



Connecting the dots in ethology: applying network theory to understand neural and animal collectives

Adam Gosztolai and Pavan Ramdya

Abstract

A major goal shared by neuroscience and collective behavior is to understand how dynamic interactions between individual elements give rise to behaviors in populations of neurons and animals, respectively. This goal has recently become within reach, thanks to techniques providing access to the connectivity and activity of neuronal ensembles as well as to behaviors among animal collectives. The next challenge using these datasets is to unravel network mechanisms generating population behaviors. This is aided by network theory, a field that studies structure–function relationships in interconnected systems. Here we review studies that have taken a network view on modern datasets to provide unique insights into individual and collective animal behaviors. Specifically, we focus on how analyzing signal propagation, controllability, symmetry, and geometry of networks can tame the complexity of collective system dynamics. These studies illustrate the potential of network theory to accelerate our understanding of behavior across ethological scales.

Addresses

Neuroengineering Laboratory, Brain Mind Institute & Interfaculty Institute of Bioengineering, EPFL, Lausanne, Switzerland

Corresponding authors: Ramdya, Pavan (pavan.ramdya@epfl.ch); Gosztolai, Adam (adam.gosztolai@epfl.ch)

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Network theory, Neural circuits, Behavior, Collective behavior, Functional recordings, Connectomics, Tracking, Network topology, Controllability, Symmetry, Geometry.

Introduction

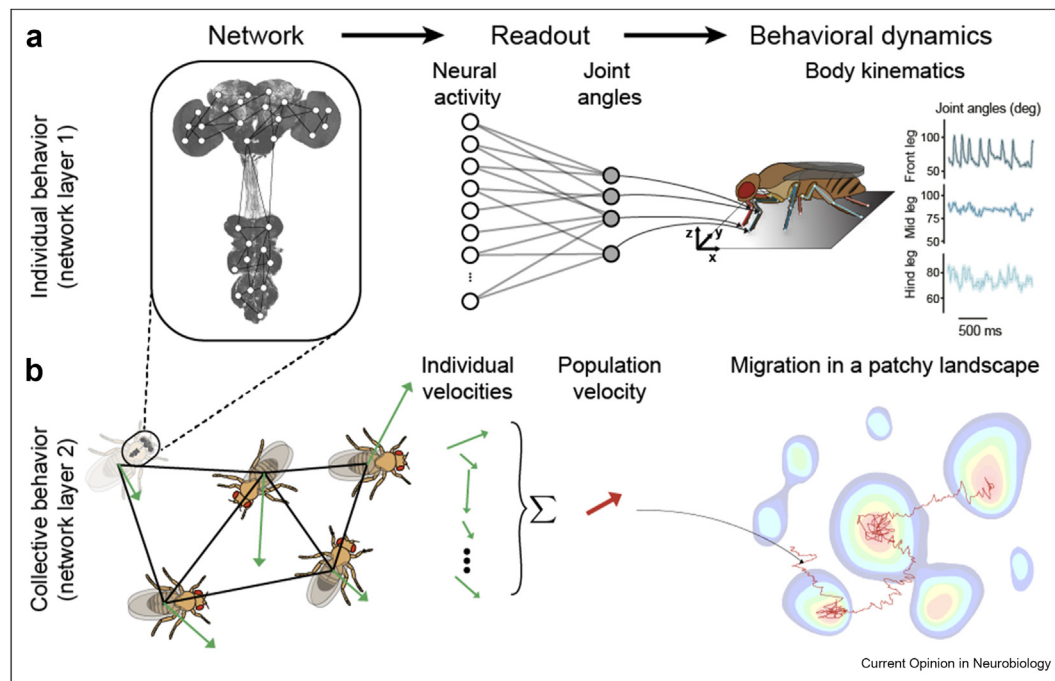
A central goal in neuroscience is to understand how animal behavior is orchestrated by the activity of formidably complex neuronal networks [1]. Parallel efforts in collective animal behavior have addressed an analogous question

at a larger scale of organization: how do population-level behaviors arise from the interactions between individual animals [2]. Both fields have, until now, favored a reductionist view by studying (i) how single neurons or small functional units regulate specific animal behaviors [3] or (ii) how simple interaction rules between self-propelled particles give rise to collective behaviors [4–6]. However, recent work is beginning to reveal that animal behavior — be it the movements of individuals or the foraging of groups — may not be fully explainable from the dynamics of individual constituent units [7–10] (Figure 1). Hence a paradigm shift is needed to move from reductionist analyses to those that embrace the complexity of distributed information processing over networks spanning multiple levels [11,12].

Network theory is a mathematical framework for modeling interacting systems as networks (or graphs) formed by a set of relations (edges) between discrete entities (nodes). Additionally, nodes can carry time-varying dynamical processes or signals [13], including the activity of neurons, or a behavioral feature (e.g., velocity) of individual animals. Because of their generality, ability to encompass different datasets, and favoring of interactions rather than spatial layouts (in physical or state space), network models are uniquely suited to bridge across the neuroscience of individual and collective animal behaviors. Importantly, they can also discover universal structure–function relationships that are robust to uncharacterized interaction parameters.

In this review, we first describe how new large-scale datasets can be characterized by different network objects. We focus on graph-based network objects and will use the terms ‘graph’ and ‘network’ interchangeably. We do not consider the use of artificial neural networks for modeling neural activity or animal behavior (these have been reviewed elsewhere [14]), nor their construction or study using graph theoretic approaches. Then, we highlight four network theoretic concepts — signal propagation, controllability, symmetry and geometry — to illustrate how the graph-based view is often rich enough to relate the time-evolution of dynamical processes on networks to network structures. Finally, we illustrate the use of these concepts for data-driven investigations of animal behavior. We put a particular emphasis on *Caenorhabditis elegans* and *Drosophila melanogaster* because for these organisms whole-brain

Figure 1



Information processing in collective animal systems occurs across hierarchical layers. (a) To orchestrate the actions of individual animals, populations of neurons interact, generating circuit dynamics. These dynamics converge and are read out by muscles, causing bodypart movements and ethological behaviors. (b) At a higher hierarchical layer, individual animals — with diverse preferences — transmit their behaviors (e.g., heading direction) as sensory signals to a social network that coordinates group dynamics, for example, moving through a patchy nutrient landscape (adapted from the study by Gosztolai et al. [15]).

connectomes, brain-wide neural recordings in behaving animals, and high-resolution population behaviors are, or soon will be, readily available.

Large-scale measurements of neural and animal interaction networks

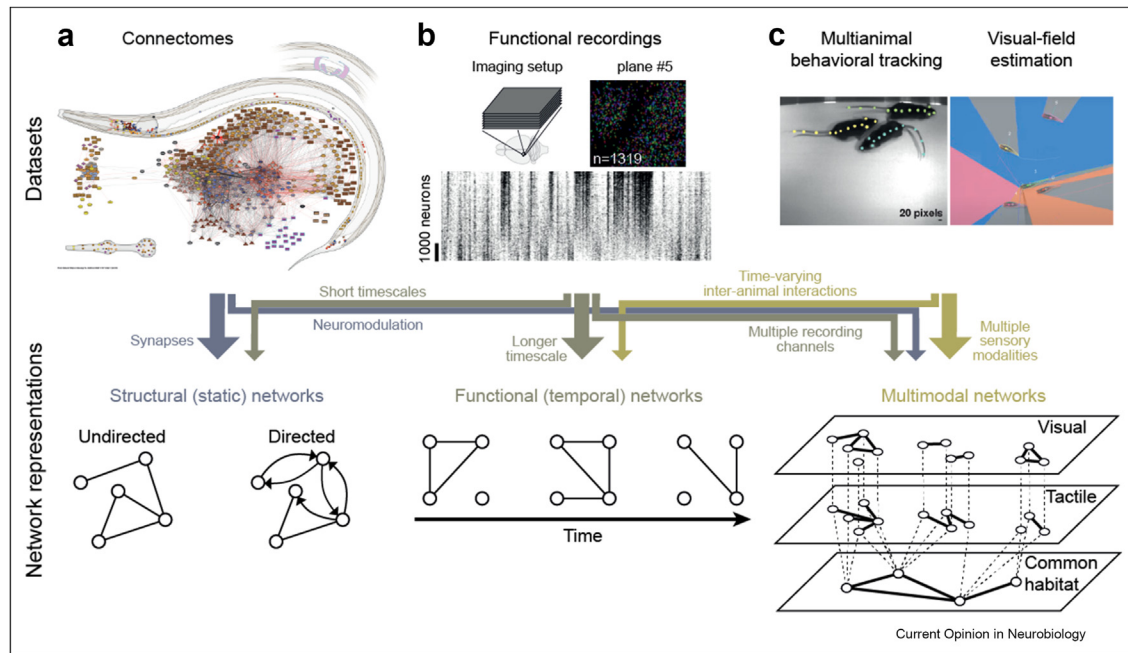
As illustrative examples, here we review three kinds of datasets that are amenable to modeling by networks and how they are defined in terms of nodes and edges. We note that other definitions are also possible and this choice is an important part of the modeling effort. Some examples are also more explicitly shown in Box 1.

Connectomic reconstruction of neural networks. A ‘connectome’ is an extensive anatomical reconstruction of neural connections — typically through semi-automated segmentation of serial section electron microscopy data (Figure 2, left). The first connectome was obtained for the hermaphrodite sex of the worm *C. elegans*, a resource that now includes nearly the complete nervous systems of both sexes (hermaphrodite and male) across development [16]. Similar reconstruction efforts are underway for the *Drosophila* central brain [17], central complex [18], olfactory system [19], motor circuits in the ventral nerve cord [20], and whole brain

of a female fly [21,22]. Beyond invertebrates, connectomes datasets have also been generated for a larval zebrafish [23], parts of mouse visual cortex [24] and human cerebral cortex [25].

Connectomes provide a structural network: individual neurons (nodes) connect to one another via directed chemical or undirected/bidirectional electrical synapses (edges). Moreover, at a finer scale, network nodes may also represent dendritic compartments as fundamental units of computation [26]. Because connectomic reconstructions typically involve one or at most a few network instances, their networks are generally considered static. This may be accurate on the time-scale of animal behaviors, except when learning and plasticity occur. Edges are typically unweighted (i.e., having unit weight), but anatomical features of axons like their diameters have sometimes been used as a proxy for edge weights [16]. This classical network model may be limiting when the heterogeneity of synaptic interactions plays an important role in network dynamics. In this case, ‘multilayer networks’ can be used to account for different network features [27,28]. Here, layers represent different modalities combined into a single mathematical object via inter-layer edges. For example, connections mediated by

Figure 2



Network descriptions of structural and functional data capturing the properties of neural and animal ensembles. (a) Connectomes describe anatomical connections of neurons or neural compartments obtained using synaptic-resolution electron microscopy reconstruction (image of *C. elegans* re-produced from the study by Hens et al. [64]). Connectomes are typically represented as static networks in contexts where synaptic plasticity is irrelevant (e.g., short timescales). Multilayer networks can represent interactions between different classes of neurons. (b) Functional recordings reveal the dynamic activity of neural populations (image reproduced from the study by Romyantsev et al. [47]). Functional networks encode a certain similarity between nodal dynamics. Because these connections covary with node dynamics, they can be represented as temporal networks, which in their simplest form are an ensemble of temporal network snapshots. (c) Animal tracking and visual field reconstructions can characterize behaviors: the output of the neural activity. Thus, they provide a bridge between individual and collective animal behaviors (images reproduced from the study by Harpaz et al. [61] and Cook et al. [63]). Inter-animal interactions can be represented using functional networks. In addition, multilayer networks can represent multiple modalities not captured by a single network layer.

neuromodulators have been modeled as different network layers [29].

Functional recordings of large-scale neural networks.

Complementing structural neuronal connectivity, optical functional recordings enable a readout of neural activity (Figure 2, middle). Although these recordings offer a lower temporal resolution than multi-electrode array recordings [30], state-of-the-art genetic reagents enable the measurement of calcium influx [31,32], voltage [33,34], or neuromodulator dynamics [35] across large swaths of neural tissue, while also more effectively conveying information about each cell's type, identity, and spatial location. These functional datasets exist for a variety of small transgenic animals including *C. elegans* [36,37], larval [38] and adult *Drosophila* [39–44], larval zebrafish [45], and rodents [46–48].

Functional recordings represent dynamic signals over network nodes. These can be used to build a 'functional network'. In this case, edge weights are not based on physical connections, but on a correlational or causative link between nodal dynamics. When edge weights represent correlational links, or 'dynamic similarity',

they typically covary with the node dynamics. Thus, functional networks are termed 'temporal' in network theory, which at its simplest can be visualized as a multilayer network with layers encoding a sequence of discrete temporal snapshots [49].

A current limitation of brain-wide imaging is that regions-of-interest cannot be easily unambiguously assigned to individually identifiable neurons. Therefore, a crucial current effort aims to couple functional and anatomical/connectomic datasets: a challenging endeavor due to inter-animal variability in cell locations as well as movement-related microscopy image deformations. Progress on this front has been mostly limited to studies of *C. elegans*, an animal for which the positions and identities of neurons are largely conserved across individuals. This fact facilitates multi-color labeling strategies to recover each neuron's identity from its spatial position and fluorescent protein expression profile [50,51]. Because this technique is not easily compatible with freely moving worms, alternative, deep learning-based methods have also been developed to recognize and track neuron positions and identities across time [52,53].

Box 1. Example network constructions

	Connectome	Functional connectome	Animal interaction network
Nodes	Neurons	Neurons	Animals
Edges	Synapses	Dynamic similarity	Pairwise social interactions
Node dynamics	–	Neural activity	Animal behaviors

Behavioral-tracking of animal collectives. A simple way to capture inter-animal interactions is by tracking their body positions in 2D space and using proximity as a readout of interactions [54]. In addition, finer-scale 3D body kinematics can be precisely measured using deep learning-based markerless motion capture and multi-camera triangulation of multiple 2D poses [55–57] or by lifting single-camera 2D poses [58]. Recent methods have extended 2D pose estimation to multi-animal settings allowing investigators to track kinematics for up to 10 animals at once [59,57,60,61] (Figure 2, right). Further insights may be gained by combining positional tracking of animals with body and head orientation measurements to infer their visual fields [62,63].

Animals (nodes) and their pairwise interactions (edges) like spatiotemporal proximity, shared group membership, or behavioral similarity must be modeled as temporal networks (Figure 2, right). Furthermore, multilayer networks can account for the same individuals interacting via different sensory modalities or individuals interacting across different spatial compartments [28].

Applications of network theory for studying neural and animal social network dynamics

The behaviors of neural and animal collectives can be thought of as dynamical signals propagating along the edges of network nodes. This is often referred to as dynamic flow or information spreading in statistical physics [67] (Figure 3A). Indeed, the activity of a node influences the likelihood that a neighboring node changes its activity which can lead to a cascade propagating throughout the network.

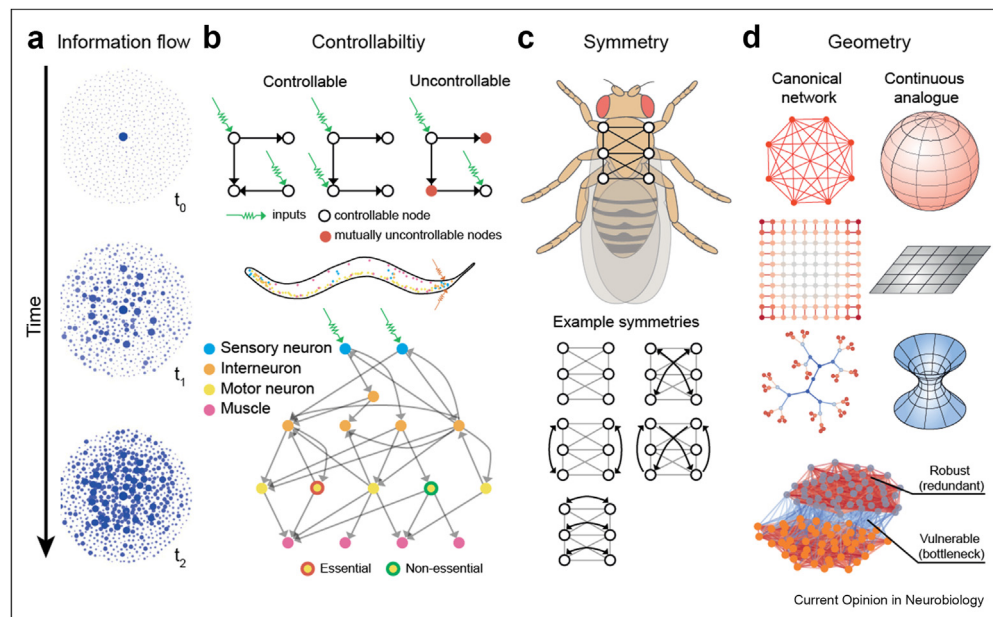
A model-based dynamical systems approach to understand the patterns of this flow entails considering nodes as state variables (e.g., the firing rate of a neuron, or swimming velocity of a fish) coupled through often nonlinear interactions. The interaction model, which can be phenomenological (e.g., Integrate-and-Fire neurons) or mechanistic (e.g., Hodgkin-Huxley neurons), explicitly describes how state variables change as a function of other variables. This framework typically entails suitably parametrizing the interaction functions and performing

simulations of the network's activity [36]. Although this approach is useful for making predictions about network activity, it is unlikely to provide generalizable insights because there is no one-to-one mapping between dynamics and parameters. For example, neural networks can exhibit the same dynamics despite morphological variations of neurons, heterogeneous circuit parameters, and neuromodulation [68–70], and conversely, networks can support different dynamics despite very small variations in connectivity [67].

The abstraction provided by network theory is powerful because it allows one to translate a network's topology to observe signal propagation patterns without requiring a detailed characterization of dynamical interactions. This hinges on describing network processes as epidemic or rumor-spreading models in which nodes adopt their neighbors' states — such as whether they are susceptible or infected. Likewise, neurons change their activity depending on the states of neighboring neurons, the interaction rules between them and their processing at nodes. Similarly, for animal collectives, epidemic models capture the process whereby changes in an individual's behavior propagates through the network [71].

To understand the role of individual neurons in network-wide signal propagation, a common simplifying assumption is to model network activity as a linear process. In *C. elegans*, this technique has been effective to predict which nodes (neurons), when removed, cause maximal disturbance in flow patterns [72]. This is likely because the worm's nervous system consists of many neurons communicating using gap junctions, which can be modeled as linear resistors. Although chemical synapses may introduce nonlinearities, their sigmoidal transfer functions are well-approximated by a linearization around their operating point [72]. However, this linear approximation may also generally apply to other organisms because nonlinear neural dynamics often evolve on a low-dimensional manifold [73,74] that is also well-approximated by linearization in the neighborhood of a point in neural space. Taking advantage of this feature, one study examined the dynamics of a linearized system and formed a new 'similarity' network where edge weights represent pairwise correlations

Figure 3



Relevant network theoretical concepts for understanding neural and animal social network dynamics (a) Network dynamics can be conceptualized as signals evolving on network nodes (edges are not shown; image reproduced from the study by Yan et al. [65]). (b) The controllability of a network quantifies the role of inputs in influencing network dynamics. The networks on the left are controllable because each node can be driven to an arbitrary state by the two inputs. The network on the right is uncontrollable because the red nodes cannot be driven to arbitrary states by the inputs. Controllability has been used to identify *C. elegans* sensory neurons that affect the global network state and thus are of likely behavioral relevance (schematic based on [66]). (c) Network symmetries are closely related to permissible network dynamics. The function of large networks can be decomposed into small network units or motifs with well-characterized symmetries and input–output relationships. Here, the symmetries of a network of six central pattern generators (CPGs) controlling insect locomotion can provide insights into functional circuit dynamics generating gaits. (d) Network geometry aims to represent network structure as a mathematical object that can better reveal network symmetries or dynamical properties. One example is edge curvature, which is typically defined based on some analogy to canonical geometries such as balls, planes or hyperboloids. Amongst other predictions, network geometry can infer a network’s robustness (redundancy) or vulnerability (bottlenecks).

between nodal dynamics [75] (Box 2). Clustering this network predicted which groups of neurons were likely to be coactive in the nonlinear system. It is known that signal propagation patterns depend on nonlinear node dynamics [67]. Yet, strikingly, for a variety of networks in neuroscience, ecology, and epidemiology, spreading behaviors fall into distinct modes depending on purely structural features. These include the shortest paths between nodes and high degree nodes (hubs) [65]. Studies aiming to understand the global effect of nonlinearities are extremely valuable for predicting how specific features of neural tuning can influence large-scale network computations.

Epidemics-inspired models are also insightful in the study of animal collectives. Indeed, animal interactions typically depend only on the relative position of individuals except, for example, in cases of crowding [76]. Modeling the behavioral changes mediated by network interactions, often termed social contagion, is simpler than modeling the evolution of a population’s state, which has traditionally been studied using approaches from the kinetic theory of gases [77]. Early ‘simple

contagion’ models considered the probability of an individual adopting a new behavior to be proportional to the number of neighbors with that behavior [78]. However, it is now recognized that this probability must include a nonlinear function of neighboring behaviors, known as a ‘complex contagion’ [79]. For example, in schooling fish, only models accounting for the cooperative effects of neighboring active individuals can explain group dynamics [80]. Thus, by simulating social cascades, it has been possible to distinguish the effect of individual–level parameters from that of the group’s structure [81]. The dynamics of signal propagation have also been extended to multilayer networks to reveal the roles of different interaction modes [27].

Controllability of network signals. In addition to network structure, network dynamics are also shaped by inputs [82], such as sensory inputs driving neural networks, or predators disturbing animal interaction networks. Inputs can affect the network locally or they can spread to the majority of nodes. ‘Controllability’ is the notion that links network signals to their inputs [75]. This measures the ability of an input to drive network

states to a desired target in finite time [83]. A special case that assumes a linear system is ‘structural controllability’, which tests whether an input to a specific node can significantly affect network dynamics. Although it is a linear property, structural controllability predicts the minimal set of inputs sufficient to control an underlying nonlinear system (Figure 3B, Box 2). When applied to connectomes, structural controllability can infer which inputs — from sensory organs or other brain regions — are behaviorally relevant. Classically, this task has been performed by ablating sensory neurons and subsequently searching for a loss of function: an approach that is experimentally intractable for larger groups of neurons or to probe combinations of neurons. One study examined structural controllability of the *C. elegans* connectome to predict sensory neuron classes, as well as single neurons within these classes, whose removal would reduce the number of controllable muscles, thus impairing locomotion [66] (Figure 3B).

Controllability has also been generalized to temporal networks, which are useful for studying animal collectives [49]. In temporal networks, signal propagation is slower but control is easier because the increased number of layers enlarges the space of possible control trajectories [49]. For example, controllability can be achieved more rapidly in a network of antenna–body interactions in ants than a network composed only of static interactions [49]. Thus, control theory can provide insights into how brains generate robust actions while also enabling diversity at the level of individual and group-level behaviors.

Understanding dynamics through network symmetries. Networks may contain ‘structural symmetries’. These are possible rearrangements of nodes that leave network topology invariant or unchanged (Figure 3C, Box 2). In neural networks, structural symmetries are required for controllability [88] and synchronization [89]. For example, central pattern generators, which are frequently used to model animal locomotion, must have ipsilateral and contralateral symmetries to generate locomotor gaits [90]. Based on this insight, one study suggested that certain *C. elegans* locomotor patterns are associated with structural symmetries in the worm’s connectome [85]. They found that circuits regulating forward/backward locomotion can be decomposed into a hierarchical system of dynamical units (filters) with well-defined symmetries. The dynamics of these units contribute to locomotion but are largely independent of the specific dynamic parameters of the neurons. This decomposition is related to network motifs — network units with well-characterized input–output behaviors [9]. As a result, evidence for network motifs between pairs of nodes can also be found experimentally by injecting a prescribed dynamic signal into one node and looking for certain dynamical signatures in other nodes [91]. Similar symmetry–function relationships are also emerging for

animals with larger nervous systems. For example, the connectivity, inputs, and outputs of the *Drosophila* central complex have recently been examined to link circuit motifs with potential functional properties [18].

Network geometry linking dynamics and structure. Further links between network symmetries, controllability, and signal propagation can be discovered using tools from the emerging field of network geometry [92]. Briefly, network geometry aims to represent a network by either identifying a continuous latent space in which it can be embedded or by defining a geometric object based on features of the network’s structure or node signals (Figure 3D, Box 2). The motivation behind constructing geometric objects is that they may be particularly suited to reveal structure–function relationships. For example, geometric notions have been exceptionally useful in identifying hidden symmetries and predicting the spatiotemporal evolution of network-driven dynamical processes [92]. A geometric approach has been used to uncover symmetries in the human functional connectome, suggesting universal organizational principles across scales [93]. Network geometry has also been used to infer information-limiting bottlenecks between regions [87] and those that are redundant for signal propagation [86,87]. Structural features like the association to a high-degree node might not highlight these properties. Thus, network geometry has the potential to predict the relevance of connections from dynamic network models or neural recordings. Network geometric ideas have also been used in collective behavior to detect dynamical transitions when a hidden parameter is varied. In the study by Runge et al. [94], the authors noticed that, in a collective system, the state of the whole system can be encoded as a probability distribution over the local connectivity of each individual. Thus, they could compare the dynamics across different conditions based on their respective probability distributions. Using this approach, they were able to detect dynamical transitions in collective behavior without temporal information but based purely on changes in the relative arrangement of individuals.

Limitations of network theoretic approaches

Thus far we have highlighted the possibilities offered by network theory when the system of interest can be abstracted as a set of nodes and interactions. However, this approximation is a modeling assumption and, thus, has shortcomings. To begin with, functional networks — where edges must be indirectly inferred from the similarity between node dynamics — can be challenging to infer. Several algorithms are available that rely on an underlying generative network model or use correlative or causative measures [95] that depend on factors such as sampling rate, unobserved nodes, noise, and sample size. In this context, missing nodes and edges can interrupt

Box 2. Common Terminology in 3D Behavioral Tracking

Controllability The activity of N neurons can be modelled as the time-evolution of a state $x(t)$ over N nodes connected by edges representing synapses. The network may be subject to inputs $u(t)$ representing sensory neurons. These neurons drive M muscles, whose activity $y(t)$ is a linear readout of $x(t)$. Although the full non-linear governing equations are necessary for prediction, finding the minimal set of sensory inputs required to control network activity can be accomplished by studying the linear system

$$\dot{x}(t) = Ax(t) + Bu(t)$$

$$\dot{y}(t) = Cx(t),$$

where A is the adjacency matrix of the connectome, B are the sensory neurons which convey external stimuli and C is a readout matrix to the muscles. This linear system is *structurally controllable* if, for almost all choices of the non-zero entries of A, B, C , the Kálmán condition holds

$$\text{rank}[CB, CAB, CA^2B, \dots, CA^{N+M}B] = N.$$

An efficient approach to find the minimal set of inputs is to transform the control problem to a geometric one [84]. First, find the *maximum matching* in the network, that is, the maximum number of edges that do not share endpoints. A node is matched if an edge in the maximum matching is directed toward it. Then, inputs at unmatched nodes form the minimum set needed to control network activity if there is a directed path from each input to every matched node (Figure 3B).

Signal propagation One way to quantify signal propagation is to compute the similarity between dynamic processes at nodes connected by an edge. For example, considering the time-evolution of a state $x(t) = (x_1(t), \dots, x_N(t))$ (such as neural activity) over N nodes, one can compute the inner product

$$\psi_{ij}(t) = \langle x_i(t), x_j(t) \rangle = x_i(t)x_j(t)^T.$$

Instead of an inner product, other measures of similarity could be considered, such as different correlations, or information theoretic measures. However, taking the inner product and assuming that $x(t)$ obeys linear dynamics, the similarity can be expressed as [75].

$$\psi(t) = B^T \frac{dG_O(t)}{dt} B,$$

where $G_O(t) = \int_0^t dt e^{A^T t} C^T C e^{At}$ is the observability Gramian of the system over a time horizon t . Thus, $\psi_{ij}(t)$ is related to control, by quantifying how predictive the node i is for the dynamics of node j over a time horizon t .

Symmetry The symmetry of a network can be formalized as an *automorphism*, a relabeling of nodes that preserves the connectivity in the sense that the same nodes are connected before and after the application of the automorphism (Figure 3C). The set of automorphisms forms a *symmetry group* of the network. The symmetry groups of a network can be found algorithmically and then factorized into subgroups. Finding these factors predicts subsets of neurons that drive distinct animal behaviors [85].

Geometry One way to capture the geometry of a network is by defining its *curvature*. There are several possible curvature notions, typically based on some analogy to the curvature of continuous spaces. A popular definition is the Ollivier-Ricci curvature of an edge, which generalizes the coarse Ricci curvature on continuous manifolds in a given direction. It measures the extent to which the edge length w_{ij} between two connected nodes i and j differs from the (weighted) average length of shortest paths between the respective neighborhoods of these nodes. Mathematically, the Ollivier-Ricci curvature of an edge ij is

$$\kappa_{ij} = 1 - W(m_i, m_j) / w_{ij},$$

where W is the optimal transport distance and m_i and m_j are distributions supported by the neighborhoods of i and j that serve to weight the importance of geodesics. For example, they can be uniform distributions [86], or weighted based on the distance of neighbors to account for the network topology at different scales [87]. Computing the curvature for all edges in the network can predict dynamically related nodes based on similar values of the curvature (Figure 3D).

signal propagation and cause network-wide differences in dynamic patterns. Thus, a naive approach should attempt to include all nodes and edges in a network analysis. That said, studies of the resilience of networks against failure (i.e., the ability of networks to maintain their function despite missing nodes and edges) offer techniques for estimating whether incomplete datasets are likely to result in erroneous predictions depending on the surrounding network topology [96]. Furthermore, the accuracy and interpretations of network theory metrics can, on a case-by-case basis, depend on network and dynamic properties including network size, stochastic dynamics or measurement noise, and the dimensionality of dynamics.

Conclusions

Recent technical advances have enabled the acquisition of large-scale datasets in neuroscience and collective behavior. These can be represented as networks of neural connectivity, functional dynamics, and also population-level inter-animal interactions. Network theory offers a set of tools that can help to distill universal principles from these data, linking structure and function, often from only a few noisy network instances. Progress in this direction will offer new avenues for investigating distributed computations performed by collective systems of neurons and animals and can advance machine learning approaches that leverage the power of bioinspired network operations.

Conflict of interest statement

Nothing declared.

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