Communication dynamics in complex brain networks

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Abstract | Neuronal signalling and communication underpin virtually all aspects of brain activity and function. Network science approaches to modelling and analysing the dynamics of communication on networks have proved useful for simulating functional brain connectivity and predicting emergent network states. This Review surveys important aspects of communication dynamics in brain networks. We begin by sketching a conceptual framework that views communication dynamics as a necessary link between the empirical domains of structural and functional connectivity. We then consider how different local and global topological attributes of structural networks support potential patterns of network communication, and how the interactions between network topology and dynamic models can provide additional insights and constraints. We end by proposing that communication dynamics may act as potential generative models of effective connectivity and can offer insight into the mechanisms by which brain networks transform and process information.

Understanding how brain function emerges from patterns of communication between large numbers of neuronal elements stands as one of the enduring challenges of modern neuroscience[1–3]. Like many complex systems, the brain exhibits a very wide range of dynamic activity and connectivity patterns that are thought to be instrumental for enabling the integration and processing of information in the course of behaviour and cognition. Although much work has addressed the complex organization of the structural and functional networks of the brain[4–8], how this complexity supports communication processes that are fundamental to the brain's computational capacities remains poorly understood. In this article, we survey recent work on brain networks that illuminates the network basis of neuronal information processing and computation.

The complex systems approach to understanding the brain is akin to approaches in other disciplines that blend concepts from network science, statistical physics and dynamical systems to study social networks, the spread of epidemics, rumours or computer viruses, the effects of perturbations or attacks on electric grids or the World Wide Web, or the functioning of gene regulatory or metabolic networks[9,10]. These approaches all model a complex real-world system as a collection of elements that are linked by pairwise (dyadic) connections. The elements (or nodes) generally exhibit simple local properties and the connections (or edges) represent the relationships between these elements (for example, they may mediate the flow of energy or information,

the transmission of a virus, the physical binding between biomolecules or the conversion of such molecules in chemical pathways). Importantly, the topology of connectivity powerfully shapes the patterns of interaction and the communication between the elements of a system, which in turn govern its global behaviour. These patterns unfold dynamically across time in response to endogenous or exogenous perturbations. We define the complete set of spatiotemporal patterns of network communication that a given system exhibits or supports as the 'communication dynamics' of the system.

Communication is particularly relevant for networks that are specialized to transmit or distribute information in a coordinated manner. In the context of brain networks, which can be estimated from both anatomical and physiological data, two parallel theoretical approaches have crystallized to advance our understanding of communication[11–13]. First, graph theory has been instrumental for characterizing topological organization and for making inferences about information flow through a network. Within this framework, the nature of graph-based inference (or prediction) of communication patterns strongly depends on how elementary communication events are conceptualized and formally defined. Second, models and simulations of dynamical systems generate communication events that temporally evolve on top of a structural graph. Essentially, this approach captures the interdependencies between anatomical structure (topology) and communication dynamics as they unfold on the network. The nature of the dynamics

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Random walk
A stochastic process that describes a succession of random steps taken on a network.

Network topology
The patterns of connectivity of a network.

Neural elements
Unit elements of a neural network. The unit is defined by the spatial scale. Neural elements can represent, for example, a single synapse, a neuron, a neuronal population or an entire brain region.

Adjacency matrix
A mathematical representation of a network as a matrix. Elements of the matrix indicate whether two nodes are connected or not.

ranges from simple linear processes such as random walk dynamics, to more complex spreading processes and consensus models and, finally, to nonlinear models that are based on neuronal biophysics and physiology.

In this Review, we examine the key contributions of these two parallel approaches to understanding communication dynamics in brain networks. We investigate what key concepts of network topology can predict about patterns of network communication. We then focus on clarifying some of the explicit and implicit assumptions behind different dynamical models, what these models have taught us about the brain and how they relate to neurobiological theories and empirical evidence. Next, we attempt to place these theoretical ideas and models within the context of computational accounts of brain function. We end by looking at possible future insights that result from the development of more advanced computational and theoretical tools and from the increasing availability of empirical data.

Conceptual framework

Network neuroscience conceptualizes brain function as emerging from the collective action of numerous systems elements and their mutual interconnections[14,15]. Brain networks extend across a broad range of spatial and temporal scales, and can be assembled from various recording and mapping techniques that capture (usually pairwise) relationships among elements. The analysis and modelling of brain networks draw from the methods and tools of network science[16–18]. Briefly, brain networks are represented as sets of neural elements (nodes) and their pairwise connections (edges), often summarized in the mathematical form of an adjacency matrix (also known as a connection matrix). The relationships between nodes and edges define the topology

of the network, and edges may be directed or undirected, weighted or unweighted, depending on the nature of the empirical data from which the networks are constructed.

In FIG. 1, we present a conceptual framework that places communication dynamics in the context of two frequently studied domains of brain networks: structural connectivity and functional connectivity. Structural connectivity and functional connectivity differ in many fundamental respects. Structural connectivity (the connectome) reflects the anatomical (physical) relationships between neural elements; that is, their synaptic connections or inter-regional projections (the 'wiring diagram'). Functional connectivity, by contrast, describes the set of pairwise statistical dependencies between the neurophysiological signals (time courses) recorded from individual neural elements. As such, functional connectivity can be expressed in many ways, from simple cross-correlations to more complex measures that attempt to infer patterns of directed influence. Although numerous studies have demonstrated similarities in the configuration of structural connectivity and functional connectivity, the relationship between the two is non-trivial. Structural connectivity acts as a 'skeleton' that constrains the flow of neural signals. Subsets of structural couplings are engaged in a time-dependent and state-dependent manner. Resulting from signalling events that occur through these active links, patterns of functional connectivity exhibit fast dynamics that explore a large number of functional network topologies upon external perturbation and in the course of spontaneous fluctuations.

Importantly, observations of anatomy or time courses alone do not disclose dynamic patterns of neuronal signalling and communication. Direct observation of individual communication events (as opposed to their
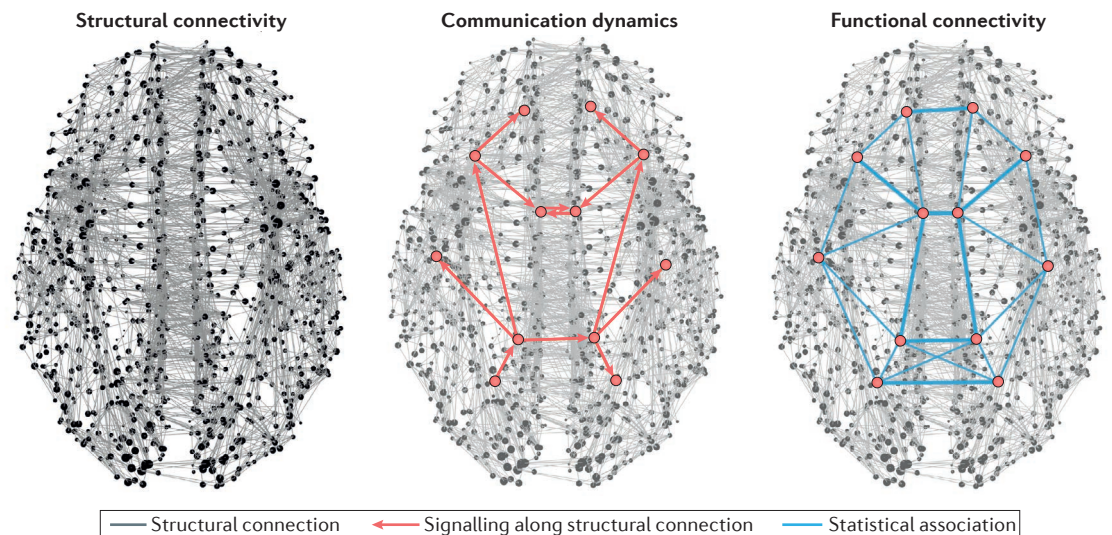

| Structural connectivity | Communication dynamics | Functional connectivity |

—— Structural connection   ←— Signalling along structural connection   —— Statistical association

Figure 1 | A conceptual framework for linking structural connectivity and functional connectivity. The left panel shows a network of structural connections (grey lines) that link distinct neural elements (brain regions; black dots). Neural activity gives rise to signalling events that propagate, at each given point in time, along distinct subsets of structural connections (middle panel; signalling routes and implicated neural elements in orange). The resulting statistical dependencies (in blue; right panel) among regional time series can be captured as functional connectivity.

effects on time courses) is difficult to achieve at the level of individual pairs of neurons or brain regions, and full coverage is currently beyond our existing technological capabilities at the systems level. However, models of communication processes and neuronal dynamics that are implemented on patterns of structural connectivity generate patterns of information flow that can be tracked and recorded *in silico*, together with their ensuing effects on time courses and functional connectivity. Our framework thus consists of a two-step generative model: the activity of neuronal elements that are coupled through structural networks generates patterns of communication (representing time-varying causal relationships between neural elements), which in turn generate dependencies among the elements' time courses that can be accessed as functional connectivity (FIG. 1). In other words, interactions between neural elements are dynamic, allowing flexible, time-varying patterns of information flow. When observed or aggregated over longer timescales, these dynamic patterns of information flow shape a (time-averaged) functional connectivity matrix. Empirical knowledge of structural and functional connectivity can then be used to test predictions made by competing models that represent hypotheses about the underlying communication dynamics.

Within the proposed conceptual framework, communication dynamics bridges structural connectivity and functional connectivity. Hence, communication dynamics in brain networks seems to be of fundamental importance for studies that characterize the brain's capacity for efficient integration and segregation of information[13,19,20], robustness and resilience to damage[21,22], and ability to adapt and self-organize in response to functional demands[23–25]. Important insight about possible, or likely, patterns of communication can be gleaned from the architecture (topology) of structural networks, with various local and global topological features supporting different aspects of local and global communication. The present account builds on the notion of coexisting segregation and integration, by showing that network topology cannot be studied in isolation, but must be considered in reference to a communication mechanism. This can be achieved by considering how network topology enables neural elements to interact with and influence each other, providing a mechanistic explanation for the emergence of statistical relationships between the constituent elements.

Network topology and communication

Several core concepts from graph theory have been applied to characterize the topology of brain networks and its role in network communication. Topological attributes have proved especially insightful in the context of the segregation and integration of information[20,26–29]. Across multiple spatial scales, brain networks have a characteristic topology that describes the system as a whole: heterogeneous degree and strength distributions, short path lengths and high clustering, a multi-scale modular organization and a densely connected core of high-degree nodes are some of the network attributes that are shared across species[30] and scales[31,32]. Embedded in the system,

neural elements derive their functionality by virtue of how they are connected — the connectivity fingerprint of each element[33,34] — and by how they contribute towards the capacity of the network to integrate and segregate information.

Routing communication. The capacity for two network nodes to communicate is fundamentally conditioned by the available paths connecting them through sequences of unique nodes and edges. Notably, even small networks contain a staggering number of possible ways to create paths between any two nodes. In communication networks, the shortest path between two nodes has a special role: the length of the shortest path is taken to be the topological distance between the nodes. Thus, the shortest path length is thought to be an indicator of the ease with which signals can be transmitted between two nodes. In neural systems that communicate via electrochemical transmission, minimizing the number of synapses between any two neuronal elements (that is, path length) is intuitively desirable. Longer paths are more susceptible to noise, are more likely to involve a greater number of distinct processing steps, incur longer transmission delays and are energetically (metabolically) more expensive to construct and use. The shortest-path statistics of a network — including the path length from one node to the rest of the network (closeness) and the propensity for nodes to occupy positions along many minimally short paths in the network (betweenness) — can be used to make predictions about the integrative capacity of individual elements and the entire network.

Is there any evidence to support shortest paths as a principal communication substrate in the brain? As a canonical example of a small-world network[35], the brain possesses near-minimal path length[36–38]. Interestingly, having a short average path seems to be a costly but desirable attribute of brain networks. Several computational studies have demonstrated that geometrically embedded networks that minimize wiring cost are characterized by physically short connections that have an overall topology that increases the mean path length[37,39,40]. The near-minimal path length observed in real neural architectures violates strict wiring minimization, requiring an additional material and energetic cost. This suggests that in the brain shortest paths are indeed utilized to ensure reliable and efficient communication, and hence stronger functional connectivity. Conversely, a longer path length between two neural elements should be associated with less direct signalling, yielding weaker functional interactions. Indeed, several studies have shown that the magnitude of functional interactions is negatively correlated with path length[41–44].

Most analyses about the integrative capacity of neural networks rely on shortest-path-based metrics[45–49] (for example, betweenness centrality, closeness centrality and graph efficiency) and thus rest on the assumption that neural elements have the ability to route information selectively through shortest paths. However, several considerations challenge the notion that communication between neural elements takes place exclusively through shortest paths. First, routing communication presupposes

Resilience
A network's ability to adapt and/or recover from structural failures.

Betweenness centrality
A nodal measure of influence determined by the proportion of shortest paths that traverse a node.

Routing
The process of sending a message or signal through a determined path.

that neural signals have access to information or knowledge about the global network topology[50–52] (BOX 1). This assumption is highly unlikely in a physiological system: it is difficult to envision how an action potential would encode its route and intended destination. Second, in many networks, reliance on shortest paths excludes most of the connections of a network from participating in communication processes, even when they provide near-optimal alternatives to the shortest path (FIG. 2a). For large-scale brain networks, this can amount to excluding more than 80% of the known fibre tracts[21]. Thus, shortest-path-based measures are insensitive to targeted edge removal as long as the subset of edges comprising shortest paths is preserved. A corollary is that the load of information flow on edges that comprise the shortest paths is disproportionately large, resulting in non-resilient communication that is prone to bottlenecks[53] and vulnerable to delays, loss of information and failure owing to damage[54,55]. Third, the trajectory of shortest paths strongly depends on how networks are defined. For example,

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Box 1 | An information spectrum of communication processes

It is no surprise that neural systems have evolved to conserve space, materials, time and energy[170]. Another costly, but less obvious, aspect of neural communication is the amount of information needed for communication processes to unfold. In the context of neural coding (that is, the neural representation of information), it was long ago suggested that there are limits on the amount of information that spike trains can encode or carry given the constraints on the metabolic energy that is available to sustain the firing rate of a neuron[171,172]. A different account of information as a costly resource that constrains communication processes emerges in the context of how signals are transferred. Are neural elements capable of directing (routing) signals through the network? Do signals travel through the network towards a predefined target neural element?

These questions are often implicitly addressed by different models of neural communication. In fact, we can map communication processes onto a continuous spectrum of information. In the figure, various communication models that take place on toy networks are placed along a spectrum of information, qualitatively representing how much (if any) information is needed for each communication process to take place. The trajectory or flow of a signal (indicated by red-coloured edges) through structural network connections varies according to each communication model. On one end of the spectrum lay communication processes that operate through routing protocols, in which neural elements must have full knowledge of the network topology to relay messages or signals through a specific path, and to a predetermined target (see the figure). Communication through optimally short paths is an example of routing, but routing can take place through multiple, sub-optimal path ensembles, such as in packet switching in Internet communication. The search information of a signal decreases with the number of paths that are admissible for the communication process to take place. The other end of the information spectrum is represented by diffusive processes, in which the global structure of the network is unknown to any neural element and the notions of a source or target node may not be defined. The (unbiased) random walk model is an example of such a process (see the figure); in this case, signal propagation is only driven by local network properties. Likewise, dynamical models that trace the activity of a neural element with time are not dependent on neural elements having information about the network topology, or the global state of the system. Similarly, communication processes based on percolation theory (for example, a local or global parameter p determines whether a node adopts an 'active' state (in red; see the figure) or not, based on the fraction of neighbouring 'active' or 'inactive' nodes) only rely on local information about the states of the node and its neighbours. Between the two extremes of the spectrum, there are various communication models that are yet to be further explored in the context of brain communication. For example, greedy-routing strategies can be efficient for certain network topologies[50] and require less information than routing communication[173]. A distance-based greedy-communication strategy consists of neural elements relaying signals to the neighbouring element that is closer to the target where the message is to be sent. Hence, each element must 'know' the distance between its neighbours and the target node, which requires considerably less information than knowing the entire network wiring diagram.

Other communication strategies that require little information include preferential strategies in which nodes preferentially transfer messages (deterministically or probabilistically) to high-degree nodes as a zoom-out strategy, followed by a zoom-in strategy, in which low-degree nodes are preferred[101,173]. These preferential strategies only require each element to know the degree of its neighbours, and to be able to determine whether it is in the zoom-in or zoom-out phase of the process.
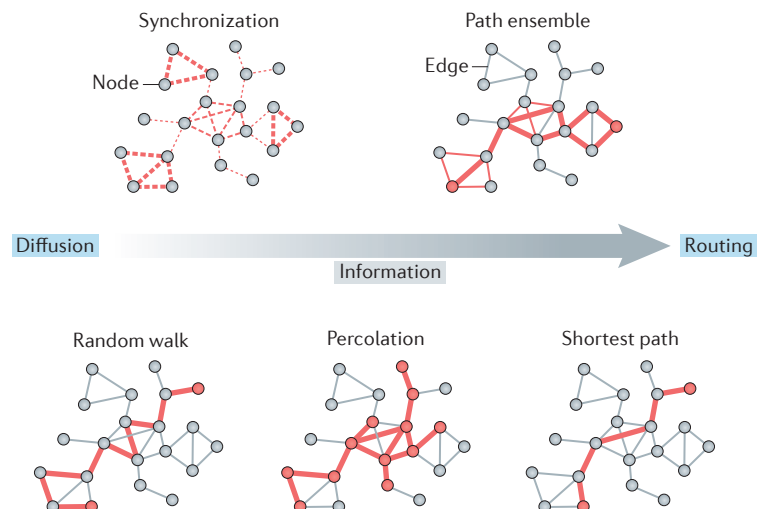
Fibre tracts
A bundle of axons connecting two brain regions.

Search information
The amount of information needed to discover a path in a network.

in the case of anatomical networks reconstructed from *in vivo* diffusion-weighted imaging, shortest paths may differ considerably depending on the choice of the measure expressing edge weight (for example, streamline count or density, fractional anisotropy, g-ratio or combinations thereof) and on how these weights are transformed to topological distance (BOX 2; FIG. 2b). Given these considerations, alternative communication models must be considered.

Parallel communication. Signal transfer that unfolds through multiple paths seems to be a more appropriate communication model for brain networks[42]. Indeed, computational analyses suggest that the recruitment of different alternative pathways can increase efficiency, robustness and resilience to brain damage[22,56,57]. In this framework, the number of paths between two neural elements has been proposed to reflect the resilience of the communication process between such elements[58]. Various measures have been developed to capture aspects of parallel and resilient communication; for

example, one measure of redundancy is defined in terms of the number of parallel paths that contain *h* links between two brain regions[59]. A similar approach[21] is based on path ensembles that comprise the *k* shortest paths between node pairs, which leads to a measure of resilience that is defined in terms of the number of edge-disjoint paths (FIG. 2c). This approach also proposes a more robust measure of distance between node pairs that takes into account the length and embeddedness of all the paths that comprise an ensemble.

It is worth noting that functional connections have a different interpretation under the lens of communication modelling. Notably, functional connections, whether static or dynamic[60,61], do not resolve the trajectories or temporal patterns of signal propagation through anatomical connections; instead, the co-variation of the activity of two neural elements expresses the aggregation of local, global, feedforward and feedback network interactions and computations[62–65]. Thus, a functional connection generally results from information flow through multiple, often polysynaptic paths,
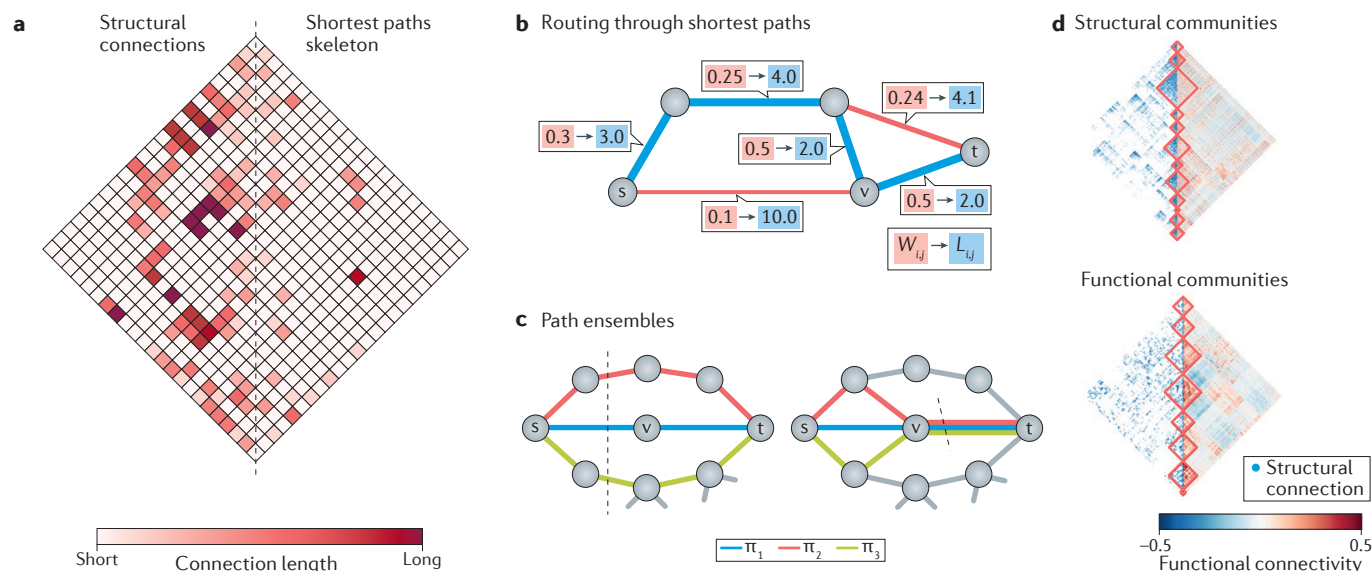

Figure 2 | **Network topology and communication. a** | Communication through shortest paths exclusively relies on a small fraction of high-strength connections, excluding most of the network connections from participating in the communication process. The schematic matrix represents a structural connectivity network (left triangle) and the structural connections comprising shortest paths (right triangle). The colour map indicates the physical length of the structural connections, and shows that long-range connections ('small-world' short-cuts) do not participate in shortest-path communication. **b** | Structural connection strengths are often interpreted as a measure of capacity for information flow. Connection strengths ($W_{i,j}$) must be mapped onto connection distances ($L_{i,j}$) to compute shortest paths. In this example, the reciprocal of the connection strengths (values in red boxes) maps strengths onto distances (values in blue boxes). Blue-coloured edges represent the shortest path between nodes 's' and 't'. Red edges are semi-metric edges; that is, the direct connection between node 's' and 'v' is topologically longer than the indirect (polysynaptic) path. Note that the shortest path length from 's' to 't' is 11, and it comprises four edges; the second shortest path length is 12, but it contains only two edges. **c** | Relaxing the assumption that signals only flow through the shortest paths allows communication through a path ensemble comprising the k shortest paths,

where k = 1 is the shortest path and as k increases, paths get progressively longer. The models illustrate three shortest paths (π_1, π_2 and π_3) on an unweighted network. Note that the second and third shortest paths (π_2 and π_3, respectively) are degenerate, as they have equal lengths. Parallel signalling through path ensembles increases the resilience of the communication process. If the paths in the ensemble have disjoint edges (left; highlighted by the dashed black line), network communication is more resilient than in path ensembles in which edges are shared by several paths (right; highlighted by the dashed black line). **d** | Structural and functional network communities rarely overlap. Neural elements that are densely interconnected (left side of the outlined red squares in the top matrix) do not trivially explain the emergence of functional modules (right side of top matrix). Likewise, neural elements that form functional modules (right side of the red-outlined squares in the lower matrix) are not always directly connected anatomically (left side of the lower matrix). This suggests that simple topological features such as direct connections and shortest paths cannot fully account for patterns of functional connectivity, which instead require a more nuanced exploration of the communication processes that lead to the observed functional interactions. Part **c** is adapted from REF. 21, Macmillan Publishers Limited. Part **d** is based on data from REF. 126.

Box 2 | Distance and communication

In the brain, distance is a multi-faceted concept. Fundamental to any network account of brain structure and function is the simple fact that the brain exists in 3D space; that is, it is geometrically embedded. This embedding defines the spatial layout of neural elements and their interconnections, and spatial proximity predicts greater likelihood of structural links[174]. Physical separation of pairs of nodes may be computed from spatial positions (Euclidean distance) or, in the case of structural networks, refers to the length of projections or axons, thus taking into account their spatial trajectory and curvature. These projection lengths are related to temporal conduction delays (which are also heavily dependent on axon calibre), which define temporal distances among node pairs.

However, physical or geometric distance is only one way in which one can express the degree to which neural elements are remote or close to each other. Network science adds the important dimension of topological distance, defined as the length of the shortest path by which two nodes can be linked. Topological distance may be expressed as the number of steps (an integer count) or in terms of the sum of edge lengths, derived from edge weights via a strength-to-distance conversion function[10,174]. In neural systems, structural-edge weights denote the strength and reliability of a connection and signals are often assumed to be more likely to flow through stronger connections. Hence, the shortest path between two neural systems is a measure of proximity in terms of the maximum capacity of information flow between two nodes. A strength-to-similarity conversion function translates edge weights from a strength (or capacity) space to a distance space, such that large edge strengths (high capacity of information flow) get mapped onto short edge distances, and vice versa. This mapping enables the computation of shortest paths — a classic minimization problem.

Despite the prevalent use of shortest paths in brain network analysis, there is no theoretical justification to support a particular conversion function. Conversion functions impose distortions of the network topology[175], and it is unclear how such distortions affect graph-based measures that are evaluated on the various weighting schemes (for example, fractional anisotropy, fibre densities, fibre count and number of synapses). The most commonly used conversion function is the reciprocal of the edge strengths (FIG. 2b). This conversion function transform yields extremely skewed distributions of edge distances, with very few, extremely short connections that are prioritized to participate in the overwhelming majority of shortest paths. Alternative conversion functions have been proposed that diminish this effect[41,175].

A lesser known implication of the strength-to-similarity conversion is that it generally yields non-metric topological distances that violate the triangle inequality. In other words, the shortest path between two nodes may not be a direct edge between them (if that edge exists), but instead, an indirect path composed of multiple edges. The semi-metric nature of brain networks has important implications on communication modelling. On the one hand, the role of long-range connections is under-represented in semi-metric topologies. A path formed by several strong, but physically short, edges is often preferred over a direct long-range, but weak-tie connection[28,102,176]. Notably, this topological effect is inconsistent with the popular idea that long-range connections provide 'small-world' shortcuts for routing signals across long distances (thus increasing the efficiency of the network). On the other hand, it has been suggested that the semi-metric nature of brain networks supports high redundancy and sharing of information among neural elements[102,177].

even in the presence of a direct anatomical connection between neural elements[66–69]. This redundancy implies that changes in or perturbations of functional connections cannot be directly interpreted as re-routing of information flow along specific paths. Despite these considerations, functional connections undoubtedly convey some information about the patterns of information flow through the underlying structure. For instance, temporal delays that maximize the lagged co-variation between pairs of neural elements can be used to infer the direction (but not the actual route) of signal propagation[70]. Alternative statistical methods used to infer the directionality of information flow, such as Granger causality[71], transfer entropy[72,73] and others[74], show that dominant patterns of information flow are associated with specific frequencies in neurophysiological recordings[75,76]. For example, posterior-to-anterior information flow has been associated with high-frequency bands, whereas the reverse pattern is dominated by a lower-frequency band[77]. However, these analyses do not take into consideration the underlying anatomical connections through which signals actually propagate. By contrast, a recent study combined structural and functional data to infer 'time-respecting' paths through which signals propagate in the human brain[78]. Time-respecting paths were defined as sequences of nodes that were structurally connected and temporally synchronized. The time-respecting paths differed from the topological

shortest paths; however, the former's length exhibited a higher correlation with functional connectivity than did the shortest path lengths.

Communication efficiency. A more realistic account of the integrative capacity of neural systems requires an important distinction between the concept of 'communication efficiency' and the commonly used graph-theoretic measure called 'global efficiency' (REF. 79). The global efficiency of a network is defined as the mean of the inverse of the shortest path length between all pairs of nodes, thus capturing the global capacity of the network to transmit information in a parallel fashion. Although this measure is frequently invoked as an index of integration of information, it is important to note that, by relying on shortest paths, it inherits the caveats associated with routing communication discussed above. Strictly speaking, global efficiency (perhaps better called 'routing efficiency' (REF. 51)) provides an upper limit on the integrative capacity of a network, not taking into account congestion or other sources of transmission delays, and assuming equal interaction likelihoods across all node pairs. By contrast, a more realistic account of communication efficiency must be sensitive to several additional constraints that are imposed by the topology and emergent dynamics of a system, and be contextualized by the communication model under consideration[80].

Connection density
The fraction of connections present in a network, or a subsystem of a network, with respect to the maximum number of possible connections.

Morphospace
A space in which possible, impossible and real-world network architectures can be mapped.

The assumption that all node pairs communicate equally, which is inherent in the topological measure of routing efficiency, merits some attention, as this assumption may not hold for brain networks. Both structurally and functionally, neural systems are characterized by a modular organization[81] that is related to specialized neural processing[82–84], that unfolds at various spatial and temporal scales[31,32,85] and that is encountered across species[30]. Structurally, modules are generally characterized by groups of nodes that preferentially link to other nodes in the same community and that are sparsely connected to the rest of the network[86]. A high within-module connection density promotes high within-module communication efficiency[87]; sparser connections between modules enable efficient inter-module integration of information[28,88,89]. Hence, efficient integration of

information is supported by both inter-module communication and intra-module communication[26,27,90], but not necessarily equally among all node pairs. Moreover, the efficiency of inter-module communication and intra-module communication may rely on different attributes, as communication can take place through different processes (for example, feedback versus feedforward processing) and on different spatial and temporal scales. Notably, a topology that optimizes segregation and integration of information through interconnected modules may not exhibit global routing efficiency as high as that of a non-modular topology. This example further illustrates the divergence between the simple capacity measure of routing efficiency and the more realistic accounts of communication efficiency (BOX 3).

A similar integration–segregation framework is postulated for modules derived as communities in functional networks[28,29,91]. Functional modules are characterized by groups of neural elements that exhibit coherent fluctuations in physiological activity, suggesting that the neural elements are communicating or, at least, modulating each other's activity[92]. Surprisingly, neural elements that are connected by dense structural connections do not trivially explain the emergence of functional modules[93,94] (FIG. 2d). This counterintuitive mismatch between structural and functional modules suggests that simple topological features such as shortest paths are insufficient to account for patterns of functional connectivity, which instead requires more complex topological attributes to model functional interactions between neural elements.

Indeed, empirically observed structure–function relationships among elements of brain networks offer insight into how neural elements may potentially communicate with each other. As mentioned above, for areas that are directly connected, the weight of the structural connection, which is often interpreted as a measure of flow capacity or bandwidth, is correlated with their functional connectivity[42,66]. Beyond direct connectivity, as the topological distance (that is, path length) between two areas increases, their functional connectivity decreases, presumably reflecting a diminished capacity for communication[41,43,44]. Moreover, functional connectivity between distant areas is greater if there are multiple paths between them, suggesting that the availability of parallel channels potentiates information transfer[56,59]. Reinforcing the importance of redundancy and resilience, the greater the number of re-entrant detours between two nodes, the greater their functional connectivity[41]. Finally, how paths are embedded in the network also influences their functional interactions[95,96]. One study[41] showed that functional connectivity between two areas is greater if the shortest path between them is more accessible to diffusing signals, allowing such signals to be transferred with greater fidelity. In this regard, shortest paths that traverse many high-degree nodes are more 'hidden' from diffusing signals, as they provide many chances for detours or, from a biological perspective, a greater potential for the signal to be corrupted by signals from other sources[97] (FIG. 3a).

Box 3 | Communication efficiency as a driving force shaping network structure

Communication processes in neural systems can also be studied from a natural selection perspective, whereby it must be asked what kind of communication process benefits most from the brain's topological attributes, and how a preference for a particular communication process might drive the evolution of these attributes. For example, communication efficiency and wiring cost are two fundamental attributes that underpin the functionality of neural systems. Minimizing wiring enforces sparsity and penalizes long-distance communication. Efficient communication imposes costs on metabolic energy and processing speed, as well as the cost associated with the amount of information needed to identify and select short paths (for example, the search information). Jointly, these multiple cost demands probably play a major part in constraining the network morphospace of possible brain architectures[178]. One idea is that the brain, like most complex systems, has resulted from selection processes in which multiple, often competing, traits and constraints must be satisfied simultaneously[36]. An optimal solution to this problem is a balance between the competing traits such that the system can be functional. Optimization is assumed to be part of the intrinsic dynamics of natural evolving systems[179], and the optimality conditions of any system are crucial for the survival and/or functionality of the system.

   However, understanding the relationship between structure and functionality from a natural selection perspective is particularly challenging in the case of biological networks. For instance, in the context of neural systems, the question of how structure supports or optimizes communication efficiency is generally addressed by two different approaches. One approach is to study and characterize the structure and wiring cost of empirical networks and then to try to infer to what extent the structure is optimal to support and promote specific communication strategies. A second approach is to generate network structures that are optimal for specific communication strategies and then compare these optimal networks to empirical networks to assess whether they are structurally similar. Although the second approach provides a direct demonstration of the optimality of an empirical network to sustain a specific set of functions (for example, communication protocols), it also ignores the fact that biological systems are not engineered with a preconceived objective. Instead, evolution often results from tinkering; that is, natural selection operates on structures (morphologies) that already exist and cannot be rebuilt from scratch for the sake of optimality[179]. These historical contingencies impose strong constraints on the repertoire of possible structures that can be derived at any given moment, limiting the ability of a network to adopt a configuration that is optimal with respect to one or more functions. Nonetheless, several aspects of the topology of neural systems reflect optimization strategies. The hierarchical modular structure of neural systems, ubiquitous across scales and species, is a case in point. Experimental and computational studies have found that a hierarchical modular organization emerges as an optimal cost-efficient solution to diverse problems such as facilitating the coexistence of functional integration and segregation[13], and enabling evolvability and adaptability[180], while minimizing wiring and energetic cost[1,4,93].

a Search information   Path transivity
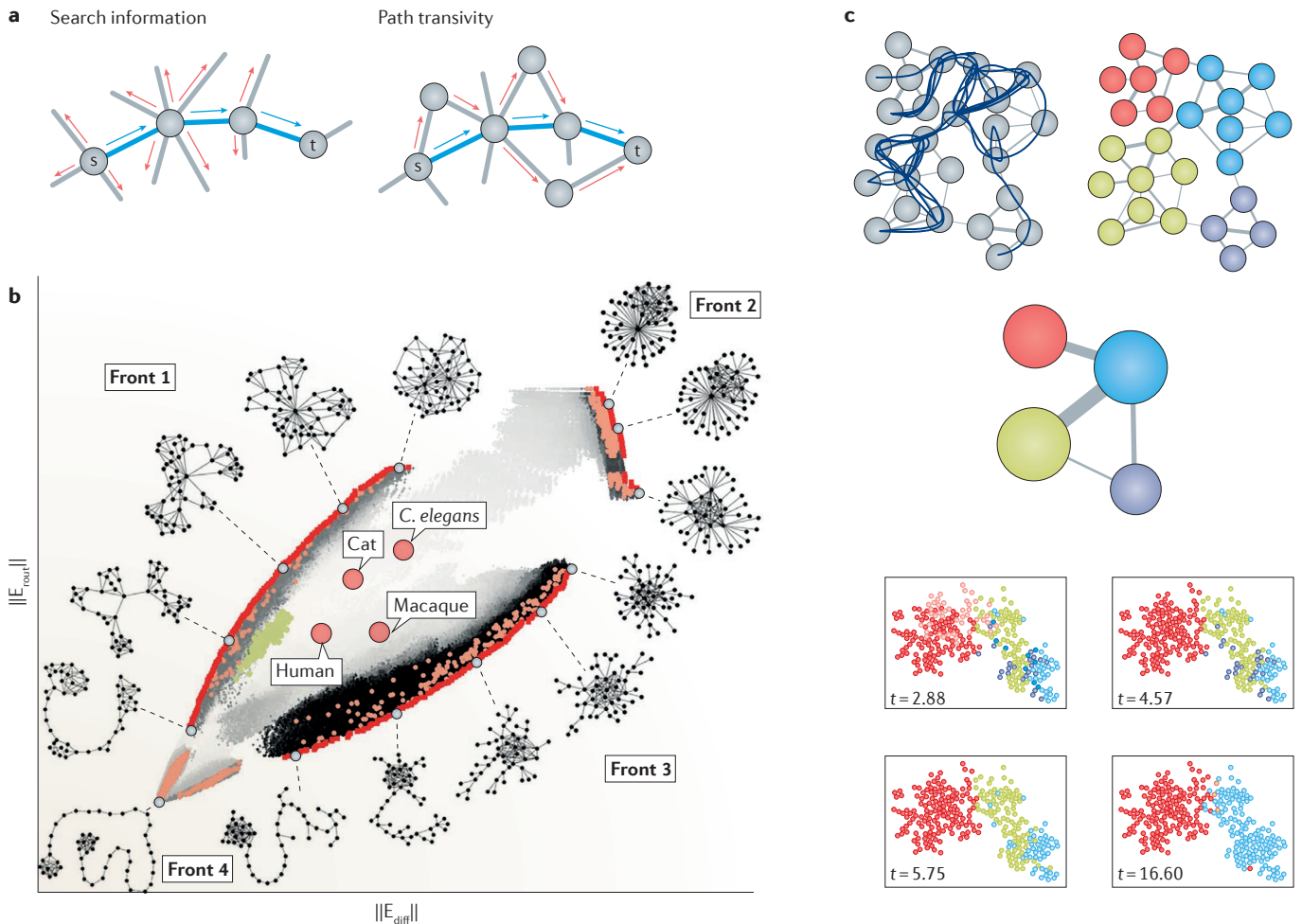

c

b

Figure 3 | **Interplay between architecture and communication dynamics.** **a** | Search information and path transitivity capture the hiddenness of a path within the network. The blue-coloured edges show the shortest path from 's' to 't'. Each intermediary node in the shortest path has several edges that act as potential detours for a signal travelling through the shortest path. In a scenario where a signal starting at node 's' and going to node 't' propagates randomly within the network, the more detours it encounters, the less likely it is that the signal will travel through the shortest path. Search information measures the amount of information (in terms of bits) that such a signal would require in order to travel through the shortest path. Conversely, path transitivity measures the number of re-entrant edges (red arrows departing and returning to the path) that would enable a signal to return to the shortest path after detouring from the path. **b** | A population of small-world topology networks (green markers) were evolved to simultaneously optimize diffusion efficiency ($\|E_{diff}\|$) and routing efficiency ($\|E_{rout}\|$), yielding an efficiency-morphospace of possible network configurations that maximize routing efficiency and minimize diffusion efficiency (front 1), maximize both routing and diffusion efficiency (front 2), maximize diffusion efficiency but minimize routing efficiency (front 3), or minimize routing and diffusion efficiency (front 4). All coloured regions indicate the existence of a possible network configuration. Notice that large regions of the morphospace are empty, indicating that the space of possible network configurations is strongly restricted. Red markers at each front show the final population of evolved networks for each front. Each front is characterized by a particular network topology. For example, networks in front 1 are modular, hence maximizing routing efficiency but minimizing diffusion efficiency, as the high ratio of intra-modular links to inter-modular links lowers the probability that diffusing signals will escape modules. Conversely, networks in front 2 are characterized by a highly connected core that supports diffusive signalling whereby highly connected hub nodes make even peripheral nodes accessible. Modular networks with a connective core (front 3) are not the most efficient on either axis, but the coexistence of these attributes may allow such networks to benefit from both diffusion and routing at different temporal and spatial scales. Empirically measured brain networks (outlined red circles) are not optimal with respect to any axis as they sustain a balance between diffusion and routing efficiency. **c** | Specialized communities or modules can be defined as groups of nodes in which information flows quickly or easily. This principle can be used to detect modules at different scales: the trajectory of a random walker on a network delineates groups of nodes (modules) that capture the random walker during various time intervals. The top panels illustrate one possible trajectory of a random walk on a small network, delineating four communities that tend to contain the trajectory of the random walker for some period of time. The colours of the nodes indicate their membership to a community. Each community can represent a single specialized neural unit that interacts with other units, in turn forming communities that are uncovered at larger temporal scales of a random walk. The bottom panels show a multi-scale flow-based partition of the *Caenorhabditis elegans* connectome, which outlines clusters of neurons (denoted by different colours) that reflect known functional circuits. Each frame represents a different timescale, as indicated by the parameter t. At short temporal scales, the trajectory of a random walker can only visit a few nodes and hence uncover small communities; for longer timescales, a random walker's trajectory can visit more nodes, uncovering larger communities. For *C. elegans*, this multi-scale process uncovers a sequence of robust partitions that are nearly hierarchically organized and that correspond to known functional circuits. Part **b** is adapted from REF. 51. The top panels in part **c** are adapted from REF. 111, Proceedings of the National Academy of Sciences. The bottom panels in part **c** are adapted from REF. 121.

The potential influence of node degree along structural paths on information transmission poses an interesting conundrum on the role of high-degree nodes, or hubs[98]. On the one hand, nodes with many connections are well positioned to facilitate integration of information both within and between specialized modules[29,40,49,86,99,100]. Moreover, highly connected nodes tend to connect with other highly connected nodes, forming a dense connective core that theoretically enables fast and direct communication between subsystems[27]. For example, most of the shortest paths in a network travel through at least one high-degree node[101], promoting re-entrant edges (FIG. 3a), a structural attribute that has been associated with stronger functional interactions[102]. On the other hand, in a decentralized scenario in which neural elements do not have knowledge about the global topology of the network, high-degree nodes facilitate detours that deflect messages away from optimal routes. Accordingly, paths that contain high-degree nodes are less likely to be followed just by chance, an attribute that has been shown to be associated with weaker functional connectivity[41]. Thus, despite the potential central role that high-degree nodes occupy in communication processes, their contribution to communication is dependent on the underlying dynamics of information flow.

Network dynamics and communication

In this section, we review communication processes from a dynamical point of view, building on the discussion above on the importance of the underlying structural topology in constraining signal propagation. As we will highlight in this section, one of the most important distinctions between dynamical and topological analyses of brain communication is the amount of information (in the statistical sense) that is needed for the communication process to unfold (BOX 1). The models we review in this section do not assume that neural elements have the capacity to access (and somehow encode) information about the global topology of the network[10,51,56,103]; instead, communication dynamics are driven by the interaction between the connectivity fingerprint and intrinsic dynamics of each node.

Flow-based communication models. One approach to model decentralized information flow is to assume that information disperses across the entire network through all possible paths and walks. The graph measure called communicability[104] operates under this hypothesis, offering an upper bound on the parallel processing capacity of the system, as all elements take part in signal transfer. Whereas routing efficiency is only sensitive to disruptions that affect shortest paths, communicability is sensitive to disruptions of all edges[105,106], supporting the intuition that perturbations of any network edge should affect the flow of information[42].

Parallel and redundant processing is important, but information that travels through all possible paths and walks can lead to an overloaded and congested system[53,107], in which loss and corruption of information are

more likely and the energetic cost required to ensure the spread of information is exceedingly high[36,108]. Moreover, communicability does not take into account how different paths and/or walks are topologically embedded in the network. Conversely, flow-based approaches that are driven by local topological properties can be energetically more efficient[109,110], as the global topology may impose constraints on how information propagates[111], thus avoiding a massively redundant amount of signals traversing the system.

The random walk is a flow-based model that describes the transfer of signals as a diffusion process that takes place on the network. At any given node, the probability that a signal — modelled by a random walker — will traverse a connection is proportional to the weight of the outgoing connections, thus assuming a preference for relaying signals through high-capacity connections. Locally, signal-diffusion dynamics depend only on the weights of the outgoing connections of nodes; globally, signal-diffusion dynamics are strongly driven by incoming connections, such that the larger the in-capacity of a node, the more likely it is that signals will arrive. Hence, under a diffusion model, high-indegree hubs have an integrative role[112], as signals naturally flow towards them, whereas low-indegree nodes are difficult to reach. Formally, these properties are captured by a pairwise statistic called the mean first-passage time, which measures the expected length of a (random) walk (in terms of number of traversed edges) between two nodes[113].

The mean first-passage time defines a topological distance between any two nodes communicating by diffusion, just like the shortest path length defines a topological distance for optimal routing. The inverse of the mean first-passage time is a global measure of diffusion efficiency that captures the integrative capacity of a network under a diffusion-based model of communication[51]. Comparative analysis of several real-world networks shows that centralized, star-like topologies and decentralized, modular topologies promote diffusion and routing efficiency, respectively. Interestingly, the topology of most real-world networks, including brain networks, achieves a balance between diffusion and routing efficiency by combining modular organization with a core of highly interconnected hubs (FIG. 3b). Modules contribute towards increasing the global routing efficiency of the system, whereas the central core contributes towards increasing the global diffusion efficiency. A computational study used a multi-objective optimization technique to investigate the capacity of human anatomical networks to evolve towards topologies that maximize or minimize diffusion and routing efficiency while preserving the wiring cost of the system[114]. The results of this investigation indicated that large-scale brain networks minimize diffusion efficiency, suggesting that the topology of brain networks is not well suited for the global spread of signals through diffusion. One possible interpretation of this finding is that large-scale topology limits diffusion to contain the spread of random perturbations and noise.

Hubs
Highly connected nodes.

Path transitivity
The frequency of detours comprising two edges (that is, of length 2) that are available along a path.

Integration and segregation through routing and diffusion. It is important to note that global measures such as routing and diffusion efficiency may not be representative of the local aspects of the network topology, as they discount the heterogeneity of the elements of the system. The inherently modular structure of neural systems suggests a different approach, in which efficiency measures are evaluated over network subsystems, as opposed to globally. Such analysis offers an alternative account of how neural systems might combine aspects of diffusion and routing. Indeed, modular structures counteract global diffusion efficiency, as modules act as structural 'basins' from which signals are unlikely to escape[115,116]. However, from a flow-based perspective, modules are characterized by clusters of nodes among which information flows quickly and easily[111], succinctly outlining network domains in which the efficient integration of information through diffusion is favoured (FIG. 3c). Thus, communication through diffusion may operate most efficiently within modules, whereas efficient flow of information between modules may necessitate routing communication.

Principles of flow-based dynamics have been used to uncover multi-scale organization of neural systems, in which modules detected at different timescales can be linked to biological and functional attributes. Under this framework, the temporal scale is defined in terms of the length of time — or the number of hops — needed before a random walker can escape a cluster of nodes[111,115]. For example, a flow-based model for multi-scale community detection on human structural networks found groups of brain regions that capture diffusive flow over various timescales[116]. Several of the detected components had a strong correspondence with unimodal functional communities, such as the visual, auditory or somatomotor systems. Interestingly, flow-based modules exhibited little correspondence with distributed systems that are generally associated with multiple cognitive states and that are characterized by containing a disproportionate number of connector hubs[117] that enable them to bridge different functional sub-subsystems[118–120]. A similar approach was implemented in the neuronal network of the nematode *Caenorhabditis elegans*, in which sequences of robust partitions of the network exhibited a nearly hierarchical organization that strongly corresponded to known functional circuits[121] (FIG. 3c).

Communication processes as a function of time. So far, we have considered the progression from targeted routing to structurally guided diffusion. The formalism adopted in the sections above emphasizes the static, long-term properties of such processes, embodied by statistics such as efficiency, communicability and mean first-passage time. Neural signalling is, however, highly dynamic. The waxing and waning of neuronal firing rates are associated with complex patterns of synchronization and desynchronization across multiple timescales. The transient reconfiguration of these communication patterns suggests that it is meaningful to consider how information may diffuse to new elements over time. In the following sections, we consider how to trace the temporal evolution of communication processes, using both computational and statistical models.

In contagion and spreading models, the state of a node depends on the states of its neighbours. In a neural context, local perturbations or signals — for example, representing the transduction of sensory stimuli — diffuse to connected elements. Neural elements are more receptive to information from topological neighbours if they are exposed to multiple simultaneous or coincident signals. By adding a finite threshold (that is, the number or proportion of neighbours that must activate before a node itself activates), the excitability of the network can be tuned parametrically, allowing a broad repertoire of emergent network behaviours.

This principle has been implemented in various random-walk models[52,122,123], threshold models[22,124–127], epidemic-spreading models[128–130] and avalanche models[131]. A simple threshold model implemented on large-scale cortical connectivity[126] found that regions that frequently co-participated in the same information cascade were more likely to exhibit stronger resting-state functional connectivity (FIG. 4a). Moreover, the anatomical embedding of polysensory networks, such as the default-mode network, favours the convergence of spatially remote signals onto these systems. Another model designed to predict functional connectivity from structural connectivity[52] demonstrated that although local dynamics of neurons and neuronal populations are nonlinear and nonstationary, the correlation structure of haemodynamic activity can be approximated by a simple, low-dimensional diffusion process that operates on the anatomical network. Altogether, applications of spreading models show that these models, despite their simplicity, may enable us to trace empirically observed patterns and characteristics of functional systems to features of underlying communication dynamics.

A natural extension to this approach is to endow individual nodes with intrinsic, biophysically realistic dynamics. Rather than simulate the spiking of millions of individual neurons, one may consider the mean activity (for example, firing rates and membrane potentials) of neuronal ensembles or populations of neurons[12,132]. The time-varying activity of a neuronal population is typically described by one or several differential equations, which are then coupled according to anatomical connectivity patterns. The collective dynamics of these neural elements, conditioned by anatomy, yield self-sustained oscillations and structured patterns of inter-regional synchrony. Large-scale nonlinear models have proved versatile, and recapitulate a range of phenomena, including electrical and haemodynamic functional connectivity patterns[66,133], clustering into intrinsic connectivity networks[134]. In addition, nonlinear dynamical systems may be configured to match, both qualitatively and quantitatively, various nonstationary behaviours that are observed in neural activity. For example, dynamical models may display multistable rhythms, with alternating periods of high and low synchrony[135].

How is communication conceptualized in such models? In the course of numerical integration, neuronal populations (nodes) influence each other's biophysical state through a diffusion-like process of passing incremental influences through the pairwise structural connections. Communication between two populations manifests as intermittent episodes of coherence[136]. Coherence among neurons enables rhythmic modulation of postsynaptic excitability, creating time windows when input gain is maximized[137] (FIG. 4b). The addition of noise in the presence of critical dynamics[138] seems to provide the best fit to empirically observed data[134,139]. Akin to stochastic resonance, this noise-induced synchronization is an attractive model for a communication system that is built around inherently low-fidelity electrochemical signal transmission[140]. The emergent communication process is richly dynamic: noisy fluctuations enables coherence to be rapidly established and dissolved, resulting in selective routing of signals[141] (FIG. 4c). This point deserves further consideration as we turn to the link between communication dynamics and communication.

Network computation and communication

So far, we have considered attributes of network topology that, in conjunction with a spectrum of dynamical models, contribute to communication processes in brain networks. Much of the interest in communication dynamics ultimately derives from their crucial role in neural computation. In this final section, we highlight several aspects of brain network communication that illuminate mechanisms by which brain networks perform computations.

Communication dynamics as effective connectivity. Functional connectivity is a major construct through which network-wide processes in the brain are described and monitored, during both rest and task conditions. It is worth reiterating that in its most common usage, functional connectivity expresses statistical dependencies among time courses (correlations) that, as has been pointed out in many empirical and modelling studies[142], do not generally represent direct neuronal signalling. More sophisticated measures have been proposed that are based on partial correlations[143,144], coherence[145] or temporal precedence cues that enable estimation of directed interactions[74,146,147]. Owing to the inherent interdependencies and (in the case of correlations) the transitivity of the individual pairwise measurements, networks constructed from bivariate estimates of functional connectivity face methodological difficulties. For example, in such constructed networks, node degree and strength may not accurately predict node influence or centrality[100], and the concept of a path (or walk) is ill-defined, as sequences of pairwise functional connections do not represent actual signalling routes.

Effective connectivity has been proposed as a more powerful and unambiguous way to capture stimulus-dependent or task-dependent patterns of causal influence among neural elements[5,148]. As effective connectivity cannot be measured directly, it is derived through a process of model construction and inference under rigorous criteria of model selection and fit. The limits on the scalability of this approach, which are imposed by the inferential nature of the process, are being addressed: for example, in recent work, effective connectivity was generated from whole-brain resting-state functional recordings[149,150]. Models of communication dynamics may offer a new perspective on effective connectivity that is complementary to 'model inversion' or inference, as they define 'forward' or generative models. The temporal sequences and spatial patterns of communication events in structural networks may be viewed as snapshots of effective (causal) connections that drive neural computation. As a generative model of effective connectivity, communication dynamics may offer a mechanistic link between the empirically more accessible domains of structural and functional connectivity (FIG. 1).

Computation by networks. The notion that computation is distributed among many elements and connections in networks is not new — it underpins most accounts of neural networks that have been presented over past decades, including the seminal advances made by connectionism and connectionist models (BOX 4). Like connectionism, network neuroscience emphasizes the role of ensembles of network nodes and edges in performing computational transformations on signals and activations. One important difference is that network neuroscience stresses the role of specific topological attributes in shaping computations. For example, as discussed earlier, the modular and core–periphery organization of many structural brain networks constrains the possible patterns of signal flow and the ease with which information can be distributed and shared[20,29,151] (FIG. 4c).

As the field advances, structural concepts such as modularity and core–periphery organization are taking on increasingly dynamic interpretations. With anatomical networks acting as scaffolds or structural skeletons that enable certain interactions while excluding many others, neuronal signalling (and the ensuing signal transformations; that is, computations) are inherently dynamic and context- or task-dependent[152,153]. Individual network elements fluctuate in their modular affiliation[25,154] and their functional connectivity with other parts of the brain[155,156], and extended functional networks reconfigure with changing task demands[156–159].

What neural mechanisms drive these changing patterns? Empirical and modelling studies suggest that changes in functional activations and connectivity can be traced to changing patterns of communication dynamics; that is, varying signal flow through specific subsets of structural connections. Models of attention and cognitive control have long suggested that these processes can act to selectively open subsets of communication paths to aid specific behaviours or computations. Synchrony[23,160] and "communication through coherence" (REF. 161) emphasize the importance of temporal (phase) relationships for sharing and transmitting signals along paths that can be dynamically

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Core–periphery
A tendency for a network to contain a densely interconnected central component.

Modularity
Propensity for nodes to form internally densely connected clusters.

a

b Bursting activity, 14 DIV

c
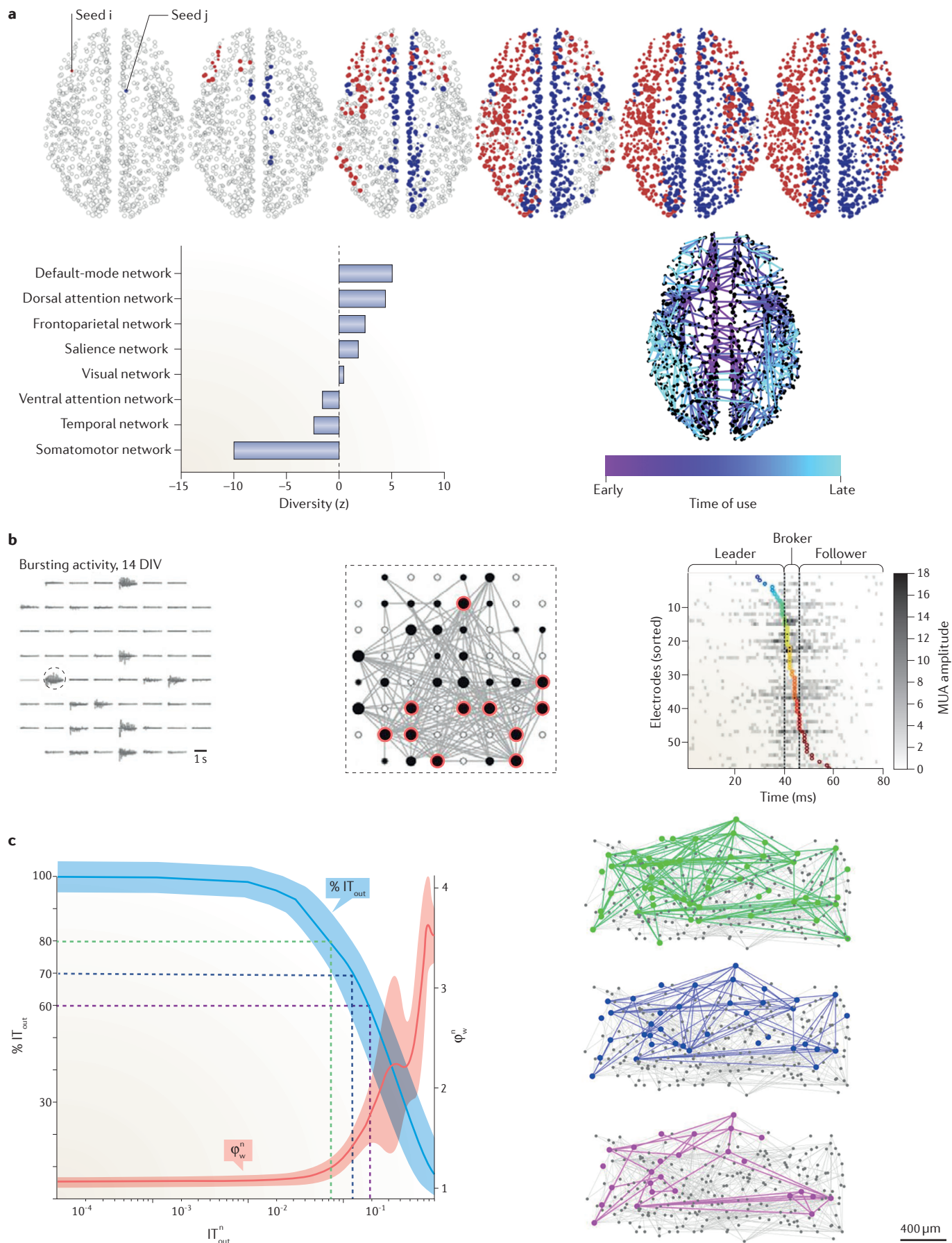
◄ Figure 4 | **Communication processes as a function of time. a** | The top row depicts a linear threshold model in which the state of a node depends on the state of its neighbours. Multiple competing signals were initiated (from seeds 'I' and 'j') and diffused over time through an anatomical network derived from diffusion-weighted imaging. The polysensory association networks (the default-mode network and the frontoparietal network) were frequently the point of convergence for remote signals in this model (reflected by their high diverse neighbourhood scores; left chart in bottom row;), suggesting that the integrative properties of these functional networks naturally arise from their anatomical embedding. Much of the spreading was mediated by a compact core of highly connected areas, including the precuneus, posterior cingulate, medial prefrontal cortex and bilateral insulae (see right image in bottom row), suggesting that this central component is crucial for mediating pairwise interactions and broadcasting of signals on the network. **b** | Multi-unit activity in dissociated hippocampal neurons reveals the development of microscopic communication patterns. Over 14 days *in vitro* (DIV), cultures exhibited an increased repertoire of spontaneous bursting activity, resulting in functional networks that increased in strength, density and size (left). Interestingly, this period was marked by a pronounced tendency for rich (highly connected) neurons to become richer, yielding a central core of highly connected hub neurons (red-ringed circles; middle panel). Multi-unit activity (MUA) exhibited distinct flow patterns and heterogeneous profiles, with some units acting as originators or 'leaders' and others acting as 'followers' (right). **c** | Organized communication patterns among cortical neurons. The weighted rich-club coefficient (ϕ_w; red) is shown for the total outgoing information transfer (IT; estimated via transfer entropy) for each neuron. The blue curve shows the cumulative outgoing information. The dashed lines (green, blue and magenta) show subnetworks (right) that cumulatively account for 80%, 70% and 60% of total outgoing information. Neurons with the greatest incoming and outgoing transfer entropy tend to interact with each other, forming a densely interconnected core. A large proportion of total information appears to pass through this small, highly privileged subset of neurons. Part **a** is adapted with permission from REF. 126, Elsevier. Part **b** is adapted from REF. 187. Part **c** is adapted from REF. 188.

reconfigured on fast timescales. The limits on the connection density, bandwidth and coding capacity of structural connections suggest that such connections participate in different communication events at different times, with effective paths opening and closing with changes in processing demands. A related model proposes that flexible routing of information is achieved through virtually instantaneous switching between different states of collective dynamics[141,162]. These ideas suggest important roles for transient synchrony and collective dynamics in distributing information in a spatially and temporally precise manner. A goal for future work is to find links between network topology and communication dynamics that can address the empirical problem of how brain networks perform computations in a manner that is adaptive, dynamic, fast and flexible. Another important future avenue is the use of appropriate experimental strategies to identify communication schemes that are used in the brain. At the microscale, communication pathways in neuronal circuits might be observed by stimulating individual neurons and tracking the pattern by which the perturbation spreads. The timing of this pattern, together with information about the underlying structural connectivity, may enable inferences about likely communication strategies. At the macroscale, the propagation of transcranial magnetic stimulation pulses can be measured with electroencephalography or magnetoencephalography[163,164], and the time at which these pulses arrive at downstream brain regions

or nodes might be used to infer likely propagation routes. Another strategy is the use of single-pulse electrical stimulation to perturb extended networks *in vivo* and the measurement of cortico-cortical-evoked potentials[165].

A final point relates to the nature of the fundamental units of neuronal signalling on which network computations are carried out. Most theories assume that neural information is encoded in spike trains and activation patterns, and yet how this information is transmitted within extended networks in a manner that maintains representational content is not well understood. Does neural information travel in the form of discrete packets, somewhat analogous to routing in telecommunication networks[54,55] and, if so, are these packets addressable to specific targets? Or is neural communication more akin to broadcasting; that is, is it primarily undirected? Most structurally guided communication models implicitly assume that signals are self-contained packets of information or signal units that are passed, essentially intact, from node to node. Routing through shortest paths operates with a single objective, which is to minimize the communication delay. This implies that the sequence of nodes that comprise the shortest path is selected not to perform a computation but only to relay an intact message from a source node to a target node. Hence, communication through shortest paths does not consider computation. Similarly, most communication models that consider parallel processing[21,58,59,80] use packets of information that are replicated and travel simultaneously through multiple pathways, affording redundancy and resilience to the system. However, such models do not consider that signals are transformed — for example, within local circuits — as they are transmitted between different subsystems or areas. By contrast, time-dependent diffusion-like models, whether discrete or continuous, express communication as an influence or modulation among neighbouring neural elements, more commensurate with a definition of communication that includes computation and signal transfer. Under this framework, the communication process consists of a sequence of time-dependent causal influences (flexible, time-dependent effective connectivity) between a set of neural elements.

Several theories (for example, the free-energy principle[166]) have posited that brain networks use some form of prediction-error propagation to encode representations. How global network architecture shapes the capacity of the system to minimize variational free energy and enact this mechanism is an exciting topic for future research[167]. More generally, how message passing and local computation can be reconciled remains unclear. Given the importance of neural signalling for computation, these and other questions regarding the nature of neural information and its transmission within extended, sparse and modular networks deserve greater attention. Models of communication dynamics can offer important insights as to the constraints and consequences that are inherent in different signalling protocols.

Box 4 | **From classic connectionism to network computation**

Classic models of information processing are based on theories that conceptualize neural computation as the transformation of activity patterns (representations), from inputs into outputs within distributed networks[181–183]. Under this framework, each neural component performs specific computations, and the results of these computations are relayed between components through neuronal connections. In simple physiological terms, neurons perform computations on their synaptic inputs and relay these outputs of these computations to other neurons through axonal connections. Neuronal signalling, then, represents the exchange of information, encoded in the form of spike trains. This exchange of information unfolds across sensory and motor systems within processing hierarchies that generate increasingly complex neuronal representations. One of the central objectives of the classic models is to identify the computational steps that underpin cognitive behaviours. How do the concepts in the classic models differ from a perspective based on concepts of network science and dynamics?

Although connectionism stresses the distributed and delocalized character of neural computation, it remains largely silent on the potential roles of network topology and emergent dynamics in the functioning of large-scale neuronal systems. Topology and dynamics, however, are central to network neuroscience: brain function relies on dynamic communication within highly structured networks[14], which enables coherent brain states that underpin behaviour and cognition[12]. These patterns are dynamic (reconfigured on multiple timescales, spontaneously and in response to varying processing demands), multi-scale (ranging over multiple spatial scales, from neurons to whole-brain systems) and rely on the highly complex organizational structure of the nervous system, the intrinsic and collective dynamics of neural elements[162], and external driving signals and noise owing to our interaction with the surrounding environment. The network view holds that functional specialization arises in large part from connectivity and interactions (in fact, it can be predicted from such patterns) rather than from specialized circuitry within isolated processing units.

Modularity plays an important part in many accounts of brain networks, both structural and functional. It also figures centrally in some computational accounts of cognition[184], in which it refers to encapsulated processing capacities akin to 'mental faculties'. However, network-based accounts of modularity represent a radical departure from models that divide the brain and mind into sets of local processors and that relegate the interconnections between these processors to relaying their outputs. Instead, network modules are directly derived from anatomical and functional brain data, and they are both multi-scale and dynamic, their boundaries shifting with fluctuations in information and communication events. Despite the sharp contrast between cognitive and network modularity, links are beginning to emerge between empirical studies of brain networks and formal accounts of cognition. For example, the flexibility of modules has been implicated in theories of learning[185] and features of network topology have been linked to the cost of cognitive control[186]. Thus, studies of brain network architecture and dynamics have begun to illuminate formal accounts of human cognition and behaviour.

Conclusion

Network neuroscience has begun to reveal how network topology and dynamics shape the flow of neuronal signals underlying brain function; however, many gaps in our knowledge remain, imposed by limits on data and of recording tools. For example, empirical access to communication dynamics is limited by the availability of observational tools that allow direct recording of elementary signalling and communication events. Hence, although it has become possible to map structural connections and record temporal dependencies among local time series, the mechanisms by which signals are transferred across the network in a manner that allows flexible and adaptive computation remain elusive. The spectrum of communication models considered in this Review may serve to guide future experimental investigation of these mechanisms. Despite limitations, there are also considerable opportunities for gaining generalizable knowledge on how brain networks operate. For example, dynamic network communication may offer a theoretical framework that can contribute to understanding behaviour and cognition, including patterns of change unfolding during development and with ageing[168]. It may also become an important tool for predicting the effects and outcomes of perturbations, including lesions and focal stimulation[163,169]. Building on topology and dynamics, the confluence of empirical and theoretical studies is poised to add significant new insights into the network basis of brain function.

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