Neural network function, density or geometry?

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Abstract

We consider an oriented network in which two subgraphs (modules $X$ and $Y$), with a given intra-modular edge density, are inter-connected by a fixed number of edges, in both directions (nodes in $X$ to nodes in $Y$, and conversely). We study the adjacency spectrum of this network, focusing in particular on two aspects: (1) the changes in the spectrum in response to varying the intra and inter-modular edge density, and (2) the effects on the spectrum of perturbing the edge configuration, while keeping the densities fixed.

Since the general case is quite complex analytically, we adopted here a combination of approaches that allowed us to formally understand some simpler particular cases, and numerically simulate some general results. After investigating the behavior of the mean and standard deviation of the eigenvalues, we conjectured the robustness of the adjacency spectrum to variations in edge geometry, when operating under a fixed density profile. We remark that, while this robustness increases with the size $N$ of the network, it emerges at small sizes, and should not be thought of as a property that holds only in the large $N$ limit. We argue that this may be helpful when studying applications on small networks of nodes (such as small brain macro-circuits).

We interpret our results in the context of existing literature, which has been placing increasing attention to random graph models, with edges connecting two given nodes with certain probabilities. Based on similar analogies, we carry out a large $N$ limit comparison between our network and a classical probabilistic model described in a recent paper by Narakuditi and Newman. We discuss whether / how properties such as Wigner’s semicircle law, or effects of community structure, still hold in the context of a model which is density based, rather than probability based.

Finally, we suggest possible applications of the model to understanding synaptic restructuring during learning algorithms, and to classifying emotional responses based on the underlying adjacency configuration of the emotion-regulatory neural circuit. In this light, we argue that future directions should be directed towards relating such underlying hardwiring to the temporal behavior of the network as a dynamical system. Understanding the effects of configuration on coupled dynamics in a system in which each node is a nonlinear oscillator is of great importance for a wide variety of applications.

**Keywords:** random matrix, oriented graph, edge density, eigenvalue spectrum, robustness.
1 Introduction

Eigenvalues of graphs are useful for controlling many graph properties and consequently have numerous algorithmic applications. Many studies have examined random graphs with a general given expected degree distribution, and established bounds or other descriptions/estimations of their adjacency spectra. While it is well known that the largest eigenvalue of such an adjacency matrix is determined by the maximum degree of the graph \(m\), and the weighted average of the squares of the expected degrees \(\langle d \rangle\) [4], recent work on random matrices has delivered more accurate estimates. For example, Chung et al. [3] have investigated an ensemble of random uncorrelated, undirected networks, and found that, in the large \(N\) limit, the expected largest eigenvalue is determined by the ratio of the second to first moment of the average degree distribution \(\langle d^2 \rangle/\langle d \rangle\), together with the expected largest degree \(d_{\text{max}}\). More generally, for directed (oriented) networks without edge degree correlations, a first order approximation to the leading eigenvalue is given by \(\langle d_{\text{in}}d_{\text{out}} \rangle/\langle d \rangle\), where \(d_{\text{in}}\) and \(d_{\text{out}}\) are respectively the in and out-degrees of the graph, and \(\langle d_{\text{in}} \rangle = \langle d_{\text{out}} \rangle = \langle d \rangle\) [17].

It is thus clear that the edge in/out degrees, as well as their correlations, have crucial effects on the leading eigenvalue. In general, a graph’s defining feature is its distribution of edges. Among other properties, edge density, edge clustering, presence of hubs, have been intensely studied. Detecting and interpreting the modularity of a network (i.e., the presence of community structures within the graph, defined as densely connected groups of nodes, with sparser inter-group connections) has been recently of particular interest. Whether the graph represents the architecture of a web network or that of a neural circuit, the structure of a dynamic disease system or of a social group of friends, modularity reflects into adjacency properties of the network, thus modulating its structural and functional properties, and implicitly controlling the temporal behavior of the system.

In this study, we focus on understanding the spectral properties of a particular type of networks. We consider oriented graphs with two subgraphs \(X\) and \(Y\), each composed of \(N\) nodes. Within both \(X\) and \(Y\), the intra-modular edge density is fixed to a fraction \(\gamma\) (out of the possible maximum of \(N^2\)). The density of the \(X\)-to-\(Y\) edges is fixed to a fraction \(\alpha\) of the \(N^2\) possible \(X - Y\) connections, and the density of the \(Y\)-to-\(X\) edges is fixed to \(\beta\) of the \(N^2\) possible \(Y - X\) connections. Throughout the paper, we will use the term “modules” for \(X\) and \(Y\) (and not the more common term of “communities,” since the latter has been used in literature in the context where the probability of two nodes within the same community to be connected by an edge is higher than for two arbitrary nodes which are not. In contrast, our \(\alpha, \beta\) and \(\gamma\) take any values of the form \(\frac{k}{N^2} \in [0,1]\), where \(k\) is a positive integer \(\leq N^2\) (allowing the cases \(\gamma < \alpha, \beta\)). In this setup, when \(\gamma = 0\) the modules are totally disconnected, and when \(\gamma = 1\) the modules are fully connected (cliques).

This graph structure may be regarded, for example, as a schematic architectural representation of a neural circuit. In the Discussion, we revisit an existing application, in which \(X\) and \(Y\) represent the excitatory, respectively inhibitory modules of a neural feedback loop, so that \(X\) projects to \(Y\) through \(\alpha\) excitatory connections, and \(Y\), in turn, modulates \(X\) through \(\beta\) feedback, inhibitory connections. In such a circuit, the overall connectivity density may remain constant during a cognitive process such as learning, even though the network may exhibit high plasticity, and constantly inspect a variety of edge geometry combinations. Throughout the process, some connections may be lost, while others appear, as part of a “synaptic probing” process which has been empirically observed and is still being studied.

The adjacency matrix of such an oriented graph is a \(2N \times 2N\) binary block matrix of the form:

\[
T = \begin{bmatrix}
S & A \\
B & R
\end{bmatrix},
\]

where the blocks \(S\) and \(R\) have fixed edge density \(\gamma\), while \(A\) and \(B\) have fixed edge densities \(\alpha\) and \(\beta\), respectively. We study the spectrum of eigenvalues of this matrix, with a particular focus on understanding how these eigenvalues are perturbed (a) when changing the density profile \((\alpha, \beta, \gamma)\) and (b) when changing only the edge distribution, while keeping densities fixed. We use a combination of analytical and numerical methods to understand the statistics (mean and standard deviation) of this
adjacency spectrum.

Our work is organized as follows. In Section 2, we focus on the particular case of two interconnected cliques, \( \gamma = 1 \) (as used in our previous modeling work). In Section 3, we generalize the connectivity scheme to relax the requirement of full connectedness of the modules (\( \gamma \leq 1 \)), and we analyze how the robustness of the spectrum changes under this relaxation. In Section 4, we put our results in the context of the existing work on eigenspectra of random graphs. We also discuss the possible significance of our results in learning and neural dynamics; as an example, we revisit an application previously worked out, in which different brain connectivity patterns reflected into different power law behavior of the neural signals, and translated into different types of emotional processing. We finally propose exploring the idea of overlaying nonlinear dynamics on this hard-wired structure, so that the nodes of the graph are coupled oscillators.

## 2 Two interconnected cliques

We first consider the case in which the modules are fully-connected (cliques, see Figure 1). This means that the diagonal blocks of the adjacency matrix \( T \) are \( S = R = M \) (where \( M \) is the appropriate size matrix with all entries equal to one). The off-diagonal \( N \times N \) blocks \( A \) and \( B \) are random binary matrices, with fractions \( \alpha \) and respectively \( \beta \) of ones. By discussing the effects of *edge density* we mean analyzing how the spectrum of \( T \) changes when the values of \( \alpha \) and \( \beta \) are varied; we will represent these changes in the form of surface plots with respect to pairs \((\alpha, \beta) \in [0,1]^2\). By discussing the effects of *geometry* we mean understanding the effects on the spectrum of the edge distribution, under the constrain of fixed densities \( \alpha \) and \( \beta \), respectively. We will measure these effects by estimating the mean and standard deviation of the eigenvalues of \( T \) over the edge geometries permissible by any fixed density pair \((\alpha, \beta)\).

![Figure 1: Schematic representation of the network for \( N = 5 \) nodes per module. Module X is shown on the left; module Y is shown on the right; they are both fully-connected, local sub-graphs of the full network. The dotted red arrows represent the X–Y connections, and the dotted blue arrows represent the Y–X connections, all generated randomly for low connectivity densities of \( \alpha = \beta = 0.25 \), to maintain clarity of the illustration.](image)

**Definition 2.1.** For fixed \( 0 \leq \alpha, \beta \leq 1 \), we call \( \mathcal{D}^{\alpha,\beta} \) the distribution of \( 2N \times 2N \) adjacency matrices \( T \) with densities \( \alpha \) and \( \beta \), respectively. We call \( \mathcal{L}^{\alpha,\beta} \) the corresponding distributions of each of the eigenvalues \( \lambda_j \) of \( T \) (with \( j = 1, 2N \)).

It is easy to see that the cardinality \(|\mathcal{D}^{\alpha,\beta}| = C_{N^2}^{\alpha N^2} C_{N^2}^{\beta N^2} \). While in general the exact eigenvalues of \( T \) depend on the representative \( T \in \mathcal{D}^{\alpha,\beta} \) (i.e., on the actual exact positions of the 1’s within the blocks \( A \) and \( B \)), we notice the following two boundary results (i.e., for \( \alpha \) or \( \beta \) in \( \{0,1\} \)):

**Lemma 2.2.** Fixing \( \alpha = 1 \) fixes the eigenvalues of \( T \), so that \(|\mathcal{L}_j^{1,\beta}| = 1 \), for all \( j=1,2N \) (i.e., the eigenvalue distributions are all trivial for \( \alpha = 1 \). More precisely, the eigenvalues of any \( T \in \mathcal{D}^{1,\beta} \) are given by
When \( \beta = 1 \), the eigenvalues of any \( T \in \mathcal{D}^{\alpha,1} \) are given by \( \lambda_1 = N + N\sqrt{\alpha} \), \( \lambda_2 = N - N\sqrt{\alpha} \), and \( \lambda_3 = 0 \) (with multiplicity 2\( N - 2 \)). Similarly, for \( \beta = 0 \), the eigenvalues of any \( T \in \mathcal{D}^{\alpha,0} \) are given by \( \lambda_1 = N \), \( \lambda_2 = \ldots = \lambda_{2N} = 0 \) (with multiplicity 2\( N - 1 \)).

Proof. Similar to that of Lemma 2.2.

When \( \alpha, \beta \neq 1 \), the distributions \( \mathcal{L}^{\alpha,\beta}_j \) are no longer trivial. If we restricted our interest to finding only the leading eigenvalue of the matrix \( T = \begin{bmatrix} M & A \\ B & M \end{bmatrix} \), there are a variety of existing tools that we could use to assist us (power method, graph Laplacian). However, even the computations involved in a task such as expanding the powers \( T^k \) (equivalent to finding all paths of length exactly \( k \) in the graph) become very complex quite fast (see Appendix). It is in this light that, from this point on, we will proceed numerically to support a few conjectures.

Our goal is to obtain descriptions of \( \mathcal{L}^{\alpha,\beta}_j \) for values of densities \( \alpha, \beta \in (0,1) \); in particular, we want to estimate their means and standard deviations, and observe how these depend on the values of \( \alpha \) and \( \beta \).
and on the size $N$ of the network. For small network sizes ($N \leq 4$), the mean and standard deviation of the entire distribution $\mathcal{L}^\alpha_\beta$ can be computed directly, for each $\alpha$, $\beta$ and $j$ (see Figure 2a and b). However, for larger values of $N$, inspecting of the whole distribution becomes computationally very expensive (e.g., for $N = 5$, we have $|D^{0.48,0.48}| = (C_{45}^{12})^2 \sim 10^{13}$ configurations, although some will produce identical spectra). So, for larger $N$s, we inspected instead only a sample $\mathcal{S} \subset D^\alpha_\beta$ (we considered $|\mathcal{S}| = 50 \times 50$, or $|\mathcal{S}| = 100 \times 100$ configurations of $T$ in $D^\alpha_\beta$), and estimated the means and standard deviations based on this sample (see Figure 2b and c for a comparison between the whole-distribution and a sample-based results for $N = 3$).

![Figure 2](image)

**Figure 2:** Expected spectrum and variation of leading eigenvalue for $N = 3$, as functions of the densities $\alpha$ and $\beta$. **A.** Means of the eigenvalue magnitudes, calculated formally over all $T \in D^\alpha_\beta$ (i.e., over all possible combinatorial configurations of the blocks $A$ and $B$), for each given pair of densities $(\alpha, \beta)$. **B.** Standard deviations of the eigenvalue magnitudes, also calculated formally over all possible combinatorial configurations. **C.** Standard deviations of the eigenvalue magnitudes, calculated using a sample of 50 representative matrices for $A$, and 50 for $B$, for each given pair of densities $(\alpha, \beta)$.

### 2.1 Estimating the large eigenvalue means

There are a few contexts in the literature on eigenspectra of random graphs that relate to our problem, among which a known result due to Juhász [11]. Viewed in the reference’s general framework, the adjacency matrix $T$ is a block matrix with (weighted) density matrix $D = \begin{bmatrix} 1 & \alpha \\ \beta & 1 \end{bmatrix}$, whose eigenvalues are $\mu_{1,2} = 1 \pm \sqrt{\alpha \beta}$. According to the main theorem in the referenced paper, $T$ has 2 eigenvalues that are large in absolute value (of order $N$), with: $\lambda_{1,2} = N \pm N \sqrt{\alpha \beta} + o(N^{1/2+\epsilon})$ in probability, while the other eigenvalues are of order $o(N^{1/2+\epsilon})$ in probability (for any $\epsilon > 0$).

Based on this result, $\hat{\lambda}_{1,2} = N \pm N \sqrt{\alpha \beta}$ would be the first candidates to check, as possible expressions for the means of the two large eigenvalues of $T$ in terms of the densities $\alpha$ and $\beta$. The formula looks particularly promising, since it seems to naturally extend the boundary expressions obtained in the two lemmas for $\alpha$ or $\beta = 1$ in $\{0, 1\}$, and since it matches almost exactly the surfaces we obtained numerically for $\hat{\lambda}_{1,2}$. However, this was quickly refuted by the direct computation of the mean and standard deviation for small network sizes ($N = 3, 4$), although the formula seems to give a very close estimate, which might be exact in the limit as $N \to \infty$. This leaves us with the question of computing and/or understanding the source of the small correction terms.

### 2.2 Spectrum variance

For a fixed $N$, we noticed that, as expected, the eigenvalue distributions get thicker at intermediate values of $\alpha$ and $\beta$. Figures 2 illustrates the surface plot (with respect to $\alpha$ and $\beta$) of the standard deviation of
Figure 3: Expected spectrum and variation of eigenvalues for $N = 7$, estimated numerically by considering a sample of 50 matrices $A$ and 50 matrices $B$, for each pair of densities $(\alpha, \beta)$. A. Surface plots of expected eigenvalue magnitudes. There are two leading eigenvalues, whose surfaces are very close to the surfaces $N \pm N\sqrt{\alpha\beta}$; the other eigenvalues are close to zero. B. Surface plot of the standard deviation estimate for the largest eigenvalue, for each pair of densities $(\alpha, \beta)$. B. Surface plot of the standard deviation estimate of the second largest eigenvalue magnitude. B. Surface plot of the standard deviation estimate of the third largest eigenvalue magnitude. Following the same logic (“higher cardinality likely produces higher variance”), one would have expected the eigenvalue standard deviations to increase when the size $N$ is increased (recall that $|D^{\alpha,\beta}| = C^{\alpha N^2}_N C^{\beta N^2}_N$, which increases greatly with $N$). Juhász’ estimate seems in tune with this, allowing a correction term of magnitude $o(N^{1/2+\epsilon})$. In reality, the “widths” of $L^{\alpha,\beta}_j$ do not seem to increase as $\sqrt{N}$, but rather saturate as $N$ increases (the case of the small eigenvalues), or even narrow down (the case of the leading eigenvalue distributions). In Figures 4a,b,c we illustrate, as surface plots, the behavior of the standard deviations for the three leading eigenvalues, for $2 \leq N \leq 7$; in Figure 4d we show that the maximum standard deviation (as approximated by our algorithm) appears to be decreasing as a function of size $N$. Based on our plots, we suspect that, for any pair $(\alpha, \beta)$, the standard deviations change slower with $N$ as $N$ increases. Computing these rates, however, seems quite difficult, since the distances between two consecutive approximate surfaces are hard to estimate numerically with enough accuracy, even for small values of $N$. 
Figure 4: Illustration of the evolution of the standard deviation of the eigenvalue magnitudes, when increasing the network size $N$. A. Each surface plot represents the standard deviation, with respect to $(\alpha, \beta)$, of the leading eigenvalue of $T$, for a different size $N$, from $N = 2$ (lightest surface, top) to $N = 7$ (darkest surface, bottom). B. Each surface plot represents the standard deviation of the second leading eigenvalue magnitude, for a different size $N$, from $N = 2$ to $N = 7$ (notice that the surfaces cross each other). C. Each surface plot represents, for a different size $2 \leq N \leq 7$, the standard deviation for a small eigenvalue of $T$ (the third in magnitude, in this case). For convenience, we plot here one minus the actual value; the figure is vertically flipped, in order to make all surfaces visible. D. Illustration of how the standard deviations of the eigenvalue magnitudes evolve when the size $N$ is increased. We plot the maximum value attained on the surface corresponding to each $N$, for a few representatives of the spectrum (for the two eigenvalues large in magnitude, as well as for the third and the last in magnitude).

We summarize our theoretical and numerical observations in this case in the form of a conjecture, which remains open to a more rigorous investigation:

**Conjecture 2.4.** In the case of fully-connected modules $\gamma = 1$ (i.e., $S = R = M$), the spectrum of the matrix $T$ varies with respect to the inter-modular densities $\alpha$ and $\beta$ of the blocks $A$ and $B$ as follows:

(i) The spectrum has two eigenvalues $\lambda_1$ and $\lambda_2$ whose means are large in magnitude, while the other $2N - 2$ have means which are small in magnitude (close to zero).

(ii) For each size $N$ and each density pair $(\alpha, \beta)$, the mean magnitudes of the two leading eigenvalues (over all adjacency configurations corresponding to $(\alpha, \beta)$), are given approximately by $N \pm N \sqrt{\alpha \beta}$. 
(iii) For any size $N$, the standard deviation of each eigenvalue magnitude is a “unimodal” surface, with a point of maximum in the open square $(0,1)^2$, and which is zero when $\alpha = 0, 1$ or $\beta = 0, 1$.

(iv) As $N$ increases, the surface-maxima saturate asymptotically. The change with $N$ (difference between two consecutive maxima) decreases as $N$ gets large.

(v) For the leading eigenvalue $\lambda_1$, the standard deviation maximum is very small (one degree of magnitude smaller than the mean $\hat{\lambda}_1$, or than the corresponding maxima for the other eigenvalues). Moreover, the standard deviation of $\lambda_1$ decreases monotonically with $N$, for each fixed pair $(\alpha, \beta)$.

3 Two interconnected modules

In this section, we relax the “full-connectedness” condition for the two modules, to explore other intra-modular edge configurations.

![Illustrations of the standard deviations of the eigenvalue magnitudes for different values of inter-modular connectivity $\gamma$, for $N = 3$. A. Each surface represents the standard deviation of the leading eigenvalue, for one value of $\gamma \in [0, 1]$ (low to high surfaces, as $\gamma$ decreases). B. Cross-section of the surfaces shown in (A), for fixed $\alpha = 5/9$. C. Similar cross-sections, shown for the second leading eigenvalue. D. Similar cross-sections, shown for a small (third in magnitude) eigenvalue.](image)

In Figure 5, we illustrate the dependence of the standard deviations not only on the inter-modular edge densities $\alpha$ and $\beta$ (represented on the $x$ and $y$-axes), but also on the intra-modular density $\gamma$ (in each
panel, different plots correspond to different values of $\gamma \in [0, 1]$). In Figure 5a, we represented the standard deviations of the leading eigenvalue, for $N = 3$ and $\gamma \leq 1$, as surface plots with respect to pairs $(\alpha, \beta)$. (For better visualization of the surfaces, we omitted the boundaries $(\alpha, 1)$ and $(1, \beta)$, where the standard deviations are zero). Notice that, for pairs $(\alpha, \beta)$ close to the corner $(1, 1)$, the surfaces are (as one would expect) barely affected by the value of $\gamma$, as long as $\gamma > 0$. More generally: although the stdev surfaces do not generally exhibit the same shape and unique centrally-placed maximum as in the particular case of Section 2, the unimodality is preserved in cross-section (in Figures 5b, c and d we show such cross-sections for the first three largest eigenvalues, for $N = 3$).

As $\gamma$ decreases, the standard deviation surfaces raise higher. However, a main property appears to be preserved from the fully-connected case $\gamma = 1$ to the more general case of $\gamma > 0$: the standard deviations don’t escape to $\infty$ as $N$ increases, but are rather bounded by a fairly small upper bound (close to 1). In the case $\gamma = 0$, however, this property breaks down. It is interesting to notice that the standard deviation for the leading eigenvalue, which is very small when $\gamma = 1$, increases slowly as $\gamma$ decreases from 1, then faster as the values of $\gamma$ get close to 0; the complete crash, however, only happens at $\gamma = 0$ (also see Figure 6). In other words, the full-connectedness of the two moduli confers very high spectral robustness to the network, which is surprisingly well preserved as one loosens this condition, pruning out random edges and lowering the intra-modular density. The property is completely lost, however, when there are none of the intra-modular edges left to connect the nodes. We further interpret this in the Discussion.

Figure 6: Behavior of eigenvalues of $T$ as $\gamma$ decreases from 1 to 0. Here, $N = 3$, and $\alpha = 5/9$. In each panel: $\gamma = 1$ (panel A), $\gamma = 4/9$ (panel B), $\gamma = 2/9$ (panel C) and $\gamma = 0$ (panel D). The curves represent the expected eigenvalue magnitudes, and the error bars represent the respective standard deviations.
If the graph is the underlying hardware for a dynamical system, the local linearization (Jacobian) matrix around the system’s equilibria is likely to depend, among other parameters, on the adjacency spectrum, in particular on the separation of eigenvalues. Here, we also illustrate how the eigenvalues are separated, and how this separation if affected when using the different connectivity schemes we considered throughout this section. Figure 6 shows the means of the eigenvalue magnitudes together with the respective standard deviations, for four level of intra-modular connectivity (each panel corresponds to a different value of $\gamma$, as described below); we fixed $\alpha = 5/9$ and allowed $\beta$ to vary in each case along the $x$-axis. When $\gamma = 1$ (Figure 6a), the standard deviations are small (as shown in Section 2), and the first and second eigenvalues (whose means are well approximated in magnitude by $N \pm N\sqrt{\alpha\beta}$) remain to a large extent separated from the other small eigenvalues. As $\gamma$ decreases from 1, this situation gradually changes, and the large expected eigenvalues decay as $N\gamma \pm N\sqrt{\alpha\beta}$ (Figure 6b,c), to eventually completely collapse at $\gamma = 0$ (Figure 6d).

4 Discussion

4.1 General comments

In this study, we have investigated, using analytical and numerical computations, the adjacency spectrum of an oriented graph, in which the nodes of two modules connect though fixed numbers of randomly placed edges within each module, as well as across modules. We concluded that, when fixing the number of both intra and inter-modular edges, the adjacency spectrum of the network remains in general sufficiently robust under particular edge configurations (geometries), suggesting that simple algorithms in such a system may also remain unaffected by constrained geometry changes.

There is a very large body of work addressing properties of random matrices [23], whose entries are drawn independently out of a given (typically normal) probability distribution. If, in addition, the matrix represents the adjacency of a random graph, so that each entry equals 1 with a given probability, there are classical methods used when looking for properties of the the spectrum, such as spectral radius, or spectral density. Our model differs from most of these approaches in that it conserves the number of edges within/between modules, rather than fixing the probability of independently having an edge that connects two given nodes in the same/different modules. In our setup, the entries of the adjacency matrix are neither independent, nor identically distributed. However, while classical results (such as Wigner’s semicircle law) require the entries to be identically distributed, various extensions have been worked out, for models which don’t necessarily abide by these properties.

Consider, for example, the configuration model [8], whose spectral properties have been addressed by numerous studies. Since its edges are not statistically independent, a direct analytical approach is very difficult; existing results range from approximating the full spectrum [6], to formally deriving the expected values of the leading eigenvalue, but only in the large $N$ limit [3]. In a recent paper, Newman et al. [13] took an indirect approach: they considered instead a model with the same degree sequence as the configuration model, but in which the number of edges between any two nodes was drawn independently from a Poisson distribution. They then showed that the spectra of the two models agree in the large $N$ limit.

Below, we illustrate the same idea, by carrying out a large $N$ limit comparison between our model and a corresponding model, with independent, stochastic edges, considered by Nadakuditi and Newman [14]. In the referenced paper, they considered a stochastic, non-oriented network with two communities, and computed the ensemble-means for the two large eigenvalues of its symmetric adjacency matrix, in the large $N$ limit. The method involved first finding the eigenvalues of the modularity matrix, then showing that these are identical in the large $N$ limit to the eigenvalues of the adjacency matrix. Their asymptotic expressions $z_1$ and $z_2$ were computed in terms of $c_{in} = np_{in}$ and $c_{out} = np_{out}$ (where, with the notations in the original text, $n$ is the matrix size, $p_{in}$ is the probability of two nodes within a module to be directly connected, and $p_{out}$ is the probability of two nodes which are not in the same module to be directly connected). More precisely:
Figure 7: Comparison between our results and those of Narakuditi-Newman [14], in the case of a two modular, non-oriented graph. We compare the values of $z_1, z_2$ (solid curves in purple and brown, respectively) with the formal means $\hat{\lambda}_1, \hat{\lambda}_2$ (dotted curves in blue and green), and their close approximations $N \pm \frac{\alpha}{N}$ (solid curves in yellow and cyan). A. Comparison for $N = 4$. B. Comparison for $N = 100$; here, we used only the approximations $N \pm \frac{\alpha}{N}$, since the formal means are computationally extremely expensive.

With our notation, $c_{in} = 2N$, $c_{out} = 2\alpha/N$ and the adjacency matrix is symmetric ($\beta = \alpha$). Accounting for the absence of loops in the referenced model, which are present in ours, we get:

\[
\begin{align*}
    z_1 &= \frac{1}{2}(c_{in} + c_{out}) + 1 \\
    z_2 &= \frac{1}{2}(c_{in} - c_{out}) + \frac{c_{in} + c_{out}}{c_{in} + c_{out}}
\end{align*}
\]

so that $z_1 > z_2$ if $\alpha < N(N - 1)$. In Figure 7, we show a comparison between our results and those of Nadakuditi and Newman, when applied to two fully-connected communities, by illustrating on the same axes $z_{1,2}$, the formal means $\hat{\lambda}_{1,2}$, and their close approximations obtained earlier as $N \pm \frac{\alpha}{N}$. The approximations get exact in the large $N$ limit, at least for values of $\alpha < N^2 - N\sqrt{2N}$, where $z_1$ has its global minimum (after which it shoots up, detaching from the graph of $\hat{\lambda}_2$).

Lastly, the reference remarks on spectral distribution of the modularity matrix (i.e., in the large $N$ limit, also the spectral radius for the adjacency matrix of the non-oriented graph studied). The spectrum consisted of a continuous semicircular band of eigenvalues, plus the singular leading eigenvalue. As long as the leading eigenvalue is well separated from the semicircular band, there is evidence of community structure in the network; when the leading eigenvalue passes the edge of the band ($z = \sqrt{c_{in} + c_{out}}$), the community structure is no longer detectable. As we have already suggested in Section 3, the property extends to the case of the oriented random graph that constitutes our study case. In Figure 8 we show, for $N = 4$, a sample (100 configurations) of the spectrum, observing the separation between eigenvalues, as the modularity of the network changes. Since the adjacency matrix is no longer symmetric, the eigenvalues are plotted in the complex plane. All eigenvalues are distributed (uniformly?) within the unit disc, except
the first two largest in absolute value, which, for $\gamma = 1$, are real and significantly larger than 1. When the “community structure” decreases (e.g., $\gamma$ decreases), first the second largest eigenvalue collides into the unit disc, and starts diffusing around its boundary. If we continue decreasing $\gamma$, the leading eigenvalue will also become indistinguishable from the pool distribution.

Figure 8: Illustration of separation of eigenvalues, when changing the community structure. The eigenvalues are plotted in the complex plane: the leading eigenvalue in absolute value is shown in red, the second largest in green, the rest in blue. All plots are for $N = 4$, and are based on samples of 100 matrix configurations, under the following restrictions: A. $\alpha = 1/4$, $\beta = 3/4$, $\gamma = 1, 3/4, 1/2, 1/4$ (from top to bottom). B. $\alpha = 1/2$, $\beta = 1/2$, $\gamma = 1, 3/4, 1/2, 1/4$ (from top to bottom).

4.2 Applications to learning

In summary: while a lot is known about certain classes of random matrices (e.g., with normal, or independent entries), little is known about other types of ensembles. Normal distributions are ubiquitous in nature; however, natural processes may involve many other sources of noise and of randomness, and studying them may become equally useful.

For example, let’s imagine the oriented graph considered in this paper to represent a network of coupled neurons, so that each edge represents a synapse with a corresponding synaptic strength, or “weight” (so that the “effective connectivity matrix” of such a network would be a weighted mutation of the adjacency matrix). Synaptic updating has been known to be for a long time the physiological basis of learning, but the exact ways in which such a process is implemented biophysically are still under investigation.

There are many different models describing, qualitatively or quantitatively, the synaptic adjustments that may take place in such a network, during a process such as learning. In general, the process is suspected to involve not only weight changes of existing synapses, but also activation of “silent” sites,
creating of new connections, or pruning of the existing ones. In terms of our model, this means that not only the edge weights, but also the edge distribution might change during learning.

A clear biological restriction to this updating game has to be that the synaptic strengths are somehow prevented to increase without bound, which is why most models incorporate a normalization scheme. However, again, there is very little agreement on how this normalization step is actually implemented by the brain. Some rules assume the process to be local (subtractive normalization [15, 9, 26, 12], a weight-dependent rule [7] or a BCM rule [5]), but one can imagine various other ways of insureing stability, possibly involving “homeostasis” or “synaptic scaling” [24, 25]. Many models support a global normalization, for which the state of the whole network is assessed at each updating step, and a specific norm is imposed at each weight update.

In this light, it becomes important to understand possible normalization mechanisms for optimal weight updating. While most models of learning introduce the updates into the weights themselves, the brain may normalize (at least in the short term) by simply maintaining the overall number of active connections in the network approximately constant, so that, in the updating process, loosely one synapse will turn off whenever a new site is activated. One would then want to understand how this architectural dynamic may promote/influence learning, and how the effects of geometry updating complement or compare with the effects of direct weight updating. Let us finally note that adding or deleting edges based on a probabilistic process (as described in Section 4.1) would be a local mechanism, equivalent to our model in the large $N$ limit. However, even for relatively large values of $N$ (see Figure 7b) for $N = 100$), the differences in the spectra are quite substantial. Since many brain networks plausibly operate with a few thousand neurons, it is safe to understand the apparent distinctions between the two models, for finite values of $N$.

Knowledge of the geometry of the network is very important when determining which connectivity schemes are plausible to use for models of learning. Choices currently used in modeling range from considering fully-connected to fully-disconnected interacting modules, or layers [16]. In our framework, convergence (learning) is not a priori prevented in either case. In developing future iterations of this model, it will also be important to explore how the learning process itself shapes the connectivity scheme. Siri et al. [19] suggest that the structure emerging during learning breaks down into different numbers of hub-like subnetworks; this might affect the spectral robustness demonstrated in our modular. Understanding the source and limits of this robustness may be an instrument that could be used to investigate which architectures favor convergence under particular learning algorithms, and which not.

4.3 Random coupled oscillators and applications to brain connectivity

Recent studies have used graph theoretical approaches not only to understand learning, but also to investigate more general organizational principles of brain networks [2, 22, 20]. With nodes and edges defined according to modality appropriate scales [21], there studies support certain generic topological properties of the human brain architecture, such as modularity, small-worldness, the existence of hubs and other connectivity density patterns [10]. These properties, if proven consistent with certain physiological, behavioral or genetic factors, may be usable to better understand neural processes, or even as biomarkers for behavioral traits or neuropsychiatric conditions.

In previous work, we have used a graph-theoretical framework to study how network density can affect the complexity of signal outputs in a control meso-circuit (the prefrontal-limbic system, viewed as a network of hemodynamic nodes). As in our theoretical framework, we used two interacting modules (one excitatory – amygdala, and one inhibitory – prefrontal cortex), thus representing schematically the prefrontal-limbic system. While conceived to be sufficiently general to maintain relevance for a variety of classes of neural control circuits, this setup wa appropriate for informing our imaging results on this system in humans, and draw conclusions on how prefrontal-limbic connectivity may drive arousal dynamics and emotional responses. With each of the $N$ nodes in either module acting as an stochastic linear damped (Ornstein-Uhlenbeck) oscillator, we studied how connectivity complexity can determine and modulate scale-free
features of the output signals. When allowing the densities $\alpha, \beta$ to vary within the interval $(0, 1]$, the frequency profiles of the solutions (measured in our case as the slopes of the log-log power spectra) shifted closer of further from white to pink to brown noise, in a consistent way which allowed us to suggest a testable framework for interpreting similar power spectral trends found in our fMRI time series. Individuals with average emotional reactivity represent well-regulated control systems, in which excitatory and inhibitory influences are balanced (these individuals exhibited fMRI signals close to pink noise in both amygdala and prefrontal regions). Anxious individuals have relatively weaker inhibitory feedback inputs from the prefrontal cortex (primarily driving amygdala signals closer to white noise). Less reactive individuals have relatively stronger excitatory inputs from the amygdala, producing stronger feedback (inducing more white noise primarily for the prefrontal cortex).

Such modeling results, in agreement with empirical finds [18] and in with existing theoretical work [1], support the necessity of two key conditions for optimal function in brain networks: first, the requirement for a well-balanced adjacency matrix. The corresponding bidirectional graph should appropriately combine robust features (e.g., fully connected populations) and random edges (e.g., due to synaptic probing) so as to allow some flexibility, yet also render sufficient stability for convergence during a cognitive process such as learning. Second, there should be well-balanced connection strengths (i.e., the weights on each adjacency edge), hence an efficient connectivity matrix driving optimal dynamics in the system.

In future work, we propose extending such analyses to understand interactions between nonlinear nodes. While biologically more plausible, nonlinearity also produces richer temporal trajectories. The dynamics of many types of coupled nonlinear oscillators have been widely investigated, in particular when the temporal architecture of the system is overlayed on a hard-wired connectivity scheme between nodes/variables. It has become clear that even trivial interaction schemes, in conjunction with nonlinear behavior, may produce highly complex phenomena. For example, symmetric weak coupling between two Wilson-Cowan excitatory/inhibitory units has been shown to produce interesting phase-space transitions (bifurcations) between stable equilibria, cycles and invariant tori, when varying the system parameters (e.g., the coupling strengths). In our framework, the aim would be not necessarily to locate these transitions in the parameter space for each adjacency configuration, but rather to understand how the bifurcations are affected statistically by changes in the edge configuration.

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