CellPress REVIEWS

Opinion

Network Neuroscience Theory of Human Intelligence

Aron K. Barbey[1,2,3,4,5,6,*,@]

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.

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.

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

[1]Decision Neuroscience Laboratory, University of Illinois at Urbana-Champaign, IL, USA
[2]Department of Psychology, University of Illinois at Urbana-Champaign, IL, USA
[3]Department of Bioengineering, University of Illinois at Urbana-Champaign, IL, USA
[4]Neuroscience Program, University of Illinois at Urbana-Champaign, IL, USA
[5]Beckman Institute for Advanced Science and Technology, University of Illinois at Urbana-Champaign, IL, USA
[6]https://www.DecisionNeuroscienceLab.org
[@]Twitter: @DecisionNeurosc

*Correspondence: barbey@illinois.edu (A.K. Barbey).

© 2017 The Author. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

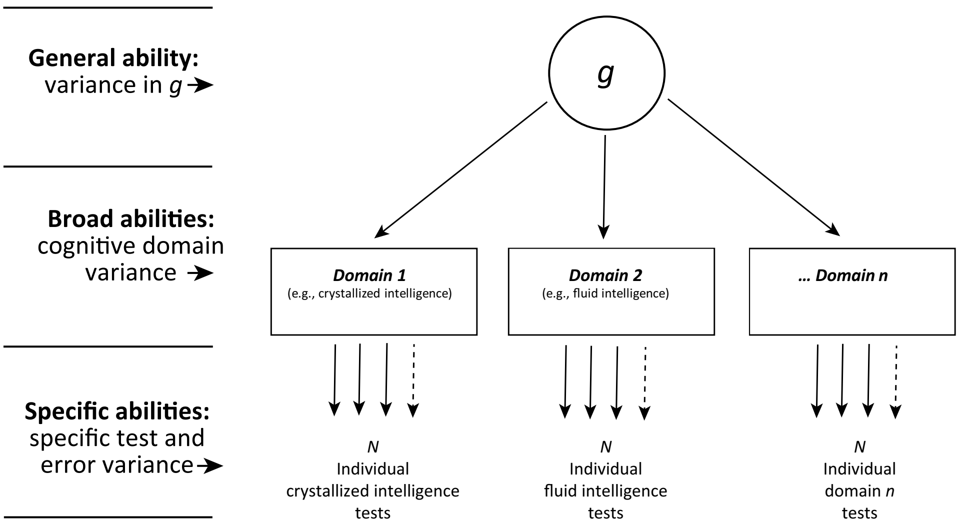

Figure 1. Hierarchical Structure of General Intelligence. At the level of specific abilities, people differ in scores on individual achievement tests, which are all positively correlated. At the level of broad abilities, strong correlations among tests measuring the same cognitive domain are present. 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 effecting 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

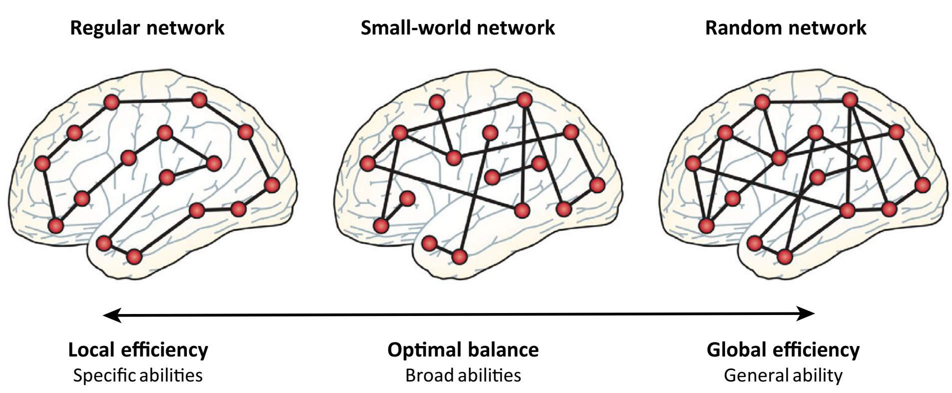

Figure 2. Small-World Network. Human brain networks exhibit a small-world topology that represents a parsimonious balance between a regular brain network, which promotes local efficiency, and a random brain network, which enables global efficiency. Adapted, with permission, from [20].

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

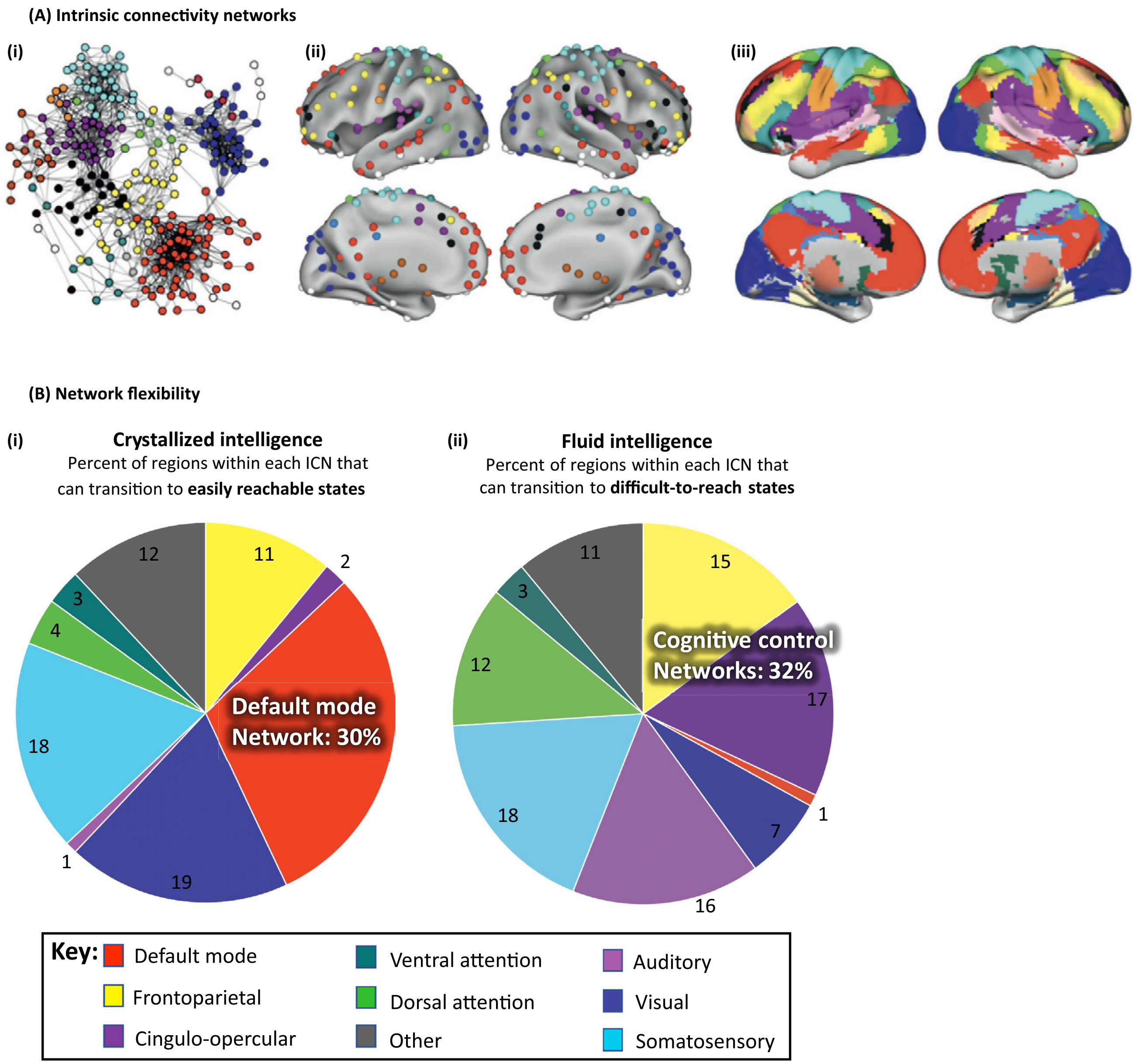

Figure 3. Intrinsic Connectivity Networks (ICNs) and Network Flexibility. (A) Functional networks drawn from a large-scale meta-analysis of peaks of brain activity for a wide range of cognitive, perceptual, and motor tasks. (i) A graph-theoretic embedding of the nodes. Similarity between nodes is represented 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

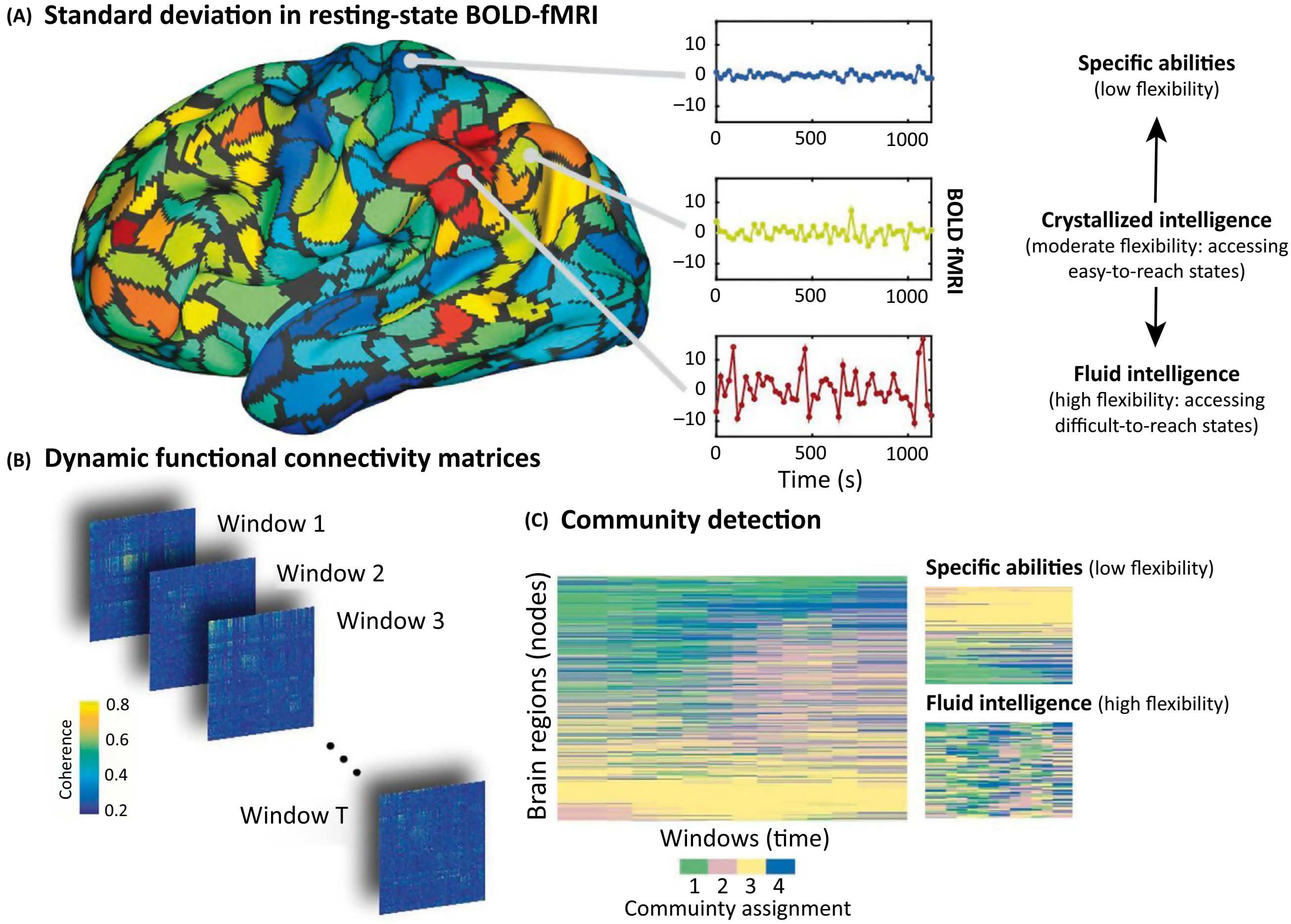

Figure 4. Dynamic Functional Connectivity. (A) Standard deviation in resting-state blood oxygen level-dependent (BOLD) fMRI reveals regions of low (blue), moderate (green), and high (red) variability. (B) Dynamic functional connectivity matrices are derived by windowing time-series and estimating the 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 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.

Acknowledgments

The work was supported by the Office of the Director of National Intelligence (ODNI), Intelligence Advanced Research Projects Activity (IARPA), via contract 2014-13121700004 to the University of Illinois at Urbana-Champaign (principal investigator: A.K.B.). The views and conclusions contained herein are those of the author and should not be interpreted as necessarily representing the official policies or endorsements, either expressed or implied, of the ODNI, IARPA, or the US Government. The US Government is authorized to reproduce and distribute reprints for Governmental purposes notwithstanding any copyright annotation thereon. The author is grateful for the helpful comments provided by Adam Hampshire and two anonymous reviewers.

References

1. Spearman, C. (1904) 'General intelligence' objectively determined and measured. *Am. J. Psychol.* 15, 201–292
2. Spearman, C. (1928) The abilities of man. *Science* 68, 38
3. Carroll, J.B. (1993) *Human Cognitive Abilities: A Survey of Factor-Analytic Studies,* Cambridge University Press
4. McGrew, K.S. and Wendling, B.J. (2010) Cattell–Horn–Carroll cognitive-achievement relations: what we have learned from the past 20 years of research. *Psychol. Sch.* 47, 651–675
5. Cattell, R.B. (1971) *Abilities: Their Structure, Growth, and Action,* Houghton Mifflin
6. Deary, I.J. (2014) The stability of intelligence from childhood to old age. *Curr. Dir. Psychol. Sci.* 23, 239–245
7. Sherrington, C.S. (1940) *Man on His Nature,* The University Press
8. Bassett, D.S. and Sporns, O. (2017) Network neuroscience. *Nat. Neurosci.* 20, 353–364
9. Fornito, A. *et al.* (2016) *Fundamentals of Brain Network Analysis,* Academic Press
10. Jensen, A.R. (1993) Spearman's g: links between psychometrics and biology. *Ann. N. Y. Acad. Sci.* 702, 103–129
11. Thomson, G.H. (1916) A hierarchy without a general factor. *Br. J. Psychol.* 8, 271–281
12. Thomson, G.H. (1919) The hierarchy of abilities. *Br. J. Psychol.* 9, 337–344
13. Thomson, G.H. (1935) The factorial analysis of human abilities. *Human Factor* 9, 180–185
14. Deary, I.J. *et al.* (2008) A conversation between Charles Spearman, Godfrey Thomson, and Edward L. Thorndike: The International Examinations Inquiry Meetings 1931–1938 (vol 11, pg 122, 2008). *Hist. Psychol.* 11, 163–163
15. Bartholomew, D.J. *et al.* (2009) Sir Godfrey Thomson: a statistical pioneer. *J. R. Stat. Soc. Ser. A Stat. Soc.* 172, 467–482
16. van der Maas, H.L. *et al.* (2006) A dynamical model of general intelligence: the positive manifold of intelligence by mutualism. *Psychol. Rev.* 113, 842–861
17. Jensen, A.R. (1998) *The G Factor: The Science of Mental Ability,* Praeger

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?

18. Pinker, S. (1994) How could a child use verb syntax to learn verb semantics. *Lingua* 92, 377–410
19. Ramón y Cajal, S. *et al.* (1999) *Texture of the Nervous System of Man and the Vertebrates,* Springer
20. Bullmore, E. and Sporns, O. (2012) The economy of brain network organization. *Nat. Rev. Neurosci.* 13, 336–349
21. Latora, V. and Marchiori, M. (2001) Efficient behavior of small-world networks. *Phys. Rev. Lett.* 87, 198701
22. Barbey, A.K. *et al.* (2015) Network topology and dynamics in traumatic brain injury. *Curr. Opin. Behav. Sci.* 4, 92–102
23. Simon, H. (1962) The architecture of complexity. *Proc. Am. Philos. Soc.* 106, 467–482
24. Bassett, D.S. and Gazzaniga, M.S. (2011) Understanding complexity in the human brain. *Trends Cogn. Sci.* 15, 200–209
25. Deco, G. *et al.* (2015) Rethinking segregation and integration: contributions of whole-brain modelling. *Nat. Rev. Neurosci.* 16, 430–439
26. Bassett, D.S. and Bullmore, E. (2006) Small-world brain networks. *Neuroscientist* 12, 512–523
27. Bassett, D.S. and Bullmore, E.T. (2017) Small-world brain networks revisited. *Neuroscientist* 23, 499–516
28. Watts, D.J. and Strogatz, S.H. (1998) Collective dynamics of 'small-world' networks. *Nature* 393, 440–442
29. Sporns, O. *et al.* (2000) Theoretical neuroanatomy: relating anatomical and functional connectivity in graphs and cortical connection matrices. *Cereb. Cortex* 10, 127–141
30. Sporns, O. *et al.* (2000) Connectivity and complexity: the relationship between neuroanatomy and brain dynamics. *Neural Netw.* 13, 909–922
31. Robinson, P.A. *et al.* (2009) Dynamical reconnection and stability constraints on cortical network architecture. *Phys. Rev. Lett.* 103, 108104
32. He, Y. *et al.* (2007) Small-world anatomical networks in the human brain revealed by cortical thickness from MRI. *Cereb. Cortex* 17, 2407–2419
33. Eguiluz, V.M. *et al.* (2005) Scale-free brain functional networks. *Phys. Rev. Lett.* 94, 018102
34. Achard, S. *et al.* (2006) A resilient, low-frequency, small-world human brain functional network with highly connected association cortical hubs. *J. Neurosci.* 26, 63–72
35. Achard, S. and Bullmore, E. (2007) Efficiency and cost of economical brain functional networks. *PLoS Comput. Biol.* 3, e17
36. Hagmann, P. *et al.* (2007) Mapping human whole-brain structural networks with diffusion MRI. *PLoS One* 2, e597
37. van den Heuvel, M.P. *et al.* (2009) Efficiency of functional brain networks and intellectual performance. *J. Neurosci.* 29, 7619–7624
38. Cole, M.W. *et al.* (2012) Global connectivity of prefrontal cortex predicts cognitive control and intelligence. *J. Neurosci.* 32, 8988–8999
39. Stam, C.J. *et al.* (2007) Small-world networks and functional connectivity in Alzheimer's disease. *Cereb. Cortex* 17, 92–99
40. Stam, C.J. (2014) Modern network science of neurological disorders. *Nat. Rev. Neurosci.* 15, 683–695
41. Zuo, X.N. *et al.* (2017) Human connectomics across the life span. *Trends Cogn. Sci.* 21, 32–45
42. Bassett, D.S. and Bullmore, E.T. (2009) Human brain networks in health and disease. *Curr. Opin. Neurol.* 22, 340–347
43. Biswal, B. *et al.* (1995) Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. *Magn. Reson. Med.* 34, 537–541
44. Buckner, R.L. *et al.* (2009) Cortical hubs revealed by intrinsic functional connectivity: mapping, assessment of stability, and relation to Alzheimer's disease. *J. Neurosci.* 29, 1860–1873
45. Bullmore, E. and Sporns, O. (2009) Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat. Rev. Neurosci.* 10, 186–198
46. Power, J.D. *et al.* (2011) Functional network organization of the human brain. *Neuron* 72, 665–678
47. Sporns, O. *et al.* (2004) Organization, development and function of complex brain networks. *Trends Cogn. Sci.* 8, 418–425
48. van den Heuvel, M.P. *et al.* (2009) Functionally linked resting-state networks reflect the underlying structural connectivity architecture of the human brain. *Hum. Brain Mapp.* 30, 3127–3141
49. Power, J.D. and Petersen, S.E. (2013) Control-related systems in the human brain. *Curr. Opin. Neurobiol.* 23, 223–228
50. Smith, S.M. *et al.* (2013) Resting-state fMRI in the Human Connectome Project. *Neuroimage* 80, 144–168
51. Park, H.J. and Friston, K. (2013) Structural and functional brain networks: from connections to cognition. *Science* 342, 1238411
52. Byrge, L. *et al.* (2014) Developmental process emerges from extended brain-body-behavior networks. *Trends Cogn. Sci.* 18, 395–403
53. Shine, J.M. *et al.* (2016) The dynamics of functional brain networks: integrated network states during cognitive task performance. *Neuron* 92, 544–554
54. Meunier, D. *et al.* (2010) Modular and hierarchically modular organization of brain networks. *Front. Neurosci.* 4, 200
55. Betzel, R.F. and Bassett, D.S. (2016) Multi-scale brain networks. *Neuroimage* Published online November 11, 2016. http://dx.doi.org/10.1016/j.neuroimage.2016.11.006
56. Power, J.D. *et al.* (2013) Evidence for hubs in human functional brain networks. *Neuron* 79, 798–813
57. van den Heuvel, M.P. and Sporns, O. (2013) Network hubs in the human brain. *Trends Cogn. Sci.* 17, 683–696
58. Guimera, R. and Nunes Amaral, L.A. (2005) Functional cartography of complex metabolic networks. *Nature* 433, 895–900
59. Bertolero, M.A. *et al.* (2015) The modular and integrative functional architecture of the human brain. *Proc. Natl. Acad. Sci. U. S. A.* 112, E6798–E6807
60. van den Heuvel, M.P. and Sporns, O. (2011) Rich-club organization of the human connectome. *J. Neurosci.* 31, 15775–15786
61. Gu, S. *et al.* (2015) Controllability of structural brain networks. *Nat. Commun.* 6, 8414
62. Bassett, D.S. *et al.* (2011) Dynamic reconfiguration of human brain networks during learning. *Proc. Natl. Acad. Sci. U. S. A.* 108, 7641–7646
63. Buchel, C. *et al.* (1999) The predictive value of changes in effective connectivity for human learning. *Science* 283, 1538–1541
64. Pascual-Leone, A. *et al.* (2005) The plastic human brain cortex. *Annu. Rev. Neurosci.* 28, 377–401
65. Betzel, R.F. *et al.* (2016) Optimally controlling the human connectome: the role of network topology. *Sci. Rep.* 6, 30770
66. Christoff, K. *et al.* (2016) Mind-wandering as spontaneous thought: a dynamic framework. *Nat. Rev. Neurosci.* 17, 718–731
67. Kucyi, A. (2017) Just a thought: how mind-wandering is represented in dynamic brain connectivity. *Neuroimage* Published online July 3, 2017. http://dx.doi.org/10.1016/j.neuroimage.2017.07.001
68. Wirth, M. *et al.* (2011) Semantic memory involvement in the default mode network: a functional neuroimaging study using independent component analysis. *Neuroimage* 54, 3057–3066
69. St Jacques, P.L. *et al.* (2011) Dynamic neural networks supporting memory retrieval. *Neuroimage* 57, 608–616
70. Schneidman, E. *et al.* (2006) Weak pairwise correlations imply strongly correlated network states in a neural population. *Nature* 440, 1007–1012
71. Granovetter, M.S. (1973) The strength of weak ties. *Am. J. Sociol.* 78, 1360–1380

72. Gallos, L.K. *et al.* (2012) A small world of weak ties provides optimal global integration of self-similar modules in functional brain networks. *Proc. Natl. Acad. Sci. U. S. A.* 109, 2825–2830
73. Dosenbach, N.U. *et al.* (2008) A dual-networks architecture of top-down control. *Trends Cogn. Sci.* 12, 99–105
74. Santarnecchi, E. *et al.* (2014) Efficiency of weak brain connections support general cognitive functioning. *Hum. Brain Mapp.* 35, 4566–4582
75. Barbey, A.K. *et al.* (2012) An integrative architecture for general intelligence and executive function revealed by lesion mapping. *Brain* 135, 1154–1164
76. Glascher, J. *et al.* (2010) Distributed neural system for general intelligence revealed by lesion mapping. *Proc. Natl. Acad. Sci. U. S. A.* 107, 4705–4709
77. Jung, R.E. and Haier, R.J. (2007) The parieto-frontal integration theory (P-FIT) of intelligence: converging neuroimaging evidence. *Behav. Brain Sci.* 30, 135–154
78. Barbey, A.K. *et al.* (2014) Architecture of fluid intelligence and working memory revealed by lesion mapping. *Brain Struct. Funct.* 219, 485–494
79. Barbey, A.K. *et al.* (2013) Architecture of cognitive flexibility revealed by lesion mapping. *Neuroimage* 82, 547–554
80. Duncan, J. *et al.* (2017) Complexity and compositionality in fluid intelligence. *Proc. Natl. Acad. Sci. U. S. A.* 114, 5295–5299
81. Duncan, J. *et al.* (2000) A neural basis for general intelligence. *Science* 289, 457–460
82. Duncan, J. (2010) The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends Cogn. Sci.* 14, 172–179
83. Kovacs, K. and Conway, A.R.A. (2016) Process overlap theory: a unified account of the general factor of intelligence. *Psychol. Inq.* 27, 151–177
84. Beggs, J.M. (2008) The criticality hypothesis: how local cortical networks might optimize information processing. *Philos. Trans. A Math. Phys. Eng. Sci.* 366, 329–343
85. Petermann, T. *et al.* (2009) Spontaneous cortical activity in awake monkeys composed of neuronal avalanches. *Proc. Natl. Acad. Sci. U. S. A.* 106, 15921–15926
86. Betzel, R.F. *et al.* (2016) A positive mood, a flexible brain. *arXiv*. Published online January 28, 2016. https://arxiv.org/abs/1601.07881
87. Mattar, M.G. *et al.* (2016) The flexible brain. *Brain* 139, 2110–2112
88. Zalesky, A. *et al.* (2014) Time-resolved resting-state brain networks. *Proc. Natl. Acad. Sci. U. S. A.* 111, 10341–10346
89. Zhang, J. *et al.* (2016) Neural, electrophysiological and anatomical basis of brain-network variability and its characteristic changes in mental disorders. *Brain* 139, 2307–2321
90. Hampshire, A. *et al.* (2012) Fractionating human intelligence. *Neuron* 76, 1225–1237
91. Cole, M.W. *et al.* (2013) Multi-task connectivity reveals flexible hubs for adaptive task control. *Nat. Neurosci.* 16, 1348–1355
92. Braun, U. *et al.* (2015) Dynamic reconfiguration of frontal brain networks during executive cognition in humans. *Proc. Natl. Acad. Sci. U. S. A.* 112, 11678–11683
93. Salthouse, T. (2012) Consequences of age-related cognitive declines. *Annu. Rev. Psychol.* 63, 201–226
94. Flynn, J.R. (1984) The mean IQ of Americans – massive gains 1932 to 1978. *Psychol. Bull.* 95, 29–51
95. Flynn, J.R. (1987) Massive IQ gains in 14 nations – what IQ tests really measure. *Psychol. Bull.* 101, 171–191
96. Flynn, J.R. (2007) *What is Intelligence? Beyond the Flynn Effect*. Cambridge University Press
97. Yankner, B.A. *et al.* (2008) The aging brain. *Annu. Rev. Pathol.* 3, 41–66
98. Zamroziewicz, M.K. and Barbey, A.K. (2016) Nutritional cognitive neuroscience: innovations for healthy brain aging. *Front. Neurosci.* 10, 240
99. Zamroziewicz, M.K. *et al.* (2017) Nutritional status, brain network organization, and general intelligence. *Neuroimage* 161, 241–250
100. Chai, L.R. *et al.* (2016) Evolution of brain network dynamics in neurodevelopment. *Netw. Neurosci.* 1, 14–30
101. Hampshire, A. *et al.* (2016) Network mechanisms of intentional learning. *Neuroimage* 127, 123–134
102. Barbey, A.K. *et al.* (2013) Dorsolateral prefrontal contributions to human intelligence. *Neuropsychologia* 51, 1361–1369
103. Duncan, J. and Owen, A.M. (2000) Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci.* 23, 475–483
104. Kitzbichler, M.G. *et al.* (2011) Cognitive effort drives workspace configuration of human brain functional networks. *J. Neurosci.* 31, 8259–8270
105. Dehaene, S. *et al.* (1998) A neuronal model of a global workspace in effortful cognitive tasks. *Proc. Natl. Acad. Sci. U. S. A.* 95, 14529–14534