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Spatial Network Growth

Technical Report No. 1

January 2005

School of Engineering and Science

Spatial network growth

Generating small-world, scale-free, and multi-cluster spatial networks

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Summary

Almost all real-world networks are distributed in space. In many of these networks, more short- than long-distance connections exist. Thus, there is a preference to minimize the length of connections. Such networks often exhibit properties of small-world, scale-free or multi-clustered networks. However, previous models for development, where only distance between nodes is considered when establishing a connection, were unable to yield spatial graphs with these properties.

I present a new model for spatial graph development that can generate small-world networks. Notably, also scale-free networks (similar to the German highway system or the yeast protein-protein interaction network) can be generated without using preferential attachment. The final topology of the network depended on whether the growing network reached spatial limits during development or not. Furthermore, different models for network evolution (limited, unlimited and preferential attachment) could be distinguished by observing the change of density and clustering coefficient over time.

Spatial growth was able to yield networks similar to real-world spatial networks. As a case study, I generated networks similar to cortical networks. I found that not only global network properties but also wiring properties were similar. In addition, multiple clusters could be generated by introducing time windows.

Contents

1 Introduction

Spatial networks are graphs that consist of nodes arranged in metric (usually 2D) space (Watts, 1999). However, the concept of space could be extended to non-metric space. A typical example are transportation networks where cities are the nodes with a two-dimensional position on the map and highways are connections between the nodes. In theoretical studies, spatial graphs are usually generated by distributing the nodes randomly in space. After the nodes are arranged, edges between the nodes are added to the network either randomly or depending on the distance between the nodes.

These models, however, fail to reproduce many features of real-world networks. One such feature is that of a small-world network (Watts and Strogatz, 1998) in which many connections between neighbors of a node exist but characteristic path length, that means the number of edges that have to be crossed to go from one node to another, is as short as that of a randomly connected network. Neighborhood connectivity is usually assessed by the *clustering coefficient* which is the average percentage of connections between neighbors of a node (Watts and Strogatz, 1998). Small-world properties were found in many biological and artificial networks, including networks extending in space such as the Internet, power grids, neural networks, and food webs (Watts and Strogatz, 1998). Another property is that of having multiple clusters, that means that nodes as well as connections between nodes are not distributed equally among space but concentrated on certain regions. Thus, there exist multiple clusters in the network. For example, in the yeast protein-protein interaction network there are relatively more interactions within the mitochondrium than between mitochondrium and other cellular compartments (Schwikowski et al., 2000). Another property of real-world networks is that highly-connected nodes or hubs exist in the network which would not occur when a random distribution of connections is assumed. The degree distribution of these real-world networks, where degree is the number of edges that a node has, follows a power-law where the probability for a node having degree k is $P(k) \propto k^{-\gamma}$ (Barabási and Albert, 1999).

I will describe a spatial growth model that can explain features of real-world networks such as scale-free degree distribution, small-world properties, optimal component placement and multiple clusters. The report consists of the following parts. First, I will give examples for spatial graphs and their properties. Next, I will give an overview of different models for network development or evolution. Then, I will give general properties of our model and will — as a case study for real-world networks — describe how brain-like networks can be generated. Finally, I will discuss applications and limits of spatial growth.

1.1 Internet

One spatial network with well-documented topology is the network of networks — the Internet. The Internet can be analyzed both on the router and the autonomous systems (AS) level. Whereas routers are the basic units redirecting packages, AS's as independent subnetworks can be identified at a global scale (Tanenbaum, 2003). Recently, a combination of spatial constraints (Waxman, 1988) and preferential attachment (Barabási and Albert, 1999) has been shown to yield a topology similar to the Internet (AS level) (Yook et al., 2002). However, all nodes were existing before the start of establishing connections thereby not modeling simultaneous growth of nodes and edges. In this study I analyze a reconstruction of the AS network based on snapshots from December 1997, December 1998, and December 1999 (Data from the Measurement and Network Analysis Group; `http://moat.nlanr.net/AS/`). The data consisted of 6,524 AS and 29,629 connections between them. The connection density was 0.07% with a higher neighborhood connectivity (clustering coefficient 67%).

1.2 Traffic networks

Cities and roads between them are geographically distributed. It was shown recently that the German highway network has a scale-free topology (Kaiser and Hilgetag, 2004b) [1]. The data of location nodes and connections was processed from the "Autobahn Informations System" (AIS), as accessible under `http://www.bast.de` (data as of 18 July 2002). Only roads defined as highways were included in the analysis. Multiple highway exits for the same city (e.g., Hagen-West and Hagen-Nord) were merged to one location representing the whole city as a node of the network. Due to the merging process and highways currently under construction, eight percent of the nodes were separated from the largest cluster and were excluded from analysis. The resulting network consisted of 1,168 highway exits or locations and 2,486 highway connections between them (Fig. 1). As for the Internet, the density of 0.18% is very low. Because of linear chains of nodes, i.e. sequences of nodes that have only connections to successors or predecessors in the chain, the clustering coefficient (0.12%) is lower than the density. In addition, the maximum degree of a node (12 highways) is very low so that no highly-connected nodes exist in the system. A similar type of organization was also found for scale-free protein-protein interaction networks (Jeong et al., 2001) (maximum degree $k_{max} \approx 20$). Therefore I term these networks with linear chains of nodes and scale-free but hub-less degree distribution *linear scale-free networks.*

1.3 Brain Connectivity Networks

As most other biological systems, the brain also is a spatial network. I analyzed the network not on the level of single neurons but on the level of large-scale structural modules (cytoarchitectonically defined areas). The analyzed connectivity networks

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[1] In our study nodes are defined as highway exits. In other studies (Gastner & Newman, cond-mat/0407680) only highway junctions and state borders were defined as nodes. This could explain why these networks did not show a scale-free degree distribution.

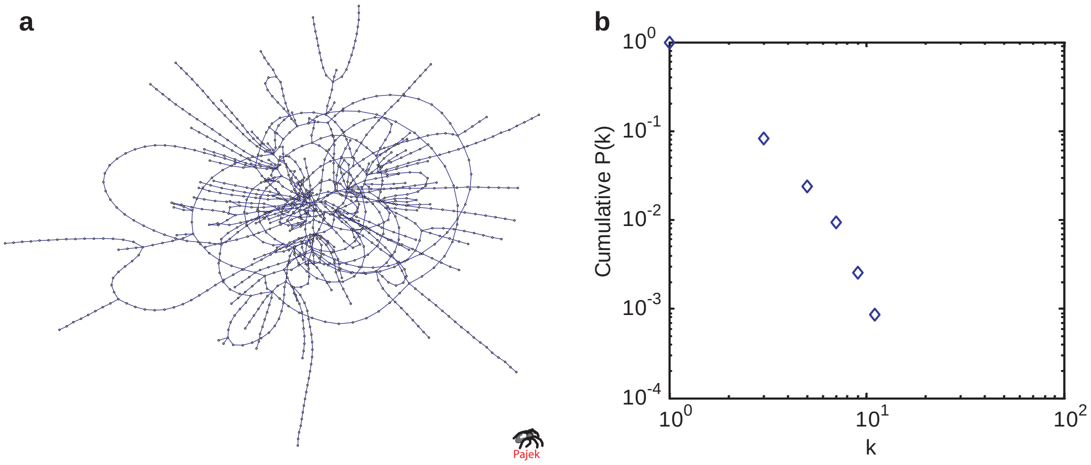

Figure 1: German highway (Autobahn) system. **a**, Positions were yielded by the free Kamada-Kawai energy minimization (Pajek software package). Linear chains of nodes can be clearly seen in the periphery of the visualization. **b**, Cumulative degree distribution ($k_{max} = 12$).

of the cat and the macaque monkey consist of brain areas or regions as nodes and the connections between the nodes as edges. In contrast to the previous networks, the brain connectivity networks were very dense (15% density for the macaque with 73 areas and 30% for the cat with 55 areas). The network showed properties of small-world networks, in that the clustering coefficient (Watts and Strogatz, 1998) was higher and the average shortest path (ASP) length comparable to similar random networks.

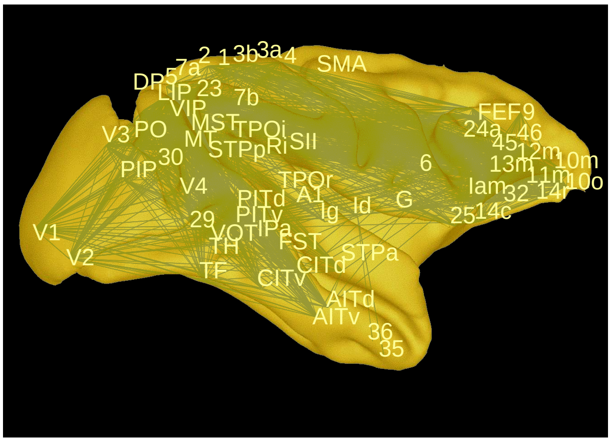

Figure 2: Schematic drawing of the macaque cortical network with 95 areas. Areas are positioned at the center of the surface region that belongs to each cortical area. Lines represent known connections between cortical areas.

In addition to connectivity networks used in previous studies (Young, 1993; Hilgetag et al., 2000), I analyzed a connectivity network together with the corresponding positions of the cortical areas (Kaiser and Hilgetag, 2004a). Connectivity among cortical areas was obtained from three studies (Felleman and van Essen, 1991; Carmichael and Price, 1994; Lewis and Van Essen, 2000), for which data was available in the CoCoMac-database (`http://www.cocomac.org`). Average spatial positions of cortical areas were estimated based on surface coloring using the CARET software (van Essen Lab, `http://brainmap.wustl.edu/caret`). The length of connections was approximated as the direct Euclidean distance between the geometric centers of two connected areas. The resulting network consisted of 95 cortical regions and 2,402 connections (Fig. 2).

1.4 Biochemical Networks

I analyzed metabolic and protein-protein interaction networks. Whereas the edge density was only 1% in these systems, the clustering coefficient was 60% and 70%, respectively. I used data from metabolic networks of 43 organisms where the nodes were metabolites and the edges were transitions or reactions (data from `http://www.nd.edu/~networks/database/`). The protein-protein interaction network of yeast (*S. cerevisiae*), on the other hand, consisted of proteins and interactions between them identified by yeast two-hybrid analysis (Schwikowski et al., 2000; Ito et al., 2001). I analyzed the largest connected component consisting of 1,846 proteins and 4,406 interactions.

2 Methods for Network Growth

2.1 Distance independent growth models

2.1.1 Growth and preferential attachment

The standard model for generating scale-free networks uses growth and preferential attachment (Barabási and Albert, 1999). Starting with m_0 initial nodes, a new node establishes a connection with an existing node i with the probability

$$P_i = \frac{k_i}{\sum k}$$

that is, the number of edges of node i (k_i) divided by the total number of edges yet established in the network. The resulting network consists of one cluster, and the degree distribution shows a power-law.

2.1.2 Hierarchical model

In order to develop modular scale-free networks, the hierarchical model for network generation has been developed (Barabási et al., 2001; Ravasz et al., 2002). Starting with one root node, for each step two units that are identical to the network generated in the previous iteration, are added and the bottom nodes of these two units are linked with the root of the network.

In contrast to real-world networks, the modules are generated in a deterministic way. This also means that the module hierarchy is strongly self-similar, leaving no space for a variety of module sizes within the same network. However, for metabolic networks it is argued that the replacement of a unit by the whole network, thereby increasing the previously existing topology, could be the result of copying and reusing existing modules and motifs (Ravasz et al., 2002).

2.2 Distance dependent growth

2.2.1 Preference for short-distance connections

Waxman (1988) proposed a connection establishment algorithm for the Internet in which the probability of a connection between two nodes decays exponentially with the spatial distance between them. In that way, the high costs for the wiring and maintenance of long-range connections can be represented.

Initially, the nodes are distributed at random. Thereafter, edges are attached to the graph. The probability that an edge is established between two nodes u and v is

$$P(u,v) = \beta\, e^{\frac{-d(u,v)}{L\ \alpha}}$$

where L is the maximum distance between two nodes, α is a factor for the distance importance (a higher value results in fewer long-range connections), and β is a scaling factor. The probability decays exponentially with the distance $d(u,v)$ between the nodes. In contrast to the other models, the location of the nodes is determined from the start, therefore, there was no growth in terms of the size of the network or number of nodes.

Diffusion as a reason for distance dependence in biological systems

Why should short-distance connections be more likely than long-distance connections? One explanation is that the concentration from the place of the production / emission of a growth factor to a distant location is decreasing. The process of diffusion building up a gradient towards the source of a molecule is dependent on the molecular mass of the molecule, the viscosity of the fluid, and the temperature. Looking at a system where a certain concentration of molecules is deposited at position $x = 0$ for the starting time $t = 0s$ the concentration at position x after time t is given by

$$c(x,t) = \frac{Q}{2\ \sqrt{\pi\ D\ t}}\ e^{\frac{-x^2}{4\ D\ t}}$$

where D is the diffusion coefficient and Q is initial amount of particles per area (Murray, 1990, p. 235).

2.3 Spatial growth model

The diffusion model is particularly plausible for biological networks, as the concentration of growth and signaling factors decays exponentially from the point of origin in the cell or the brain. Therefore, the probability for establishing a connection with a certain brain area or to interact with a certain protein will decrease with spatial distance to the growth factor source or the protein, respectively. In the spatial growth model nodes are generated step by step, and whenever a new node is added to the network, its connections to the existing network are established.

This method can take borders or limits of development into account. The generation of new cortical regions is limited within the skull. In addition, apoptosis factors limit the generation of neurons so that growth beyond the limits of the skull does not occur. In that way new nodes cannot be formed at the borders of the network, that is, distant from the existing network. As new nodes can only be generated within the limits of the existing network, the core of the network is increasing its connection density.

At each step a new node was added at a randomly chosen position. Thereafter, for all existing nodes the probability for establishing an edge between the new node u and an existing node v was

$$P(u, v) = \beta \ e^{-\alpha \ d(u,v)}$$

where β is a scaling factor and α controls the probability for establishing long-range connections. New nodes that did not establish connections with existing nodes were removed from the network. The procedure was repeated until the desired number of nodes was reached.

I only used the normal exponential decay. The distance between two nodes could be less than one. Therefore, using the square of the distance would yield a relatively *higher* probability for near nodes contradicting exponential decay.

As the initial spatial distribution of nodes would have been an additional parameter for network growth, I started network generation with one defined initial node at the center of the network space. In that way the initial distances to the border for the growing network were identical for all trials.

3 Results

3.1 General properties of spatial growth networks

3.1.1 Parameter domains for different network types

For very small β (< 0.01), sparse networks were generated (Fig. 3a) in which only a small proportion of all possible edges was established. The resulting networks were highly linear, that is, exhibiting one-dimensional chains of nodes, independent of limited or virtually unlimited growth (parameter α). The histograms of chain-lengths found in these networks, indicating the number of nodes in the chains,

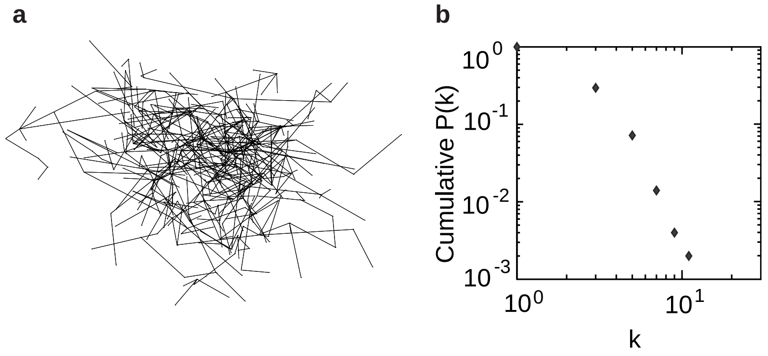

Figure 3: **a**, Sparse network (density 0.42%) with 500 nodes obtained by limited growth ($\alpha = 2$, $\beta = 0.001$). **b**, Double-logarithmic plot of the cumulative degree probability $P(k)$ that a node possesses k edges for the network shown in **a**. The plot is based on uniform bins of data. A power-law of the degree distribution ($\gamma = 2.43$) can be observed.

were similar to those of random networks with the same density. Unlike in random networks, however, the clustering coefficient was lower than the network density, and despite lacking clusters and hubs with large degree k, these networks possessed a power-law degree distribution, with high ASP (Fig. 3b, to avoid systematic errors known to occur for linearly histogrammed data plotted on logarithmic scales, the plot uses data bins of uniform width). The power-law exponent was small, in the range of [1.7; 2.1]; and in the simulated networks of 100 nodes the cut-off for the maximum degree of the scale-free networks was 16. Given their low maximum degree, these networks with low clustering and long linear chains of nodes were called linear scale-free.

For higher edge probability ($\beta \rightarrow 1$), a noteworthy difference between limited and virtually unlimited growth became apparent. While it was impossible to generate high network density under virtually unlimited growth conditions, the introduction of spatial limits resulted in high density and clustering, as well as low ASP. This was due to the fact that, in the virtually unlimited case, new nodes at the borders of the existing network were surrounded by fewer nodes and therefore formed fewer edges than central nodes within the network. In the limited case, however, the network occupied the whole area of accessible positions. Therefore, new nodes could only be established within a region already dense with nodes and would form many connections.

Figure 4 shows the relation between small-world graph properties and growth parameters α and β for networks consisting of 100 nodes. The ratio of the clustering coefficient in spatial growth compared to random networks was larger than one (indicating small world graphs), if the values for α and β were high (Fig. 4a). The ASP in the generated networks normalized by the ASP in random networks with similar density was similar for low values of α and high values of β. For

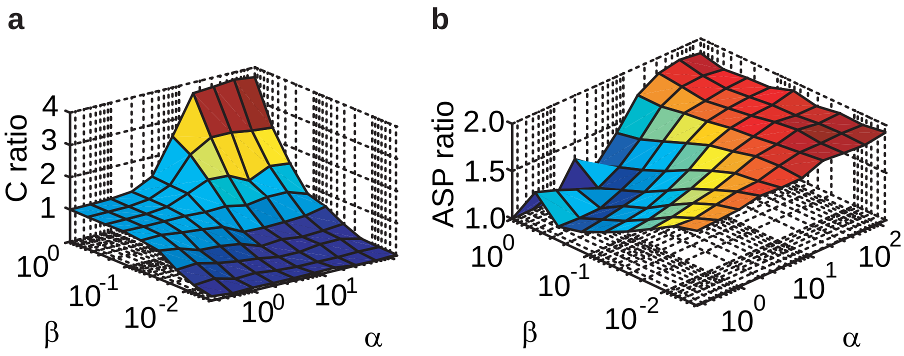

Figure 4: Comparison of small-world properties of spatial and random networks for N=100 nodes. Each data point represents the average for 50 networks. **a**, Ratio of the clustering coefficient C of the generated networks divided by the clustering coefficient for comparable random networks. A large ratio is one feature of small-world networks. **b**, Ratio of the average-shortest paths, ASP, of spatial-growth and comparable random networks.

these networks the likelihood of edge formation was high and — because of the low value of α — independent from spatial distance. Such networks resembled random growth, with the clustering coefficient possessing the same value as the density ($C/C_{random} \approx 1$).

In a small interval of intermediate values for α ($\alpha \approx 4$, $\beta = 1$), networks exhibited properties of small-world networks (ASP and clustering coefficient shown in Fig. 5a). Here, the ASP was comparable to that in random networks of the same size ($\lambda \approx \lambda_{random}$), while the clustering coefficient was 39% higher than in random networks (Watts, 1999, p. 114). An overview of the parameter space and the resulting random, small-world, virtually unlimited or linear scale-free networks is given in Figure 5b.

In contrast to limited growth, virtually unlimited growth simulations with high β resulted in inhomogeneous networks with dense cores and sparser periphery. It is difficult to imagine realistic examples for strictly unlimited development, as all spatial networks eventually face internal or external constraints that confine growth, may it be geographical borders or limits of their energetic and material resources. However, virtually unlimited growth may be a good approximation for the early development of networks before reaching borders.

I tried an alternative approach for generating scale-free networks. The idea was to increase the probability that new nodes settle in dense areas inside the network rather than at positions where only few nodes existed. Therefore, a node only survived if it established more connections than the average connectivity. A node inside a cluster had more links than a node at more sparse locations of the network. Consequently, its probability to survive was higher. The resulting network covered a smaller area of the network space, as it was more likely that nodes survived at the core of the network rather than at it's borders (Fig. 6). The density was increased

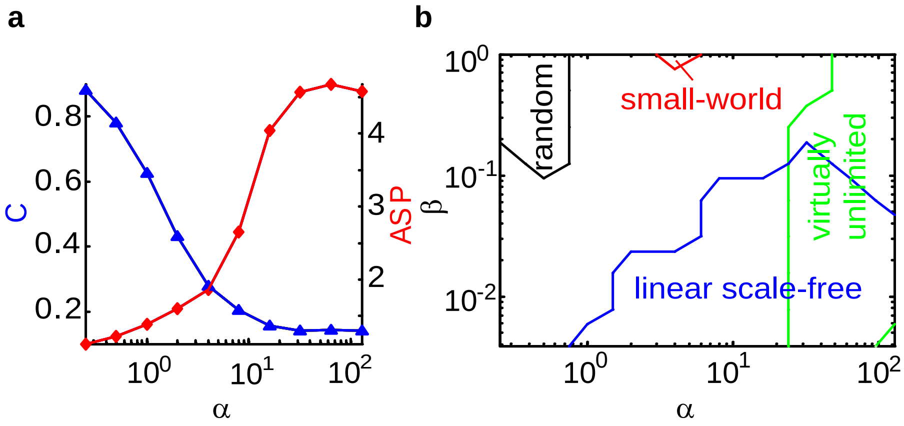

Figure 5: Exploration of model parameter space. **a**, For dense networks ($\beta = 1$, $N = 100$ nodes), an increased dependence of edge formation on distance (parameter α) led to an increase of ASP (diamonds) and a decrease in clustering coefficient C (triangles). **b**, Overview of network types for different spatial growth parameters ($N = 100$ nodes). Low values of α made edge formation independent from distance and resulted in random networks. For large values of α only nodes near the existing network could establish connections, and the hard borders were not reached (virtually unlimited). The area labeled linear scale-free was a region in which networks were sparse and highly linear and showed a scale-free degree distribution. Only a small part of the parameter space displayed properties of small-world networks.

and the ASP for the unlimited case is now similar to the limited case. However, no hubs occurred and no scale-free degree distribution could be generated. As new nodes inside clusters had the same probability to establish links with peripheral as well as central nodes, the increase in connectivity did not favor a small number of nodes and did not result in hub formation.

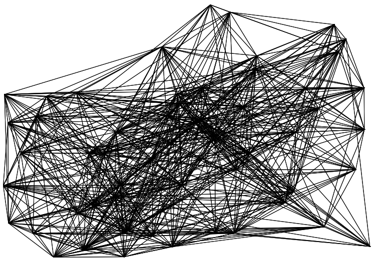

Figure 6: Preferential crowding condition for limited growth. The core of the network has a higher node density. However, no power-law degree distribution was found.

3.1.2 Distinguishing Types of Network Development

Different network growth types can be distinguished by assessing the evolution of network density and clustering coefficient. Growth with preferential attachment as well as spatial growth lead to clustering coefficients, $C(N)$, that depend on the current size of the network, that is, the number of nodes, N (Fig. 7a). While $C(N)$ decreases with network size for networks generated by the BA-Model (Barabási and Albert, 1999), it remains constant for spatial-growth networks. Virtually unlimited or limited spatial growth can thus be distinguished, since density decreases with network size for unlimited growth, while remaining constant for limited growth (Fig. 7b).

Example: Evolution of metabolic networks. I applied this concept to classifying the development of real-world biological networks. The evolution of metabolic systems, for instance, can be seen as an incorporation of new substances and their metabolic interactions into an existing reaction network. Reviewing 43 metabolic networks in species of different organizational level (Jeong et al., 2000), the clustering coefficient of these systems remained constant across the scale (Ravasz et al., 2002), whereas their density (Fig. 7c) decreased with network size. This indicated features of virtually unlimited network growth. The relation between the number of links and nodes in these systems was linear (Fig. 7d), with a slope of 5.2, so that the number of interactions of a metabolite was not increasing with network size. Such linear growth may ensure that the metabolic systems remain connected (with the number of reactions larger than substances, as a necessary condition for connectedness), while not becoming too complex too quickly (as, for instance, with exponential addition of new reactions).

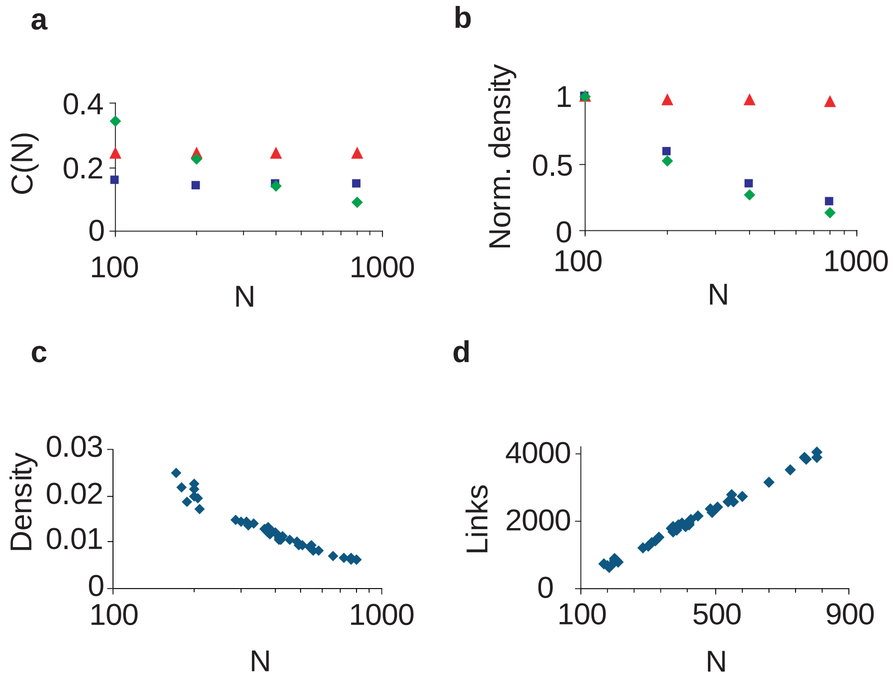

Figure 7: Comparison of the dependence of clustering coefficient $C(N)$ and density on network size (number of nodes, N). **a**, For the simulated networks the clustering coefficient remained constant for limited (triangles, $\alpha = 5$, $\beta = 1$) and virtually unlimited (boxes, $\alpha = 200$, $\beta = 1$) spatial growth, but decreased for growth with preferential attachment (diamonds). **b**, Density was independent of network size only for limited spatial growth. **c**, Density depending on network size (N) for the metabolic networks of 43 different organisms (15). **d**, A critical measure for network development was the dependence of network size on the number of links. For metabolic networks, this relationship was strongly linear.

Example: Evolution of the Internet. The development of the Internet was considered at the autonomous system (AS) level, that is, for independent sub-networks. Over the years, the number of autonomous systems has been increasing. Whereas the clustering coefficient did not shrink and even seemed to increase, the density has been decreasing with network size (Fig. 8). Therefore, the current development of the Internet shows properties of unlimited spatial growth. Indeed, current maps still show sparsely populated countries to which the network can expand (Yook et al., 2002, Fig. 1). In order to determine the exact growth mechanisms, it would be interesting to investigate if new nodes form at dense geographical regions, that is, within the network, or at sparse regions at the network borders.

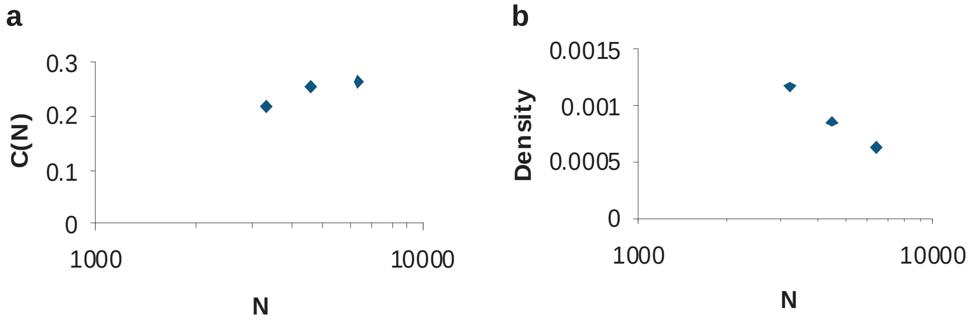

Figure 8: Evolution of the Internet. Clustering coefficient C(N) and density depending on the size of the AS-network. **a**, After an increase from 1997 to 1998 the clustering coefficient remained constant. **b**, Density of the network was decreasing with network size.

Networks grow in time and space. New cities and roads are constantly build. During development, brain areas and new fibers are established. Therefore, data about nodes and edges in the traffic system, the Internet, or the neural system should be available for different times and therefore network sizes. If the connection density is decreasing with increasing network size, an unlimited network can be assumed. I would not be surprised, however, if the growth of many real-world networks would be found limited by borders.

3.2 Case study: cortical connectivity networks

Here, I analyze cortical networks of the cat and the macaque monkey. I will investigate whether properties of these networks can result from spatial growth. First, I will test whether spatial growth limits are necessary to generate networks that are similar to cortical networks.

3.2.1 The role of borders for development

The connectivity networks of cat and macaque are compared with generated spatial growth networks under the limited (border) as well as the virtually unlimited condition. The parameter β was not changed, therefore, the density and clustering coefficient differed between bordered and unlimited case. Both for the cat (Tab. 1) and the macaque (Tab. 2), limited growth could yield similar network properties of clustering coefficient and ASP, but the virtually unlimited condition led to larger ASP (almost a factor of 2) and decreased clustering coefficient (about 2/3 of the original value).

It appears to be impossible to generate a high density as in the cat network and low ASP's as for cat and macaque network without borders. In fact, the ASP for the unlimited networks is much higher than for comparable random networks (ASP 2.8) excluding them from being small-world networks. It appears that small-world networks, indeed, only occur in *small* (limited) and not in infinite network spaces.

Table 1 Cat brain connectivity network and artificially generated networks. Clustering coefficient cl, density d, average shortest path ASP and the maximum degree of the resulting network are shown.

	cl	d	ASP	$max.\ deg.$
Cat_{55}	0.55	0.3	1.82	31
border (α=5)	0.5	0.34	1.7	29
unlimited (α=200)	0.3	0.08	3.9	10

Table 2 Macaque brain connectivity network and artificially generated networks. Clustering coefficient cl, density d, average shortest path ASP and the maximum degree of the resulting network are shown.

	cl	d	ASP	$max.\ deg.$
$\mathrm{Macaque}_{73}$	0.46	0.16	2.2	39
border (α=8)	0.4	0.17	2.2	23
unlimited (α=200)	0.3	0.07	4.1	12

3.2.2 Total wiring length in cortical and simulated networks

I compared the wiring length of networks generated with our model in three dimensions with the wiring length of cortical systems connectivity in one hemisphere of the macaque monkey.

For the macaque cortical network as well as comparable generated networks (length scaled to account for different embedding space), the total length of all connections was comparable (macaque: 32,364 mm; spatial growth simulation: 36,562 mm).

I note that networks generated by spatial growth show optimal component placement (Cherniak, 1995), in that reordering node positions leads to an increase in total wiring length. In contrast to previous approaches to yield optimal wiring, such as the vector mechanics model (Cherniak et al., 1999), spatial growth does not need *a posteriori* optimization. In favoring nearby nodes for connection establishment during each individual step, our greedy spatial growth algorithm leads to the global property of optimal component placement.

3.2.3 Multiple clusters

Within the aforementioned algorithm multiple cluster can occur. When a new node faraway from the existing network does survive, candidate nodes in its vicinity are likely to establish a connection to such a *pioneer node*. However, the probability that a node distant to the existing network can survive, that is, establishes at least one long-distance connection to the existing network, is still low. Therefore, it can not be guaranteed that such a node occurs during development and that multiple clusters arise. Furthermore, there is no control over the size of occurring clusters.

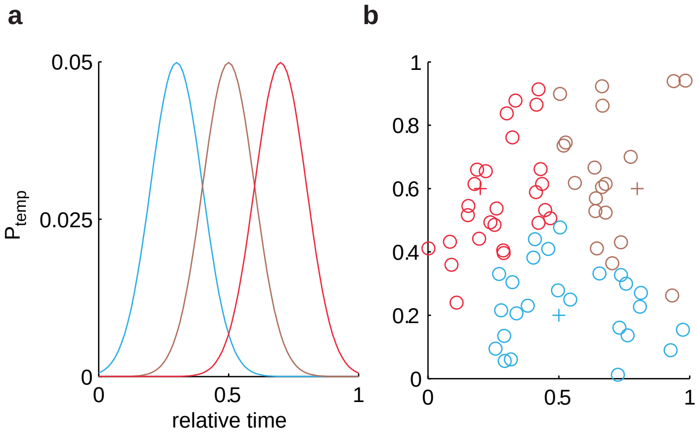

Figure 9: **a**, Temporal dependence P_{temp} of the projection establishment depending on the time and the type of the node. Relative time was normalized in that 0 stands for the beginning of the development and 1 for the end of network growth. The three seed nodes had different time windows which were partially overlapping. **b**, 2D projection of node positions. The color represents the time window corresponding to one of the three seed nodes (+).

Therefore, I introduced a different factor that can ensure the occurrence of multiple clusters: *time windows* for development. In addition, time windows have been found during cortical development (Rakic, 2002). The formation of many cortical areas overlaps in time but ends at different time points with highly differentiated sensory areas (e.g., area 17) finishing last. Based on this finding, we explored a wiring rule by which network nodes were most likely to be connected if they developed during the same time window.

I used the following algorithm for growth depending on distance as well as time windows (cf. Fig. 9a). First, three seed nodes were placed at spatially distant locations (cf. Fig. 9b). New nodes were placed randomly in space. The time window of the new node was the same as that of the nearest seed node as it was assumed to originate from this node. Second, the new node u established a connection with an existing node v with probability $P(u,v) = P_{temp}(u) * P_{temp}(v) * P_{dist}(u,v)$. Third, if no connections were established, the node was removed from the network.

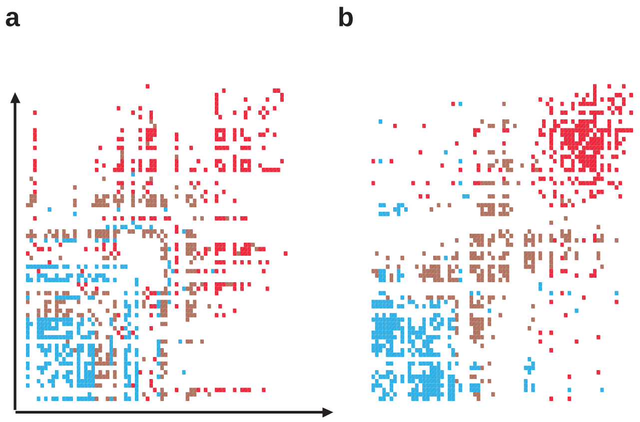

Figure 10: **a**, Timed adjacency matrix. **b**, Clustered adjacency matrix

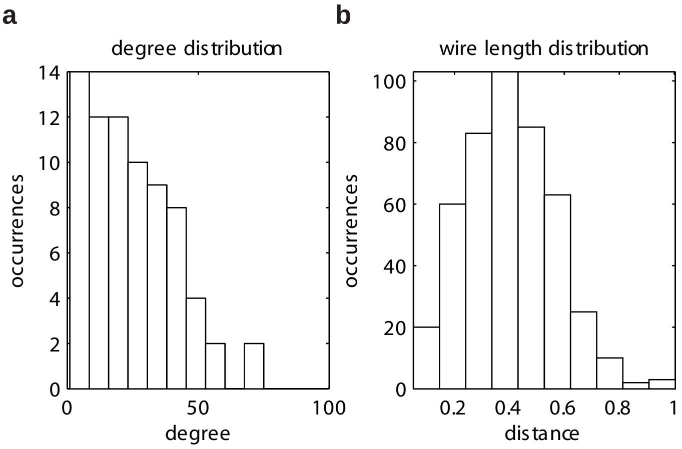

Figure 11: **a**, Whereas most nodes had fewer than 30 (incoming or outgoing) connections, also highly connected nodes did exist. **b**, Distribution of 'fiber' lengths in the generated networks. Long-distance connections also occurred.

The timed adjacency matrix shows the development of connections over time (Fig. 10a). Different colors represent the time-window of the nodes. The reordered matrix represents the same network in such a way that nodes with similar connectivity were placed nearby in the adjacency matrix (Fig. 10b). The resulting network exhibited both long-distance connections and highly connected nodes (Fig. 11). Using time windows generated defined clusters depending on the number of different time windows that govern development. In addition to the number of clusters, the size of clusters could be varied changing the width of the corresponding time window.

In conclusion, spatial growth and time windows can represent various global network properties as well as the general cluster architecture. Although having similar general properties, the time window approach remains preliminary. More information about cortical time windows and the positions of clusters in the cortex has to be included in order to compare the simulation results with the existing cortical network.

4 Discussion

I have proposed a different kind of spatial-growth mechanism, incorporating both limited and virtually unlimited growth, that can produce a variety of metric real-world networks. The metric is not limited to Euclidean space as in the discussed examples, but may also use measures of similarity to define the link probability e.g., social relations (Watts et al., 2002).

Spatial limits seem to occur in biological networks, as the skull limits neural growth at the network border and in the cell different reaction compartments (mitochondria, ER, cell core) and distant positions of proteins in the membranes limit the interaction of molecules. Furthermore, it has been shown, that the spatial separation of molecule interaction is critical in the early chemical evolution of metabolic pathways (Szabó et al., 2002).

Also in artificial networks such as the Internet, and transportation networks the spatial distance limits edge formation. Moreover, borders can exist, as undersea connections are much more expansive (and therefore unlikely) than overland connections with the same distance. These geographic borders like sea, mountains, deserts and so on can limit network growth resulting in a higher clustering coefficient and density of the network and might be the reason for small-world properties.

In contrast to previously studied spatial graphs (Watts, 1999), networks generated by our model were always connected. Moreover, the approach was able to generate small-world graphs, which is thought not to be possible in the spatial graph model in which positions are chosen randomly before edge formation (Watts, 1999). Finally, the model was also able to produce scale-free networks with relatively low maximum degree, similar to, for example, the German highway system. A systematic evaluation of model parameter space was carried out at the specific network size of 100 nodes, which was feasible computationally. It would be interesting to also evaluate larger or smaller network sizes and to investigate for them, if small-world networks can be generated in a larger range of parameters α and β.

A model with three distinct classes of nodes and different time windows resulted in three clusters in the wiring architecture. Therefore, multiple clusters may arise from spatially distributed origins for spatial growth development as well as different time windows for establishment of connections.

In conclusion, I have presented a network growth algorithm which is able to yield networks with high correlation coefficient and low ASP as found in small-world networks by using borders for network growth. Moreover, the clustering coefficient remains independent from the network size as found e.g. for metabolic networks (Ravasz et al., 2002). I was also able to show that scale-free spatial networks can be generated *without* preferential attachment, only relying on the distance between two nodes. The generated scale-free network was found similar to the linear German highway systems and could be applied to other systems which are scale-free and unclustered.

Acknowledgment

I am grateful for critical comments on this manuscript by Dr. Claus C. Hilgetag. This work was financially supported by a fellowship of the International University Bremen as well as a PhD fellowship from the German National Academic Foundation (Studienstiftung des deutschen Volkes). Part of this report has already been published (Kaiser and Hilgetag, 2004a; Kaiser and Hilgetag, 2004b; Sporns et al., 2004).

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