

6 Human Intelligence and Network Neuroscience

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Introduction

Flexibility is central to human intelligence and is made possible by the brain's remarkable capacity to reconfigure itself – to continually update prior knowledge on the basis of new information and to actively generate internal predictions that guide adaptive behavior and decision making. Rather than lying dormant until stimulated, contemporary research conceives of the brain as a dynamic and active inference generator that anticipates incoming sensory inputs, forming hypotheses about that world that can be tested against sensory signals that arrive in the brain (Clark, 2013; Friston, 2010). Plasticity is therefore critical for the emergence of human intelligence, providing a powerful mechanism for updating prior beliefs, generating dynamic predictions about the world, and adapting in response to ongoing changes in the environment (Barbey, 2018). This perspective provides a catalyst for contemporary research on human intelligence, breaking away from the classic view that general intelligence (*g*) originates from individual differences in a fixed set of cortical regions or a singular brain network (for reviews, see Haier, 2017; Posner & Barbey, 2020).

Early studies investigating the neurobiology of *g* focused on the lateral prefrontal cortex (Barbey, Colom, & Grafman, 2013b; Duncan et al., 2000), motivating an influential theory based on the role of this region in cognitive control functions for intelligent behavior (Duncan & Owen, 2000). 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. For example, the Parietal-Frontal Integration Theory (P-FIT) was the first to propose that “a discrete parieto-frontal network underlies intelligence” (Jung & Haier, 2007) and that *g* reflects the capacity of this network to evaluate and test hypotheses for problem-solving (see also Barbey et al., 2012). A central feature

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of the P-FIT model is the integration of knowledge between the frontal and parietal cortex, afforded by white-matter fiber tracks that enable efficient communication among regions. Evidence to support the fronto-parietal network's role in a wide 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 (Duncan, 2010). 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 (Kovacs & Conway, 2016). Thus, contemporary theories suggest that individual differences in g originate from functionally localized processes within specific brain regions or networks (Table 6.1; for a comprehensive review of cognitive neuroscience theories of intelligence, see Chapter 5, by Euler and McKinney).

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 (Barbey, 2018). 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. This chapter surveys recent evidence within the rapidly developing field of network neuroscience that assess the nature and mechanisms of general intelligence (Barbey, 2018; Girn, Mills, & Christoff, 2019) (for an

Table 6.1 *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	✓	✗	✗	✗	✗	✗
P-FIT Theory*	✗	✓	✗	✗	✗	✗
MD Theory	✗	✓	✗	✗	✗	✗
Process Overlap Theory	✗	✗	✓	✗	✗	✗
Network Neuroscience Theory	✗	✗	✓	✓	✓	✓

* The P-FIT theory was the first to propose that “a discrete parieto-frontal network underlies intelligence” (Jung & Haier, 2007).

introduction to modern methods in network neuroscience, see Chapter 2, by Hilger and Sporns). We identify directions for future research that aim to resolve prior methodological limitations and further investigate the hypothesis that general intelligence reflects individual differences in network mechanisms for (i) efficient and (ii) flexible information processing.

Network Efficiency

Early research in the neurosciences revealed that the brain is designed for efficiency – to minimize the cost of information processing while maximizing the capacity for growth and adaptation (Bullmore & Sporns, 2012; Ramón y Cajal, Pasik, & Pasik, 1999). Minimization of cost is achieved by dividing the cortex into anatomically localized modules, comprised 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), increasing the signal transmission speed (conservation of time) and promoting local efficiency (Latora & Marchiori, 2001). This compartmentalization of function enhances robustness to brain injury by limiting the likelihood of global system failure (Barbey et al., 2015). Indeed, the capacity of each module to function and modify its operations without adversely effecting other modules enables cognitive flexibility (Barbey, Colom, & Grafman, 2013a) and therefore confers an important adaptive advantage (Bassett & Gazzaniga, 2011; Simon, 1962).

Critically, 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 (Deco, TONI, Boly, & Kringelbach, 2015) (Figure 6.1). Local efficiency is embodied by a regular network or lattice, in which each node is connected to an equal number of its nearest neighbors, supporting direct local communication in the absence of long-range connections. In 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.

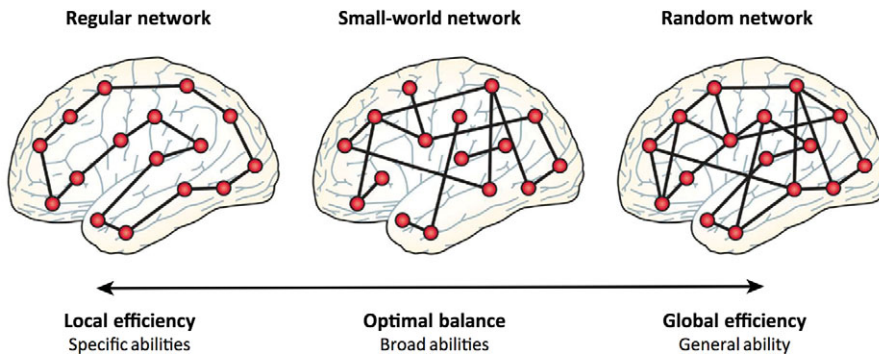


Figure 6.1 *Small-world network. Human brain networks exhibit a small-world topology that represents a parsimonious balance between a regular brain network, which promotes local efficiency, and a random brain network, which enables global efficiency. Figure modified with permission from Bullmore and Sporns (2012)*

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 small-world topology (Bassett & Bullmore, 2006, 2017; Watts & Strogatz, 1998). A small-world network embodies (i) short-distance connections that reduce the wiring cost (high local clustering), along with (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, providing a parsimonious architecture for human brain organization (Robinson, Henderson, Matar, Riley, & Gray, 2009; Sporns, Tononi, & Edelman, 2000a, b; van der Maas et al., 2006). Evidence further indicates that efficient network organization is based on routing strategies that combine local and global information about brain network topology in an effort to approximate a small-world architecture (Avena-Koenigsberger et al., 2019).

Research in network neuroscience has consistently observed that the topology of human brain networks indeed exemplifies a small-world architecture, which has been demonstrated across multiple neuroimaging modalities, including structural (He, Chen, & Evans, 2007), functional (Achard & Bullmore, 2007; Achard, Salvador, Whitcher, Suckling, & Bullmore, 2006; Eguluz, Chialvo, Cecchi, Baliki, & Apkarian, 2005), and diffusion tensor magnetic resonance imaging (MRI) (Hagmann et al., 2007). Alterations in the topology of a small-world network have also been linked to multiple disease states (Stam, 2014; Stam, Jones, Nolte, Breakspear, & Scheltens, 2007), stages of lifespan development (Zuo et al., 2017), and pharmacological interventions (Achard & Bullmore, 2007), establishing their importance for understanding human

health, aging, and disease (Bassett & Bullmore, 2009). 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.

Small-World Topology and General Intelligence

The functional topology and community structure of the human brain has 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 6.2a) (Achard et al., 2006; Biswal, Yetkin, Haughton, & Hyde, 1995; Buckner et al., 2009; Bullmore & Sporns, 2009; Power & Petersen, 2013; Power et al., 2011; Smith et al., 2013; Sporns, Chialvo, Kaiser, & Hilgetag, 2004; van den Heuvel, Mandl, Kahn, & Hulshoff Pol, 2009). Functional brain networks largely converge with the structural organization of networks measured using diffusion tensor MRI (Byrge, Sporns, & Smith, 2014; Hagmann et al., 2007; Park & Friston, 2013), together providing a window into the community structure from which global information processing emerges.

The discovery that global brain network efficiency is associated with general intelligence was established by van den Heuvel, Stam, Kahn, and Hulshoff Pol (2009), who observed that g was positively correlated with higher global efficiency (as indexed by a globally shorter path length) (for earlier research on brain network efficiency using PET; see Haier et al., 1988). Santarnecchi, Galli, Polizzotto, Rossi, and Rossi (2014) further examined whether this finding reflects individual differences in connectivity strength, investigating the relationship between general intelligence and global network efficiency derived from weakly vs. strongly connected regions. Whereas strong connections provide the basis for densely connected modules, weak links index long-range connections that typically relay information between (rather than within) modules. The authors replicated van den Heuvel, Stam, et al. (2009) and further demonstrated that weakly connected regions explain more variance in g than strongly connected regions (Santarnecchi et al., 2014), supporting the hypothesis that global efficiency and the formation of weak connections are central to general intelligence. Further support for the role of global efficiency in general intelligence is provided by EEG studies, which examine functional connectivity as coherence between time series of distant EEG channels measured at rest. For instance, Langer and colleagues provide evidence for a positive association between g and the small-world topology of intrinsic brain networks derived from EEG (Langer, Pedroni, & Jancke, 2013; Langer et al., 2012).

Complementary research examining the global connectivity of regions within the prefrontal cortex also supports a positive association with measures

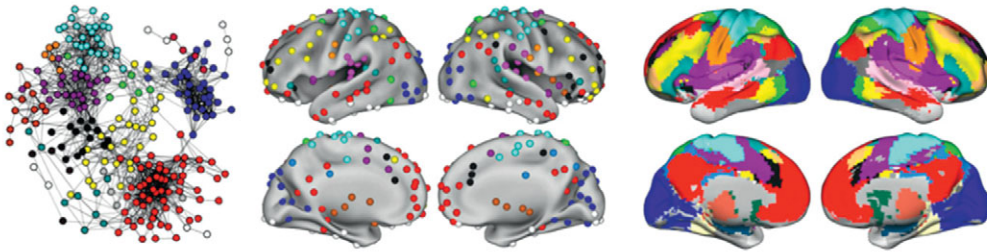
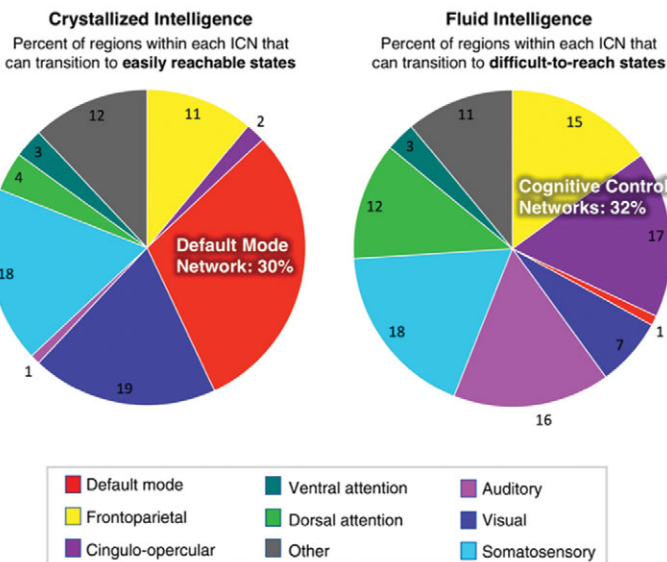
(A) Intrinsic Connectivity Networks**(B) Network Flexibility**

Figure 6.2 *Intrinsic connectivity networks 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. Upper left figure represents 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. Middle and right sections present the nodal and voxel-wise network distribution in both hemispheres. Figure modified with permission from Power and Petersen (2013). (B) Left graph 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. Right graph 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. Figure modified with permission from Gu et al. (2015)*

of intelligence. For example, Cole, Ito, and Braver (2015) and Cole, Yarkoni, Repovš, Anticevic, and Braver (2012) observed that the global connectivity of the left lateral prefrontal cortex (as measured by the average connectivity of this region with every other region in the brain) demonstrates a positive association with fluid intelligence. Converging evidence is provided by Song et al. (2008), who found that the global connectivity of the bilateral dorsolateral prefrontal cortex was associated with general intelligence. To integrate the diversity of studies investigating the role of network efficiency in general intelligence – and to account for null findings (Kruschwitz, Waller, Daedelow, Walter, & Veer, 2018) – it will be important to examine differences among studies with respect to resting-state fMRI data acquisition, pre-processing, network analysis, and the study population.

A central question concerns whether resting-state fMRI is sufficiently sensitive or whether task-based fMRI methods provide a more powerful lens to examine the role of network efficiency in general intelligence. Indeed, a growing body of evidence suggests that functional brain network organization measured during cognitive tasks is a stronger predictor of intelligence than when measured during resting-state fMRI (Greene, Gao, Scheinost, & Constable, 2018; Xiao, Stephen, Wilson, Calhoun, & Wang, 2019). This literature has primarily employed task-based fMRI paradigms investigating cognitive control, specifically within the domain of working memory (for a review, see Chapter 13, by Cohen and D’Esposito).

For example, fMRI studies investigating global brain network organization have revealed that working memory task performance is associated with an increase in network integration and a decrease in network segregation (Cohen & D’Esposito, 2016; see also Gordon, Stollstorff, & Vaidya, 2012; Liang, Zou, He, & Yang, 2016). Increased integration was found primarily within networks for cognitive control (e.g., the fronto-parietal and cingular-opercular networks) and for task-relevant sensory processing (e.g., the somatomotor network) (Cohen, Gallen, Jacobs, Lee, & D’Esposito, 2014). Thus, global brain network integration measured by task-based fMRI provides a powerful lens for further characterizing the role of network efficiency in high-level cognitive processes (e.g., cognitive control and working memory). Increasingly, scientists have proposed that high-level cognitive operations emerge from brain network dynamics (Breakspear, 2017; Cabral, Kringelbach, & Deco, 2017; Deco & Corbetta, 2011; Deco, Jirsa, & McIntosh, 2013), motivating an investigation of their role in general intelligence.

Network Flexibility and Dynamics

Recent discoveries in network neuroscience motivate a new perspective about the role of global network dynamics in general intelligence – marking an important point of departure from the standard view that

intelligence originates from individual differences in a fixed set of cortical regions (Duncan et al., 2000) or a singular brain network (Barbey et al., 2012; Duncan, 2010; Jung & Haier, 2007) (Table 6.1). Accumulating evidence instead suggests that network efficiency and dynamics are critical for the diverse range of mental abilities underlying general intelligence (for earlier research on brain network efficiency using PET; see Haier et al. (1988)).

Network Dynamics of Crystallized Intelligence

Global information processing is enabled by the hierarchical community structure of the human brain, with modules that are embedded within modules to form complex, interconnected networks (Betzler & Bassett, 2017; Meunier, Lambiotte, & Bullmore, 2010). This infrastructure is supported, in part, by nodes of high connectivity or hubs (Buckner et al., 2009; Hilger, Ekman, Fiebach, & Basten, 2017a, b; Power, Schlaggar, Lessov-Schlaggar, & Petersen, 2013; van den Heuvel & Sporns, 2013). 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 (Guimera & Nunes Amaral, 2005). Hubs are therefore essential for transferring information within and between ICNs and provide the basis for mutual interactions between cognitive processes (Bertolero, Yeo, & D'Esposito, 2015; van der Maas et al., 2006). 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 (van den Heuvel & Sporns, 2011).

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 (Gu et al., 2015). 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 (Gu et al., 2015), engaging highly accessible representations of prior knowledge and experience that are a hallmark of crystallized intelligence (Carroll, 1993; Cattell, 1971; McGrew & Wendling, 2010). 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 (Bassett et al., 2011; Buchel, Coull, & Friston, 1999; Pascual-Leone, Amedi, Fregni, & Merabet, 2005). 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 (Betzell, Gu, Medaglia, Pasqualetti, & Bassett, 2016; Gu et al., 2015) (Figure 6.2b). This network is known to support semantic and episodic memory representations that are central to crystallized intelligence (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016; Kucyi, 2018; St Jacques, Kragel, & Rubin, 2011; Wirth et al., 2011) 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 (Betzell, Gu et al., 2016; Gu et al., 2015).

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 (Schneidman, Berry, Segev, & Bialek, 2006). 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 (Bassett & Bullmore, 2006, 2017; Granovetter, 1973). 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 (Gallos, Makse, & Sigman, 2012; Granovetter, 1973).

Research investigating their role in brain network dynamics further indicates that weak connections enable the system to function within many difficult-to-reach states (Gu et al., 2015), 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 (Gu et al., 2015) (Figure 6.2b). Together, these networks are known to support cognitive control, enabling the top-down regulation and control of mental operations (engaging the

fronto-parietal network) in response to environmental change and adaptive task goals (maintained by the cingulo-opercular network) (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008).

Converging evidence from resting-state fMRI and human lesion studies strongly implicates the fronto-parietal network in cognitive control, demonstrating that this network accounts for individual differences in adaptive reasoning and problem-solving – assessed by fMRI measures of global efficiency (Cole et al., 2012; Santarnecchi et al., 2014; van den Heuvel, Stam, et al., 2009) and structural measures of brain integrity (Barbey, Colom, Paul, & Grafman, 2014; Barbey et al., 2012, 2013a; Glascher et al., 2010). From this perspective, the fronto-parietal network's role 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 (Duncan, Chylinski, Mitchell, & Bhandari, 2017). Thus, rather than attempt to localize individual differences in fluid intelligence to a specific brain network, this framework instead suggests that weak connections within the fronto-parietal and cingulo-opercular networks (Cole et al., 2012; Santarnecchi et al., 2014) 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 (Duncan et al., 2000), a primary brain network (Barbey et al., 2012; Duncan, 2010; Jung & Haier, 2007), or the overlap among specific networks (Kovacs & Conway, 2016). Accumulating evidence instead suggests that network flexibility and dynamics are critical 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 (Beggs, 2008; Petermann et al., 2009) (Figure 6.1). 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 6.1).

Rather than reflect a uniform topology of dynamic states, emerging evidence suggests that ICNs exhibit different degrees of variability (Betz, Gu et al., 2016; Mattar, Betz, & Bassett, 2016) – elucidating the network architecture that supports flexible, time-varying profiles of functional

connectivity. Connections between modules are known to fluctuate more than connections within modules, demonstrating greater dynamic variability for connector hubs relative to provincial hubs (Zalesky, Fornito, Cocchi, Gollo, & Breakspear, 2014; Zhang et al., 2016). Thus, the modular community structure of specific mental abilities provides a stable foundation upon which the more flexible, small-world topology of broad mental abilities is constructed (Hampshire, Highfield, Parkin, & Owen, 2012). The dynamic flexibility of ICNs underlying broad mental abilities (Figure 6.2b) is known to reflect their capacity to access easy- vs. difficult-to-reach states, with greatest dynamic flexibility exhibited by networks that are strongly associated with fluid intelligence, particularly the fronto-parietal network (Figure 6.3) (Braun et al., 2015; Cole et al., 2013; Shine et al., 2016).

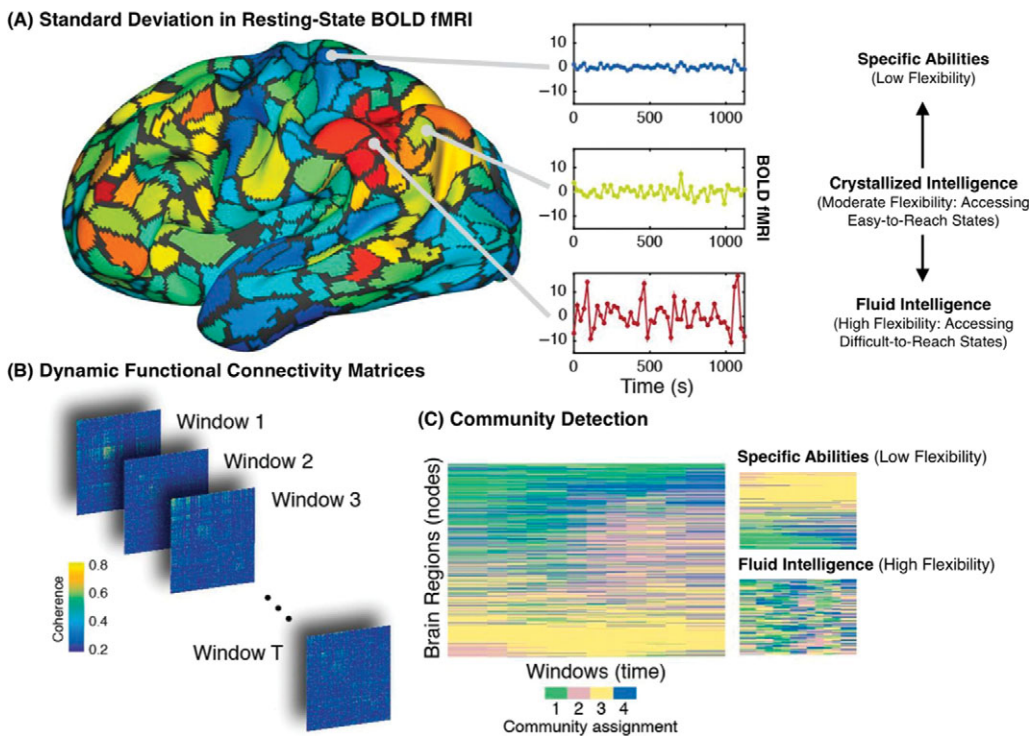


Figure 6.3 *Dynamic functional connectivity.* (A) *Standard deviation in resting-state BOLD fMRI reveals regions of low (blue), moderate (green), and high (red) variability.* (B) *Dynamic functional connectivity matrices are derived by windowing time series and estimating the functional connectivity between pairs of regions. Rather than remain 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 network's modular structure at each time point, revealing regions of low or high temporal dynamics.* Figure modified with permission from Mattar et al. (2016)

Functional Brain Network Reconfiguration

Accumulating evidence examines the dynamic reconfiguration of brain networks in the service of goal-directed, intelligent behavior. Recent findings indicate that the functional reconfiguration of brain networks (i.e., greater network flexibility) is positively associated with learning and performance on tests of executive function. For example, Bassett et al. (2011) found that functional network flexibility (as measured by changes in the modular structure of brain networks) predicted future learning in a simple motor task. Converging evidence is provided by Braun et al. (2015), who examined functional brain network reconfiguration in a continuous recognition memory task (i.e., *n*-back) and observed that higher cognitive load was associated with greater network reorganization within frontal cortex.

In addition, Jia, Hu, and Deshpande (2014) examined functional brain network dynamics in the context of resting-state fMRI, investigating the stability of connections over time. The authors found that performance on tests of executive function was associated with the average stability of connections examined at the whole brain level, with greater brain network reconfiguration (i.e., lower stability) predicting higher performance. Notably, the highest level of functional brain network reconfiguration was observed within the fronto-parietal network (Jia et al., 2014; see also, Hilger, Fukushima, Sporns, & Fiebach, 2020). Taken together, these findings support the role of flexible brain network reconfiguration in goal-directed, intelligent behavior.

Additional evidence to support this conclusion is provided by studies that investigate the efficiency of functional brain network reconfiguration in the context of task performance. For example, Schultz and Cole (2016) examined the similarity between functional connectivity patterns observed at rest vs. during three task conditions (language, working memory, and reasoning). The authors predicted that greater reconfiguration efficiency (as measured by the similarity between the resting-state and task-based connectomes) would be associated with better performance. Consistent with this prediction, the authors found that individuals with greater reconfiguration efficiency demonstrated better task performance and that this measure was positively associated with general intelligence. This finding emphasizes the importance of reconfiguration efficiency in task performance and supports the role of flexible, dynamic network mechanisms for general intelligence.

Network Neuroscience Theory 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, followed by the transfer of skills to easily reachable network states as knowledge and experience are acquired to guide problem-solving. 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 (Chai et al., 2017). A recent study by Finc et al. (2020) examined the dynamic reconfiguration of functional brain networks during working memory training, providing evidence that early stages of learning engage cognitive control networks for adaptive behavior, followed by increasing reliance upon the default mode network as knowledge and skills are acquired (Finc et al., 2020), supporting the predictions of the Network Neuroscience Theory.

A primary direction for future research is to further elucidate how the flexible reconfiguration of brain networks is related to general intelligence, with particular emphasis on mechanisms for cognitive control. Although brain networks underlying cognitive control have been extensively studied, their precise role in specific, broad, and general facets of intelligence remain to be well characterized (Mill, Ito, & Cole, 2017). Future research therefore aims to integrate the wealth of psychological and psychometric evidence on the cognitive processes underlying general intelligence (Carroll, 1993) and cognitive control (Friedman & Miyake, 2017) with research on the network mechanisms underlying these processes (Barbey, Koenigs, & Grafman, 2013; Barbey et al., 2012, 2013b) in an effort to better characterize the cognitive and neurobiological foundations of general intelligence.

Conclusion

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. Rather than attribute individual differences in general intelligence to a single brain region (Duncan et al., 2000), a primary brain network (Barbey et al., 2012; Duncan, 2010; Jung & Haier, 2007), or the overlap among specific networks (Kovacs & Conway, 2016), 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 (Table 6.1). This framework sets the stage for new approaches to understanding individual differences in general intelligence and motivates important questions for future research, namely:

- 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 and do mechanisms for cognitive control figure prominently? 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?

As the significance and scope of these issues would suggest, many fundamental questions about the nature and mechanisms of human intelligence remain to be investigated and provide a catalyst for contemporary research in network neuroscience. 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

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