Graph Analysis of Cortical Networks Reveals Complex Anatomical Communication Substrate

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Abstract

Sensory information entering the nervous system follow independent paths of processing such that specific features are individually detected. However, sensory perception, awareness and cognition emerge from the combination of information. Here we have analyzed the cortico-cortical network of the cat, looking for the anatomical substrate which permits the simultaneous segregation and integration of information in the brain. We find that cortical communications are mainly governed by three topological factors of the underlying network: 1) a large density of connections, 2) segregation of cortical areas into clusters and 3) the presence of highly connected hubs aiding the multisensory processing and integration. Statistical analysis of the structure of shortest paths reveals that, while information is highly accessible to all cortical areas, the complexity of cortical information processing may arise from the rich and intricate alternative paths in which areas can influence each other.

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Traditionally, complex dynamical systems are characterized by a large number of nonlinearly interacting elements. The recent discovery of an intricate and nontrivial interaction topology among the elements in natural systems introduces a new ingredient to the spectrum of complexity. A network representation provides the system with a form (topology) which can be mathematically tractable towards uncovering its functional organization and the underlying design principles. The term *complex* is coined because most real systems have neither a regular nor a completely random topology, but survive in some intermediate state, probably governed by rules of self-organization. For example, the axonal pathways (white matter) transmitting electrical information between regions of the cerebral cortex (grey matter) form a complex network with very particular properties. Information of different modality (visual, auditory, etc.) entering the nervous system follows particular paths of processing, typically separated from the processing paths of other modalities. This segregation permits specialized information processing. However, achieving a coherent and comprehensive perception of the real world requires that information of all modalities are combined. Cortico-cortical networks of the macaque monkey and cat have been found to be organized into clusters, facilitating the segregation of areas specialized in one sensory modality. Where and how the integration happens, is still unknown. In this paper, we present a statistical analysis of the cortico-cortical communication paths. We find that cortical processing is governed by very short paths, allowing for fast behavioral responses. Moreover, cortical areas may influence each other via different alternative paths, suggesting rich and complex information processing capabilities. Of particular interest, we find that communication between areas of different modality is mediated by few, highly connected areas, emphasizing the central role of these hubs for the multisensory information processing and integration.

I. INTRODUCTION

The mammalian nervous system is a complex system par excellence. Composed of over 10^{10} neurons, it is responsible for collecting and processing information, and providing adaptive responses which permit the organism to survive in a constantly changing environment [1, 2]. In order to characterize the connectional organization of the nervous system and to understand its functional implications, the complex network approach has been applied in recent years, particularly at the level of the cerebral cortex. The long-range fibers linking the cortical areas form a complex network which is neither regular nor completely random. Cortico-cortical networks of the macaque and cat have been found to possess small-world properties [3, 4], i.e. short average pathlength l and large clustering coefficient C, meaning that cortical areas are at a very short topological distance from each other and are cohesively linked. A stochastic optimization method detected a small number of distinctive clusters in cortical networks of cat and macaque [3, 5]. Clusters are formed by areas which are more frequently linked with each other than with areas in other clusters. Moreover, the detected clusters closely coincide with functional subdivisions of different modalities [6, 7], e.g. they contain predominantly visual or auditory areas (see Figure 1).

The capacity of the nervous system to simultaneously process different kinds of information relies, to a large extent, on the circuitry where the stimulus is received and processed. It has been widely argued that, to achieve its function, the cortical connectivity should be organized into a balance between segregation (specialization) and integration (binding) [8]. Processing of detailed sensory information, e.g. detection of object orientation in visual stimuli or detection of frequency in auditory stimuli, is processed performed in differentiated cortical regions. But at the same time, the emergence of a coherent perception, and the comprehensive understanding of the environment as a whole, requires that specialized information of different modalities and features can be integrated. The clustered organization of the cortical networks reveals the anatomical substrate for segregation. How and where does the integration of information happen, is still unclear [9].

In this paper, we perform a large-scale statistical analysis of the communication paths within the cortico-cortical connectivity of the cat. The aim is to study how the topological organization is related to the potential information processing capabilities of the cortex. As a working approximation, we consider that information in cortical networks flows only along

FIG. 1: Weighted adjacency matrix W of the corico-cortical connectivity of the cat comprising of 826 directed connections between 53 cortical areas [6, 7]. The connections are classified as weak (open circles), intermediate (blue stars) and dense (red filled circles) according to the axonal densities in the projections between two areas. For visualisation purposes, the non-existing connections (0) have been replaced by dots. The network has clustered organization, reflecting four functional subdivisions: visual, auditory, somatosensory-motor and frontolimbic.

shortest paths. In Section II the global classification of cortical networks is critically revised by comparison to different ensembles of surrogate networks and network models. We find that while cortical networks share characteristics of small-world networks, they contain a broad degree distribution, with some hubs connecting up to 60% of all the areas. The comparison includes a novel manner to detect the optimal rewiriing probability of small-world networks. In Section III the pairwise distance and communication paths between cortical areas is analysed. We find that cortico-cortical communications are governed by direct connections and paths of length two, assuring fast information processing and behavioral responses. However, deeper analysis of the shortest paths reveals the capacity of the cortex to process information in parallel and to simultaneously generate complex responses. In particular, the fundamental role of the hubs is highlighted, by supporting and centralizing the multisensory communications.

Cortico-Cortical Connectivity of the Cat

In this paper we analyse the cortical connectivity of the cat because it is, up to date, the most complete data set of its kind. It was created by Jack W. Scannell after a collation of an extensive literature reporting anatomical tract-tracing experiments [6, 7]. It consists of a parcellation into 53 cortical areas and 826 fibers of axons between them as summarized in Figure 1. The connections are weighted according to the axonal density of the projections between areas. The connections originally reported as *weak* or *sparse* were classified with 1 and, the connections originally reported as *strong* or *dense* with 3. The connections reported as *intermediate* strength, as well as those connections for which no strength information was available, were weighted with 2.

After application of data mining methods [5, 6], the network was found to be organized into distinguishable clusters. Even if the analysis made use uniquely of the topological properties of the network, cortical areas known to have similar function were naturally clustered together giving rise to the four functional subdivisions (visual, auditory, somatosensory-motor and frontolimbic) displayed in Figure 1. From the 826 connections, 470 are *internal*, i.e. they connect two areas in the same cluster, and 356 are *external*, i.e. connect two areas in distinct clusters. The cortical data of the macaque monkey, although very relevant for comparison to the abundant behavioral experiments, is still rather sparse for an statistical analysis of the characteristic here presented. Nevertheless, based on the current literature, we expect that the general conclusions obtained are suitable for understanding cortical organization in a large family of mammals.

II. CLASSIFICATION OF CORTICAL NETWORKS

The cortico-cortical networks of cat and macaque have been classified as small-world networks due to their large clustering coefficient C and their small average pathlength l. On the other hand, robustness analysis has revealed similarity to scale-free (SF) networks [10]. In this section we perform a critical and detailed revision of this classification scheme by comparing the cortical network of the cat to network models and surrogate networks of same size, $N = 53$ nodes, and similar density of links $\rho_{cat} = \frac{L}{N(N-1)} \approx 0.3$:

1. Small-world networks after the model of Watts and Strogatz (W-S) [11]. Starting from a regular ring-lattice in which vertices are connected to their $z = 8$ closest neighbors, links are rewired with a given probability p_{rew}. The resulting networks contain $L = 424$ undirected links and have, hence, almost the same density as the studied cortical network of the cat. The use of undirected links is justified because, of the 826 links in the cortical network of the cat, 73% of them are reciprocal. On the contrary, random directed graphs have reciprocity equal to ρ which, in this case, is much smaller than the observed fraction of reciprocal links.

2. Scale-free (SF) networks with exponent $\gamma = 1.5$ have been generated following the method in [17], which consists of a modification of the configuration model. Certainly, with only 53 nodes the obtained networks cannot achieve a SF degree distribution, nevertheless, they display a broad distribution, see Figure 3(b).

3. Random graphs are constructed, for consistency, out of the set of small-world networks with $p_{rew} = 1.0$.

4. Random rewired digraphs of the same size $N = 53$, number of directed links $L = 826$ and degree distribution $N(\boldsymbol{k})$ as the connectivity of the cat. The set was generated by application of typical rewiring algorithms which conserve the input and the output degrees of every vertex [12–15].

A. Optimal p_{rew} in W-S model

Before performing a comparative analysis, a proper rewiring parameter for the W-S networks needs to be chosen. Therefore, ensembles of 100 graphs have been generated with probabilities ranging from $p_{rew} = 0.0$ (the initial lattice) to $p_{rew} = 1.0$ (equivalent to random graphs). The clustering coefficient C and the average pathlength l of each ensemble was measured and the results plotted, Figure 2(a), normalized by the values of the initial lattice $C(0)$ and $l(0)$ as in the original reference [11]. According to Figure 2(a), it seems that there is no small world regime in our case, because for $p_{rew} > 0.08$ the normalized average pathlength $l(p)/l(0)$ overcomes the curve for $C(p)/C(0)$. The reason for such a behavior lies on the large density of connections in the networks here generated, $\rho = \frac{2L}{N(N-1)} \approx 0.3$. As a result, the initial lattice already possesses a short average pathlength ($l = 2.15$), which is only 20% larger than the pathlength in the random graph ($p_{rew} = 1.0$). Nevertheless, the aim of the W-S model is to generate networks which are *complex* in the sense that they are neither regular nor completely random. Therefore, instead of normalizing by $C(p)/C(0)$ and $l(p)/l(0)$ (which resembles only the deviation from the regular lattice), $C(p)$ and $l(p)$ should be appropriately rescaled to capture the essence of topological complexity as stated above. Hence, we rescale C and l such that $C' = l' = 1$ only if the network is completely regular ($p_{rew} = 0$) and $C' = l' = 0$ only if the network is random, by the following transformations:

$$C'(p) = \frac{C(p) - C(1)}{C(0) - C(1)} \tag{1}$$

$$l'(p) = \frac{l(p) - l(1)}{l(0) - l(1)}, \tag{2}$$

where $C(1)$ and $l(1)$ are the values of the random graph ($p_{rew} = 1.0$). It is a well known theoretical result that the clustering coefficient of a random graph equals its density of

FIG. 2: Small-world properties of W-S networks of equivalent size and link density as the cortical network of the cat. (a) As in reference [11], the quantities are displayed normalized by the values of the initial regular lattice $C(0)$ and $l(0)$. (b) $C(p)$ and $l(p)$ are rescaled to display the complexity of the networks such that, $C'(p) = l'(p) = 1$ only if $p_{rew} = 0.0$ (regular lattice) and $C'(p) = l'(p) = 0$ only if $p_{rew} = 1.0$ (random graph). At $p_{rew} \approx 0.09$ (dashed line) the difference between the rescaled C' and l' is maximal.

links, hence, $C(1) = \frac{2L}{N(N-1)}$ in the case of undirected graphs. Analytical estimates of the pathlength of random graphs capture the scaling behaviour [16] and are not accurate enough for the use here intended. Hence, $l(1)$ should be numerically computed as the ensemble average.

After rescaling C and l, Figure 2(b), the *small world regime* becomes apparent. As an optimal rewiring probability, we choose the p_{rew} for which the difference between $C'(p)$ and $l'(p)$ is maximal, because it captures the networks of maximal complexity. In the following we consider the set of W-S networks with $p_{rew} = 0.09$ (dashed line in Figure 2(b)) for comparison to the properties of the cortical network of the cat. Note that the optimal p_{rew} can be different depending on the density of links.

B. Comparison to random graph models

Once an optimal rewiring probability for the W-S random graphs has been adequately selected, we can now compare the properties of different random graph models to the cortical network of the cat. With respect to the *small-world* characteristics, Table I, the W-S networks ($p_{rew} = 0.09$) have clustering and pathlength similar to those of the cortical network of the cat. For a more consistent comparison, in Figure 3(a) the rescaled values C' and l' of the networks are displayed. The blue line corresponds to ensembles of W-S networks for different rewiring parameters. From $C' = l' = 1$ corresponding to the initial ring-lattice ($p_{rew} = 0.0$), the W-S model moves towards the origin with increasing p_{rew}. The green triangle in the origin corresponds to the rescaled characteristics of random graphs ($p_{rew} = 1$). The optimal W-S networks ($p_{rew} = 0.09$) lie closer to the cortical network than the rewired, SF and random networks. Notice that W-S networks with p_{rew} between 0.1 and 0.2 would lie closer to the cat than the optimal ones.

	Cat cortex	Random	Rewired	Watts-Strogatz	Scale-free
C	0.50	0.31 ± 0.01	0.400 ± 0.005	0.57 ± 0.01	0.37 ± 0.01
l	1.83	1.702 ± 0.002	1.737 ± 0.004	1.82 ± 0.01	1.686 ± 0.004

TABLE I: Average clustering and shortest pathlength of the cat cortical network and equivalent random network models of the same size $N = 53$ and link density $\rho \approx 0.3$. 'Rewired' additionally conserves the same input and output degree sequence. Values are the average over 100 realizations.

FIG. 3: Classification of the cat cortical network and comparison to ensembles of random null-models and generic models. (a) *Small-World diagram* displaying the re-scaled clustering C' and pathlength l' of the different networks: cat cortex (●), random graphs (▲), rewired (⧫), scale-free (▼) and Watts–Strogatz networks (■). (b) Cumulative degree distribution $p_c(k)$ of the cat cortical network and of the random models. Error bars are very small in both figures, and hence, not shown.

Despite the similarity in the small-world characteristics, the Watts and Strogatz model cannot be considered as a plausible model to explain the cortical organization because: 1) W-S networks do not display clustered organization, and more striking 2) the W-S networks have homogeneous degree distribution. On the contrary, the network of the cat cortex possesses a broad (inhomogeneous) degree distribution, e.g. some hubs connect up to 60% of all other areas. As shown in Figure 3(b), the difference in the cumulative degree distributions, $P_c(k)$, of the cat and the W-S networks is prominent [?]. On the other hand, the cumulative degree distribution of SF graphs with $N = 53$, $L = 423$ and exponent $\gamma = 1.5$ (solid line of Figure 3(b)) closely follows the real distribution of the cat cortex [?], what explains the similar attack tolerance behavior [10]. This resemblance in the degree distribution is also observed in the fact that in the complexity space, Figure 3(a), the rewired networks (green cross) lie very close to the SF networks (purple ▼).

Nevertheless, SF networks have a very small clustering coefficient (Table I) and thus, random SF graphs cannot be considered as a suitable model for cortical networks. In the end, the W-S and SF random models are minimal models intended to capture only *certain* global properties observed in real systems, but cortical networks have a very rich internal organization. For practical purposes, it is simply relevant to learn that cortical networks have few important organization properties: *1)* a large density of links causing a very short

FIG. 4: (a) Distance matrix D_{ij} of the cortico-cortical network of the cat. Cortical areas separated by distance $d = 1$ (dark blue), $d = 2$ (light blue), $d = 3$ (yellow) or $d = 4$ (red). (b) Path multiplicity matrix M_{ij} representing the number of distinct shortest paths (of length D_{ij}) from area i to area j. On average, there exist 5.2 alternative paths between every pair of areas.

pathlength, *2)* a large clustering coefficient arising from the clustered organization, and *3)* a broad degree distribution with few areas playing the role of highly connected hubs. Because of the small size of the network, whether the degree distribution follows a power-law or not is a rather irrelevant matter.

III. CORTICAL COMMUNICATION PATHS

As stressed in the previous section, the cortico-cortical connectivity of the cat is characterized by a very short average pathlength of only $l = 1.83$. This implies that, within the cortex, information is highly accessible to all cortical areas regardless of the sensory origin of the information. The ensembles of surrogate networks, random and rewired networks, displayed yet a shorter l, Table I. To understand this difference, we consider the distance matrix $\boldsymbol{D}$ (Figure 4(a)). Its elements D_{ij} represent the number of links crossed to travel from node i to node j and take integer values $D_{ij} = 1, 2, 3, \ldots$ The distribution of distances $n(d)$ is obtained by counting the number of pairs of nodes at distance $D_{ij} = d$. We find that in the cortical network 87.4% of all pairs communicate either through direct connections ($D_{ij} = 1$) or paths of length $d = 2$; $n(1) = 826$ and $n(2) = 1584$ respectively (Figure 5(a)). The most distant cortical areas are separated by 4 steps. However, only five pairs, all with paths starting from auditory area VP, are separated by $D_{ij} = 4$. We consider these few cases as an exception, probably originated from the limitations of the data.

The distance matrices $\boldsymbol{D}$ of surrogate networks have been computed and their distance distributions $n(d)$ extracted. We emphasize the following observations: *1)* Despite the fact that random and rewired networks have very different degree distributions $p(k)$, they have an almost identical distribution of distances $n(d)$, Figure 5(a). *2)* Surrogate networks contain almost no pairs of nodes at distance $d = 3$ while the cortical network of the cat possesses $n(3) = 341$ pairs (12% of all pairs), most of them corresponding to *external* communication paths between areas in different clusters, Figure 5(c). Besides, none of the

FIG. 5: Number of pairs of cortical areas $n(d)$ at distance $D_{ij} = d$. a) All cortical areas considered, b) only distance between areas in the same community, c) only distance between areas in different communities.

generated surrogate networks contained pairs of nodes at distance $D_{ij} = 4$. *3)* The *internal* connectivity in the cortical network, i.e. communication between two areas in the same anatomical cluster, is significantly governed by direct links, Figure 5(b).

The explanation of these observations lies in the clustered organization of the cortical network, which surrogate networks lack. Clusters are composed by subsets of nodes densely connected among them, but sparsely connected to the nodes of other clusters. This inhomogeneous distribution of link density causes the internal communications inside a cluster to happen most often through direct links. On the contrary, communication paths between cortical areas in different communities tend to be longer.

Multiple and alternative communication paths

The picture described above raises the question of how complex cortical information processing could be with respect to the macroscopic scale here analyzed. Certainly, at the microscopic level each cortical area is composed of millions of neurons with different functions and connectivity. But if cortico-cortical communications are governed by direct links and paths of length 2, it might be argued that there is little room for complex and flexible information processing as it is expected to happen in the brain. However, while serial information processing might be reduced to a few steps, the computational power of the network should not be underestimated. In general there is more than one shortest path between two nodes, what might foster rich and flexible computation capabilities. We define the *path multiplicity matrix* $\mathbf{M}$, Figure 4(b), whose elements M_{ij} are the number of shortest paths (of length D_{ij}) running from area i to area j. Additionally, the number of shortest paths of a fixed length, $m(d) = \sum_{ij} M_{ij}$ for which $D_{ij} = d$, have been counted and displayed in Figure 6(a).

We find a total of $m(2) = 6648$ paths of length $d = 2$, meaning that on average, pairs of nodes at distance $d = 2$ are connected by $\langle m(d) \rangle = \frac{m(d)}{n(d)} = 4.1$ different shortest paths. All paths of length 2 from a node i to another node j are necessarily ‘parallel’ to each other,

FIG. 6: Analysis of the path multiplicity. (a) Total number of shortest paths $m(d)$ between cortical areas at distance $D_{ij} = d$. (b) Average number of shortest paths $\langle m(d) \rangle$ between areas at distance $D_{ij} = d$. (c) and (d) Probability $p_d(M_{ij})$ that a pair of nodes at distance d is connected by M_{ij} shortest paths.

say, they go from i to j following non-crossing routes. For example, the visual information entering the cortex through the primary visual cortex, area ‘17’, has three independent manners (paths) of influencing the processing performed by visual area ALLS:

1: 17 → 19 → ALLS
2: 17 → PLLS → ALLS
3: 17 → AMLS → ALLS

For paths of longer size this is rarely the case. In general, two paths can run ‘parallel’ to each other, but a third path could be parallel to only one of them. For illustration, let us consider some of the shortest paths from visual area ‘19’ to primary auditory area AI:

1: 19(V) → PMLS(V) → 35(FL) → AI(A)
2: 19(V) → 21b(V) → EPp(A) → AI(A)
3: 19(V) → 7(V) → EPp(A) → AI(A)
4: 19(V) → 20a(V) → P(V) → AI(A)
5: 19(V) → 5Am(SM) → 35(FL) → AI(A)

Paths 2, 3 and 4 are all parallel to path number 1, but paths 2 and 3 are not parallel to each other because both run through the auditory hub EPp. Moreover, in the example above we also observe that the paths between visual ‘19’ and auditory AI may include areas in different sensory systems. From these observations, we conclude that the mixture of parallel and intricate alternative paths of communication between cortical areas might give rise to complex information processing properties, including multisensory modulation and integration. The parallel and alternative paths may also provide robustness to the communications. The short paths between every cortical region assures fast processing and behavioral responses.

Due to its combinatorial nature, the average number of shortest paths $\langle m(d) \rangle$ rapidly increases with d. In Figure 6(b), $\langle m(d) \rangle$ of the cortical network of the cat and of the surrogate networks is plotted for shortest paths of length $d = 1, 2$ and 3. Interestingly, while the distribution $n(d)$ of both surrogate network models is almost identical, Figure 5(a), $\langle m(d) \rangle$ of the cortical network and of the rewired networks are very similar. On the contrary, random graphs contain twice the number of shortest paths between each pair nodes at distance $d = 3$ than the rewired and the cortical networks. To stress this observation, in Figures 6(c) and (d) the distribution $p_d(M_{ij})$ of the values M_{ij} for pairs of nodes at distance $d = 2$ and $d = 3$ are plotted. The distribution $p_d(M_{ij})$ represents the probability that a pair of nodes at distance $D_{ij} = d$ is connected by M_{ij} shortest paths. For both $d = 2$ and $d = 3$, $p_d(M_{ij})$ of the cortical network and of the rewired networks follow very close to each other, with maximal probabilities peaking around $M_{ij} \approx 3$, and $M_{ij} \approx 15$. On the contrary, the $p_3(M_{ij})$ distribution of random networks peaks for values $M_{ij} \approx 40$. These observations strongly indicate that the presence of hubs in the cortical and the rewired networks limits the random dispersion of paths acting as mediators between low degree nodes. In terms of the cortical network, hubs help communicate the areas segregated in different communities.

IV. CONCLUSIONS AND DISCUSSION

Sensory neurons transduce environmental information into electrical signals which follow a bottom-up processing along the nervous system. The capacity of the nervous system to simultaneously process different kinds of information relies, to a large extent, on the circuitry where the stimulus is received and processed. But in order to achieve a coherent and unified perception of the reality, sensory information needs to be integrated together at some point [18] and at some time [19–21], and for that the paths of information need to converge. In this paper, we have reviewed the large-scale organization of cortico-cortical networks and have performed a statistical analysis of its communication paths in an effort to understand how the anatomical substrate of connections (the network topology) may support the simultaneous functional necessities for specialization and integration. We find there are three major features governing the organization of cortical connectivity: a large density of connections, the clustered organization into functional communities and the presence of highly connected hubs.

As a consequence of the large density of links, cortico-cortical communications are governed by either direct connections or paths of length 2. This assures fast processing and behavioral responses. This observation is in agreement with recent results [22–24], where it has been shown that neural organization might favor short information processing rather than short axonal paths. Instead, a prominent hypothesis in the field is that the nervous system tends to minimize the wiring length because of the energetic benefits of propagating electrical impulses through shorter axons. Another consequence is that, within the cortex, information is highly accessible to all cortical areas regardless of its sensory origin. In other words, the processing of information of an area can be widely affected by the outcome of other areas.

The organization into clusters, giving rise to a large clustering coefficient, permits that sensory information of different modalities is segregated and processed "independently". Areas within the same cluster are mainly connected by direct connections, while communication between areas in different communities, tends to follow longer paths.

The cortical network of the cat also contains highly connected hubs, some of them link to nearly 60% of the network. Our statistical analysis has revealed that the presence of hubs drastically reduces the random dispersion of paths, by acting as mediators in the communication between cortical areas in different clusters. This property highlights the central role that these hubs may play for the integration of multisensory information [25–30].

Summarizing, the results here presented, after statistical analysis the long-range connectivity of the cat, uncover the rich and complex information processing capabilities of the cerebral cortex. On the one hand, the predominance of short processing paths ensures fast responses, on the other hand, the large number of alternative and intricate paths in which two areas may influence on each other opens the door to a large variety and flexible information processing.

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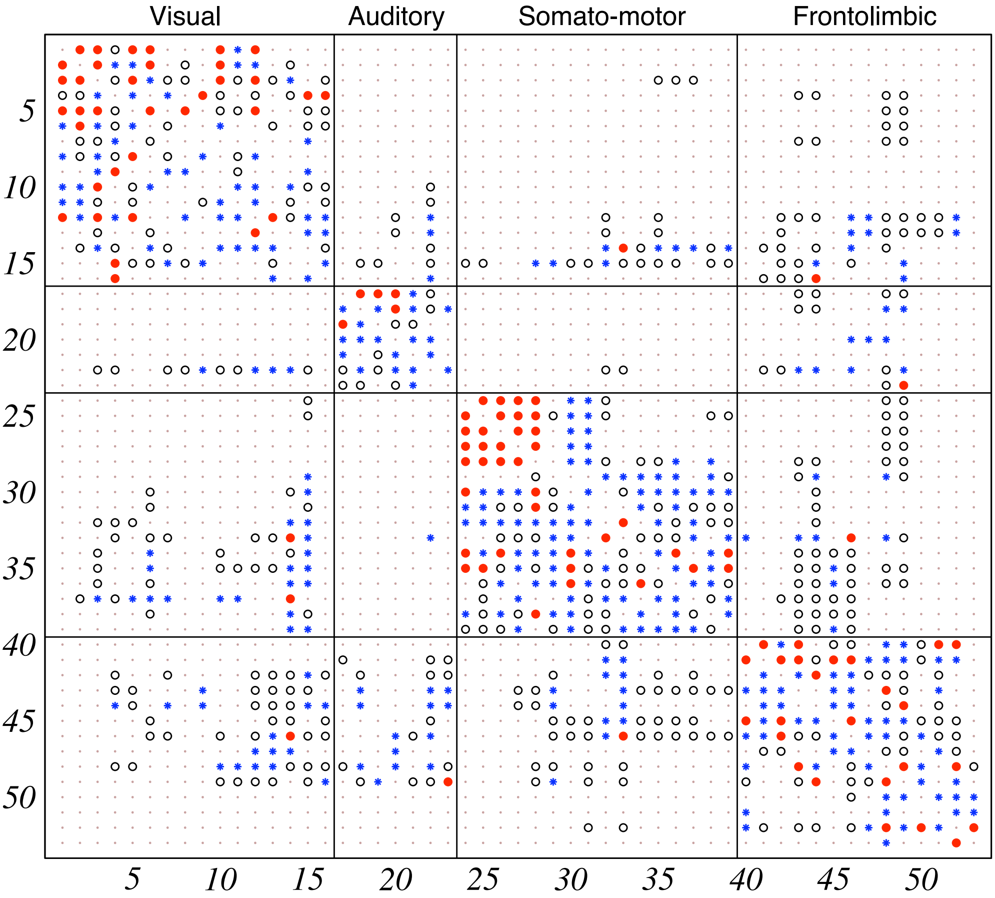
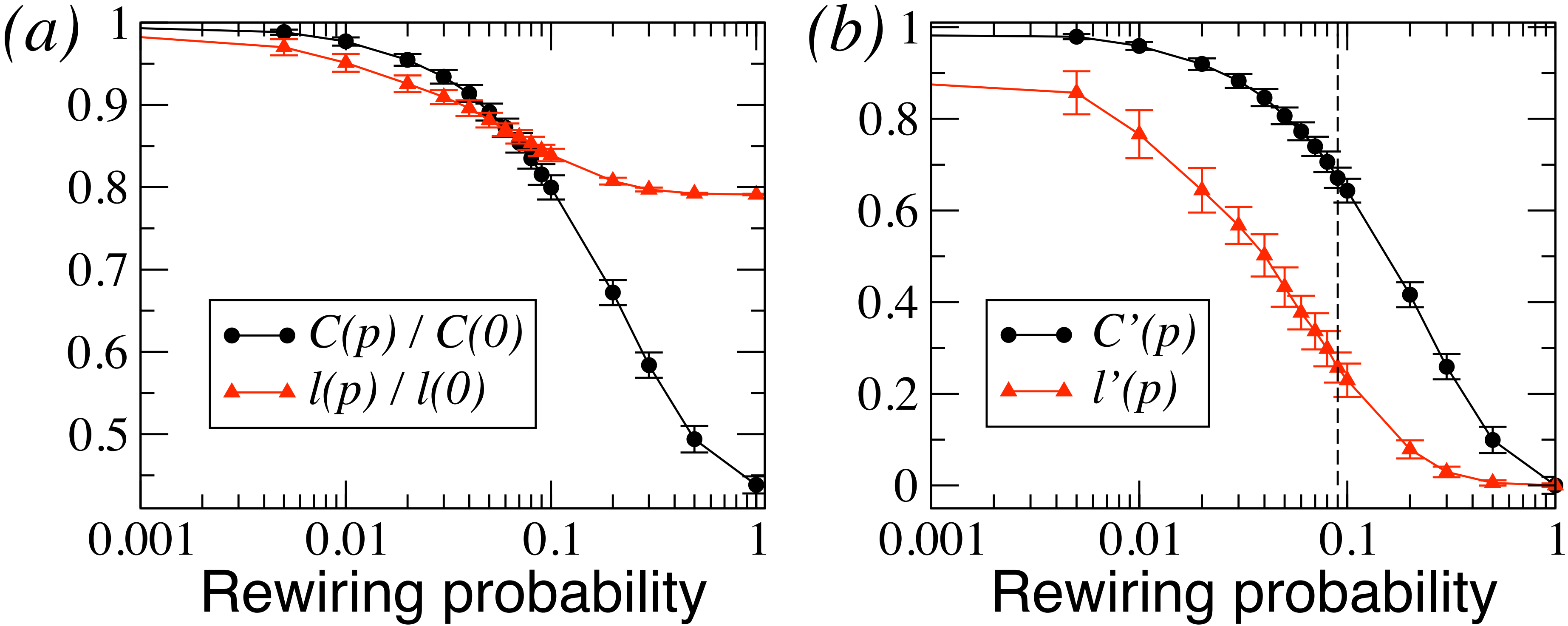
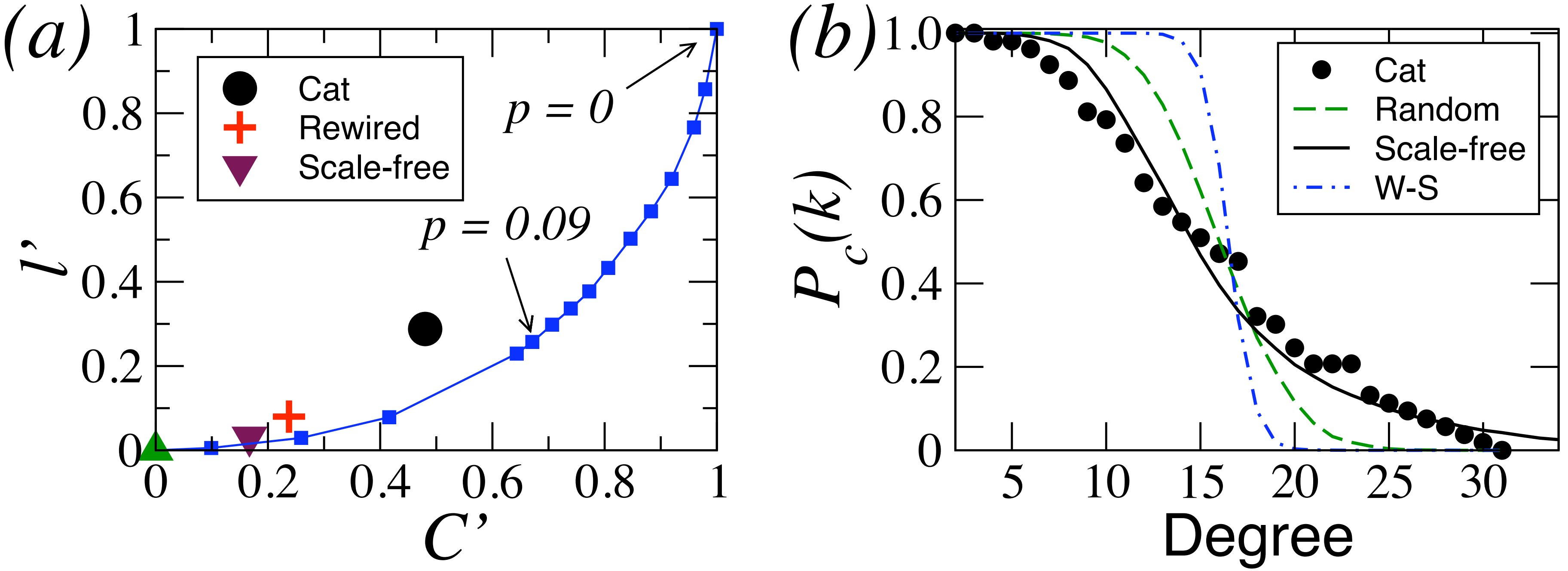
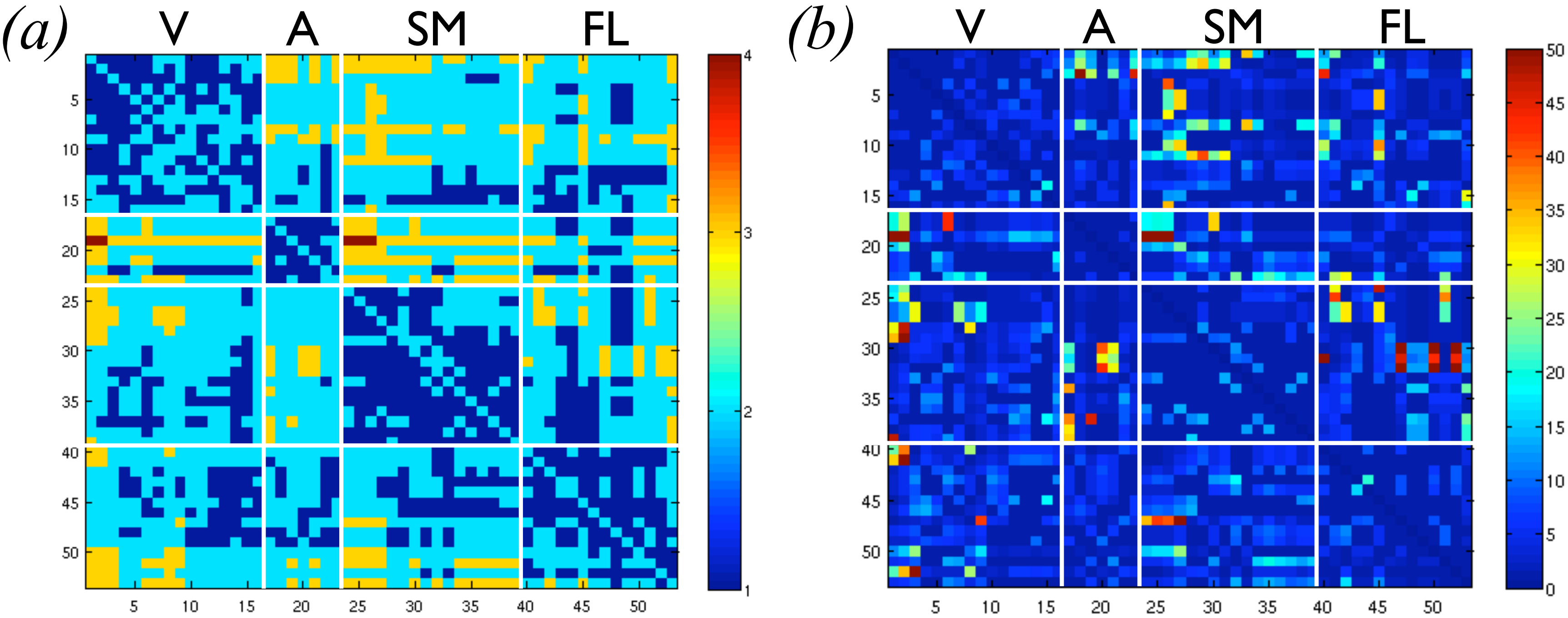
[] $P_c(k)$ is defined as the probability that a randomly chosen node has degree larger of equal to k

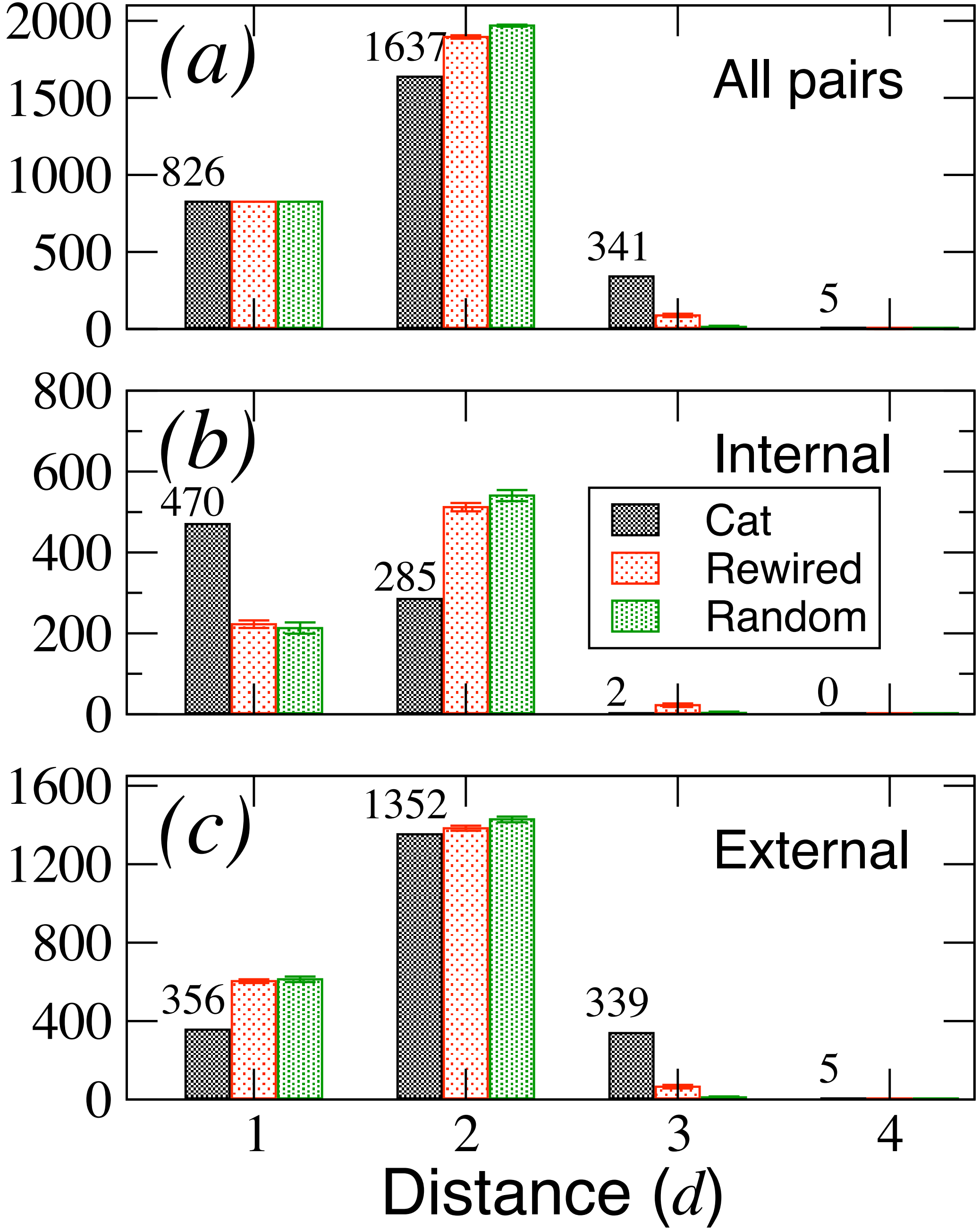
[] The exponent $\gamma = 1.5$ is approximately the one that best fitted in a range between 1.2 and 3.0.

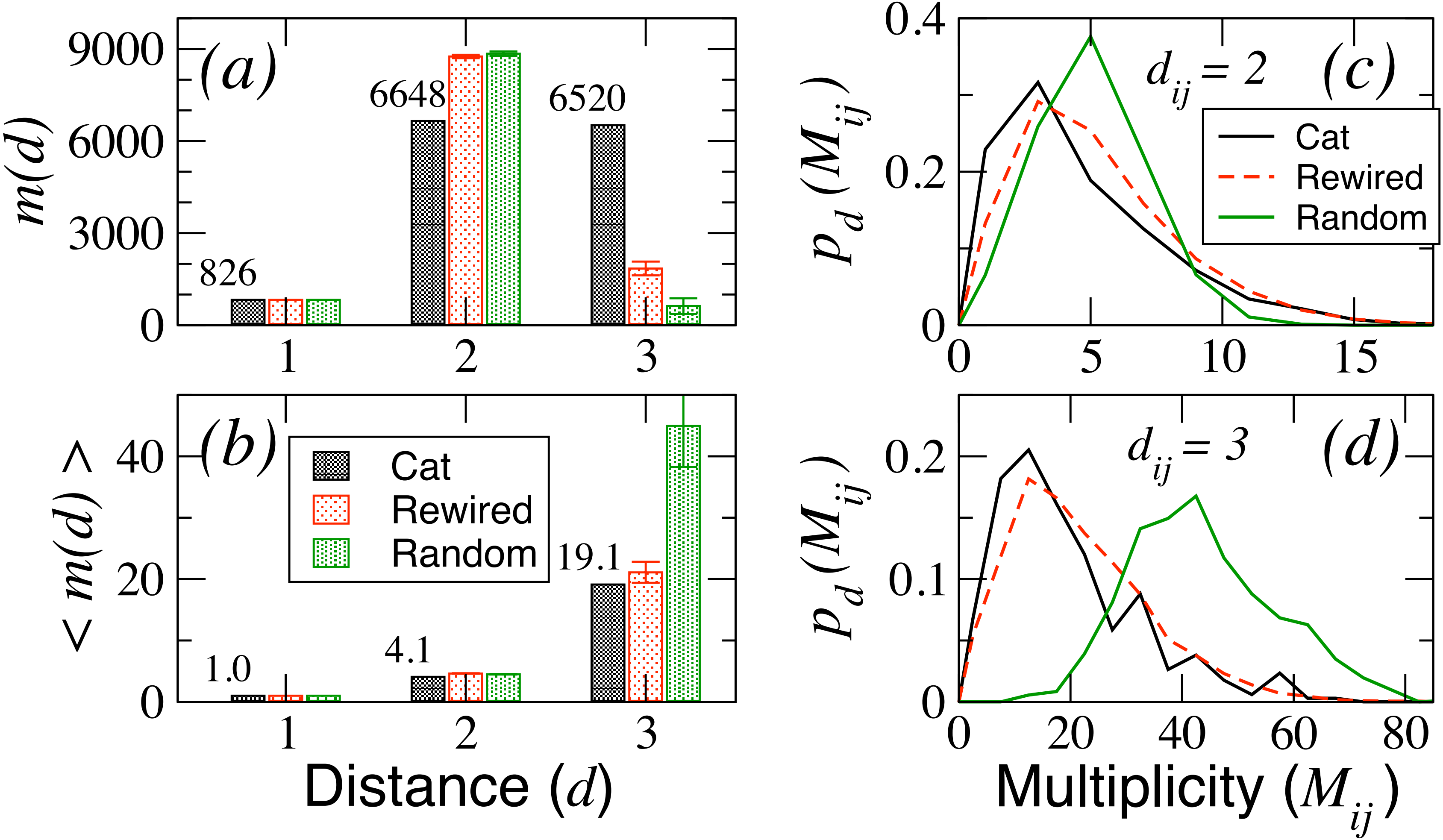

Visual
Auditory
Somato-motor
Frontolimbic
5
10
15
20
25
30
35
40
45
50
5
10
15
20
25
30
35
40
45
50


(a)
(b)
1
0.9
0.8
0.7
0.6
0.5
0
0.2
0.4
0.6
0.8
0.001
0.01
0.1
Rewiring probability
$C(p) / C(0)$
$l(p) / l(0)$
$C'(p)$
$l'(p)$


(a)
Cat
Rewired
Scale-free
p = 0
p = 0.09
l'
C'
0
0.2
0.4
0.6
0.8
1
(b)
Cat
Random
Scale-free
W-S
$P_c(k)$
Degree
0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
25
30


(a)
V
A
SM
FL
5
10
15
20
25
30
35
40
45
50
1
2
3
4
(b)
V
A
SM
FL
5
10
15
20
25
30
35
40
45
50
0
5
10
15
20
25
30
35
40
45
50


(a)
All pairs
2000
1500
1000
500
0
826
1637
341
5
(b)
Internal
800
600
400
200
0
470
285
2
0
Cat
Rewired
Random
(c)
External
1600
1200
800
400
0
356
1352
339
5
1
2
3
4
Distance (d)


(a)
m(d)
9000
6000
3000
0
826
6648
6520
1
2
3
(b)
< m(d) >
40
20
0
1.0
4.1
19.1
Cat
Rewired
Random
Distance (d)
(c)
d_ij = 2
p_d (M_ij)
0.4
0.2
0
5
10
15
(d)
d_ij = 3
0.2
0.1
20
40
60
80
Multiplicity (M_ij)