Analysis [2].

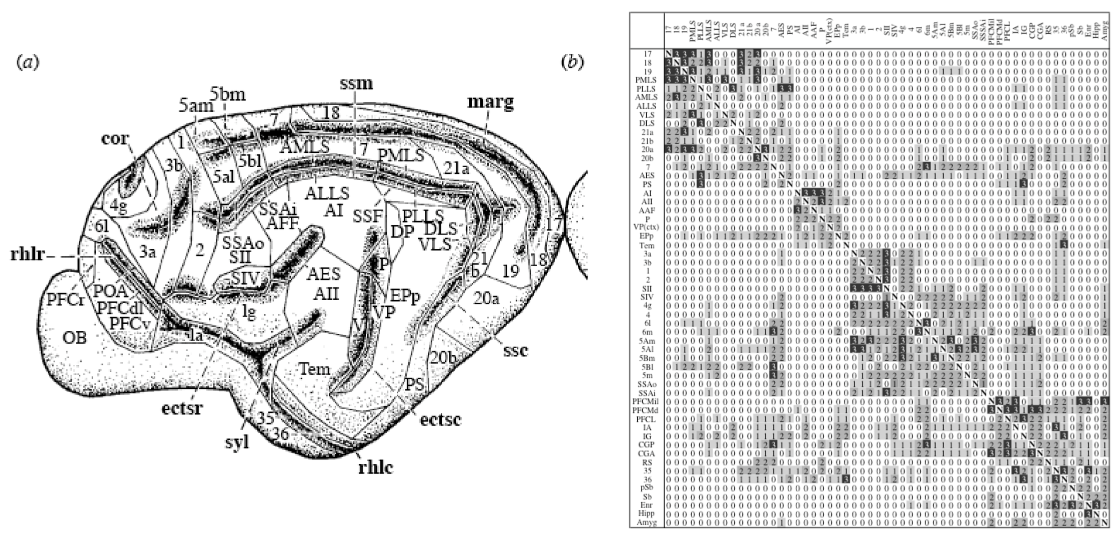


Figure-1: CAT CORTEX
a) Map of cat cortex as divided by [4]. b) Cat cortico-cortical adjacency matrix as given by [3]

CLASSIFICATION

Classification of cortical networks is highly limited by their small size, anyway, we make this effort in order to obtain some hints about the evolutionary proccess that might have shaped the cortico-cortical connectivity. Even if degree distribution shows no power law, three properties support the idea of ***SF cortical networks***:

1. Some high degree vertices are present.
2. Robustness studies [4] suggest similar behaviour to SF network under random vertex or edge removal.
3. Its cumulative degree distribution resembles that of generated SF network with similar properties.

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

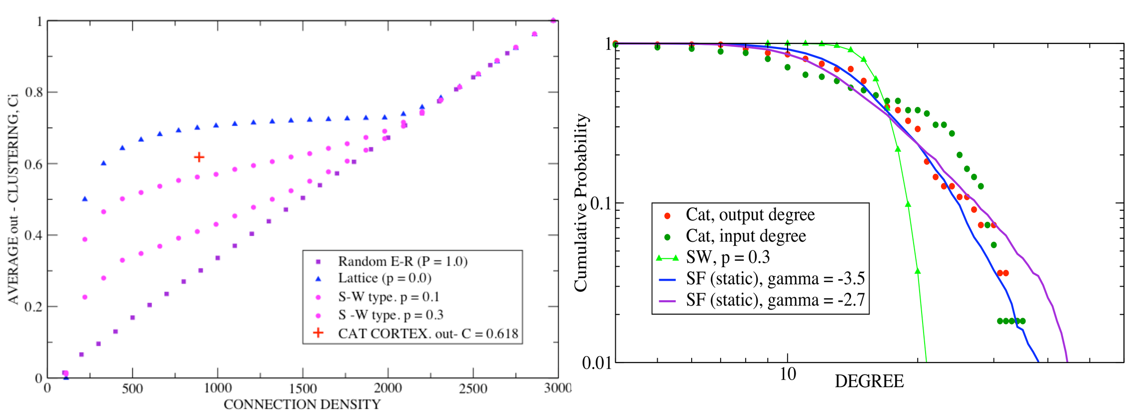
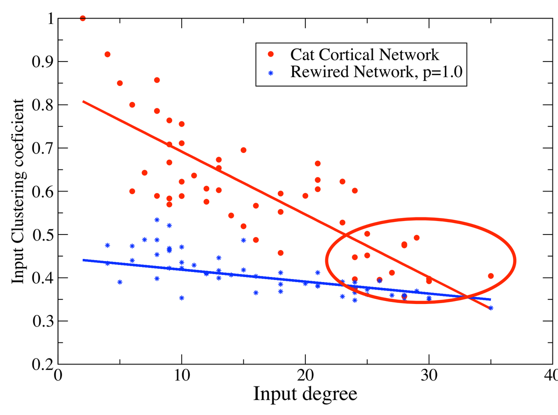


Figure-2: CLASSIFICATION OF CAT CORTEX
Comparison of cat cortex properties to randomly generated networks of same size. a) Out-Clustering coeficient b) Cumulative degree distributions cat cortex and of randomly generated W-S and SF networks.

We conclude that, even if cat cortical network is claimed to be a SW network [1], **cat cortex seem to lie somewhere in between SF networks and W-S model networks**.

STRUCTURAL INTEGRATION

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 because these areas extend their connections communicating the different clusters together while low degree areas make only local connections within their cluster. Rewiring connections of the network while conserving both input and output degrees, distroys the modular organization as observed by the decrease in the slope of the C/k relationship. Thus, **degree distribution alone can not explain the modular organization of the network.**



	in-Clust	out-Clust
Cat Cortex	0.60	0.62
Visual	0.65	0.65
Auditory	0.87	0.84
Frontolimb.	0.79	0.81
Sens-Motor	0.72	0.74
Integrator	0.80	0.80

.**Figure-3: THE 5TH CLUSTER:**
a) Modular organization is revealed by anticorrelation of clustering and degree. b) The areas with highest-k and lowest-C show besides a high clustering coeficient far higher than expected by degree distribution.

Besides, we find these cortical areas with high-k/low-C to form another highly connected cluster not mentioned in previous studies whose members spam along the different sensorial modalities. Therefore, we do believe **this new cluster to be involved in the integration of incomming sensorial information from different modalities**. Its high clustering coeficient also suggests strong implication in the highest level neural processings such as consciousness and cognitive processes.

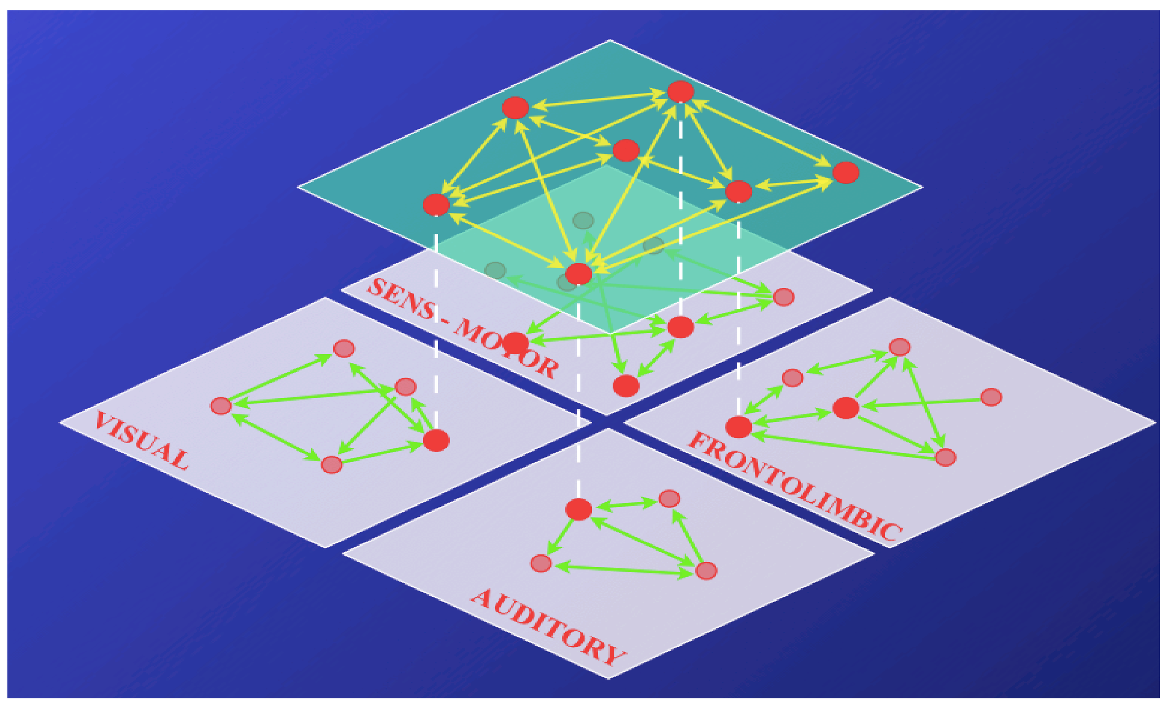


Figure-4: INTEGRATION OF INFORMATION:
The cluster formed by high-k / low-C vertices might be involved in integration and processing of information at highest level.

FUNCTIONAL INTEGRATION

In order to test the relevance of this new cluster for integration of information we proceed to make simulations with very simple local dynamics so that propagation of activity would exclusively depend on the network structure. Activity of an area is modeled by the following map:

$$a_i(t+1) = \frac{2}{\pi}\arctan\left(\alpha \sum_j W_{ij}\, a_j(t)\right)$$

where a_i is the activation level of a cortical area, α is a nonlinear parameter and W_{ij} is the normalized adjacency matrix. Initially, only one single area was stimulated (a(0) = 0.5), either primary visual cortex (area '17') or primary auditory cortex (area 'AI') in order to simulate real sensorial input. Parameter α = 0.4 was chosen for slow saturation.

Then, we proceed to selectively remove the input connections of the 'Integrator cluster', isolating it from receiving any external signal. For comparison, we also remove randomly the same number of connections and simulate the propagation of activity. As result, it is observed that:

1) even if structurally, after removal of 241 links, **the network is still highly connected and modular** (figure-6),

2) functionally, **only the non-trivial, selective, removal of links that isolate the 'Integrator Cluster' can brake the communications between the different clusters**, confirming the importance of this cluster in the integration of different sensorial information coming into the brain.

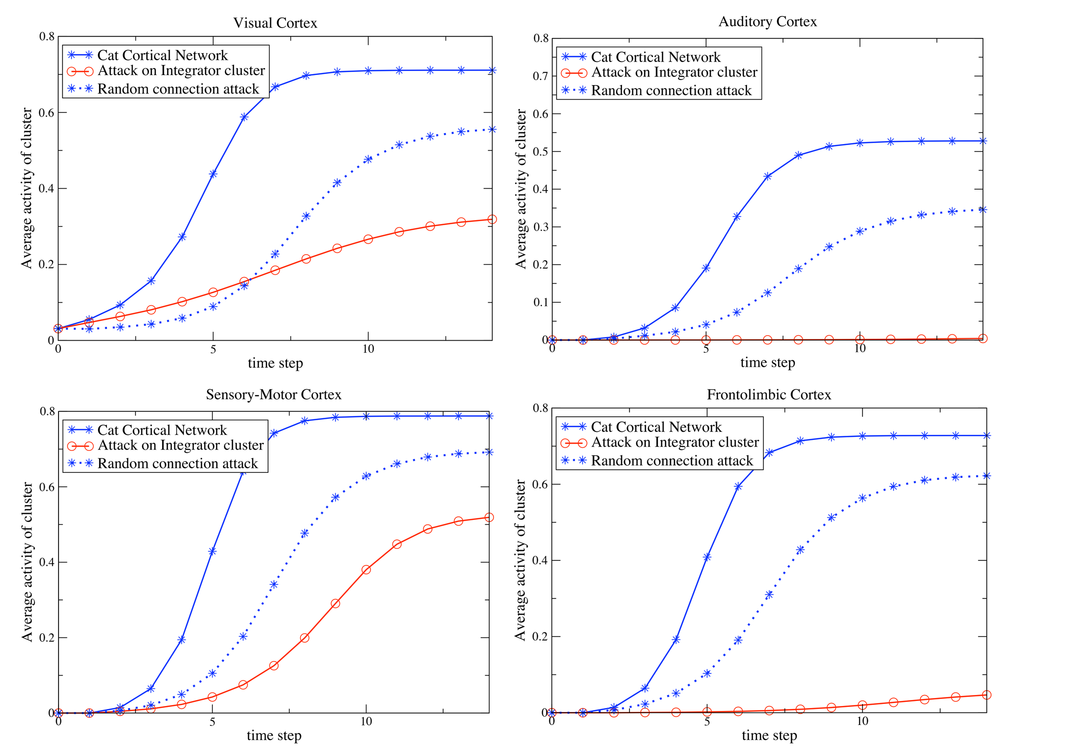


Figure-5: DISCONNECTION OF CLUSTERS:
Visual Stimulation. Comparison of random link attack and selective attack on input links of the 'integrator cluster.' The latter largely affects the propagation of activity among modal clusters.

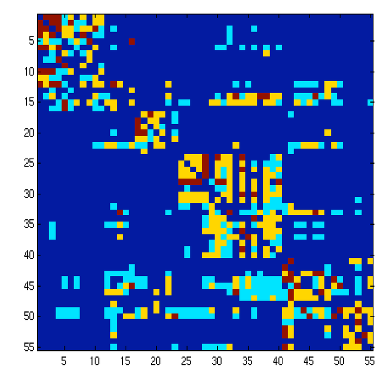


Figure-6: LINK ATTACK:
Connectivity after selective attack on external links of 'Integrator cluster', shows non-trivial attack procedure neccessary to functionally disconnect the clusters.

WEIGHTS 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.

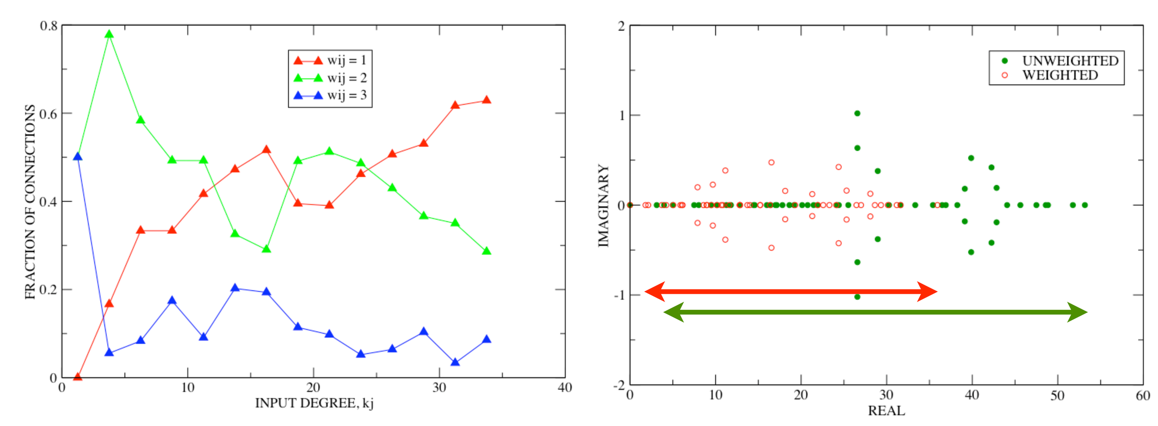


Figure-7: CONNECTION WEIGHTS
a) Inhomogeneous weight distribution and b) eigenvalues of weighted and unweighted Laplacian, may be a sign for enhancement of synchronization [5].

FUTURE WORK

1.Use of a biologically realistic model to simulate the local dynamics and perform more interesting measures.

2.Further structural test using a novel algorithm to find communites and confirm the existence of such a '5th Cluster'.

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

All computations have been programmed using: python