

Opinion

Network Neuroscience Theory of Human Intelligence

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An enduring aim of research in the psychological and brain sciences is to understand the nature of individual differences in human intelligence, examining the stunning breadth and diversity of intellectual abilities and the remarkable neurobiological mechanisms from which they arise. This Opinion article surveys recent neuroscience evidence to elucidate how general intelligence, g , emerges from individual differences in the network architecture of the human brain. The reviewed findings motivate new insights about how network topology and dynamics account for individual differences in g , represented by the Network Neuroscience Theory. According to this framework, g emerges from the small-world topology of brain networks and the dynamic reorganization of its community structure in the service of system-wide flexibility and adaptation.

Spearman's Enigmatic g

Research in the psychological and brain sciences has long sought to understand the nature of individual differences in human intelligence, examining the stunning breadth and diversity of intellectual abilities and the remarkable cognitive and neurobiological mechanisms from which they emerge. The foundations of modern research in this effort were established in the early 20th century by Charles Spearman, who developed the correlation method and applied this technique to examine academic achievement within four branches of school study (i.e., English, French, classics, and mathematics) [1,2].

Spearman discovered that correlations in performance reflected characteristics of each discipline, observing that 'English and French, for instance, agree with one another in having a higher correlation with Classics than with Mathematics' [1]. Evidence that all branches of school study were not equally correlated motivated Spearman to conclude that they were influenced, in part, by mental abilities that were specific to each discipline. Beyond identifying the contribution of specific mental abilities, Spearman observed that the correlations among the four branches of school study were always positive. This finding, which is now well-established and named the positive manifold, provided evidence that all cognitive tests measure something in common. Spearman referred to this commonality as the general factor, g , which represents the component of individual differences variance that is common across all tests of mental ability.

These early findings motivated Spearman's two-factor model which held that performance on tests of mental ability jointly reflect (i) a specific factor, s , that is unique to each test, and (ii) a general factor, g , that is common across all tests [1,2]. Contemporary research has further elaborated Spearman's model to include an intermediate level of broad abilities that account for the variance that is shared across similar domains of cognitive ability. For example, the well-established Cattell–Horn–Carroll theory distinguishes between performance on tests of prior knowledge and experience, referred to as crystallized intelligence, from those that require

Trends

Accumulating evidence from network neuroscience indicates that g depends on the dynamic reorganization of brain networks, modifying their topology and community structure in the service of system-wide flexibility and adaptation.

Whereas crystallized intelligence engages easy-to-reach network states that access prior knowledge and experience, fluid intelligence recruits difficult-to-reach network states that support cognitive flexibility and adaptive problem-solving.

The capacity to flexibly transition between networks states therefore provides the basis for g – enabling rapid information exchange across networks and capturing individual differences in information processing at a global level.

This framework sets the stage for new approaches to understanding the neural foundations of g , examining individual differences in brain network topology and dynamics.

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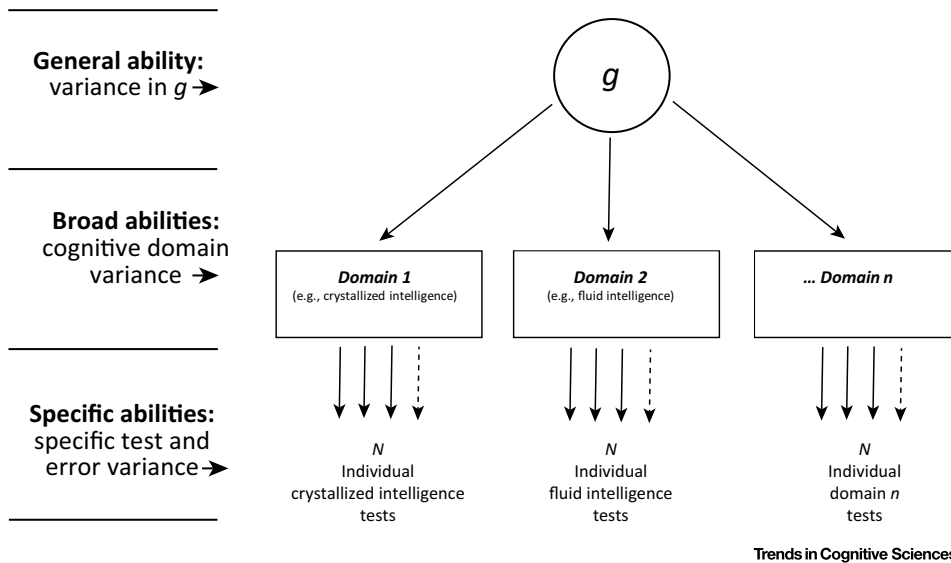


Figure 1. Hierarchical Structure of General Intelligence. At the level of specific abilities, people differ in scores on individual achievement tests, which are all positively correlated. At the level of broad abilities, strong correlations among tests measuring the same cognitive domain are present. At the level of general ability, people who perform well in one domain also tend to perform well in others, and therefore a general factor (g) can be derived. Adapted, with permission, from [6].

adaptive reasoning in novel situations, called fluid intelligence [3–5]. Taken together, the specific, broad, and general factors of intelligence account for the hierarchical pattern of correlations that are observed among tests of mental ability [3,6] (Figure 1).

Spearman's discoveries ushered in a new era of research on individual differences in human intelligence and uncovered fundamental mysteries about the nature and origins of g that stand as one of the most significant and enduring challenges for modern research in the psychological and brain sciences. Despite the fact that g represents the largest component of the common factor variance, its psychological foundations have remained largely invisible and beyond the reach of further scientific examination. The enigmatic nature of g arises from the fact that it is not a measure of specific knowledge, skills, or strategies for problem-solving. These aspects of task performance are simply a vehicle for the measurement of g . The general factor instead accounts for individual differences in information processing at a global level. Thus, we cannot understand the causal underpinnings of g by appealing to specific cognitive processes or by directly examining the psychological tests from which the general factor is derived. Research on the nature and origins of g must therefore extend beyond psychology to examine the neurobiological mechanisms that shape individual differences in cognitive ability.

This Opinion article surveys recent evidence from the burgeoning field of network neuroscience in an effort to elucidate how g – reflected in the positive manifold and the hierarchical pattern of correlations among tests – emerges from individual differences in the network topology and dynamics of the human brain.

Network Perspective

An enduring vision captured by early research in the neurosciences conceives of the human brain as a dynamic network of interconnected elements – ‘an enchanted loom where millions of flashing shuttles weave a dissolving pattern’ – revealing a complex topology echoed among the

stars, ‘as if the Milky Way entered upon a cosmic dance’ [7]. This celestial view seeks to discover the rich constellation of elements and connections that comprise the human brain at multiple levels of organization – from molecular foundations to higher-level systems – and continues to inspire modern research in the psychological and brain sciences, raising new possibilities for understanding the nature of human intelligence from a network perspective.

At the frontiers of research in this effort is the interdisciplinary field of network neuroscience [8,9] which applies methods from mathematics, physics, and computer science to enable the formal measurement and modeling of the interactions among network elements, thereby providing a powerful new lens for examining the emergence of global network phenomena. This rapidly developing field holds great promise for advancing research on the nature and origins of g , which represents a global network phenomena *par excellence*. Indeed, the general factor captures the variance that is common across all tests of mental ability and demonstrates predictive validity across a broad landscape of socially important variables – accounting for academic, professional, economic, and health outcomes [10].

It was therefore shortly after the discovery of g that Spearman’s contemporary, Godfrey Thomson, proposed that the general factor represents a global network phenomenon [11–13]. Thomson held that g emerges from the interaction among the many elements of the brain, which he referred to as neural arcs or bonds [14,15]. According to Thomson’s Sampling Theory of Mental Ability, each item on an achievement test samples a number of these bonds [11–13]. He proposed that the degree of overlap among bonds accounted for the correlation between tests and the resulting positive manifold. Thus, Thomson’s theory was the first to show that Spearman’s discovery of the general factor of intelligence is consistent with a network perspective.

Thomson’s legacy can be found in modern psychological theories which posit that g originates from the mutual interactions among cognitive processes [16]. Individual differences in g are known to be influenced, for example, by language abilities [10,17], which facilitate a wealth of cognitive, social, and affective processes through mutual interactions (i.e., reciprocal causation) [18]. The central idea of the Mutualism Model is that change or growth in one aspect of mental ability is (i) partially autonomous (owing to developmental maturation), and is also (ii) based on growth in other areas (owing to the mutual interaction between cognitive processes). By accounting for both the autonomous and interactive nature of cognitive processes, this model is able to explain individual differences in the general factor of intelligence – accounting for the positive manifold and the hierarchical pattern of correlations among tests [16].

Advances in network neuroscience have further sharpened Thomson’s notion of neural bonds, revealing principles of brain organization that support (i) the modularity of cognitive processes (enabling the autonomy of mental processes), and (ii) the dynamic reorganization of this modular architecture in the service of system-wide flexibility and adaptation (enabling mutual interactions between cognitive processes). The following sections review these principles of brain organization and introduce a Network Neuroscience Theory for understanding individual differences in the general factor of intelligence based on the small-world topology and network dynamics of the human brain. This framework relies upon formal concepts from network neuroscience and their application to understanding the neurobiological foundations of g .

Small-World Network

Through the incisive lens of his 19th century microscope, Ramón y Cajal observed that ‘the neuron and its various components are simply morphological adaptations governed by the laws

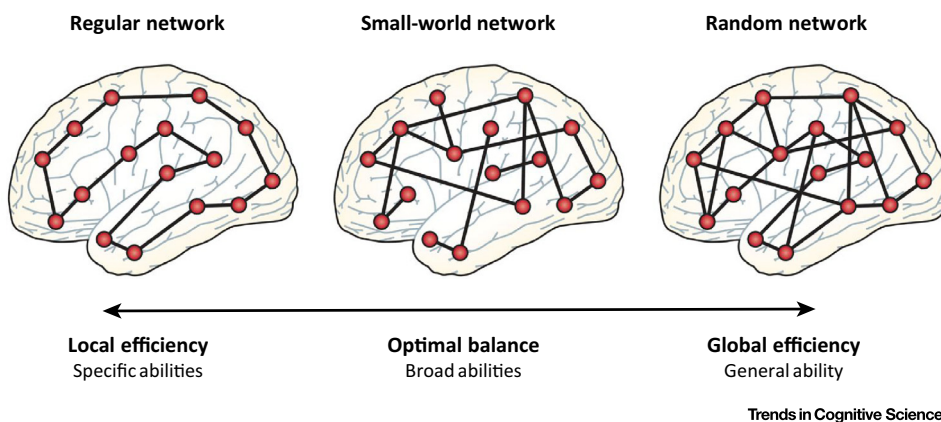
of conservation for time, space, and material' [19]. These principles provide the modern foundation for understanding the organization of the human brain, which is fundamentally designed for efficiency – to minimize the cost of information processing while maximizing the capacity for growth and adaptation [19,20].

Minimization of cost is achieved by dividing the cortex into anatomically localized modules, composed of densely interconnected regions or nodes. The spatial proximity of nodes within each module reduces the average length of axonal projections (conservation of space and material), thereby increasing signal transmission speed (conservation of time) and promoting local efficiency [21]. This compartmentalization of function enhances robustness to brain injury by limiting the likelihood of global system failure [22]. Indeed, the capacity of each module to function and modify its operations without adversely affecting other modules enables cognitive flexibility and therefore confers an important adaptive advantage [23,24].

Crucially, however, the deployment of modules for coordinated system-wide function requires a network architecture that also enables global information processing. Local efficiency is therefore complemented by global efficiency, which reflects the capacity to integrate information across the network as a whole and represents the efficiency of the system for information transfer between any two nodes. This complementary aim, however, creates a need for long-distance connections that incur a high wiring cost. Thus, an efficient design is achieved by introducing competing constraints on brain organization, demanding a decrease in the wiring cost for local specialization and an opposing need to increase the connection distance to facilitate global, system-wide function.

These competing constraints are captured by formal models of network topology [25] (Figure 2). Local efficiency is embodied by a regular network or lattice in which each node is connected to an equal number of its nearest neighbors, thus supporting direct local communication in the absence of long-range connections. By contrast, global efficiency is exemplified by a random network in which each node connects on average to any other node, including connections between physically distant regions.

Recent discoveries in network neuroscience suggest that the human brain balances these competing constraints by incorporating elements of a regular and random network to create a



Trends in Cognitive Sciences

Figure 2. Small-World Network. Human brain networks exhibit a small-world topology that represents a parsimonious balance between a regular brain network, which promotes local efficiency, and a random brain network, which enables global efficiency. Adapted, with permission, from [20].

small-world topology [26–28]. A small-world network embodies (i) short-distance connections that reduce the wiring cost (high local clustering) as well as (ii) long-distance connections that provide direct topological links or short-cuts that promote global information processing (short path length). Together, these features enable high local and global efficiency at relatively low cost, thus providing a parsimonious architecture for human brain organization [29–31] and capturing the modular (autonomous) and global (interactive) network topology that is essential to general intelligence [16].

Research in network neuroscience has consistently observed that the topology of human brain networks indeed exemplifies a small-world architecture, and this has been demonstrated across multiple neuroimaging modalities including structural [32], functional [33–35], and diffusion tensor MRI [36]. Emerging neuroscience evidence further indicates that general intelligence is directly linked to characteristics of a small-world topology, demonstrating that individual differences in g are associated with network measures of global efficiency [37,38]. Alterations in the topology of a small-world network have also been linked to multiple disease states [39,40], stages of lifespan development [41], and pharmacological interventions [35], establishing their importance for understanding human health and disease [42].

Network Neuroscience Theory

Recent advances in network neuroscience further elucidate the functions afforded by a small-world architecture, motivating new insights about how brain network topology and dynamics account for individual differences in specific and broad facets of general intelligence, represented by the Network Neuroscience Theory.

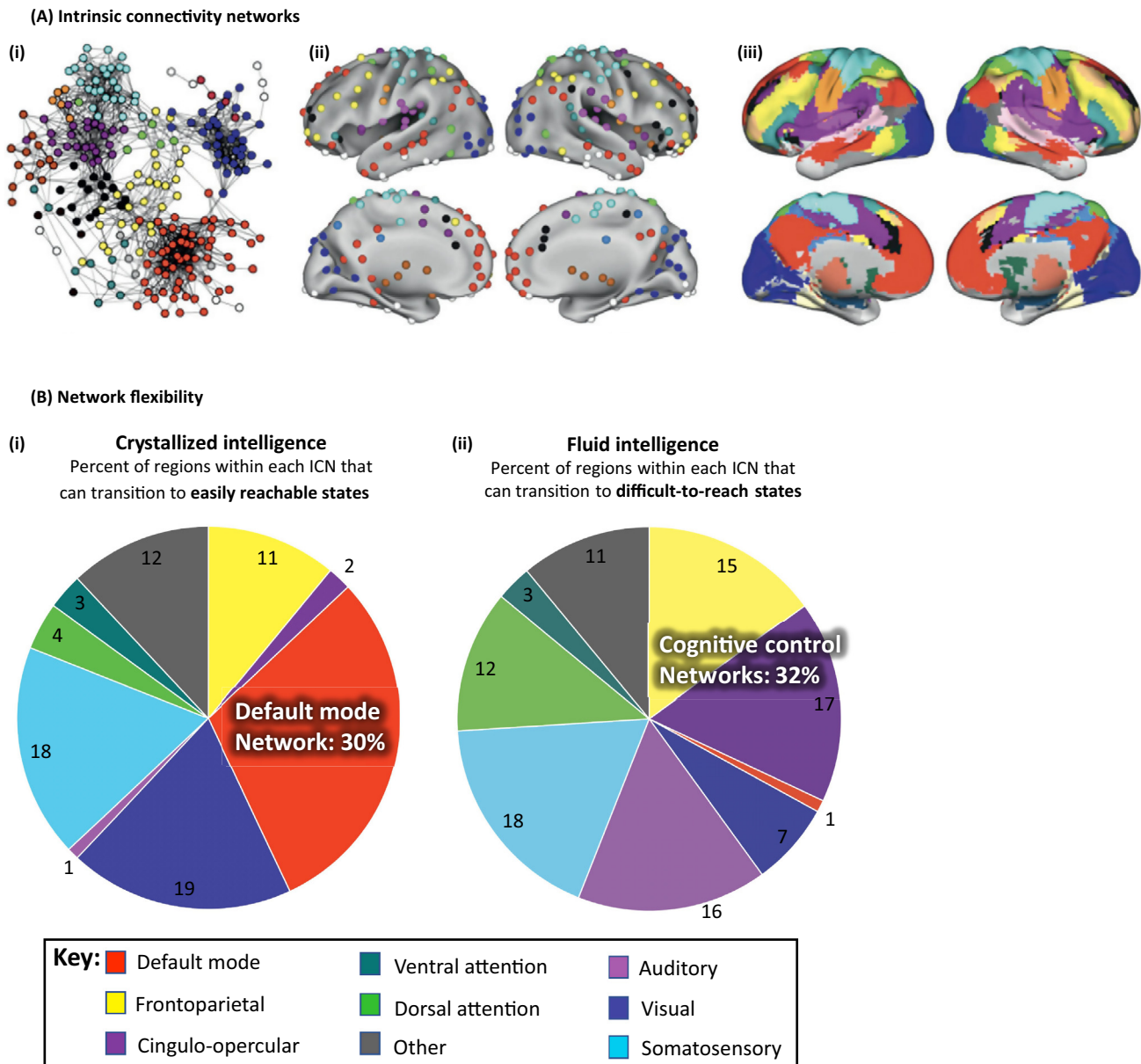
Modularity of Specific Mental Abilities

Functional specialization is built into the community structure of modules which comprise densely interconnected regions that together perform specific cognitive operations. Modularity therefore provides the basis for specialized information processing (Figure 1) – as originally expressed in Spearman’s specific factor, s , which captures the variance in task performance that is unique to specific tests of mental ability [1,2]. According to this view, the emergence of functional specialization and autonomous information processing [16] originates from the drive for local efficiency and the conservation of time, space, and material that it affords [19].

Small-World Topology of Broad Mental Abilities

Spearman’s model of general intelligence has been further elaborated in modern theories to include an intermediate level of cognitive domains that are broader than specific abilities but are less comprehensive than g [3–5] (Figure 1). Well-established broad abilities include crystallized intelligence, which underlies performance on tests of previously acquired knowledge, and fluid intelligence, which reflects the capacity for adaptive reasoning in novel environments. From a network neuroscience perspective, the formation of broad abilities reflects the competing forces of local versus global efficiency, resulting in an economic tradeoff in which locally efficient modules are embedded within modules to create a broader set of cognitive abilities whose topology enables a more globally efficient, small-world network [26–28] (Figure 2).

The functional topology and community structure of the human brain have been extensively studied through the application of resting-state functional MRI which examines spontaneous low frequency fluctuations of the blood oxygen-level dependent (BOLD) signal. This method demonstrates coherence in brain activity across spatially distributed regions to reveal a core set of intrinsic connectivity networks (ICNs; Figure 3A) [34,43–50]. Functional brain networks



Trends in Cognitive Sciences

Figure 3. Intrinsic Connectivity Networks (ICNs) and Network Flexibility. (A) Functional networks drawn from a large-scale meta-analysis of peaks of brain activity for a wide range of cognitive, perceptual, and motor tasks. (i) A graph-theoretic embedding of the nodes. Similarity between nodes is represented by spatial distance, and nodes are assigned to their corresponding network by color. (ii) and (iii) The nodal and voxel-wise network distribution in both hemispheres. Adapted, with permission, from [49]. (B) (i) Illustrates the percent of regions within each intrinsic connectivity network that can transition to many easy-to-reach network states, primarily within the default mode network. (ii) Illustrates the percent of regions within each intrinsic connectivity network that can transition to many difficult-to-reach network states, primarily within cognitive control networks. Adapted, with permission, from [61].

largely converge with the structural organization of networks measured using diffusion tensor MRI [36,51,52], together providing a window into the community structure from which global information processing and broad facets of intelligence emerge. Instead of originating from a specific brain network, a growing body of evidence suggests that individual differences in

crystallized and fluid intelligence reflect global, system-wide dynamics [37,38,53] and the capacity to flexibly transition between network states.

Network Dynamics of Crystallized Intelligence

Global information processing is enabled by the hierarchical community structure of the human brain, where modules are embedded within modules to form complex, interconnected networks [54,55]. This infrastructure is supported, in part, by nodes of high connectivity or hubs [44,56,57]. These regions serve distinct roles either as provincial hubs, which primarily connect to nodes within the same module, or as connector hubs, which instead provide a link between distinct modules [58]. Hubs are therefore essential for transferring information within and between ICNs, and provide the basis for mutual interactions between cognitive processes [16,59]. Indeed, strongly connected hubs together comprise a rich-club network that mediates almost 70% of the shortest paths throughout the brain and is therefore important for global network efficiency [60].

By applying engineering methods to network neuroscience, research from the field of network control theory further elucidates how brain network dynamics are shaped by the topology of strongly connected hubs, examining their capacity to act as drivers (network controllers) that move the system into specific network states [61]. According to this approach, the hierarchical community structure of the brain may facilitate or constrain the transition from one network state to another, for example by enabling a direct path that requires minimal transitions (an easy-to-reach network state) or a winding path that requires many transitions (a difficult-to-reach network state). Thus, by investigating how the brain is organized to form topologically direct or indirect pathways (comprising short- and long-distance connections), powerful inferences about the flexibility and dynamics of ICNs can be drawn.

Recent studies applying this approach demonstrate that strongly connected hubs enable a network to function within many easy-to-reach states [61], engaging highly accessible representations of prior knowledge and experience that are a hallmark of crystallized intelligence [3–5]. Extensive neuroscience data indicate that the topology of brain networks is shaped by learning and prior experience – reflecting the formation of new neurons, synapses, connections, and blood-supply pathways that promote the accessibility of crystallized knowledge [62–64]. The capacity to engage easy-to-reach network states – and therefore to access crystallized knowledge – is exhibited by multiple ICNs, most prominently for the default mode network [61,65] (Figure 3B). This network is known to support semantic and episodic memory representations that are central to crystallized intelligence [66–69] and to provide a baseline resting state from which these representations can be readily accessed. Thus, according to this view, crystallized abilities depend on accessing prior knowledge and experience through the engagement of easily reachable network states, supported, for example, by strongly connected hubs within the default mode network [61,65].

Network Dynamics of Fluid Intelligence

Although the utility of strongly connected hubs is well-recognized, a growing body of evidence suggests that they may not fully capture the higher-order structure of brain network organization and the flexibility of information processing that this global structure is known to afford [70]. Research in network science has long appreciated that global information processing depends on the formation of weak ties, which comprise nodes with a small number of connections [26,27,71]. By analogy to a social network, a weak tie represents a mutual acquaintance that connects two groups of close friends, providing a weak link between multiple modules. In

contrast to the intuition that strong connections are optimal for network function, the introduction of weak ties is known to produce a more globally efficient small-world topology [71,72].

Research investigating their role in brain network dynamics further indicates that weak connections enable the system to function within many difficult-to-reach states [61], reflecting a capacity to adapt to novel situations by engaging mechanisms for flexible, intelligent behavior. Unlike the easily reachable network states underlying crystallized intelligence, difficult-to-reach states rely on connections and pathways that are not well-established from prior experience – instead requiring the adaptive selection and assembly of new representations that introduce high cognitive demands. The capacity to access difficult-to-reach states is exhibited by multiple ICNs, most notably the frontoparietal and cingulo-opercular networks [61] (Figure 3B). Together, these networks are known to support cognitive control, enabling the top-down regulation and control of mental operations (engaging the frontoparietal network) in response to environmental change and adaptive task goals (maintained by the cingulo-opercular network) [73].

Converging evidence from resting-state fMRI and human lesion studies strongly implicates the frontoparietal network in cognitive control, demonstrating that this network accounts for individual differences in adaptive reasoning and problem-solving – as assessed by fMRI measures of global efficiency [37,38,74] and structural measures of brain integrity [75–79]. From this perspective, the role of the frontoparietal network in fluid intelligence reflects a global, system-wide capacity to adapt to novel environments, engaging cognitive control mechanisms that guide the dynamic selection and assembly of mental operations required for goal achievement [80]. Thus, rather than attempting to localize individual differences in fluid intelligence to a specific brain network, this framework instead suggests that weak connections within the frontoparietal and cingulo-opercular networks [38,74] drive global network dynamics – flexibly engaging difficult-to-reach states in the service of adaptive behavior and providing a window into the architecture of individual differences in general intelligence at a global level.

Network Dynamics of General Intelligence

Recent discoveries in network neuroscience motivate a new perspective about the role of global network dynamics in general intelligence – breaking away from standard theories that account for individual differences in g on the basis of a single brain region [81], network [77,82], or the overlap among specific networks [83] (Box 1). Accumulating evidence instead suggests that network flexibility and dynamics are crucial for the diverse range of mental abilities underlying general intelligence.

According to Network Neuroscience Theory, the capacity of ICNs to transition between network states is supported by their small-world topology – which enables each network to operate in a critical state that is close to a phase transition between a regular and random network [84,85] (Figure 2). The transition toward a regular network configuration is associated with the engagement of specific cognitive abilities, whereas the transition toward a random network configuration is linked to the engagement of broad or general abilities (Figure 2).

Instead of reflecting a uniform topology of dynamic states, emerging evidence suggests that ICNs exhibit different degrees of variability [86,87] – elucidating the network architecture that supports flexible, time-varying profiles of functional connectivity (Figure 4). Connections between modules are known to fluctuate more than connections within modules, demonstrating greater dynamic variability for connector hubs relative to provincial hubs [88,89]. Thus, the modular community structure of specific mental abilities provides a stable foundation upon

Box 1. Cognitive Neuroscience Theories of Human Intelligence

Cognitive neuroscience theories of human intelligence propose that g originates from individual differences in functionally localized regions or networks of the brain. Early studies investigating the neurobiology of g implicated the lateral prefrontal cortex (PFC) [81,102], motivating an influential theory based on the role of this region in cognitive control functions for intelligent behavior [103]. The later emergence of network-based theories reflected an effort to examine the neurobiology of intelligence through a wider lens, accounting for individual differences in g on the basis of broadly distributed networks. The landmark Parietofrontal Integration Theory (P-FIT) appeals to the frontoparietal network to explain individual differences in intelligence [75], proposing that g reflects the capacity of this network to evaluate and test hypotheses for problem-solving [77]. A central feature of the P-FIT model is an emphasis on the integration of knowledge between frontal and parietal cortex, afforded by white-matter fiber tracks that enable efficient communication among regions. Evidence to support the role of the frontoparietal network role in a broad range of problem-solving tasks later motivated the Multiple-Demand (MD) Theory, which proposes that this network underlies attentional control mechanisms for goal-directed problem-solving [82]. Finally, the Process Overlap Theory represents a recent network approach that accounts for individual differences in g by appealing to the spatial overlap among specific brain networks, reflecting the shared cognitive processes underlying g [83] (cf Thompson [11–13]). Thus, contemporary theories suggest that individual differences in g originate from functionally localized processes within specific brain regions or networks (Table I).

Network Neuroscience Theory adopts a new perspective, proposing that g originates from individual differences in the system-wide topology and dynamics of the human brain. According to this approach, the small-world topology of brain networks enables the rapid reconfiguration of their modular community structure, creating globally coordinated mental representations of a desired goal-state and the sequence of operations required to achieve it (cf [104,105]). The capacity to flexibly transition between network states therefore provides the foundation for individual differences in g , engaging (i) easy-to-reach network states to construct mental representations for crystallized intelligence based on prior knowledge and experience, and accessing (ii) difficult-to-reach network states to construct mental representations for fluid intelligence based on cognitive control functions that guide adaptive reasoning and problem-solving (see Figure 3B in main text). Thus, network flexibility and dynamics provide the foundation for general intelligence – enabling rapid information exchange across networks and capturing individual differences in information processing at a global level.

Table I. Summary of Cognitive Neuroscience Theories of Human Intelligence

	Functional localization			System-wide topology and dynamics		
	Primary region	Primary network	Multiple networks	Small-world topology	Network flexibility	Network dynamics
Lateral PFC Theory [103]	✓	x	x	x	x	x
P-FIT Theory [75]	x	✓	x	x	x	x
MD Theory [82]	x	✓	x	x	x	x
Process Overlap Theory [83]	x	x	✓	x	x	x
Network Neuroscience Theory	x	x	✓	✓	✓	✓

which the more flexible, small-world topology of broad mental abilities is constructed [90]. The dynamic flexibility of ICNs underlying broad mental abilities (Figure 3B) is known to reflect their capacity to access easy- versus difficult-to-reach states, with greatest dynamic flexibility being exhibited by networks that are strongly associated with fluid intelligence, particularly the frontoparietal network (Figure 4) [53,91,92].

Research in network neuroscience also motivates new hypotheses about lifespan development and generational change in crystallized and fluid intelligence. A wealth of evidence indicates that fluid abilities selectively decline in older adulthood, while crystallized intelligence is largely preserved [93]. Population studies have also shown that fluid intelligence is more sensitive to generational change than is crystallized intelligence, and systematic increases in fluid abilities are observed across generations [94–96]. Together, these findings suggest that fluid intelligence is influenced by cognitive decline and generational change to a greater extent than is crystallized intelligence. Network Neuroscience Theory accounts for this pattern of findings on the basis of global network dynamics, whereby fluid intelligence exhibits higher variability with age and across generations due to greater network flexibility (Figure 3B) and higher dynamic connectivity than crystallized intelligence (Figure 4A). According to this view, age-related decline in fluid intelligence is due to alterations in the network topology and dynamics of the aging brain [97], whereas generational change has a beneficial effect on fluid intelligence owing to improvements in education and lifestyle factors, such as diet and nutrition [98,99], that

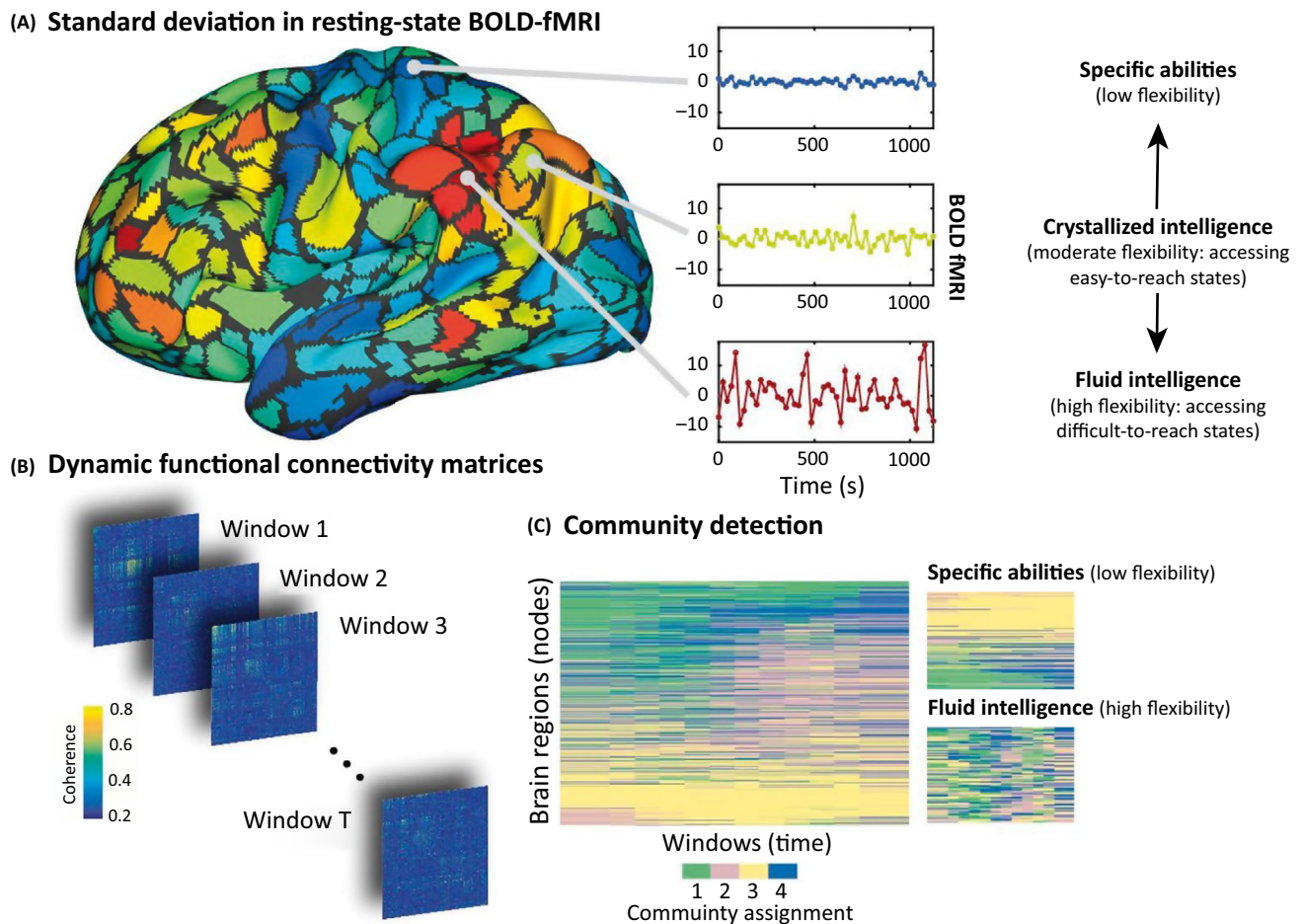


Figure 4. Dynamic Functional Connectivity. (A) Standard deviation in resting-state blood oxygen level-dependent (BOLD) fMRI reveals regions of low (blue), moderate (green), and high (red) variability. (B) Dynamic functional connectivity matrices are derived by windowing time-series and estimating the functional connectivity between pairs of regions. Instead of remaining static, functional connectivity matrices demonstrate changes over time, revealing dynamic variability in the connectivity profile of specific brain regions. (C) Dynamic functional connectivity matrices can be used to assess the modular structure of the network at each timepoint, revealing regions of low or high temporal dynamics. Adapted, with permission, from [87].

are known to enhance network flexibility. This framework also motivates new predictions about the role of network dynamics in learning, suggesting that the early stages of learning depend on adaptive behavior and the engagement of difficult-to-reach network states [100], followed by the transfer of skills to easily reachable network states as knowledge and experience are acquired to guide problem-solving [101]. Indeed, recent findings suggest that the development of fluid abilities from childhood to young adulthood is associated with individual differences in the flexible reconfiguration of brain networks for fluid intelligence [100].

In summary, Network Neuroscience Theory proposes that general intelligence depends on the dynamic reorganization of ICNs – modifying their topology and community structure in the service of system-wide flexibility and adaptation. Whereas crystallized intelligence engages easy-to-reach network states that access prior knowledge and experience, fluid intelligence instead recruits difficult-to-reach network states that support cognitive flexibility and adaptive

Trends in Cognitive Sciences

problem-solving (Figure 3B). Thus, the capacity to flexibly transition between network states provides the foundation for individual differences in g – supporting the rapid exchange of information across networks and capturing individual differences in cognitive processing at a global level.

Concluding Remarks

Network Neuroscience Theory raises new possibilities for understanding the nature and mechanisms of human intelligence, suggesting that interdisciplinary research in the emerging field of network neuroscience can advance our understanding of one of the most profound problems of intellectual life: how individual differences in general intelligence – which give rise to the stunning diversity and uniqueness of human identity and personal expression – originate from the network organization of the human brain. The reviewed findings elucidate the global network architecture underlying individual differences in g , drawing upon recent studies investigating the small-world topology and dynamics of human brain networks. Instead of attributing individual differences in general intelligence to a single brain region [81], network [77], or the overlap among specific networks [83], the proposed theory instead suggests that general intelligence depends on the dynamic reorganization of ICNs – modifying their topology and community structure in the service of system-wide flexibility and adaptation (Box 1). This framework sets the stage for new approaches to understanding individual differences in general intelligence, examining the global network topology and dynamics of the human brain – from the level of molecules and synapses to neural circuits, networks, and systems (see Outstanding Questions). By investigating the foundations of general intelligence in global network dynamics, the burgeoning field of network neuroscience will continue to advance our understanding of the cognitive and neural architecture from which the remarkable constellation of individual differences in human intelligence emerge.

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Outstanding Questions

What are the neurobiological foundations of individual differences in g ? Does the assumption that g originates from a primary brain region or network remain tenable, or should theories broaden the scope of their analysis to incorporate evidence from network neuroscience on individual differences in the global topology and dynamics of the human brain?

To what extent does brain network dynamics account for individual differences in specific, broad, and general facets of intelligence? To gain a better understanding of this issue, a more fundamental characterization of network dynamics will be necessary.

In what respects are ICNs dynamic, how do strong and weak connections enable specific network transformations, and what mental abilities do network dynamics support?

How does the structural topology of ICNs shape their functional dynamics and the capacity to flexibly transition between network states? To what extent is our current understanding of network dynamics limited by an inability to measure more precise temporal profiles or to capture higher-order representations of network topology at a global level?

How can we facilitate interdisciplinary investigations of human intelligence from a network neuroscience perspective, integrating research across psychology, neuroscience, mathematics, physics, and computer science?

What unifying theories and modeling approaches can be applied to integrate research across disciplines to develop a more comprehensive understanding of global network dynamics – from the level of molecules and synapses to neural circuits, networks, and systems?

What implications does a network neuroscience perspective have for understanding how intelligence emerges through evolution and development, is cultivated through learning and experience, or is altered through cognitive aging, psychiatric illness, and neurological disease?

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