Defined Vocabulary for Nervous System Network Analysis

This is a working vocabulary compiled mostly from the pioneering work of Olaf Sporns and colleagues (see bibliography at the end). It complements the defined vocabulary in our *Foundational Model of Nervous System Structural Connectivity* (Swanson & Bota 2010). Preferred synonyms are **bolded**. Also see Wikipedia articles, *Glossary of graph theory* and *List of graph theory topics*.

Adjacency matrix: See **connection matrix**, although strictly speaking, the term may refer only to a matrix with binary connections (see Sporns 2012a, p. 16).

Allometric scaling: "Allometric scaling concerns the relationships between body size (scale) and other anatomical, functional or metabolic properties of organisms. These scaling relationships are often described by power laws" (Bullmore & Sporns 2012, p. 338). See Wikipedia *Allometry*.

Anatomical connections: See **structural connections**.

Arc: See **connection**.

Assortativity: "A measure of the tendency for nodes to be connected to other nodes of the same or similar degree" (Bullmore & Sporns 2009, p. 195). More specifically, it is "The correlation between the degrees of connected nodes. Positive assortativity indicates that high-degree nodes tend to connect to each other." (Bullmore & Sporns 2009, p. 188). "The correlation coefficient for the degrees of neighboring nodes. Positive assortativity indicates that edges tend to link nodes of similar degree, while negative assortativity indicates that high-degree nodes preferentially connect with low-degree nodes." (Sporns 2011, p. 9).

Betweenness centrality: "The betweenness centrality of an individual node is defined as the fraction of all shortest paths in the network that pass through the node. A node with high betweenness centrality can control information flow because it is at the intersection of many short paths." (Sporns 2011, p. 15).

Bidirectional connection: Two directed connections between a pair of nodes; see Kötter & Stephan (2003). A nonpreferred synonym is reciprocal connection.

Binary connections: "Denotes the presence or absence of a connection" (Rubinov & Sporns 2010, p. 1060). Synonyms are binary links and binary edges.

Block model: "Model-based community (module) detection method whose parameters are selected to maximize the likelihood that the model generated an observed network." (Sporns & Betzel 2016, p. 19.9).

Brain architecture: "Multiple lines of empirical and computational evidence suggest that brain architectures balance competing spatial, metabolic, and functional demands. Rather than being optimal for any single factor, brain connectivity jointly satisfies these multiple demands. The combination of these demands is likely to have shaped the neuronal morphology and connection topology of nervous systems ranging from *C. elegans* to humans." (Sporns 2011, p. 128). "Graph theoretical analyses have allowed us to make some first steps toward elucidating important architectural features of structural brain networks." (Sporns 2011, p. 102). Also see **network architecture**.

Brain connectivity: "Description of structural or functional connectivity between brain network elements (i.e., brain regions, neurons)." (Heuvel & Sporns 2013, p. 683). See more inclusive **nervous system connectivity** and **neural connectivity**.

Centrality: "Measures of the relative importance of a node or edge within the overall architecture of a network. Several centrality metrics have been proposed, including (among many others) degree, betweenness, closeness, eigenvector, and pagerank centrality." (Heuvel & Sporns 2013, p. 683). "A topological measure of the importance or influence of a node or edge for network organization." (Bullmore & Sporns 2012, p. 342). "Many measures of centrality are based on the idea that central nodes participate in many short paths within a network, and consequently act as important controls of information flow (Freeman 1978)…Measures of centrality may have different interpretations in anatomical and functional networks. For instance, anatomically central nodes often facilitate integration, and consequently enable functional links between anatomically unconnected regions. Such links in turn make central nodes less prominent and so reduce the sensitivity of centrality measures in functional networks." (Rubinov & Sporns 2010, p. 1064). "The node degree gives a first indication of centrality, especially in networks with a broad or scale-free degree distribution." (Sporns 2011, p. 327). "In general, centrality measures identify elements that are highly interactive and/or carry a significant proportion of signal traffic. A node that is highly central in a structural network has the potential to participate in a large number of functional interactions. Conversely, a node that is not central is unlikely to be important in a network-wide integrative process. Furthermore, the loss of nodes or edges with high structural centrality tends to have a larger impact on the functioning of the remaining network." (Sporns 2011, p. 16).

Characteristic path length: The most commonly used measure of network functional integration that is the average shortest path length between all pairs of nodes in the network (Rubinov & Sporns 2010). "The average of all finite distances in a network. A short path length implies the existence of many short paths between node pairs."

Circuit: "A circuit can be a closed walk allowing repetitions of vertices [nodes] but not edges [connections]; however, it can also be a simple cycle, so explicit definition is recommended when it is used." (Wikipedia, *Glossary of graph theory*); also see **cycle**, closed path.

Cliques: "High levels of local clustering among nodes of a network" (Bullmore & Sporns 2009, p. 189), or "A group of fully connected nodes" (Sporns & Betzel 2016, p. 19.10) Synonyms include families, **clusters**.

Cliquishness: See **clustering coefficient,** cliques.

Closed path: See **cycle**.

Closeness centrality: "The closeness centrality of an individual node is the inverse of the average path length between that node and all other nodes in the network. A node with high closeness centrality can reach all other nodes via short paths and may thus exert more direct influence over the nodes." (Sporns 2011, p. 15).

Clusters: "If the nearest neighbors of a node are also directly connected to each other they form a cluster." (Bullmore & Sporns 2009, p. 188). Basically, a cluster is a densely interconnected group of nodes (see Rubinov & Sporns 2010, p. 1061). Synonyms include cliques, families.

Clustering: "The tendency of small groups of nodes to form connected triangles. Many triangles around a central node imply that the connected neighbors of the node are also neighbors of each other, forming a cluster or clique." (Heuvel & Sporns 2013, p. 683). "A measure that captures the 'cliquishness' of a local neighborhood, based on the number of triangular connections between groups of three nodes." (Bullmore & Sporns 2012, p. 340). It is a simple measure of functional segregation and is based on the number of triangles in the network, "with a high number of triangles implying segregation. Locally, the fraction of triangles around an individual node is known as the *clustering coefficient* and is equivalent to the fraction of the node's neighbors that are also neighbors of each other (Watts & Strogatz 1998). The mean clustering coefficient for the network hence reflects, on average, the prevalence of clustered connectivity around individual nodes." (Rubinov & Sporns 2010, p. 1061). "Clustering is significant in a neurobiological context because neuronal units or brain regions that form a densely connected cluster or module communicate a lot of shared information and are therefore likely to constitute a functionally coherent brain system…Conversely, neuronal units that belong to different clusters or modules do not share as much information and remain functionally segregated from each other. Thus, measures of clustering and modularity highlight a particular aspect of the functional organization of the brain, its tendency to form segregated subsystems with specialized functional properties. The identification of modules in brain networks is an important first step toward the characterization of these subsystems." (Sporns 2011, pp. 12-13).

Clustering coefficient: "The clustering coefficient quantifies the number of connections that exist between the nearest neighbors of a node as a proportion of the maximum number of possible connections…associated with high local efficiency of information transfer and robustness" (Bullmore & Sporns 2009, p. 188). "The fraction of triangles around an individual node is known as the *clustering coefficient* and is equivalent to the fraction of the node's neighbors that are also neighbors of each other (Watts & Strogatz 1998). The mean clustering coefficient for the network hence reflects, on average, the prevalence of clustered connectivity around individual nodes." (Rubinov & Sporns 2010, p. 1061). "The clustering coefficient of a node captures the degree to which its neighbors are also neighbors of each other (the 'cliquishness' of a network neighborhood)." (Sporns 2011, p. 17). See **clustering**.

Communicability: "A measure of global information flow based on the number of walks between nodes (Estrada & Hatano 2008)" (Sporns 2011, p. 14). Also see **integration**, **walks**.

Community: "In networks, communities refer to modules, densely interconnected sets of nodes." (Heuvel & Sporns 2013, p. 683).

Community detection: See **module detection**.

Community structure: See **modular structure**.

Complex graph: See **complex network**.

Complex network: An informal description of a network with certain topological features, such as high clustering, small-worldness, the presence of high-degree nodes or hubs, assortativity, modularity or hierarchy, that are not typical of random graphs (networks) or regular lattices. Most real-life networks are complex by this definition, and analysis of complex networks therefore forms an important methodological tool for systems biology." (Bullmore & Sporns 2009, p. 187; also see Bullmore & Sporns 2012, Box 1). The interplay between functional segregation and global integration in the nervous system was first explored theoretically by Tononi, Sporns, & Edelman (1994), who introduced the measure neural complexity (C_N)—"The crucial insight was that the information dynamics of the network depended on how its elements were structurally coupled." (Sporns 2012b, p. 883). "Neither 'armchair theorizing' nor formal mathematical analysis is sufficient to deal with the rich spatiotemporal structure of complex systems. Instead, computer simulations of such systems are necessary to form and test hypotheses and to gain mechanistic insight." (Sporns 2011, p. 47). "While there is much ongoing discussion about how complexity should be mathematically defined and measured in real systems, there is some agreement across different problem domains and fields of science about the ingredients that are shared by most, if not all, complex systems. First, as discussed by Herbert Simon [1962], most complex systems can be decomposed into components and interactions, possibly on several hierarchical levels. Second, complexity is a mixture of order and disorder, or regularity and randomness, which together account for the nontrivial, nonrepeating nature of complex structures and their diverse dynamics" (Sporns 2011, p. 279). "The interactions of components in a nearly, but not fully decomposable system [decomposable: all communication occurs strictly within subsystems or modules] generate phenomena that cannot be reduced to or predicted from the properties of the individual components considered in isolation…These emergent phenomena cannot be fully explained by dissecting the system into components, nor can their full functionality be revealed by an examination of isolated components or interactions alone. In many cases, different levels of scale interact." (Sporns 2011, p. 280). "There are two main categories of complexity measures. Measures in one category measure complexity by how difficult it is to describe or build a given system…A second category of complexity measures captures the degree to which a system is organized or the 'amount of interesting structure' it contains, and these measures are highly relevant in the context of biological and neural systems." (Sporns 2011, p. 281). See **lattice network** and **random network**.

Complexity: See **complex network**.

Computer simulations: "Neither 'armchair theorizing' nor formal mathematical analysis is sufficient to deal with the rich spatiotemporal structure of complex systems. Instead, computer simulations of such systems are necessary to form and test hypotheses and to gain mechanistic insight…The extraordinary variety and complexity of neural activity patterns requires computational modeling of empirical data to achieve an understanding of the system that is both explanatory and predictive. Models are the basis of most, perhaps all, empirical investigation in neuroscience…one important implication of computational modeling is the necessity to explicitly parameterize potentially ill-defined and qualitative concepts. The basis of all computational models is a set of state equations that govern the temporal evolution of the dynamic variables." (Sporns 2011, p. 47).

Connected graph: See **connected network**.

Connected network: A network (graph) where "all pairs of nodes are linked by at least one path of finite length" (Sporns 2011, p. 9), sometimes called strongly connected.

Connection: “A connection expresses the existence and/or strength of a relationship, interaction, or dependency between two nodes in the network. Connections can be binary or weighted and they can be directed or undirected. Connections are also referred to as edges” (Heuvel & Sporns 2013, p. 683). A connection is multiple if there is at least one other connection with the same endnodes (for example, more than one route between two nodes); Wikipedia, *Glossary of graph theory*. Other synonyms are link and arc.

Connection density: “A topological measure that describes the number of edges (connections) in a network as a proportion of the maximum possible number of edges, namely $(N^2 – N)/2$ for an undirected network of N nodes.” (Bullmore & Sporns 2012, p. 340). The mean network degree is most commonly used as a measure of *density*, or the total “wiring cost” of the network. The directed variant of the degree distinguishes the number of inward links from the number of outward links, while the weighted variant of the degree, sometimes termed the strength, is defined as the sum of all neighboring link weights (Rubinov & Sporns 2010). Simply put, connection density “is the actual number of edges in the graph as a proportion of the total number of possible edges and is the simplest estimator of physical cost—for example, the energy or other resource requirements—of a network.” (Bullmore & Sporns 2009, p. 188). Kötter & Stephan (2003) also used “density” as a network participation index for individual nodes, and thus a synonym for node strength (see Sporns 2011, pp. 63-65).

Connection distances: “Spatial measures that describe the physical distance between nodes that are connected by an edge in the network; often approximated as the Euclidean distance (ordinary or ‘straight-line’ distance between two points in Euclidean space) between nodes.” (Bullmore & Sporns 2012, p. 339).

Connection matrix: “The most basic representation of a graph or network in matrix format, with the entries a_{ij} of the matrix equal to the weight of the connection between node i and node j. The entries a_{ij} are zeros or ones for binary graphs. (Sporns 2012a, p. 16). “In a weighted graph, the entries of the matrix equal the weight of the connection (if present).” (Sporns 2011, p. 327). “All networks are represented by their connectivity (adjacency) matrices. Rows and columns in these matrices denote nodes, while matrix entries denote links (connections). The order of nodes in connectivity matrices has no effect on computation of network measures but is important for network visualization” (Rubinov & Sporns 2010, p. 1060). That is, a “matrix can be displayed in many different ways depending on the ordering of the nodes along the rows and columns. Reordering the nodes does not change the structure of the graph and all graph measures are completely invariant with respect to these permutations.” (Sporns 2011, pp. 22-23). “A summary of all pairwise associations (connections) between network nodes, rendered in the form of a square (for binary connections) matrix.” (Heuvel & Sporns 2013, p. 683). “An association matrix…is often made sparse by removing weak relationships (‘thresholding’) in order to examine the structure of the strongest pairwise associations” (Sporns 2011, p. 38). “choices made in parsing the system into nodes and in estimating measures of their mutual association will influence the results obtained from network analysis” (Sporns 2011, p. 38). Kötter & Stephan (2003, p. 1262) “explicitly distinguish between (i) connections that exist, (ii) connections that are absent, and (iii) connections of unknown status.” Also see adjacency matrix.

Connection weight: “Weights in anatomical (structural) networks may represent size, density, or coherence of anatomical tracts, while weights in functional and effective networks may represent respective magnitudes or correlational or causal interactions…Weak and non-significant links may represent spurious connections, particularly in functional or effective networks…These links tend to obscure the topology of strong and significant connections and as a result are often discarded, by applying an absolute, or a proportional weight threshold” (Rubinov & Sporns 2010, p. 1060).

Connectional fingerprint: See **connectivity fingerprint**.

Connectivity: In network science, “A set of connections among nodes, forming a network of either structural or functional relationships.” (Sporns 2011, p. 327).

Connectivity fingerprint: The set of all input and output connections of a node, originally at the level of gray matter regions, that can be shown in an input diagram and an output diagram (see Passingham et al. 2002, Fig. 1; Kötter & Stephan 2003; Behrens & Sporns 2011, Fig. 2a; Sporns 2011, p. 62). Also see **functional fingerprint**.

Connectivity matrix: See **connection matrix**.

Connectome: “The complete description of the structural connections between elements of a nervous system” (Bullmore & Sporns 2009, p. 189). The most complete or global definition is, “A comprehensive network map of the anatomical connections of a species’s nervous system.” (Heuvel & Sporns 2013, p. 683). Such a complete connectome has been called a neurome when it includes the innervated parts of the body like muscles and glands (Bota et al. 2015). The “central motivating hypothesis is that the pattern of elements and connections as captured in the connectome places specific constraints on brain dynamics, and thus shapes the operations and processes of human cognition.” (Sporns et al. 2005, p. 249). “The archetypical brain network has a short path length (associated with high global efficiency of information transfer), high clustering (associated with robustness to random error), a degree distribution compatible with the existence of hubs, and a modular community structure. Furthermore, anatomical networks are sparsely connected, especially between nodes in different modules, and the ‘wiring length’ (the physical distance that connections span) is close to minimal. This profile of topological and geometric properties is typical not just of brain networks but also of many other complex networks, including transport systems and intracellular signalling pathways.” (Bullmore & Sporns 2009, p. 196). “Our understanding of the brain as an integrated functional system will be incomplete so long as we do not have a comprehensive description of its structural elements and interconnections…However, the quest for the brain’s wiring diagram cannot replace the search for theoretical principles that underlie brain network organization. Reliable and detailed maps of structural brain connectivity are necessary, but not sufficient, for formulating theoretical principles that capture the functioning of the brain as an *integrated system* with emergent and complex properties…Simply put, in order to understand how brain networks function, one must first know how their elements are connected.” (Sporns 2011, p. 76). The term was introduced by Sporns et al. (2005); see Sporns (2012b, p. 885).

Connectomics: "The central rationale for human connectomics builds on the premise that structural brain connectivity can serve as a basis for understanding brain dynamics and behavior" (Behrens & Sporns 2011, p. 5). The term was introduced by Hagmann (2005).

Connector hub: "A high-degree network node that displays a diverse connectivity profile across several different modules in a network." (Heuvel & Sporns 2013, p. 683). "Hubs that mediate a high proportion of inter-modular (often long-distance) connections." (Bullmore & Sporns 2012, p. 345). Formally, a hub with a high *participation coefficient* and a low *within-module degree z-score* (Rubinov & Sporns 2010).The concept was introduced by Guimerà & Amaral (2005). Also see **provincial hub**.

Core: A network core is "A group of nodes that share a large number of mutual connections, rendering them resistant to damage. Cores are identified by using a recursive procedure that prunes away weakly connected nodes." (Heuvel & Sporns 2013, p. 683).

Cost: Connection density…is the simplest estimator of the physical cost—for example, the energy or other resource requirements—of a network." (Bullmore & Sporns 2009, p. 188). Also see **wiring cost**.

Critical dynamics: "If a system is dynamically on the cusp of a phase transition between random and regular dynamics, it is said to be in a critical state or demonstrating critical dynamics." (Bullmore & Sporns 2012, p. 342). See **criticality**.

Criticality: "State situated between complete randomness and order, a hallmark of which is the absence of a characteristic scale of description." (Sporns & Betzel 2016, p. 19.20). See **critical dynamics**.

Cycle: "A path that returns to its origin, and thus links a node to itself. Cycles are also referred to as loops." (Sporns 2011, p. 327). But see **loop**. "A walk that starts and ends at the same vertex [node] but otherwise has no repeated vertices or edges, is called a cycle or closed path."; Wikipedia, *Glossary of graph theory* and *Cycle (graph theory)*.

Decomposable system: A system in which all communication takes place within modules or subsystems, a concept introduced by Herbert Simon (1962); see http://p2pfoundation.net/Decomposable_System

Degeneracy: "The capacity of systems to perform similar functions despite differences in the way they are configured and connected" (Sporns 2011, pp. 68-69). "Degeneracy is the capacity of a system to perform an identical function with structurally different sets of elements…Thus, a degenerate system can deliver constant performance or output even when some of its structural elements are altered, compromised, or disconnected. Unlike redundancy, degeneracy does not require duplication of system components. Degeneracy is ubiquitous in complex networks with sparse and recurrent structural connectivity. For example, communication patterns in such networks can occur along many alternative paths of equivalent length, a property that protects the network from becoming disconnected if nodes or edges are disrupted." (Sporns 2011, pp. 211-212).

Degree: See **node degree**.

Degree distribution: "The degrees of all nodes in the network comprise the degree distribution, which is an important marker of network development and resilience.

The mean network degree is most commonly used as a measure of density, or the total 'wiring cost' of the network." (Rubinov & Sporns 2010, p. 1061). Degree distribution is an indirect measure of resilience that reflects network vulnerability to insult (Barabasi & Albert 1999, Rubinov & Sporns 2010).

Density: See **connection density**.

Diameter: For a graph, "The maximum finite distance between any pair of nodes."(Sporns 2011, p. 327). "The global maximum of the distance matrix is also called the graph diameter." (Sporns 2011, p. 9).

Directed connection: Connection with a "from-to" relationship between two nodes. For a given node, connections may be efferent (output, from) or afferent (input, to), and for a pair of nodes, connections may be unidirectional or bidirectional; see Kötter & Stephan (2003). A synonym is **directed edge**.

Directed edge: See **directed connection**.

Directed graph: "A graph that contains directed edges, also referred to as a digraph. Directed edges link a source node to a target node, and the direction of the edge defines the direction of information flow." (Sporns 2011, p. 327).

Directed network: See **directed graph**.

Directionality: The presence or absence of a "from-to" relationship between two nodes; see **directed connection**, **directed network**, **undirected connection**, **undirected network**.

Distance: "The distance between a pair of nodes is equal to the length of the shortest path between them. If no path exists, the distance is infinite." (Sporns 2011, p. 327). It is important to bear in mind that this is topological distance, not necessarily physical distance; see Sporns (2011, p. 11).

Distance matrix: "The entries of the distance matrix contain the distances (the lengths of the shortest paths) between all pairs of nodes. The entries are 'Inf' [infinite] if no path exists." (Sporns 2011, p. 328; for an example see Sporns 2011, Fig. 2.8A). The distance matrix is used to compute the characteristic path length (Sporns 2012a, p. 17). "The global maximum of the distance matrix is also called the graph diameter." (Sporns 2011, p. 9).

Economy: "Applied to brain network organization, economy refers to the careful management of resources in the service of delivering robust and efficient performance." (Bullmore & Sporns 2012, p. 338).

Edge: "A term [synonym] for a network **connection**." (Heuvel & Sporns 2013, p. 683).

Edge-disjoint paths: "Two paths (between a pair of nodes) are edge-disjoint (or edge independent) if they have no edges in common, and they are an important concept for characterizing network flows." (Sporns 2012b, p. 883).

Effective connections: "Effective connectivity attempts to go beyond structural and functional connectivity by identifying patterns of causal influence among neural elements." (Sporns 2011, p. 36). "Direct or indirect causal influences of one region on another and may be estimated from observed perturbations (Rubinov & Sporns 2010, p. 1060, based on Friston et al. 2003). "The pattern of causal effects of one neural element over another. Effective connectivity may be computed on the basis of temporal precedence cues (Granger causality, transfer entropy) or on the basis of a causal model (e.g., dynamic causal modeling)." (Sporns 2011, p. 328). Also see Friston (2011), Sporns (2014, p. 658).

Efficiency: see **global efficiency**.

Eigenvector centrality: "Eigen vector centrality takes into account interactions of different lengths and their dispersion, relying on walks rather than shortest paths. The measure captures indirect influence patterns by which nodes that are adjacent to highly central nodes become highly central themselves. Eigenvector centrality has not yet been widely applied to biological or neuroscience data sets." (Sporns 2011, p. 16).

Emergent properties: See **reductionism**.

Entropy: "A foundational measure of information theory is entropy, whose origins trace back to thermodynamics. In Boltzmann's formulation, entropy links the macrostate of a system (e.g., its temperature) to a probability distribution of its microstates (e.g., the kinetic energy of gas molecules). In the context of Shannon's information theory (Shannon, 1948), the entropy of a system is high if it occupies many states in its available state space with equal probability. In that case, an observation of the state of the system provides a high amount of information because the outcome of the observation is highly uncertain. If the system visits only very few states, then its entropy is low and its observation delivers little information." (Sporns 2011, p. 283).

Families: See cliques (Bullmore & Sporns 2009, p. 189).

Fingerprint: See **connectivity fingerprint**, **functional fingerprint**, **motif fingerprint**.

Functional connections: "The basis of all functional connectivity is time series data from neural recordings." (Sporns 2011, p. 37). "Measured as the statistical dependence between the time series of two network nodes (e.g., brain regions, neurons)." (Heuvel & Sporns 2013, p. 683). "Statistical association—for example, significant correlations—between neurophysiological measurements recorded from anatomically distinct neurons or regions at several time points." (Bullmore & Sporns 2012, p. 339). "Functional connections correspond to magnitudes of temporal correlations in activity and may occur between pairs of anatomically unconnected regions. Depending on the measure, functional connectivity may reflect linear or nonlinear interactions, as well as interactions at different time scales." (Rubinov & Sporns 2010, p. 1060). "Other measures of functional connectivity are mutual information or coherence." (Sporns 2011, p. 328). *It is important to realize that this particular definition of functional connectivity is statistical only in nature*, "Because it expresses statistical relationships, functional connectivity does not make any explicit reference to causal effects among neural elements or to an underlying structural model of the anatomy. Hence, an observed statistical dependence between two nodes does not allow the inference of a causal interaction between them. Effective connectivity describes the network of causal effects between elements…" (Sporns 2011, p. 37).

Functional fingerprint: Functional domains are arranged in a circle around a node of interest, with relative involvement shown by distance from the center (see Sporns 2014, Fig. 3a).

Functional integration: "The ability to rapidly combine specialized information from distributed brain regions. Measures of integration characterize this concept by estimating the ease with which brain regions communicate and are commonly based on the concept of a path." (Rubinov & Sporns 2010, p. 1061). See **paths** and **path length**.

Functional segregation: "The ability for specialized processing to occur within densely interconnected groups of brain regions. Measures of segregation primarily quantify the presence of such groups, known as clusters or modules, within the network. Measures of segregation have straightforward interpretations in anatomical (structural) and functional networks. The presence of clusters in anatomical networks suggests the potential for functional segregation in these networks, while the presence of clusters in functional networks suggests an organization of statistical dependencies indicative of segregated neural processing." (Rubinov & Sporns 2010, p. 1061).

Global efficiency: "A topological measure of the reciprocal or inverse of the path length between nodes. In brain networks, global efficiency is often used as a measure of the overall capacity for parallel information transfer and integrated processing." (Bullmore & Sporns 2012, p. 338). A measure of network functional integration that is the average inverse shortest path length (Rubinov & Sporns 2010). "Efficiency is inversely related to path length but is numerically easier to use to estimate topological distances between elements of disconnected graphs." (Bullmore & Sporns 2009, p. 188). "A fully connected network has maximal global efficiency since all distances are equal to one (all pairs of nodes are linked by an edge), while a fully disconnected network has minimal global efficiency since all distances between nodes are infinite." (Sporns 2011, p. 13). "In neural terms, a network with high (global) efficiency places all its nodes at short distances from each other, which enables them to interact more directly, thus promoting high functional integration." (Sporns 2011, p. 14). Also see **information flow**, **path length**, and **characteristic path length**.

Global integration: see **integration**.

Graph: "A mathematical description of a network, comprising a collection of nodes and a collection of edges." (Heuvel & Sporns 2013, p. 683). "Simple models of a system that are based on a set of nodes and the edges between them. The nodes represent agents or elements, and the edges represent interactions or connections between nodes." (Bullmore & Sporns 2012, p. 337). "When describing a real-world system, a graph provides an abstract representation of the system's elements and their interactions." (Bullmore & Sporns 2009, p. 186). "The terms 'network' and 'graph' are often used interchangeably." (Sporns 2011, p. 16). "A graph is a simple graph if it has no multiple edges or loops, a multigraph if it has multiple edges, but no loops, and a multigraph or pseudograph if it contains both multiple edges and loops (the literature is highly inconsistent)."; Wikipedia, *Glossary of graph theory*—also see **loop** and **connection** (edge).

Graph diameter: "The global maximum of the distance matrix is also called the graph diameter." (Sporns 2011, p. 9).

Graph measures: "Based on the insights they deliver, they can be classified into measures reporting on aspects of segregation, integration, and influence. Segregation (or specialization) refers to the degree to which a network's elements form separate cliques or clusters. Integration refers to the capacity of the network as a whole to become interconnected and exchange information. Influence measures report on how individual nodes or edges are embedded in the network and the extent to which they contribute to the network's structural integrity and information flow." (Sporns 2013, p. 249).

Graph theory: "A branch of mathematics that deals with the formal description and analysis of graphs." (Bullmore & Sporns 2009, p. 186). "The fundamental growth in the statistical mechanics of complex networks, and the power and elegance of graph theoretical analysis, suggests that this approach will play an increasingly important part in our efforts to comprehend the physics of the brain's connectome." (Bullmore & Sporns 2009, p. 196). Graph theory was first applied to neural circuitry in a very specialized way by Changeaux et al. (1973); see Sporns, Tononi, & Edelman (2000), who noted that "Representing networks as graphs has the important advantage of a parsimonious structural description that allows comparisons of different connection patterns within a common theoretical framework" (p. 127), and called their approach theoretical neuroanatomy. "Around 1990, when I completed my PhD and embarked on my postdoctoral research, no one in neuroscience was interested in graph theory…What prevented the early use and adoption of network approaches, apart from the skeptical attitude of most neuroscientists against anything 'theoretical', was the lack of suitable network data sets…From the beginning, we approached the graph structure of the brain as a 'causal skeleton' from which neural dynamics and distributed information emerged." (Sporns 2012b, pp. 882-883). "Modern graph theory offers a virtually unlimited range of analytic tools, with continual innovations across an extraordinarily wide range of applications in science and technology. Graphical tools naturally fit the organization of the brain (the brain *is* a network, after all), and they provide a coherent theoretical framework that links networks across scales (neurons, populations, brain regions) and modes (structural, functional, effective)." (Sporns 2012b, p. 884). "In all cases, the use and interpretation of graph models has to be motivated by the specific functionality of the neural system at hand." (Sporns 2011, p. 30). "Graph theoretical analyses have allowed us to make some first steps toward elucidating important architectural features of structural brain networks." (Sporns 2011, p. 102). The first paper explicitly to use and illustrate graph theory for a neural network, the primate visual cortex, was by Young (1992, Fig. 1). The application of graph theory to fMRI was pioneered by Achard et al. (2006); see (Sporns 2012b, p. 884).

Heavy-tailed degree distributions: "A term that is generally used to mean that the proportion of high-degree nodes (nodes with a large number of edges connecting them to other nodes (hubs) is greater than in random graph (network)." (Bullmore & Sporns 2012, p. 340).

Hierarchical modularity: "Organization of a module into submodules, of submodules into sub-submodules, and so on." (Sporns & Betzel 2016, p. 19.20; also see Behrens & Sporns 2011, Fig. 4c). "Modularity has a major role in constraining the dynamics of neural activity as well. For example, modular networks give rise to more complex dynamics than random networks (Sporns et al. 2000), and they promote metastability (Wildie & Shanahan 2012) and synchronizability (Arenas et al. 2006) as well as the separation of timescales (Pan & Sinha 2009). These effects are particularly evident in networks that exhibit hierarchical modularity, i.e., are characterized by the existence of modules-within-modules across multiple spatial scales (Kaiser et al. 2010). Network models suggest that hierarchical modularity is an important structural ingredient for enabling the dynamic regime of criticality (Rubinov et al. 2011), which is characterized by spontaneous and persistent fluctuations, long transients following perturbations, and high information transfer." (Sporns & Betzel 2016, p. 19.20). See **modular structure**.

Hub: "Hubs are nodes with high degree, or centrality." (Bullmore & Sporns 2009, p. 188). "A node occupying a central position in the overall organization of a network." (Heuvel & Sporns 2013, p. 683). "A topologically important or central node, as defined by one of several possible measures of centrality, including degree centrality (number of edges) or betweenness centrality." (Bullmore & Sporns 2012, p. 337). "The most central or influential nodes in a network are often referred to as 'hubs,' but it should be noted that there is no unique way of detecting these hubs with graph theory tools. Instead, a conjunction of multiple influence measures (eg, degree, betweenness, vulnerability) should be used when attempting to identify hub nodes" (Sporns 2013, pp. 250-251). "The existence of hub nodes is essential to maintain network-wide information flow. Their loss or dysfunction has disproportionate effects on the integrity and functionality of the remaining system. Studies of social or technological systems have shown that hubs are points of vulnerability that may become subject to 'targeted attack.'…However, despite their highly central structural embedding and diverse functionality, hub nodes should not be mistaken for 'master controllers' or 'homunculus regions,' capable of autonomous control or executive influence. Their influence derives from their capacity to connect across much of the brain and promote functional integration, not from special intrinsic processing power or capacity for 'decision making.' Hubs enable and facilitate integrative processes, but they do not represent their outcome, which instead is found in the distributed and global dynamics of the brain." (Sporns 2011, pp. 124-125).

Hypergraph: A graph in which an edge can connect with any number of vertices (nodes); see Wikipedia, *Hypergraph*.

Indegree: "In directed graphs the indegree and outdegree correspond to the number of incoming and outgoing edges, respectively." (Sporns 2011, p. 8).

Influence: "Influence measures report on how individual nodes or edges are embedded in the network and the extent to which they contribute to the network's structural integrity and information flow…The simplest index of influence is the node degree, and in many (but not all) cases the degree of a node will be highly correlated with other more complex influence measures. Many of these measures capture the 'centrality' of network elements, for example expressed as the number of short communication paths that travel through each node or edge…Another class of influence measures is based on the effect of node or edge deletion on short communication paths or network dynamics. For example, vulnerability measures the decrease (in some cases, the increase) in global efficiency due to the deletion of a single node or edge. The most central or influential nodes in a network are often referred to as 'hubs,' but it should be noted that there is no unique way of detecting these hubs with graph theory tools." (Sporns 2013, pp. 249-250).

Information flow: "Network-wide communication and functional integration are facilitated by short path lengths…This aspect of the topology of structural brain networks has been quantified as 'brain efficiency.' Efficiency as a network measure was first introduced by Latora & Marchiori (2001) to express the capacity of networks to facilitate information exchange…[they] noted that the coexistence of high local and high global efficiency allows the network to balance localized processing, fault tolerance, and large-scale functional integration." (Sporns 2011, pp. 139-140).

Integration: Integration refers to the capacity of the network as a whole to become interconnected and exchange information…Measures of integration are generally based on the concept of communication paths and their path lengths…and the global average of all distances across the entire network is called the network's characteristic path length. Closely related to this measure is the global network efficiency, which is computed as the average of the inverse of all distances (path lengths)…Short path lengths promote functional integration since they allow communication with few intermediate steps, and thus minimize effects of noise or signal degradation." (Sporns 2013, pp. 249-250). This concept of integration was originally formulated as "multi-information" by McGill (1954); see (Sporns 2012b, p. 883). "Both measures (path length and global efficiency) take into account only short paths, while alternative but longer paths and the total number of short paths are neglected. Other measures of global connectivity take these alternative routes into account. One example is the communicability, a measure of global information flow based on the number of walks between nodes (Estrada & Hatano 2008)" (Sporns 2011, p. 14).

Intermodular connections: Integrating links or connections between **modules**; see Rubinov & Sporns (2010, p. 1062), Bota et al. (2015, p. E2099).

Intramodular connections: Connections (links, edges) within **modules**; see, for example, Bota et al. (2015, p. E2099).

Labeled graph: A graph whose nodes or connections have names or labels; the former is a **node-labeled graph**, the latter a **connection-labeled graph**. A graph with no labels is an **unlabeled graph**. See Wikipedia, *Glossary of graph theory*.

Lattice network: "In contrast to random graphs (networks), lattice graphs have an ordered pattern of connections between nodes. Examples of lattice graphs include the ring or grid lattice, where edges link nearby nodes in one or two dimensions, respectively. By their construction, lattice graphs have connections that are 'locally dense.' Connected nodes tend to have same neighbors, but distances between nodes vary greatly, with some shortest paths traversing a large number of intermediate nodes. Hence, in contrast to random graphs, lattice graphs have much higher clustering but also much longer characteristic path lengths." (Sporns 2011, p. 17). Lattice networks are arranged to minimize the number of connections and thus have a low cost, but also have low efficiency, and thus do "not favor global integration of information processing; there are not enough topologically direct connections between regions that are physically far apart." (Bullmore & Sporns 2012, Box 1). Lattice networks have a lattice topology that can be displayed as a lattice graph. Also called a regular lattice network.

Levels of analysis: For the **nervous system**, four nested hierarchical levels of analysis have been defined: macro (gray matter regions), meso (cell types), micro (individual cells), and nano (synapses between cells); see Swanson & Lichtman (2016). It has also been referred to as a "hierarchy of scales" (see Sporns 2011, p. 258), or scales of analysis. "Neural dynamics at each scale is determined not only by processes at the same scale but also by the dynamics at smaller and larger scales (Breakspear & Stam 2005). For example, the dynamics of a large neural population depend on the interactions among individual neurons unfolding at a smaller scale, as well as on the collective behavior of large-scale brain systems, and even on brain-body-environment interactions." (Sporns 2011, p. 258).

Line: Synonym for **edge** (Harary 1973, p. 2).

Line graph: "Network transformation in which edges in the original network are linked to one another if they share a node." (Sporns & Betzel 2016, p. 19.10). Google line graph wikipedia.

Link: An edge with two distinct endnodes; Wikipedia, *Glossary of graph theory*. See **connection** and **loop**.

Local efficiency: "A nodal measure of the average efficiency within a local subgraph or neighborhood." (Sporns 2011, p. 139). See **information flow**.

Loop: Definitions vary. It commonly refers to an edge that begins and ends on the same node; Wikipedia, *Glossary of graph theory*. But see **cycle**.

Modeling: see **computer simulations**.

Modular structure: "A partition that induces the division of a network into modules, usually such that no modules overlap" (Sporns & Betzel 2016, p. 19.4). "A given network can be decomposed into a set of non-overlapping, overlapping, or hierarchically arranged modules." (Sporns 2011, p. 328). "In a sense, modules allow a system to buffer the effects of randomly introduced fluctuations…Taken together, there are many reasons to view modularity as essential for the generation of stable heritable variation and for the emergence of new solutions to unanticipated changes in the environment." (Sporns & Betzel 2016, p. 19.19-20). "Modular networks give rise to more complex dynamics than random networks (Sporns et al. 2000)" (Sporns & Betzel 2016, p. 19.20). "More sophisticated measures of (functional) segregation not only describe the presence of densely interconnected groups of regions (clusters of nodes), but also find the exact size and composition of these individual groups. This composition, known as the network's modular structure (community structure), is revealed by subdividing the network into groups of nodes, with a maximally possible number of within-group links, and a minimally possible number of between-group links." (Rubinov & Sporns 2010, p. 1061). "The sub-global organization of a complex network. Modularity is an example of community structure, but not all network communities are simply modular." (Bullmore & Sporns 2012, p. 340). The degree of modularity is usually computed using optimization algorithms rather than exactly to save time, and some algorithms allow for nodes participating in more than one module, and methods are also being developed "to detect a hierarchy of modules (the presence of smaller modules inside larger modules)…(and) overlapping modular network structure, and hence acknowledge that single nodes may simultaneously belong in multiple modules." (see Rubinov & Sporns 2010, p. 1061). "Highly modular graphs often consist of densely clustered communities, but high clustering alone does not necessarily indicate the existence of modules or communities (see, e.g., regular graphs, below)." (Sporns 2011, p. 12). Methodological issues are discussed in detail in (Sporns & Betzel 2016, p. 19.3), who pointed out that "Importantly, modules can be detected in a purely data-driven way, based only on the topology of the network, and understanding which nodes belong to which modules can yield important insights into how networks function." (p. 19.3).

Modularity: "The scoring of a partition according to whether the internal densities of its modules are greater or less than the expected density." (Sporns & Betzel 2016, p. 19.3). Also see **clustering**.

Modularity maximization: "A set of community (modularity) detection methods aimed at uncovering partitions that maximize the modularity quality function." (Sporns & Betzel 2016, p. 19.4)

Module: "A group of nodes that maintain a large number of mutual connections and a small number of connections to nodes outside their module." (Heuvel & Sporns 2013, p. 683). "Despite great heterogeneity in methods and statistical practices, virtually all studies across all species support the existence of modules in both structural and functional brain networks. Theoretical work points to the importance of modules for promoting stability and flexibility, conserving wiring cost, and enabling complex neuronal dynamics." (Sporns & Betzel 2016, p. 19.21). "Thus, measures of clustering and modularity highlight a particular aspect of the functional organization of the brain, its tendency to form segregated subsystems with specialized functional properties. The identification of modules in brain networks is an important first step toward the characterization of these subsystems." (Sporns 2011, p. 13). See **modular structure**.

Module detection: "A set of tools used for identifying a network's community (modular) structure based on its topology." (Sporns & Betzel 2016, p. 19.4).

Motif fingerprint: The frequency of occurrence of different motifs around an individual node is known as the *motif fingerprint* of that node and is likely to reflect the functional role of the corresponding brain region (Sporns & Kötter 2004). See **motifs**.

Motifs: Local connectivity patterns in a network, such as two nodes connected bidirectionally, or thee nodes connected in a triangle. "To aid in the analysis of connection patterns in local neighborhoods, large networks or graphs can be decomposed into smaller 'building blocks' or 'networks-within-networks.' Such subgraphs, or motifs (Milo et al., 2002; 2004a), form a basic structural alphabet of elementary circuits." (Sporns 2011, p. 11). "The significance of a motif in the network is determined by its frequency of occurrence, usually normalized as the *motif z-score* by comparison with ensembles of random null-hypothesis networks (Milo et al., 2002). The frequency of occurrence of different motifs around an individual node is known as the *motif fingerprint* of that node and is likely to reflect the functional role of the corresponding brain region (Sporns & Kötter 2004). The frequency of occurrence of different motifs in the whole network correspondingly represents the characteristic motif profile of the network" (Rubinov & Sporns 2010, p. 1063). "The distribution of different motif classes in a network provides information about the types of local interactions that the network can support." (Bullmore & Sporns 2009, p. 188), and thus different structural motifs facilitate specific classes of dynamic or functional behavior (see Sporns 2011, pp. 108-109). "Every network can be uniquely decomposed into a set of motifs of a given size, and the distribution of different motifs can reveal which subgraphs occur more frequently than expected, relative to an appropriate null model." (Sporns 2013, p. 249). "For example, for directed networks there are exactly 13 possible connected 3-node motifs." (Sporns 2011, p. 328). "Comparison of motif classes across networks of different origin (e.g., neuronal, cell transcription, and ecology; Milo et al., 2004a) may require the construction of domain-specific random models." (Sporns 2011, p. 107). The foundational paper is by Sporns & Kötter (2004).

Neighbors: "A node's neighbors are all nodes that are connected to it with either directed or undirected connections." (Sporns 2011, p. 328).

Nervous system: A structure-function system of the animal body, like the circulatory and digestive systems (see Swanson & Bota 2010). At the cellular level, the structural and logic unit of nervous system circuitry is the neuron, and the nodes of the system can be described at four nested hierarchical levels (scales) of analysis, macro (gray matter regions), meso (cell types), micro (individual cells), and nano (synapses between cells) (see Swanson & Lichtman 2016). At one extreme, the circuitry comprising the nervous system can be described abstractly as either a mathematical network or graph, which is a topological representation, or as a physical object, which is a geometric or topographic representation in Euclidean space. See **topology**.

Network: "A mathematical representation of a real-world complex system and is defined by a collection of nodes (vertices) and links (edges) between pairs of nodes." (Rubinov & Sporns 2010, p. 1060). "Broadly, brain networks fall into two different categories. Structural networks represent anatomical wiring diagrams, while functional networks are derived from estimates of interactions among time series of neuronal activity…functional networks represent patterns of correlations that do not necessarily coincide with direct neuronal communication" (Sporns 2014, p. 652). "Brain networks span multiple spatial scales, from the microscale of individual cells and synapses to the macroscale of cognitive systems and embodied organisms…In this hierarchy, no single level is privileged over another. The notion that brain function can be fully reduced to the operation of cells or molecules is as ill-conceived as the complementary view that cognition can be understood without making reference to its biological substrates. Only through multiscale network interactions can molecules and cells give rise to behavior and cognition. Knowledge about network interactions on and across multiple levels of organization is crucial for a more complete understanding of the brain as an integrated system." (Sporns 2011, pp. 2-3). "The terms 'network' and 'graph' are often used interchangeably." (Sporns 2011, p. 16).

Network architecture: "Graphs of real-world networks fall into distinct classes that have characteristic architectural features. These architectural features reflect the processes by which the graph was constructed or developed, and they have an extremely important role to play in the function of the network as a whole." (Sporns 2011, p. 15). Important examples include random network, regular lattice network, small-world network, scale-free network, hierarchical network. "Different classes of network architecture can be qualitatively arranged within a space of possible networks (Solé & Valverde 2004)." (Sporns 2011, p. 22; see his Fig. 2.5). Also see **brain architecture**.

Network comparison: "Complex network analysis may be useful for exploring connectivity relationships in individual subjects or between subject groups." (Rubinov & Sporns 2010, p. 1065). They go on to discuss this emerging field.

Network neuroscience: It is a subfield of network science (see Börner et al. 2007): "the cross-disciplinary study of the structure and function of complex interconnected systems" (Sporns 2015, p. 1)—as applied to neuroscience (see Sporns & Betzel 2016). "A major appeal of network models is that they establish a firm link from neuroscience to a rapidly expanding theoretical framework for understanding complex networked systems." (Sporns 2014, p. 659). "While measures of segregation, integration, and influence can express structural characteristics of a network from different perspectives, recent developments in characterizing network communities or modules can potentially unify these different perspectives into a more coherent account of how a given network can be decomposed into modules (segregation), how these modules are interconnected (integration), and which nodes or edges are important for linking modules together (influence). Community (module) detection is an extremely active field in network science." (Sporns 2013, p. 251).

Network participation indices: They "measure relatively simple statistics of individual nodes such as the density, convergence/divergence [afferents/efferents, inputs/outputs, indegree/outdegree, to/from], and symmetry of a node's afferent and efferent connections. Respectively, these indices have identified regions that are more or less densely connected, that engage in widespread or more restricted interactions, and that predominantly receive or emit connections. Kötter and Stephan [2003] proposed that network participation indices could be related to modes of information transfer and thus be useful for defining nodes as either 'senders,' 'receivers,' or 'relays.'" (Sporns 2011, pp. 63-65).

Network resilience: See **resilience**.

Neurome: A complete network map of the structural (anatomical) connections of a species's nervous system at the macro, meso, micro, or nano level of analysis, including innervated parts of the body like muscles and glands (Bota et al. 2015, Swanson & Lichtman 2016).

Node: The agents or elements of a network, with edges representing interactions or connections between nodes (see Bullmore & Sporns 2012, p. 337). It "may represent a neuron, a neuronal population, a brain region, a brain voxel, or a recording electrode." (Sporns 2011, p. 328). A synonym is vertex.

Node convergence/divergence: A network participation index that involves a ratio of input connections/output connections [afferents/efferents, indegree/outdegree, to/from) for a node; "brain structures that are believed to have integrative 'binding' functions may be imagined to receive afferents from a particularly large set of brain areas. By contrast, a central executive structure might be characterized by a predominance of efferent connections." (Kötter & Stephan 2003, p. 1263).

Node degree: A basic and important network measure, for "an individual node, [degree] is equal to the number of links (connections) connected to that node, which in practice is also equal to the number of neighbors of the node (for undirected connections). Individual values of the degree therefore reflect importance of nodes in the network…The degrees of all nodes in the network comprise the degree distribution, which is an important marker of network development and resilience. The mean network degree is most commonly used as a measure of density, or total 'wiring cost' of the network. The directed variant of the degree distinguishes the number of inward links from the number of outward links, while the weighted variant of the degree, sometimes termed strength, is defined as the sum of all neighboring link weights." (Rubinov & Sporns 2010, p. 1061). "In directed graphs the indegree and outdegree correspond to the number of incoming and outgoing edges, respectively." (Sporns 2011, p. 8). "The degree has a straightforward neurobiological interpretation: nodes with a high degree are interacting, structurally or functionally, with many other nodes in the network." (Rubinov & Sporns 2010, p. 1064). "In brain networks, node degree and node strength may be simply viewed as a measure of direct interaction: high-degree or high-strength nodes can be interpreted to directly interact with a large number of other nodes." (Sporns 2011, p. 9). "The degree (or strength) can be highly informative in networks with very inhomogeneous degree distributions. In such networks, nodes with high degree are often essential for maintaining global connectedness. The degree is less informative about node importance in networks with fairly homogeneous degree distributions." (Sporns 2011, p. 15). "In modular anatomical networks, degree-based measures of within-module and between-module connectivity may be useful for heuristically classifying nodes into distinct functional groups (Guimerà & Amaral 2005). The *within-module degree z-score* is a localized, within-module version of degree centrality. The complementary *participation coefficient* assesses the diversity of intermodular interconnections of individual nodes. Nodes with a high within-module degree but with a low participation coefficient (known as provincial hubs) are hence likely to play an important part in the facilitation of modular segregation. On the other hand, nodes with a high participation coefficient (known as connector hubs) are likely to facilitate global intermodular integration." (Rubinov & Sporns 2010, p. 1064). "The node degree gives a first indication of centrality, especially in networks with a broad or scale-free degree distribution." (Sporns 2011, p. 327). It is computed from the distance matrix (Sporns 2012a, p. 17).

Node density: For an individual node, a synonym for **node strength**; see Sporns (2011, pp. 63-65). See **network participation indices**.

Node strength: "The sum of all edge (connection) weights (incoming and outgoing) for all edges (connections) attached to a given node." (Sporns 2011, p. 17). "In brain networks, node degree and node strength may be simply viewed as a measure of direct interaction: high-degree or high-strength nodes can be interpreted to directly interact with a large number of other nodes." (Sporns 2011, p. 9).

Node symmetry: A network participation index that measures the extent to which a node has bidirectional (symmetrical) versus unidirectional (asymmetrical) connections; "Clearly, symmetrical connectivity patterns indicate cooperative interactions, whereas, say, structures with a relay function would be characterized by asymmetrical connectivity since the afferent and efferent areas are different." (Kötter & Stephan 2003, p. 1263).

Node transmission index: see **node convergence/divergence**.

Null-hypothesis network: "It is important to note that values of many network measures are greatly influenced by basic network characteristics…(so) the significance of network statistics should be established by comparison with statistics calculated on null-hypothesis networks that have simple random or ordered topologies but preserve basic characteristics of the original network. The most commonly used null-hypothesis network has a random topology but shares size, density and binary degree distribution of the original network." (Rubinov & Sporns 2010, p. 1061).

Outdegree: "In directed graphs the indegree and outdegree correspond to the number of incoming and outgoing edges, respectively." (Sporns 2011, p. 8).

Overlapping communities: See **overlapping modules**.

Overlapping modules: Here, "Nodes can be affiliated with more than one subnetwork simultaneously." (Sporns & Betzel 2016, p. 19.10, where methodology is discussed).

Parcellation: "A subdivision of the brain into anatomically or functionally distinct areas or regions." (Heuvel & Sporns 2013, p. 683). "Parcellation schemes that lump heterogeneously connected brain regions into single nodes may be less meaningful. In addition, a parcellation scheme should completely cover the surface of the cortex, or of the entire brain, and individual nodes should not spatially overlap…networks may only be meaningfully compared if they share the same parcellation scheme" (Rubinov & Sporns 2010, p. 1060). Modern parcellation of gray matter regions (see Swanson 1991, 1992; Kötter et al. 2001) and neuron types (see Bota & Swanson 2007) are based on multimodal or polythetic approaches location, local structure, connections, gene expression patterns and so on.

Participation coefficient: "A graph-theoretical measure that expresses the distribution of edges of a node across all modules in a network." (Heuvel & Sporns 2013, p. 683). "Once a network has been partitioned into modules, individual network nodes can be classified based on how they are embedded within and between communities. Two measures that have proven fruitful in this endeavor are a node's participation coefficient and the z-score of its within-community degree (Guimerà & Amaral 2005). The participation coefficient, p_i, expresses the degree to which a node's connections are distributed across communities. If its value is close to zero, most of its connections fall within a single community. The z-score of a node's within-community degree, z_i, expresses the number of connections a node makes to other nodes in the same community in terms of standard deviations above or below the mean. Positive z-scores indicate that a node is highly connected to other members of the same community (module); negative z-scores indicate the opposite." (Sporns & Betzel 2016, p. 19.7-8). "High-degree nodes that maintain a diverse set of between-modules connections have a high participation coefficient. Such nodes, called connector hubs, are likely to facilitate intermodular communication and integration. On the other hand, high-degree nodes that have few or less diverse between-modules connections have a low participation index. These nodes, called provincial hubs, mostly participate in interactions within their own module and thus promote the cohesion of a single community (module)." (Sporns 2011, p. 15).

Paths: "Sequences of distinct nodes and links (connections) and in anatomical (structural) networks represent potential routes of information flow between pairs of brain regions." (Rubinov & Sporns 2010, p. 1061). "In many cases, a given pair of nodes can be connected by numerous paths." (Sporns 2011, p. 328). "A path is a trail in which all vertices (except possibly the first and last) are distinct." (Wikipedia, *Glossary of graph theory*). See **path length**.

Path length: "A measure of network topology. In a binary graph, the path length between two nodes is the minimal number of edges (connections) that must be traversed to get from one node to another." (Bullmore & Sporns 2012, p. 339). "Path lengths in weighted networks correspond to the sum of the edge lengths. Edge lengths are inversely related to edge weights since edge weights express the coupling strength and thus the proximity between nodes, not their distance. To compute path lengths for weighted graphs, one must first transform edge weights to lengths." (Sporns 2011, p. 13). "The distance between two nodes is the length of the shortest path linking the nodes and is often of particular interest (Sporns 2011, p. 9). Path length (distance) "refers only to the topology of the graph, not its metric or spatial embedding." (Sporns 2011, p. 16). "Lengths of paths…estimate the potential for functional integration between brain regions, with shorter paths implying stronger potential for integration…The average shortest path length between all pairs of nodes in the network is known as the *characteristic path length* of the network (e.g., Watts & Strogatz 1998) and is the most commonly used measure of functional integration. The average inverse shortest path length is a related measure known as *global efficiency* (Latora & Marchiori 2001). Unlike the characteristic path length, the global efficiency may be meaningfully computed on disconnected (e.g., lesioned or diseased) networks, as paths between disconnected nodes are defined to have infinite length, and correspondingly zero efficiency. More generally, the characteristic path length is primarily influenced by long paths (infinitely long paths are an illustrative extreme), while the global efficiency is primarily influenced by short paths…While a binary path length is equal to the number of links in the path, a weighted path length is equal to the total sum of individual link lengths. Link lengths are inversely related to link weights, as large weights typically represent strong associations and close proximity. Connection lengths are typically dimensionless and do not represent spatial or metric distance." (Rubinov & Sporns 2010, pp. 1061-1062). "Random and complex networks have short mean path lengths (high global efficiency of parallel information transfer) whereas regular lattices have long mean path lengths." (Bullmore & Sporns 2009, p. 188). "Structural paths that are shorter or are composed of fewer steps generally allow signal transmission with less noise, interference, or attenuation. Given two networks of equal size and density of connections, shorter path length or greater (global) efficiency is likely to reflect better overall communication in the corresponding network. It will also be a network with greater efficiency, another metric that is of significance in the context of brain networks. Efficiency is less sensitive to the presence of 'outliers,' disconnected or very weakly connected nodes, than the path length. In neural terms, a network with high efficiency places all its nodes at short distances from each other, which enables them to interact more directly, thus promoting high functional integration." (Sporns 2011, p. 14). See **functional integration**.

Phase transition: "The occurrence of phase transitions in network growth is significant because the sudden appearance of new structural network properties may have consequences for the network's dynamic behavior. Phase transitions have been suggested as important steps in the spontaneous emergence of collectively autocatalytic sets of molecules in the origin of life (Kauffman, 2000). Their potential role in neural development is still entirely unexplored." (Sporns 2011, p. 236).

Point: Synonym for **node** (Harary 1973, p. 2).

Provincial hub: "A high-degree network node that mostly connects to nodes within its own module." (Heuvel & Sporns 2013, p. 683). Formally, it has a high *within-*

module degree z-score and a low *participation coefficient* (Rubinov & Sporns 2010). The concept was introduced by Guimerà & Amaral (2005). Also see **connector hub**.

Random graph: "In random graphs each pair of nodes has an equal probability, *p*, of being connected. Large random graphs have Gaussian degree distributions. It is now known that most graphs describing real-world networks significantly deviate from the simple random-graph model." (Bullmore & Sporns 2009, p. 189). Random graphs have high efficiency but also have a high cost (see Bullmore & Sporns 2012, Box 1). The class of random network where edges between nodes are randomly assigned with fixed probability is known as an Erdös-Renyi graph (Sporns 2011, p. 328). "A random network (graph) is constructed by starting with a disconnected set of nodes and connecting pairs of nodes with a uniform probability. Random networks are composed of nodes with fairly uniform degree, and so the degree distribution has a characteristic scale defined by the mean degree. Pairs of nodes in sufficiently dense random networks are typically connected by short paths. On the other hand, nodes that are directly connected maintain uncorrelated patterns of connections, and it is very unlikely for two neighbors of a node to also be neighbors of each other. As a result, random networks have short characteristic path lengths but low levels of clustering." (Sporns 2011, p. 17). A synonym is **random network**; also see **network architecture**.

Random network: A network with the properties of a **random graph**.

Random walk: "A traversal over a network where each step from one node to another is randomly chosen." (Sporns & Betzel 2016, p. 19.8)

Reachability matrix: "The binary entries of the reachability matrix record if a path (of any length) exists between a pair of nodes." (Sporns 2011, p. 328).

Reciprocal connection: see **bidirectional connection**.

Reductionism: "Reductionist approaches have only limited success when applied to complex biological systems. For example, a recent review on cellular networks states that 'the reductionist approach has successfully identified most of the components and many interactions but, unfortunately, offers no convincing concepts and methods to comprehend how system properties emerge' (Sauer et al., 2007, p. 550). The authors continue to propose that 'the pluralism of causes and effects in biological networks is better addressed by observing, through quantitative measures, multiple components simultaneously, and by rigorous data integration with mathematical models,' [which is] the research program of the emerging discipline of systems biology (Kitano, 2002). The highly interconnected, hierarchical, and dynamic nature of biological systems poses a significant experimental and theoretical challenge, one that is not adequately addressed by the reductionist paradigm." (Sporns 2011, p. 278). "The interactions of components in a nearly, but not fully decomposable system [decomposable: all communication occurs strictly within subsystems or modules] generate phenomena that cannot be reduced to or predicted from the properties of the individual components considered in isolation…These emergent phenomena cannot be fully explained by dissecting the system into components, nor can their full functionality be revealed by an examination of isolated components or interactions alone. In many cases, different levels of scale interact." (Sporns 2011, p. 280).

Regular lattice network: see **lattice network**; also called a regular lattice graph.

Regular network: see **lattice network**; also called a regular graph.

Resilience: The capacity of a network to resist functional deterioration by damage is heavily determined by which nodes and connections are affected, and "Complex network analysis is able to characterize such network resilience properties directly and indirectly. Indirect measures of resilience quantify anatomical features that reflect network vulnerability to insult. One such feature is the *degree distribution* (Barabasi & Albert, 1999). For instance, complex networks with power-law degree distributions may be resilient to gradual random deterioration, but highly vulnerable to disruptions of high-degree central nodes…Another useful measure of resilience is the *assortativity coefficient* (Newman 2002). The assortativity coefficient is a correlation coefficient between the degrees of all nodes on two opposites ends of a link" (Rubinov & Sporns 2010, p. 1065). Other indirect measures are also available. "Direct measures of network resilience generally test the network before and after a presumed insult…When testing resilience in such a way, it is prudent to use measures that are suitable for the analysis of disconnected networks. For instance, the global efficiency would be preferable to the characteristic path length as a measure of integration." (Rubinov & Sporns 2010, p. 1065).

Resting-state network: "A set of brain regions that show coherent functional connectivity during task-free spontaneous brain activity." (Heuvel & Sporns 2013, p. 683).

Rich-club organization: "The propensity of a set of high-degree nodes in a network to be more densely interconnected than expected on the basis of their node degree alone." (Heuvel & Sporns 2013, p. 683). "Related to the core, a rich club is a set of high-degree nodes that are more strongly interconnected than expected by chance." (Sporns 2012a, p. 17). For the origins of this approach see Colizza et al. (2006).

Robustness: "The degree to which the topological properties of a network are resilient to 'lesions' such as the removal of nodes or edges." (Bullmore & Sporns 2012, p. 337). "The importance of an individual node to network efficiency can be assessed by deleting it and estimating the efficiency of the 'lesioned' network. Robustness refers either to the structural integrity of the network following deletion of nodes or edges or to the effects of perturbations on local or global network states." (Bullmore & Sporns 2009, p. 188). "Robustness and evolvability are supported by the modular organization of biological systems, found everywhere from gene and protein networks to complex processes of embryonic development…Modularity promotes robustness by isolating the effects of local mutations or perturbations and thus allowing modules to evolve somewhat independently. Networks of dependencies between system elements reduce the dimensionality of the global phenotypic space and effectively uncouple clusters of highly interacting elements from each other." (Sporns 2011, p. 141). In contrast to engineered systems, biological systems rely on network mechanisms [in preference to redundancy] for robustness to extrinsic and intrinsic perturbations." (Sporns 2011, p. 210).

Scale-free network or **graph**: See **scale-free organization**.

Scale-free organization: "A network with a degree distribution that follows a power-law (scale-free or scale-invariant) function." (Heuvel & Sporns 2013, p. 683). "The term 'scale-free' refers to the fact that a power-law distribution has no characteristic scale—'zooming in' on any segment of the distribution [for example, the macro, meso, micro, or nano levels or scales of analysis] does not change its shape, and the assignment of a characteristic scale for the degree of the network nodes is therefore meaningless." (Sporns 2011, p. 20). "A power law implies that the probability of finding a node with a degree that is twice as large as an arbitrary number decreases by a constant factor. This relationship holds over the entire distribution. For example, if the probability of finding a node with a degree of 10 was 0.4, then doubling the degree to 20 might reduce the probability to 0.1, and doubling it again to 40 lowers the probability to 0.025 (this particular power-law distribution has an exponent of 2)." (Sporns 2011, p. 20). "The most notable characteristic in a scale-free network is the relative commonness of vertices with a degree that greatly exceeds the average. The highest-degree nodes are often called 'hubs', and are thought to serve specific purposes in their networks, although this depends greatly on the domain. The scale-free property strongly correlates with the network's robustness to failure. It turns out that the major hubs are closely followed by smaller ones. These smaller hubs, in turn, are followed by other nodes with an even smaller degree and so on. This hierarchy allows for a fault tolerant behavior. If failures occur at random and the vast majority of nodes are those with small degree, the likelihood that a hub would be affected is almost negligible. Even if a hub-failure occurs, the network will generally not lose its connectedness, due to the hubs. On the other hand, if we choose a few major hubs and take them out of the network, the network is turned into a set of rather isolated graphs. Thus, hubs are both a strength and a weakness of scale-free networks." (Wikipedia: Scale-free network, Characteristics). For origins of the concept see Barabási & Albert (1999).

Scales of analysis: see **levels of analysis**; see Sporns (2011, p. 258).

Segregation: "Segregation (or specialization) refers to the degree to which a network's elements form separate cliques or clusters…An important measure of segregation is the clustering coefficient of a given node, essentially measuring the density of connections among a node's topological neighbors…Another aspect of connectivity within local (ie, topologically connected) sets of network nodes is provided by the analysis of network motifs, constituting subgraphs of 'building blocks' of the network as a whole." (Sporns 2013, p. 249). "It is often a realistic assumption that a large number of processing characteristics and functional contributions of a node are determined by its interactions within a local neighborhood. Importantly, this neighborhood is defined in terms of topological distance and does not necessarily imply close physical proximity. Several measures of local connectivity evaluate the extent to which the network is organized into densely coupled neighborhoods, also known as clusters, communities, or modules." Sporns (2011, p. 11). Also called local segregation; see Sporns (2011, p. 11).

Shortest path length: "The shortest path length between two nodes reflects the minimal number of links (connections or edges) that have to be crossed to travel from one node to another node in the network." (Heuvel & Sporns 2013, p. 683).

Simulated annealing: "A computer algorithm used to find a good approximation to the global optimum of a function over a large search space." (Bullmore & Sporns 2012, p. 343).

Simulations: See **computer simulations.**

Small-world network or **graph**: See **small-world organization**.

Small-world organization: "Originally described in social networks, the 'small world' property combines high levels of local clustering among nodes of a network (to form families or cliques) and short paths that globally link all nodes of the network. This means that all nodes of a large system are linked through relatively few intermediate steps, despite the fact that most nodes maintain only a few direct connections—mostly within a clique of neighbours. Small-world organization is intermediate between that of random networks, the short overall path length of which is associated with a low level of local clustering, and that of regular networks or lattices, the high-level of clustering of which is accompanied by a long path length…Evidence for small-world attributes has been reported in a wide range of studies of genetic, signalling, communications, computational and neural networks. These studies indicate that virtually all networks found in natural and technological systems have non-random/non-regular or small-world architectures and that the ways in which these networks deviate from randomness reflect their specific functionality." (Bullmore & Sporns 2009, p. 189). "A network whose average clustering coefficient is similar to that of a regular lattice network and whose characteristic path length is similar to that of a random network." (Sporns 2011, p. 17; for an example see Sporns 2011, Fig. 2.8B). "It is commonly thought that such an organization reflects an optimal balance of functional integration and segregation" (Rubinov & Sporns 2010, pp. 1062-1063). "It is important to note that the presence of the small-world topology by itself provides only limited information about network architecture. For example, it is possible for two small-world networks to exhibit very different patterns of connectivity. One could say that there exist a number of different types of small-world architectures." (Sporns 2011, p. 20). For origins of the concept see Travers & Milgram (1969) and for an elegantly simple explanation of the phenomenon see Watts & Strogatz (1998).

Spatially embedded network: A network viewed from the topographic, physical perspective, rather than viewed as a topological graph; see Sporns (2011, p. 195), Bullmore & Sporns (2012, Box 1).

Sparse coding: "A type of neural code that represents information by the activation of a small subset of the available neurons and/or by activation of neurons over a brief instant of time." (Bullmore & Sporns 2012, p. 340).

Strength: See **node strength**.

Structural connections: "A description of the anatomical (physical) connections between network nodes (i.e., brain regions, neurons); for example, reconstructed anatomical projections derived from diffusion MRI, directed anatomical pathways derived from neural tract tracing, or synaptic connections between individual neurons." (Heuvel & Sporns 2013, p. 683). "Structural connectivity refers to maps of anatomical connections between pairs of nodes, corresponding to the popular notion of the 'wiring diagram'." (Sporns 2015, p. 3). "Structural connections only constrain, but do not rigidly determine, functional interactions in the brain. This is particularly true for the patterns of dynamic coupling and coherence observed over short time scales." (Sporns 2011, p. 257).

Subsystem: See **module**.

Thresholding: See **connection matrix** and **connection weight**.

Topography: As applied to a network, the layout pattern of interconnections, defined in terms of physical reality or Euclidean space (see Swanson & Bota 2010). As opposed to **topology**.

Topology: "The geometric relation between nodes defined by their connecting edges, irrespective of any metric distances or spatial embedding." (Sporns 2011, p. 16). "Applied to a network, the layout pattern of interconnections, defined in terms of the relations of nodes and edges." (Bullmore & Sporns 2012, p. 337). As opposed to **topography**.

Transitivity: "A collectively normalized variant of the clustering coefficient" that avoids disproportionate influence of nodes with a low degree (Sporns 2011, p. 11).

Undirected connections: Connection with no "from-to" relationship between the two nodes.

Undirected network: "A network comprising undirected connections (edges)." (Heuvel & Sporns 2013, p. 683). "In structural connectivity, undirected edges indicate reciprocal anatomical coupling." (Sporns 2011, p. 328), although this is ambiguous because some structural methods (like DTI) do not have clear information about directionality, requiring an undirected connection, in distinction to a directed, bidirectional connection (with two directed connections between a pair of nodes). The reticular theory of nervous system organization (e.g., Gerlach and Golgi in the 19th century) postulated an undirected (unpolarized) network.

Vertex: Synonym for **node** in a network (Rubinov & Sporns 2010).

Walk: A sequence of nonunique edges, as opposed to an ordered sequence of unique edges and intermediate nodes (a path); see Sporns (2011, p. 9).

Weighted connections: See **connection weight**. Synonyms are weighted links and weighted edges.

Wiring cost: "The material and metabolic expenditure associated with supporting an organism's neuronal wiring" (Sporns & Betzel 2016, p. 19.16; also see p. 19.20). "The fixed cost of making anatomical connections between neurons, often approximated by the wiring volume of anatomical connections." (Bullmore & Sporns 2012, p. 338). "Mean network degree is most commonly used as a measure of density, or the total 'wiring cost' of the network." (Rubinov & Sporns 2010, p. 1061). Also see **cost**.

Wiring diagram: See **structural connections**.

Z-score of within-module node degree: See **participation coefficient**.

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