

Spatially Embedded Dynamics and Complexity

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To gain a deeper understanding of the impact of spatial embedding on the dynamics of complex systems, we use a measure of interaction complexity developed within neuroscience using the tools of statistical information theory. We apply this measure to a set of simple network models embedded within Euclidean spaces of varying dimensionality to characterize the way in which the constraints imposed by low-dimensional spatial embedding contribute to the dynamics (rather than the structure) of complex systems. We demonstrate that strong spatial constraints encourage high intrinsic complexity and discuss the implications for complex systems in general.
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1. INTRODUCTION

From its outset, complexity science has concentrated on how simple properties can give rise to complex organization and behavior. The interplay between, inter alia, nonlinear, local interactions, physical constraints, noise, and processes of copying or competitive exclusion has been shown to give rise to self-organization, autocatalysis, path dependence, and emergent behavior in many different ways [1, 2]. Most real-world complex systems are spatially extended systems. For example, nervous systems, ecologies, economies, cities, etc., all exhibit multiple scales of spatial organization. The impact that this spatial embedding has on

the behavior of these systems is not well understood. In particular, the role of spatial constraints in influencing the ability of these systems to exhibit organized behavior is an open question.

It is clear that projecting a system of interacting elements into a low-dimensional space such that interactions tend to occur only between elements that are near to one another must restrict the possible ways in which the system elements can be “connected.” This restriction might be viewed as a frustrating constraint that prevents, or at least mitigates against, useful kinds of organization that rely upon “long-range” connections. However, embedding a system’s interactions within a space also imposes potentially useful local correlations and symmetries on its organization “for free.” In fact, studies show that spatial embedding of this kind can predispose systems to exhibit behavior that would otherwise be unstable [3, 4]. Might the constraints imposed by low-dimensional spatial embeddings actually be critical to enabling complex

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systems to arise and persist? This notion casts spatial constraints as potentially “enabling” rather than frustrating, in that they might naturally steer or bias a system’s organization in a potentially useful fashion [5].

Here, we are interested in the relationship between spatial constraints, network topology, and interaction complexity, an information–theoretic measure developed to characterize the way in which both vertebrate and invertebrate nervous organization might influence nervous function [6]. Before we introduce this measure, we first briefly describe some examples of the way in which space can influence network dynamics. By applying an approximation of the interaction complexity measure to a simple spatially embedded network and varying the dimensionality of the space, we characterize and explain the relationship between the structural properties conferred by spatial embedding and any attendant influence on interaction complexity. We conclude with a discussion of the implications for complex systems in general.

2. NETWORKS IN SPACE

The recent explosion of interest in the “new science of networks” [7–9] has focused attention on the application of graph–theoretic approaches to the characterization of natural and engineered systems. Although the influence of space was at least implicit in certain of the first graph structures discussed and used in this literature, its contribution has only started to be systematically explored relatively recently [10, 11].

For instance, Stanley Milgram’s now infamous demonstration of the “six degrees of separation” that apparently link members of society to each other through mutual acquaintance relies upon space [12]. The instruction to each of Milgram’s experimental subject was to deliver a package to a person identified only by name and place of residence. Subjects were thus clearly required to combine their social and geographical knowledge to meet this challenge. The role of spatial knowledge and the spatial structure of social networks is not often recognized in discussion of the surprisingly short routes that the successfully delivered packages took.

Here, we wish to explicitly explore the relationship between spatial embedding and the properties that it confers on both the network topology of complex systems and their consequent behavior. Several modeling studies suggest that this relationship may be significant. We describe two below.

Boerlijst and Hogeweg [3] demonstrate the power of spatial embedding in their model of molecular self-organization in “hypercycles” [13]. A hypercycle comprises a set of molecular species, where each species supports the persistence of some of the others and, in total, they achieve the persistence of the entire set. Although such organizations appear to offer a route by which persistent cooperative collaboration might arise spontaneously, such organizations can be parasitized by free-riding molecular species that benefit from

interacting with some member(s) of the hypercycle, but do not support the hypercycle’s persistence in return. In Boerlijst and Hogeweg’s model, parasitization of this kind destroyed hypercycles when the population was well mixed (i.e., non-spatial). When the same system of molecular species was embedded within a lattice such that individual molecules could only interact with their close spatial neighbors, the hypercycles that arose were spatially organized as rotating spirals and were also able to resist parasites.

Di Paolo [4] shows the importance of spatial embedding for complex organization in a somewhat different context. He shows that an altruistic behavior is unstable in a well-mixed nonspatial model: exploitation quickly undermines any tendency toward cooperation. However, the same altruistic behavior is prevalent in the same model when individuals are distributed across a two-dimensional continuous plane. When their interactions are spatially constrained, individuals spontaneously organize into clusters of altruistic individuals, each surrounded by an annulus of non-altruists.

In both of these studies, systems were able to achieve a sophisticated mode of functional organization only when they were embedded within a low-dimensional space. No such organization could persist when the system’s components were entirely well mixed and its interactions were, as a consequence, unconstrained. What of systems that lie between these two extremes? The notion of exploring systems that lie between order (e.g., a lattice) and disorder (e.g., a random graph) is familiar within complexity science since complexity measures typically seek to capture the nature of systems that are neither completely random nor completely regular. A familiar rhetorical device is taken from the statistical mechanics of gases and crystals. Although the low-level organization of a gas can be idealized as random and that of a crystal can be idealized as regular, the aggregate behavior of each is readily derivable. For intermediate systems at the phase transition between solid and fluid, however, this relationship is less clear. Complexity, it is claimed, exists in this middle ground between order and disorder [2].

Here, we explore the behavior of systems that lie between the two extremes reported by Di Paolo and Boerlijst and Hogeweg by relaxing the constraints imposed by spatial embedding through increasing the dimensionality of the metric space within which the network nodes are located. As the dimensionality increases (while the density of connections is held constant) the spatially imposed correlations amongst the system’s interactions diminish, until, in the limit of an infinite dimensional space, a random, uncorrelated graph is achieved, equivalent to a well-mixed system.

Because we are interested in the complexity of the interactions between the elements described by such a network, rather than the structure of the network itself, we use a measure of interaction complexity developed within neuroscience and described in the following section.

3. INTERACTION COMPLEXITY

Central to cognitive processing within the nervous system is the ability of the brain to integrate distributed information to produce coherent cognitive behavior. For example, information from audio, visual, and olfactory input must be successfully integrated and used to inform subsequent motor output [6]. In contrast, a great deal of experimental work demonstrates that separate neural regions are specialized and hence quasi-independent. For instance, in the mammalian brain, different neural areas are functionally specialized for detection of visual attributes such as shape, motion, and color.¹ Neural systems must balance this functional segregation at the level of neural modules with the requirement for functional integration at the level of the organism. Tononi et al. [6] proposed an interaction complexity measure that captures this tension within a single metric.

In this article, we will refer to this measure as TSE complexity. We describe it as a measure of interaction complexity because it is principally concerned with capturing the nature of the interactions amongst parts of a system rather than the static structure of the system, per se. Despite being conceived within a specific neuroscience context, TSE complexity has received widespread attention across the behavioral and brain sciences, from fields as diverse as autonomous robotics [17], neural imaging [18, 19], local dynamics of the mammalian brain [20], and the exploration of theories of sleep, consciousness, and schizophrenia [21].

TSE complexity is derived (see Refs. 6, 22, 23, and 24) by considering an isolated set of n “neural components” (nodes for brevity) and a stationary multivariate stochastic process $\mathbf{X}(t) \equiv \{X_i(t) \mid i = 1, \dots, n\}$ running on the system, where $X_i(t)$ is to represent the activation state at time t of the i th node. First, the integration associated with the system is introduced:

$$\mathcal{I} \equiv \sum_{i=1}^n H_i - H, \quad (1)$$

where H denotes the entropy $H(\mathbf{X}(t))$ of the full process $\mathbf{X}(t)$ and H_i the entropy $H(X_i(t))$ of the individual activation $X_i(t)$. Note that by stationarity these quantities and hence \mathcal{I} itself do not depend on time t . \mathcal{I} may be interpreted as a measure of the deviation from independence of the individual components of the system. TSE complexity is then defined to be:

¹It is interesting to note that neuroscientists have been convinced that spatial organization of this kind is implicated in the complexity of neural behavior since the first staining technologies began to reveal the structure of animal brains [14, 15] and that spatial constraints have recently been invoked to account for the circuit complexity of cortical structures [16].

$$C \equiv \sum_{k=1}^{n-1} \left(\frac{k}{n} \mathcal{I} - \langle \mathcal{I} \rangle_k \right) \quad (2)$$

$$= \sum_{k=1}^{n-1} \left(\langle H \rangle_k - \frac{k}{n} H \right), \quad (3)$$

where $\langle \cdot \rangle_k$ denotes an average over all subsystems of size k . In the special case where the $\mathbf{X}(t)$ are multivariate Gaussian, the entropy H may be expressed simply in terms of the $n \times n$ covariance matrix $\Omega \equiv \overline{\mathbf{X}(t)^\top \mathbf{X}(t)}$, where the overbar represents an average over the statistical ensemble [25]. Again, by stationarity Ω does not depend on time t . We then have $H = \frac{1}{2} \ln([2\pi e]^n |\Omega|)$ so that:

$$C = \frac{1}{2} \sum_{k=1}^{n-1} \left(\langle \ln |\Omega| \rangle_k - \frac{k}{n} \ln |\Omega| \right). \quad (4)$$

Like other notions of complexity, this measure is low when either all elements are independent and hence completely segregated or the system is completely integrated. Complexity is maximal in a system that is globally integrated at the level of large subsystems but simultaneously exhibits a high degree of segregation between smaller subsystems.

Tononi et al. [6] considered an $n \times n$ connectivity matrix, C , where C_{ij} is to be interpreted as the weight on the connection from (efferent) node i to (afferent) node j , and a linear regressive neural process $\mathbf{X}(t)$ driven by uncorrelated Gaussian noise. However, there is an error in their calculation of the covariance matrix. In Ref. 26, this error is corrected via introduction of the continuous-time multivariate Ornstein-Uhlenbeck process [27]:

$$d\mathbf{X}(t) = -\mathbf{X}(t) \cdot (I - C) dt + d\mathbf{W}(t), \quad (5)$$

where I is the identity matrix and $\mathbf{W}(t)$ a multivariate Wiener process with identity covariance matrix.² Equation (5) may be viewed as a linearized, noisy continuous-time recurrent neural network (CTRNN) with I corresponding to a leak current term [28–30]. $\mathbf{X}(t)$ will then be multivariate Gaussian so that (4) applies. The condition for stationarity of (5) is shown to be:

$$\Re(\lambda) < 1 \text{ for every eigenvalue } \lambda \text{ of } C \quad (6)$$

and the covariance matrix Ω is shown to satisfy:

$$2\Omega = I + C^\top \Omega + \Omega C. \quad (7)$$

²Note that the noise input to different nodes is uncorrelated. If we allow noise levels to differ per node, then we may recover an equivalent equation to (5) by a simple linear transformation of the connectivity matrix and a rescaling of activation levels.

Several subsequent statistical measures derived from information theory have attempted to quantify properties analogous to complexity. These include information integration and causal density. Information integration, ϕ , is defined as the effective information across the bipartition of a network that exhibits the least mutual information [31] and has been extended recently [32]. Here, a balance between integration and segregation is captured as the lower bound of the potential for a system to integrate information. In contrast, although causal density [33] also has its foundations in information theory, it is developed from the notion of Granger causality [34] rather than mutual information. Granger causality is a statistical measure of causality in which a causes b if knowledge of the history of a helps predict the future of b more than knowledge of the past of b alone. Causal density is calculated as the fraction of interactions among elements that are Granger causally significant. Again, like TSE complexity, it is argued that high causal density indicates the presence of globally integrated but dynamically independent elements [35].

Despite their wide application, a comprehensive understanding of the behavior of these measures and how they relate to one another has yet to be established. Initial work in this vein considering the relationship between network structure, dynamics, and complexity is reported in Refs. 26, 36, and 37.

4. A SIMPLE MODEL

Here, we explore ensembles of spatially constrained networks each constructed over 128 nodes distributed uniformly in hypercubes of various dimensionality, varying the length scale of the interaction between the nodes. It is worth noting that to control for the average distance between nodes varying with the dimensionality, d , of the hypercube within which they are embedded, we preserve the average magnitude of spatial relationships between pairs of nodes by scaling all distances by $1/\sqrt{d}$. We use continuous-valued connection matrices to represent weighted connections between pairs of nodes given by $\omega_{ij} = \exp(-|\mathbf{r}_j - \mathbf{r}_i|/\sigma)$, where $|\mathbf{r}_j - \mathbf{r}_i|$ is the distance between nodes i and j . Connection weights between pairs of nodes thus fall off exponentially with distance at a rate which is defined by the interaction length, σ .

Figure 1 shows how complexity, \mathcal{C} , varies with the log of the interaction length, $\log_{10}(\sigma)$. The first point to note is that for low-dimensional spaces, complexity rises and falls with interaction length.³ As the dimensionality of the space increases and the strength of spatial constraints weaken,

³As the covariance matrix of a 1- d lattice is of Gaussian Toeplitz form, this agrees with previous results demonstrating that scaling in such matrices is associated with a rise and fall in complexity [6].

peak complexity is reduced, until the contribution of space disappears.

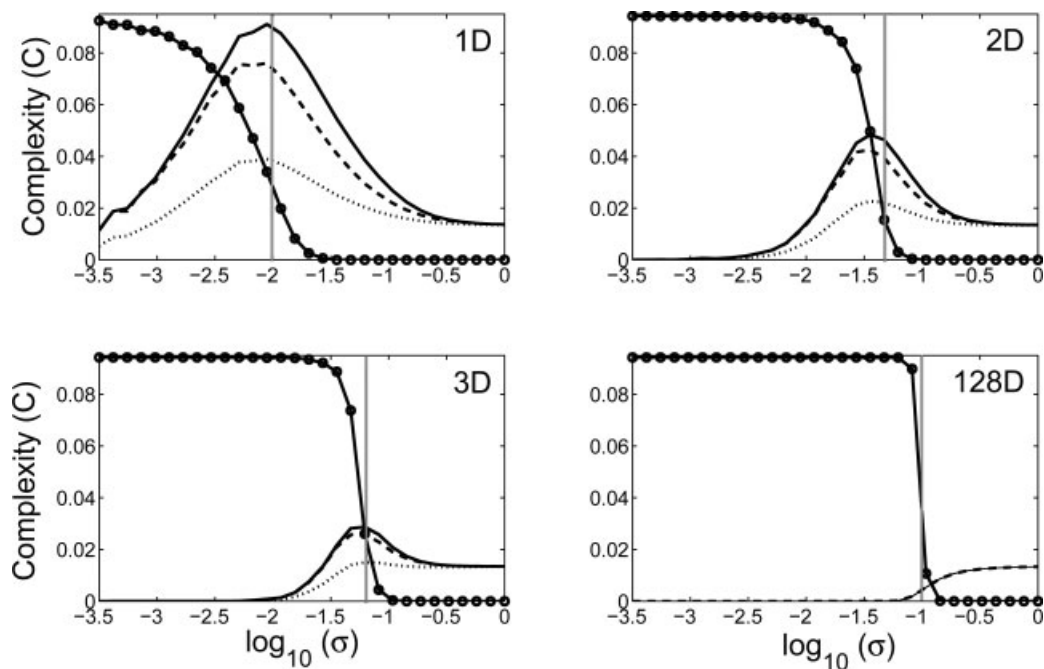
Consider first the case of nodes embedded in a low-dimensional space. Where σ is very small, even the closest nodes are far enough apart that the weighted connection between them is of negligible strength. Consequently, the network comprises a number of effectively isolated units with low interaction complexity because of the lack of network integration. As the interaction length increases, connection weights between nearby nodes begin to increase, and islands of strongly connected nodes are obtained. As a consequence, interaction complexity increases. Eventually, interaction length increases to the extent that all network nodes are close enough to each other to be strongly connected. Although the dynamics on such a network are strongly integrated at the level of the whole, interaction complexity is low because there is little or no functional segregation at the level of the parts.

Each plot in Figure 1 also presents values of complexity for two null models in which some aspect of the spatial structure inherent in the original spatially embedded networks is extinguished. In this way, we are able to decompose the contribution of spatial embedding to a network's interaction complexity. First, dotted lines represent the complexity of networks in which each node retains the same distribution of afferent connection strengths as in the original network, but these weighted connections are randomly assigned rather than determined by spatial proximity. To achieve this, the entries of each row in the original weight matrix are shuffled, preserving the values of a node's afferent weights (and their sum) but assigning them at random to the population of nodes. Dashed lines represent the complexity of networks generated by a second null model in which the connection strengths of the original spatial networks are shuffled as before, but in a manner that preserves reciprocity (i.e., $\omega_{ij} = \omega_{ji}$). Should a shuffle swap matrix element ω_{ij} with $\omega_{i'j}$, we must also swap elements ω_{ji} and $\omega_{j'i}$. It is worth noting that in this case the sum of the magnitude of the afferent weights may not be preserved.

To a significant degree, the effect of spatial organization on complexity is clearly accounted for by the reciprocal nature of spatial interactions (and to a larger degree than the mere distribution of afferent weights). However, particularly in low dimensions, the impact of spatial constraints exceeds that of mere reciprocity, suggesting that higher order structures are significant (see Ref. 26 for a complete account).

Why do we see a peak in complexity at a particular length scale for each value of d ? In fact, this peak coincides with a particular degree of network "connectance." To demonstrate this, we discretize each weighted, spatially embedded network, by reinterpreting each entry in the weight matrix as the probability that a pair of nodes will be connected with a weight equal to unity. In this way, each continuous matrix can be mapped to an ensemble of binary networks from which a

FIGURE 1



Plots of complexity versus the log of the interaction length, $\log_{10}(\sigma)$, for networks embedded within 1-d, 2-d, 3-d, and 128-d hypercubes. All networks comprise $N = 128$ nodes, with 30 networks being generated for each data point. Solid curves represent the mean complexity, \mathcal{C} , of spatially embedded systems with continuous weights varying inversely with distance. Dotted and dashed lines indicate the complexity of networks derived from two null models in which aspects of spatial organization are extinguished (see text). Gray vertical lines mark the peaks of complexity for discretized networks with the same interaction length, which agree well with the peak in complexity for the associated continuous system. The scaled number of discretized network components is also presented (circles), falling from N (a totally disconnected system) to unity (a supercluster).

random sample can be drawn and their properties calculated. For each binary network, we enumerate the number of disconnected network components (isolated fragments of network). As this value falls to unity with increasing σ , the graph is becoming completely connected, indicating the onset of a single giant component or supercluster [38, 39]. Figure 1 shows that maximal complexity coincides with the onset of this giant component in the binary ensembles. The gray vertical line also indicates that maximal complexity of the binary networks themselves agrees with that of the continuous weighted networks from which they are derived. These results suggest that complexity is associated with the achievement of a single strongly coupled component in a continuous network. Furthermore, the interaction length required for onset of the strong component (and thus high complexity) increases with increasing spatial dimensionality.

5. DISCUSSION

The results reported here demonstrate that spatial constraints on connectivity contribute directly to interaction complexity. A network comprising a uniform random distribution of locally connected nodes enjoys increased

complexity as a result of the strong spatial constraints imposed by a low-dimensional embedding. As these constraints are relaxed (by increasing the dimensionality of the space) or eroded (by shuffling the connection strengths), complexity falls. The pairwise reciprocity of spatial network connectivity (itself stemming from the fact that the distance from node i to node j must be equivalent to the distance in the reverse direction) is strongly implicated in the elevated complexity of spatially embedded networks, but does not entirely account for it. Rather, the property stems from spatial embedding imposing correlations at several topological scales.⁴

Interestingly, our results also suggest that high network complexity is associated with the onset of a strongly coupled supercluster. The fact that the coupling strength required for its onset is much smaller in networks embedded within

⁴We are able to show, using a graph-theoretic analysis, that the TSE complexity measure is directly dependent on the frequency of loop motifs within the network (Barnett, Buckley, and Bullock, manuscript in preparation)

low-dimensional spaces suggests that stronger spatial constraints may make high complexity achievable with fewer/weaker network connections.

Open questions that could be addressed in further work include the following. Which graph-theoretic properties of the supercluster are associated with high complexity, e.g., its size, clustering coefficient, modularity, etc? To what extent do the results presented here carry over to networks where, in general, $\omega_{ij} \neq \omega_{ji}$, but there remains an influence of spatial separation on node connectance.

6. CONCLUSION

Here, we have demonstrated that spatially constrained network topologies exhibit complexity that differs from equivalent random nonspatial graphs. We have shown how spatial structure can impact on interaction complexity via its influence on topological structure. In summary, the inherent constraints imposed on a system by projecting it into a low-dimensional space can be enabling for complexity in that these constraints predispose systems to exhibit elevated levels of complex interactivity for free.

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