Cognitive Neuroscience Theories of Intelligence

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Network neuroscience research into intelligence has emphasized two primary neurobiological mechanisms that underlie cognitive ability: the flexible, dynamic integration of multiple brain networks during information processing, and the topology and connectivity of highly-connected hub nodes that drive or coordinate network reconfiguration. Several cognitive neuroscience theories of intelligence appeal to these properties when drawing on neuroscience evidence to explain individual differences in cognitive ability. In this chapter, we review cognitive neuroscience hypotheses and theories of human intelligence—including neural speed and neural efficiency hypotheses, the Parieto-Frontal Integration Theory and Multiple Demand Theory, Process Overlap Theory and Network Sampling Theory, predictive processing models, the Watershed Model, and the Network Neuroscience Theory. While these theories each draw on a well-established body of neuroscience evidence, they are also each tied to the research methods and techniques that gave rise to them—complicating efforts to compare their claims and predictions. In reviewing the neuroscience evidence for current neuroscience theories, we discuss the methodological challenges of studying general intelligence with neuroscience data, identify the particularly promising strengths of network sampling- and topology- based theories of intelligence, and finally, raise several key questions for future research into intelligence and cognitive ability to address.

Introduction

Neuroscience research demonstrates that the human brain is a complex network, structured to provide both the widespread global integration and specialized regional connectivity that support general and specific cognitive abilities. The development and maintenance of cognitive abilities appear to emerge from the remarkably dynamic nature of the brain—both the slower adaptation of structural connections during learning, and the faster functional reconfiguration of brain networks while performing functional tasks. This network-based perspective has become highly influential in cognitive neuroscience, motivating a wealth of models and formal theories which associate individual differences in the psychological structure of human intelligence with underlying neurobiological networks.

In this chapter, we provide an overview of the exciting current research into cognitive neuroscience theories of intelligence. We begin with an overview of psychology re-search into intelligence, highlighting the recent emergence of psychology theories that approach cognitive ability from a network perspective. We then enter a discussion of general neuroscience accounts of intelligence, including the mitochondrial efficiency, neural speed, and neural efficiency hypotheses. Next, we discuss the early development of brain network models, focusing on the Parieto-Frontal Integration Theory and Multiple Demand Theory. We then transition to more recent models that sample intelligence from multiple brain networks, including Process Overlap Theory and Network Sampling Theory. Finally we discuss the most dynamic models of intelligence, covering predictive processing models, the Watershed Model of fluid intelligence, and the Network Neuroscience Theory. Along the way, we highlight the relationship between development in neuroscience methods and theories of intelligence, and point to the particularly promising strengths of network-based theories of intelligence. We conclude by summarizing current issues, challenges, and future directions for the field as a whole, outlining several questions for future applications for network neuroscience research into the study of intelligence research to address.

What are Brain Networks?

The field of Network Neuroscience (D. S. Bassett and Sporns, 2017) proposes to study the structure and function of the brain by interrogating the architecture and topology of brain networks. Networks are emergent phenomena that characterize the complex behavior of many real world systems (M. Newman, 2003). The dominant research paradigm used in cognitive neuroscience to image brain network topology (e.g., see Yeo et al., 2011) is functional Magnetic Resonance Imaging (fMRI; Davis and Poldrack, 2013; Poldrack, 2008), which localises changes in blood flow to specific regions in the brain to produce a mathematical graph of synchronous brain network connectivity, known as the connectome (Sporns, 2011). Several other structural and functional neuroimaging modalities can also be used to generate connectivity data. Researchers represent networks of brain connectivity data using a graph $G = (V, E)$ (see M. E. J. Newman, 2010 for an introduction), such that regions in the brain are represented by V, a set of vertices, and ordered pairs of either directed or undirected edges E represent connectivity between those brain regions. Many real-world systems can be characterized using networks to highlight important

organizational properties, which has helped to facilitate the widespread adoption network science as an interdisciplinary field (Mitchell, 2009). In cognitive neuroscience, key network properties (Medaglia et al., 2015) that have inspired research and theory into human intelligence include the degree distribution of node connectivity (van den Heuvel and Sporns, 2013) and small-world properties (D. S. Bassett and E. Bullmore, 2006; D. S. Bassett and E. T. Bullmore, 2017). Connectivity data show that long-range connections (van den Heuvel et al., 2012) across the brain are facilitated by a rich-club (van den Heuvel and Sporns, 2011) of densely interconnected hub regions, that enabling fast and efficient (Langer et al., 2012) connectivity between disparate, specialized brain regions. Research into the features of brain network topology that support these moment-to-moment changes in network connectivity profiles (Avena-Koenigsberger et al., 2019; Gu et al., 2015; Senden et al., 2014; Shine et al., 2016; Vázquez-Rodríguez et al., 2017), often termed network reconfigurations, highlight that the brain is an inherently dynamic system (Sporns et al., 2000a), where communication between brain networks depends on controlling activity in the connectome through a series of functional states (Srivastava et al., 2020). Regions that compose brain networks are known to be highly overlapped (Schultz and Cole, 2016; Yeo et al., 2014), such that a single brain region can map to membership in many possible brain networks, flexibly reconfiguring its connectivity profile to serve different cognitive demands McIntosh, 2000; Pessoa, 2014; Yeo et al., 2014). Neuroscience research into intelligence increasingly draws on these network perspectives and methods, proposing that the structure of cognitive abilities and individual differences is directly reflected in the underlying organization and topology of brain networks (Barbey et al., 2014; Betzel and D S Bassett, 2017; Cole et al., 2014; van den Heuvel et al., 2009), and associating intelligence with the dynamic reconfigurations of those brain networks during cognition (e.g., Barbey, 2018; Shine et al., 2016; Soreq et al., 2021).

Psychometric Theories of Human Intelligence

The fundamental finding in psychometric research into intelligence (Spearman, 1904) is Spearman's observation of the positive manifold: the invariable and inevitable positive correlation between a subject's performance across all cognitive tests. This general factor, g, characterizes the shared variance common to all cognitive abilities, reflecting that all cognitive tests measure something in common. However, variance in ability that is unique to particular tests will also exist, as Spearman reasoned when noting that the correlation between cognitive abilities was not perfect (for example, on a test of French language versus a test of mathematics). Soon thereafter emerged a second key observation: the introduction of the hierarchical model of cognitive abilities (Spearman, 1904, developed further in Spearman, 1927). This factorial

structure approach to intelligence estimates specific cognitive abilities from observed performance on various cognitive tests (Thomson, 1951), which then construct a hierarchy of cognitive abilities. Today, this dominant view of intelligence is best characterized by Catell-Horn-Carrol theory: a latent variable g (general intelligence) causes all shared variance in broad intellectual abilities (e.g., general intelligence, fluid intelligence, short-term memory), which can each be measured from specific tests of narrow cognitive abilities (inductive reasoning, perceptual speed, free-recall memory) (Flanagan and Dixon, 2014; Schneider and McGrew, 2018). This consensus remained dominant throughout the 20th century—and indeed, research continues to identify the positive manifold (e.g., Caemmerer et al., 2020) in all studies conducted using modern psychometric testing batteries. However, a critical issue with psychometric research into intelligence remains. Several alternative explanations of the positive manifold exist, beyond the reflective factor model first identified by Spearman, and in most cases behavioral data alone is not able to distinguish between these these competing theoretical explanations. This motivates the the use of neuroscience data in studying theories of intelligence, ideally to map the neural substrates and network operations that underpin specific cognitive abilities (Pessoa, 2014; Varoquaux et al., 2018), affording empirical tests of the various formal structures of intelligence proposed by behavioral theories. Relevantly, developments in psychometric theories of g somewhat mirror the development of cognitive neuroscience theories of intelligence, reflecting an emerging trend towards formal network models of human intelligence.

From the early beginnings of the 20th century, alternative theories of intelligence have adopted a network perspective, arguing against the consensus model of a reflective factor structure underlying intelligence, and against the existence of g. One long-standing perspective against g is the view that the positive manifold instead emerges from many overlapping cognitive processes (Bartholomew et al., 2009; Maxwell, 1972; Thurstone, 1934), a position termed sampling theorem. Instead of associating the positive manifold with a causal latent factor g, sampling theorem rejects the existence of a single unifying factor. Network representations are often employed when appealing to sampling theorem, either in explaining intelligence as an overlapping network of cognitive abilities (Hampshire et al., 2012), or explicitly identifying those networks of cognitive ability with human brain networks (Kovacs and Conway, 2016; McIntosh, 2000; Soreq et al., 2021). Other formal models of intelligence, such as the mutualism model (van der Maas et al., 2006) or the wiring model (Savi et al., 2019), provide more novel explanations for the structure of intelligence, again grounded in network representations (Savi et al., 2021). Briefly, we will give an overview of influential structural models for the positive manifold, providing context and grounding for the

remainder of our discussion into cognitive neuroscience theories of intelligence.

Among factor structure models, CHC theory represents the final synthesis of the general factor g and hierarchical models of mental ability, reflecting the culmination of almost a century of research. Originally proposing a two-factor model, Spearman, 1927 hypothesized that g reflected a form of mental capacity for work, represented in individual difference variance common across all tests of mental ability. Contrasting views in the factor structure tradition followed, maintaining the existence of g (Thurstone, 1948) but proposing that it can be decomposed into a larger and larger set of specific mental abilities. Theorizing began to center on two primary broad facets of intelligence, fluid intelligence (Gf) and crystallized intelligence (Gc), originating from a bifactor models of intelligence proposed by Hebb, 1949 that was further developed by Cattell, 1963 (Brown, 2016). Fluid intelligence reflects adaptive problem solving skills that are independent of prior experience or training, and crystallized intelligence reflects previously acquired knowledge and skills (Carroll, 1993; Cattell, 1971; McGrew and Wendling, 2010). Horn and Cattell, 1966 continued to refine this model, culminating ultimately in the development of CHC theory (Carroll, 1993; Flanagan and Dixon, 2014; Schneider and McGrew, 2018), where Carroll's three-stratum factor proposes that g produces variance across up to 16 broad abilities (e.g., Gf, Gc, Gq; Schneider and McGrew, 2018) that produce many more narrow abilities. As we will later discuss in further detail, neuroscience evidence lends support to a mapping between hierarchical cognitive abilities and hierarchical brain network organization (Betzel and D S Bassett, 2017; Meunier et al., 2010; Román et al., 2014), which alongside behavioral evidence (Caemmerer et al., 2020) continue to lend support to the factor modeling perspective.

Following Spearman's identification of g, G. H. Thompson proposed that intelligence may represent a global network phenomena (Thomson, 1916; Thomson, 1919), originating research into the sampling theory of intelligence. Thomson suggested that the positive manifold results from the overlap of shared cognitive processes, proposing that each cognitive test necessarily measures more than one cognitive ability at once, producing the overlap in mental processes that produces the statistical appearance of the positive manifold (Thomson, 1951; Thorndike et al., 1926). Sampling models have been revived in recent years, with behavioral work (Bartholomew et al., 2013; Jensen, 2006) that has has applied sampling theory to both domain-specific and domain-general processes, and also neuroscience evidence (Kovacs and Conway, 2016; Soreq et al., 2021) of network network operations both providing evidence to support the role of network sampling in intelligence.

Most recently, explanations of the positive manifold have been generated from a fully network perspective (Colom et al., 2010; van der Maas et al., 2019), accounting for g through reciprocal interactions between a network of underlying cognitive abilities. One such formal network model of intelligence emerges from mutualism theory (van der Maas et al., 2006; van der Maas et al., 2019), which proposes that the positive manifold and the hierarchical structure of cognitive abilities both emerge from reciprocal exchanges between elements of an extended network of cognitive processes during development (see also Kievit, 2020; Kievit et al., 2017; Ou et al., 2019; Peng and Kievit, 2020). Mutualism theory accounts for Gf and Gc (van Der Maas et al., 2017) by modeling cognitive abilities as a network, where local interactions between elements replace the reflective factor structure of g as the cause of the internal structure of cognitive abilities (Kan et al., 2020). In this account, a mental ability can develop in a somewhat autonomous manner, but will also change or grow due to growth in other areas, via mutual exchanges. A related theory, the wiring model (Savi et al., 2019), adopts an entirely dynamic account of network development. Wired intelligence theory models individual-specific networks of cognitive ability, accounting in particular for knowledge acquisition and the development of crystallized intelligence. In an ensemble, these network models can formally account for the "Matthew effect" (Merton, 1968) of divergent developmental outcomes in cognitive ability, adopting an idiographic perspective (Molenaar, 2004) to deploy dynamic network models that capture the cognitive development of single individuals. Wired intelligence may represent a promising new direction as a formal model for interdisciplinary research into skill acquisition, particularly applied to the study of individual differences in cognitive training (e.g., D. S. Bassett et al., 2011; Daugherty et al., 2020; Finc et al., 2020; Ree and Earles, 2006; Román et al., 2019; Román et al., 2017; Zwilling et al., 2019), where arguments made for transfer and neuroplasticity are closely aligned with those made for the emergence of g during development and education (Ackerman and Lohman, 2003; Nisbett et al., 2012).

Unlike factor and sampling approaches to intelligence, cognitive neuroscience theories of intelligence have yet to devote empirical effort to directly testing formal network models of the positive manifold. However, neuroscience research has indirectly argued in favor of the extended developmental (Byrge et al., 2014) and neurobiological (Barbey, 2018) network interactions that are entailed by formal network models, suggesting that future neuroscience work in this space may be warranted. Critically, both mutualism and wiring theory allow for individuals to be formally modeled by individualized network models, suggesting future interdisciplinary research into formal network models of intelligence that could make contact with current cognitive neuroscience trends towards methods for prediction (e.g., Finn and Rosenberg, 2021; Gabrieli et al., 2015) and individual differ-

ences modeling (e.g., Daugherty et al., 2020; Kievit et al., 2016; McFarland, 2017; Soreq et al., 2021).

Neuroscience Theories of Intelligence

Neuroscience research into human intelligence has extended our understanding of the structure of the positive manifold by identify neurobiological structures and mechanisms that underpin cognitive abilities. Building on that research, network neuroscience has emphasized two primary neurobiological mechanisms that underlie cognitive ability: the flexible, dynamic integration of brain networks during information processing (Braun et al., 2015; Cohen and D'Esposito, 2016; Nee, 2021; Ray et al., 2020; Shine et al., 2016; Wang et al., 2021), and the topology and connectivity of highly-connected hub nodes (Bertolero et al., 2018; Cole et al., 2013; Power et al., 2013; Senden et al., 2014; Senden et al., 2018; van den Heuvel and Sporns, 2013) that drive or coordinate efficient network reconfiguration. Continually updating neural representations of prior knowledge to account for new information affords for both the long-term changes to neural architecture (Byrge et al., 2014; Chai et al., 2017) and the moment-to-moment neural representation of predictions (Bubic et al., 2010; Ficco et al., 2021) that facilitate adaptive behavior and decision making. Contemporary network neuroscience research conceives of the brain as an active and dynamic inference generator, anticipating incoming sensory inputs and forming hypotheses about that world that can be tested against incoming sensory signals (Clark, 2013; Friston, 2010).

Building on previous research that identifies the positive manifold and the factor structure of intelligence with individual brain regions and networks (see Haier, 2017), network neuroscience theories of intelligence instead propose that individual differences in intelligence emerge from the global architecture of brain network topology. The balanced organization of these networks affords critical dynamics, through the active generation and reconfiguration of functional network states. This ability to optimally integrate networks together from disparate regions is critical to producing intelligence, facilitating a process where cognitive operations are implemented by discrete and specialized functional modules (e.g., Bertolero et al., 2015), and performing novel tasks requires recruiting those assembling those modules and subnetworks into an efficient configuration (as in the Multiple Demand theory; Camilleri et al., 2018), a process afforded by brain network organization that can balance this competing needs of local structure and efficient global communication, perhaps explaining their ubiquitous presence in many real-world systems, the brain included (D. S. Bassett and E. T. Bullmore, 2017) and their relationship to intelligence (e.g., Langer et al., 2012).

Network neuroscience theories of intelligence can be conceptualized along a spectrum of resolution, from individual brain networks to global whole-brain properties. Neurobiological localization has proven a successful framework for the study of many specific cognitive abilities, and a wealth of existing neuroscience evidence highlights the importance of specialized brain regions and networks, supporting localist theories of intelligence that primarily ascribe intelligence to spatially localized neurobiology. Current evidence in network neuroscience (D. S. Bassett and Sporns, 2017) highlights the critical role of brain network topology and dynamics in cognitive abilities, suggesting that the architecture and topology supporting the positive manifold spans the entire connectome (Dubois et al., 2018; Suprano et al., 2019). A balance of strong connections supporting efficient functional integration (Deco et al., 2015; Gallos et al., 2012; Langer et al., 2012) and weak connection supporting functional segregation (Bertolero et al., 2018; Bertolero et al., 2015; Gallos et al., 2012) produce a modular (Hilger et al., 2017) and small-world (D. S. Bassett and E. Bullmore, 2006; D. S. Bassett and E. T. Bullmore, 2017) neural architecture, enabling the dynamic and flexible reorganization of brain activity during cognition. The critical role of global network flexibility in higher cognition identified by network neuroscience (D. S. Bassett et al., 2011; Braun et al., 2015; Cabral et al., 2017; Finc et al., 2020; Shine et al., 2016) suggests that perspective which localize intelligence to single regions and networks may fail to account for the systemwide neural properties that underpin individual differences in intelligence.

While cognitive neuroscience theories of intelligence each draw from a well-established body of neuroscience, they are also each tied to the research methods and techniques that gave rise to them——somewhat complicating efforts to compare their claims and predictions.

General Neuroscience Theories of Intelligence

The dependency between research methods and theories of intelligence can be illustrated with a brief survey of non-fMRI neuroscience accounts of the biological basis of *g*. Drawing on distinct modalities of research—event-related potentials (ERPs; Woodman, 2010), positron emission tomography (PET; Lameka et al., 2016), and interdisciplinary neuroscience—theorists have arrived at explanations for *g* at levels of resolution that are difficult to directly reconcile with cognitive neuroscience data, or with the formal psychometric accounts of the positive manifold. Briefly, we discuss the cellular efficiency, neural speed, and neural efficiency theories motivated by these research modalities, each of which reduce the underlying *g* to a single underlying cause or mechanism. These theories may each be noteworthy to cognitive neuroscientists for their orthogonal research methodologies taken to accounting for *g*, and for the illustrative difficulties inherent in reconciling their evidence with current cognitive neuroscience theories.

The efficiency of mitochondrial functioning (Geary, 2018;

Geary, 2019) has recently been proposed as a novel mechanism that accounts for intelligence, prompting a diversity (Geary, 2020) commentary and critique from intelligence researchers. The theory shares similarities with previous efforts (see Matzel et al., 2020) to effectively reduce (P. M. Churchland and P. S. Churchland, 1992) differences in g to a lower-level biological mechanism—in this case, by postulating that the functioning of brain systems at all levels of resolution depends on the health and energy production of cellular mitochondria. One potential merit of explanations for the positive manifold pitched at a biological level is their potential to make more direct contact with theories (Dickens and Flynn, 2001) and data (Tucker-Drob and Bates, 2016) on the genetic heritability of intelligence, although as many commentators note (Matzel et al., 2020; Savi et al., 2020; Stankov, 2020; Sternberg, 2020), mitochondrial efficiency is purely correlational, with hypothesis-driven testing yet to be done. However, research into the molecular genetics of intelligence (for a review, see Deary et al., 2021) has begun to make some general, if modest, progress towards associating the heritabilitiy of intelligence with cognitive traits and neuroimaging data, although mechanisms for these correlational associations are currently lacking. While the Watershed Model and Network Neuroscience Theory (see below; Barbey, 2018; Kievit et al., 2016) are at least consistent with genetic explanations for the heritability of intelligence, cognitive neuroscience has yet to make any significant contact with genetics research, arguably due to the mismatch in methods and perspectives adopted by their respective fields. Regardless, multidisciplinary approaches to formally model the positive manifold that merge cognitive neuroscience, psychometrics, and systems biology may yet emerge during the 21st century.

A more established neuroscience account of g, neural speed, emerges from research using EEG (Schubert et al., 2017; Schubert et al., 2019, also see Jensen, 2006). One of the most well-replicated findings in the field is the negative association between intelligence and reactions time (Der and Deary, 2017), which can be measured with moderate success from the latencies of ERP components. Research in this area is recently transitioning to a focus on more narrowly defined cognitive tasks and operations—to great success, with a model of ERP waves able to account for 90% (Schubert et al., 2017) of variance in general intelligence, markedly higher than the 20% (Dubois et al., 2018) to 40% (Feilong et al., 2021) of variance currently accounted for by cognitive neuroscience methods. However, conventional ERP evidence necessarily lacks spatial localization, where as MRI evidence lacks temporal specificity. The differing lingua franca of these respective methodologies complicate any attempts to formally integrate ERP data on neural speed with cognitive neuroscience methods, short of performing simultaneous recording (Kruggel et al., 2000; Moore et al.,

2021; Scrivener, 2021) via MRI-EEG, highlighting the close bond between research method and theoretical perspective that current theories of intelligence remain subject to.

A final influential view is the neural efficiency hypothesis (Haier et al., 1988; Neubauer and Fink, 2009), which primarily associates intelligence with glucose metabolism efficiency (perhaps here making some contact with mitochondrial functioning), based on support from a variety of PET, EEG (Nussbaumer et al., 2015), fMRI (Dunst et al., 2014), and diffusion (Genç et al., 2018) studies. However, current formulations of neural efficiency are somewhat imprecisely defined, and in some cases fall prey to the well-understood problem in cognitive neuroscience of redescribing neural activation as "efficiency" (Poldrack, 2015), complicating efforts to translate these various findings into a formal mechanistic explanation of g that makes contact with conception of network efficiency (e.g., Langer et al., 2012; Santarnecchi et al., 2017b; Schultz and Cole, 2016) that has been well-studied in cognitive neuroscience. Overall, neural and biological accounts of the positive manifold make intriguing claims about the underlying nature of g. These accounts can successfully explain various modality-specific phenomena, suggesting, at the least, that the empirical findings and open questions posited by their frameworks may important for any comprehensive theoretical account of the cognitive neuroscience of intelligence to address.

Cognitive Neuroscience Theories of Intelligence

Neuroimaging studies of the cognitive neuroscience of intelligence have explained individual differences in the positive manifold by appealing to the structure and topology of brain networks. At a more localized level of resolution, several cognitive neuroscience theories have proposed that intelligence emerges from the connectivity of specialized neurobiological substrates, both at the level of individual brain regions and brain networks. Early studies investigating the neurobiology of g implicated the lateral prefrontal cortex (PFC; Duncan and Owen, 2000; Duncan et al., 2000), motivating an influential theory based on the role of this region in cognitive control of functions for intelligent behavior (Barbey et al., 2013b). Lateral PFC theory predicts that intelligence depends primarily on functional activity within frontoparietal regions. Current research continues to support the key role of PFC in many functional tasks, demonstrating granular functional specialization of neural substrates within the region (Gilbert et al., 2010; Kamigaki, 2019; Yamasaki et al., 2002) and emphasizing its important role as a specialized region important to cognitive abilities. However, efforts to examine the neurobiology of intelligence through a wider lens led to the development of cognitive neuroscience Theories of Intelligence, accounting for individual differences in g in terms of the function and topology of broadly distributed brain networks.

The landmark Parieto-Frontal integration theory (P-FIT; Jung and Haier, 2007) predicts that intelligence emerges from integrated neural activity within the frontoparietal network. A central feature of the P-FIT model is an emphasis on the integration of knowledge between an integrated network of frontal and parietal cortex (along with anterior cingulate, temporal, and occipital cortical areas), afforded by white-matter fiber tracks that enable efficient communication in the service of problem-solving and hypothesis testing. A wealth of neuroimaging evidence exists for the importance of a pre-frontal network in facilitating human intelligence (Barbey et al., 2014; Barbey et al., 2012; Barbey et al., 2013b; Braun et al., 2015; Cole et al., 2012; Daugherty et al., 2020; Duncan and Owen, 2000; Duncan et al., 2000; Gilbert et al., 2010; Gläscher et al., 2010; Jung and Haier, 2007; Kamigaki, 2019; Pineda-Pardo et al., 2016; Yamasaki et al., 2002), suggesting that the frontoparietal network serves a key role across may problem-solving contexts, responsible for displaying a general profile of task-based activation across a variety of cognitive operations (Cole et al., 2014; Cole et al., 2013; Vakhtin et al., 2014).

Evidence to support this general role of the frontoparietal network in a broad range of problem-solving tasks helped motivate the Multiple Demand (MD) Theory, which proposes that the Multiple Demand network underlies attentional control mechanisms for goal-directed problem-solving (Camilleri et al., 2018; Duncan, 2010), recruiting from a core set of regions in midcingulate cortex, bilateral anterior insula, inferior frontal junction and gyrus, right middle frontal gyrus, and right inferior parietal cortex and intraparietal sulcus. MD theory accounts for intelligence and problem-solving using a flexible network of frontoparietal and cingulo-opercular regions (Camilleri et al., 2018; Diachek et al., 2020; Fedorenko et al., 2013). While many frontoparietal connections are also entailed by Multiple Demand system, the network includes additional vertices central in attentional networks (Mineroff et al., 2018) and cingulo-opercular systems (Camilleri et al., 2018). reflects the inclusion frontopareital systems with a second, relatively dissociable (Crittenden et al., 2016) cingulo-opercular system. With the functional recruitment of the the frontoparietal system serving a more general processing role for a broad set of cognitive abilities, connectivity in the cingulo-opercular system codes for more differentiable cognitive operations, possibly representing more individualized and topologically local activation patterns, compared to the more globally recruited architecture present in the frontoparietal system.

Current research lends broad support for the importance of the frontoparietal network, with two recent meta-analyses (Basten et al., 2015; Santarnecchi et al., 2017a) highlighting the convergence of neuroimaging evidence in support of the P-FIT theory. However, parsing the extent to which network patterns of functional connectivity map to a specific theory can be challenging, as the regional definition of each theory are nested and somewhat overlapping. Further, the progression of neuroimaging research methods in the intervening decade has complicated the methodology of comparing older neuroscience studies with more recent theories, for example with P-FIT formulated at the resolution of Broadmann areas, while current neuroimaging studies afford much a higher topological resolution. It also remains unclear to what extent current research into dynamic patterns of functional connectivity (Shine et al., 2016), or the mesoscale topology of networks that supports global dynamic connectivity (D. S. Bassett et al., 2013; Elliott et al., 2020), can be mapped onto these localist theories. Together, these mapping problems may suggest a mismatch between the original neuroscience methods and perspectives that provide support for localist network theories, and more global and dynamic perspective deployed in more recent network neuroscience studies.

Network Sampling Theories of Intelligence

More recently, the revival of the sampling theory of intelligence (Thomson, 1916; Thorndike et al., 1926) has inspired a new thrust of theoretical and empirical neuroscience work, associating intelligence and cognition with the integration and overlap of processing across multiple brain networks. Process Overlap theory (Kovacs and Conway, 2016) predicts that intelligence emerges from the functional integration of several task-relevant brain regions and networks. Process Overlap theory accounts for intelligence as the spatial and functional overlap of brain networks to facilitate overlapping cognitive processes (Kovacs and Conway, 2016), building on evidence for the central role of the frontoparietal network in general and fluid intelligence (Barbey et al., 2014; Jung and Haier, 2007) to suggest that overlapping cognitive abilities are instantiated by the overlap of functional brain networks (e.g., see Meunier et al., 2010; Román et al., 2014). While in main a psychometric theory, Process Overlap theory draws support from consistent patterns across several neuroscience findings, aligning with neuroimaging evidence for localized frontoparietal hubs (Barbey et al., 2013b), dedicated systems for executive function and cognitive control (Niendam et al., 2012), global prefrontal cortex connectivity (Cole et al., 2012), and the importance of globally efficient functional connectivity (E. Bullmore and Sporns, 2012; Santarnecchi et al., 2014). Process Overlap argues that the overlap in cognitive abilities which produces the positive manifold results from an overlap in functional brain networks, such that the overlap of cognitive processes proposed by the theory is reflected directly in the joint functional activation of overlapping brain networks.

Previous research suggests that intrinsic functional patterns observed in resting state data constrain and shape task-evoked functional states (Bolt et al., 2017)—and further, that the degree of functional reconfiguration required between

resting and task-based connectivity is lower for individuals with higher intelligence (Schultz and Cole, 2016). Recent neuroimaging evidence (Soreq et al., 2021) has built on these findings, and on the sampling theory of psychometric *g*, to propose the Network Sampling Theory. Using functional neuroimaging data, Soreq et al., 2021 demonstrate that task-evoked functional network states can accurately classify cognitive states during a battery of psychometric tasks, suggesting that high-dimensional network sampling operations may support flexible network reconfiguration across a diverse set of cognitive tasks. This perspective aligns closely with the neuroscience and psychometric predictions of Process Overlap theory, and also aligns with the network dynamics perspective of Network Neuroscience Theory, where greater fluid abilities depend on increasingly complex and difficult-to-reach network states. Particularly for high-performing individuals, Soreq et al., 2021 find that multivariate network states that reflect underlying cognitive operations can be accurately classified, and that more complex cognitive operations are associated with greater network complexity. Overall, these evidence suggest that that cognitive faculties relate to the way in which the brain expresses these task-optimal network states. Intriguingly, the authors suggest that sampling theory provides a possible neurobiological explanation for factor differentiation (Detterman and Daniel, 1989), the phenomenon where intelligence explains a greater proportion of variance across tasks for lower-intelligence individuals. Higher-intelligence individuals may display more specific network states, reducing the level of overlap in network sampled across cognitive tasks. This sampling-based accounts provide an intriguing explanation for the neurobiology and dynamics of the positive manifold.

Predictive Processing Model

Predictive Processing (Euler, 2018) has also been recently proposed as a plausible integrative framework for the neuroscience of intelligence. Contemporary network neuroscience research conceives of the brain as an active and dynamic inference generator, anticipating incoming sensory inputs and forming hypotheses about that world that can be tested against incoming sensory signals (Clark, 2013; Friston, 2010). Predictive Processing builds on this perspective by integrating it with neuroscience evidence for the importance of the frontoparietal (Jung and Haier, 2007) and Multiple Demand (Duncan, 2010) networks, by proposing a hierarchy (Huang and Rao, 2011) of predictive (e.g.,Bubic et al., 2010; Ficco et al., 2021) representations in the brain, such that intelligence is the ability to overcome the uncertainty that emerges when predictions and incoming signals are mismatched. This prediction-based perspective aligns with evidence for of a hierarchy of overlapping brain networks reflecting the structure of *g* (Betzel and D S Bassett, 2017; Román et al., 2014; Soreq et al., 2021), and also maps to

accounts for *g* based on network dynamics (Barbey, 2018; van der Maas et al., 2006). However, Predictive Processing goes further than these accounts by proposing that a single physiological principle—suppressing prediction errors—underlies all neurocognitive activity and ability. While neural mechanisms for top-down prediction error have been identified (Mayer et al., 2015), evidence from network topology for the role of prediction in guiding network dynamics is lacking. Though Predictive Processing proposes uncertainty to be the central mechanism for intelligence, present formulations (Euler, 2018) of the model associate *g* with a single primary brain network, potentially at odds with current cognitive neuroscience theories which argue for the importance of multi-network dynamics or global activity and topology (e.g., Barbey, 2018; Kievit et al., 2016; Kovacs and Conway, 2016; Soreq et al., 2021).

Watershed Model of Fluid Intelligence

The Watershed Model of fluid intelligence (Kievit et al., 2016) draws primarily on neuroscience evidence for the role of microstructural white matter integrity (Lebel and Deoni, 2018; Roberts et al., 2013; Sampaio-Baptista and Johansen-Berg, 2017) in cognitive ability and development. The Watershed Model proposes that a hierarchical structure unifies the directed relationship between white matter integrity and general intelligence (Penke et al., 2012), where white matter integrity predicts processing speed (Penke et al., 2010), and processing speed predicts intelligence (Schubert et al., 2017; Schubert et al., 2015). As a conceptual framework, the Watershed Model affords for hierarchical relationships between lower-level sources of individual variance (e.g., genotypes) that gradually accumulate to influence individual differences in intermediate variables (e.g., white matter microstructure, processing speed), that ultimately produce large individual differences in the phenotypic outcome of the model (e.g., fluid intelligence). Kievit et al., 2016 validate their Watershed Model using cross-sectional data, measuring white matter integrity via tract-specific Fractional Anisotropy values acquired using Diffusion Tensor Imaging (Fox et al., 2012). Though Kievit et al., 2016 do not present their theory as a cognitive neuroscience account, the relationship between structural brain network topology (Hagmann et al., 2007), underlying white matter integrity (Frey et al., 2021), and cognition (Na et al., 2018; Zhai et al., 2020) has lead both Parieto-Frontal Integration (Jung and Haier, 2007) and Network Neurosience (Barbey, 2018) Theory to make explicit claims about the importance of underling white matter structure to cognitive ability, which are broadly supported by in a wealth of neuroimaging evidence (Barbey et al., 2015; Barbey et al., 2014; Barbey et al., 2013b; Basten et al., 2015; Byrge et al., 2014; Gläscher et al., 2010; Hilger et al., 2017; Na et al., 2018; Park and Friston, 2013; Pineda-Pardo et al., 2016; Román et al., 2017). Watershed models may be easily

extended to include measures of network structure and topology, as the conceptual strengths of the framework may permit future inclusion of directed relationships between underlying white matter structure and brain network topology, affording investigation into the network architecture that underlies intelligence. As it stands however, neuroscience data that directly support the Watershed Model of fluid intelligence are, as in other models, bound up with the methodologies of a single imaging modality and conceptual framing.

Network Neuroscience Theory of Intelligence

Recent work in network neuroscience suggests that systemwide brain network topology (Deco et al., 2015; Frey et al., 2021; Na et al., 2018; Sporns et al., 2000b) and dynamics (Barbey et al., 2015; Cabral et al., 2017; Chai et al., 2017; Shine et al., 2016; Sporns et al., 2000a) are critical sources of individual differences in cognitive ability. Aligning with this perspective, the Network Neuroscience Theory of intelligence (Barbey, 2018) proposes that intelligence results primarily from the flexible and dynamic reconfiguration of brain networks. The theory argues that network properties supporting intelligence are not isolated to specific brain networks identified by localist neuroscience theories of intelligence—instead, they are distributed across the entire connectome and reflected in functional edges that support both integration and segregation, enabling efficient and flexible dynamics across the entire connectome. This multi-network description of the underpinning of intelligence differs fundamentally from more localist theories, instead proposing that intelligence is produced by whole-brain, multi-network connectivity and dynamics, supported by an efficient and modular underlying architecture.

Network Neuroscience Theory adopts the perspective that *g* originates from individual differences in the network topology and dynamics of the entire connectome. The theory emphasizes the mechanistic importance of small-world brain networks (D. S. Bassett and E. Bullmore, 2006; D. S. Bassett and E. T. Bullmore, 2017) in producing the functional dynamics (Zalesky et al., 2014) and resulting connectivity displayed during cognition (Nee, 2021), where the organization of functional brain networks, and their network reconfigurations, are constrained and supported by underlying white-matter structural connectivity of intrinsic brain networks (Gu et al., 2015; Park and Friston, 2013). Small-world topologies (a combination of high local clustering and efficient pathways for long-distance communication) optimally facilitate the structural connectivity and functional integration of distant brain areas (E. Bullmore and Sporns, 2012; Gallos et al., 2012; van den Heuvel et al., 2009), affording network efficiency through both global functional integration (Langer et al., 2012) and flexible local connectivity (Bertolero et al., 2018; Dubois et al., 2018; Santarnecchi et al., 2014). The resulting topological balance of integrated and segre-

gated edges (Cohen and D'Esposito, 2016; van Vreeswijk and Sompolinsky, 1996; Wang et al., 2021) produces critical network dynamics that balance the connectome in a maximally connected and flexible state (Beggs, 2008; Fekete et al., 2021; Vázquez-Rodríguez et al., 2017), facilitating the dynamic brain network reconfigurations that give rise to both efficient and specialized information processing (D. S. Bassett et al., 2011; Braun et al., 2015; Finc et al., 2020; Shine et al., 2016).

One important respect in which this view differs from other cognitive neuroscience theories, such as Process Overlap (Kovacs and Conway, 2016) or Network Sampling (Soreq et al., 2021), is by emphasizing the constraints that brain network architecture places on flexibly reconfiguring brain networks during task-based cognition (e.g., Barbey et al., 2013a; Bolt et al., 2017; Cole et al., 2014; Dehaene et al., 1998; Gu et al., 2015; Kitzbichler et al., 2011) and across development (Byrge et al., 2014; Na et al., 2018; Oldham and Fornito, 2019; Zuo et al., 2017). In particular, Network Neuroscience predicts the importance of both segregation and integration across brain networks for facilitating intelligence via small-world organization—where as Process Overlap predicts that intelligence depends only on functional network integration. Small-world networks enable a balance between specialized, locally connected information processing and global connectome-wide communication (Gallos et al., 2012; Watts and Strogatz, 1998), resulting in modular autonomy between neural systems (Barbey, 2018; Barbey et al., 2015; Meunier et al., 2010) and efficient network integration (Achard and E. Bullmore, 2007; Avena-Koenigsberger et al., 2019; Khambhati et al., 2018) that reflects the modular and integrated hierarchy of cognitive abilities (Román et al., 2014; Spearman, 1904; Spearman, 1927; van den Heuvel et al., 2009).

Network Neurosience Theory therefore argues that brain network modularity and segregation (Bertolero et al., 2018; Bertolero et al., 2015; Gallos et al., 2012) support both global and local integration and connectivity (Langer et al., 2012; Santarnecchi et al., 2017b; van den Heuvel et al., 2009), resulting in a small-world network architecture (D. S. Bassett and E. T. Bullmore, 2017) and topological balance (Wang et al., 2021) of connections that affords network reconfigurations from a critically balanced state (Beggs, 2008; Fekete et al., 2021; Vázquez-Rodríguez et al., 2017) to either topologically similar, or to topologically distant network states (Gu et al., 2015), in the service of task demands. This importantly allows the Network Neuroscience Theory to propose that *g* emerges from the information processing abilities of the brain, and that individual differences in two broad abilities, crystallized intelligence and fluid intelligence, are respectively facilitated by transitions to easy-to-reach network states (supported by strongly connected hub nodes) and difficult-to-reach network states (supported by diffuse, weak

functional connections). In this way, the theory makes contact with cognitive theories of intelligence at multiple levels of their factor structure (both general and broad), representing an advance from theories that focus on single modalities of neuroscience data, or single levels in the hierarchy of cognitive abilities. Further, this network dynamics perspective permits Network Neuroscience Theory to explain observations about the positive manifold, such as the observed factor structure of *g* (Schneider and McGrew, 2018) and factor differentiation (Detterman and Daniel, 1989), in terms of brain network dynamics, and to further explain individual differences in those network transitions in terms of the underlying architecture and topology of brain networks that support flexibility, modular structure and small-world organization. Though evidence for Network Neuroscience theory remains primarily indirect, it suggests intriguing potential as an explanation for intelligence, and more generally for the modular and parallelized organization of cognitive abilities (Barbey, 2018; Barbey et al., 2015; Robinson et al., 2009). Research in Network Neuroscience therefore represents a promising path forward towards elucidating the neurobiological underpinning of *g*, motivating future research into the precise mechanistic role of human brain network organization (Mill et al., 2017) and brain network dynamics (Girn et al., 2019) in broad and general facets of intelligence.

Conclusions

What indeed are the neurobiological foundations of individual differences in *g*? Several primary questions remain to motivate future research and theory development.

I: To what extent can current methods in network neuroscience be used to successfully reconcile the sometimes overlapping claims made by current cognitive neuroscience theories to more precisely elucidate the neurobiological foundations of *g*?

II: Does the assumption that *g* originates from a primary brain region or network remain tenable, or should theories instead broaden their explanatory scope to incorporate evidence for individual differences in the global topology and dynamics of the human brain?

III: To what extent can individual differences in broad and general facets of intelligence be accounted for by brain network dynamics? Do top-down mechanisms for cognitive control figure prominently in facilitating these network reconfigurations, or do network dynamics depend instead on more emergent processes, potentially facilitated by prediction and error?

As this chapter highlights, a formally precise and unifying theory of the cognitive neuroscience of *g* remains a challenge to formulate—due in part to the spatially and temporally overlapping nature of the existing theories, and the indirect nature of the neuroscience evidence for them. Neuroscience research demonstrates that the human brain is a complex network, structured to provide both the widespread global integration and specialized regional connectivity that support general and specific cognitive abilities. The development and maintenance of cognitive abilities appear to emerge from the remarkably dynamic nature of the brain—both the slower adaptation of structural connections during learning, and the faster functional reconfiguration of brain networks while performing functional tasks. At many levels of resolution—psychometric (van der Maas et al., 2006), developmental (Savi et al., 2019), cellular (Geary, 2019, neural (Neubauer and Fink, 2009; Schubert et al., 2017), regional (Duncan et al., 2000), network (Barbey, 2018; Duncan, 2010; Jung and Haier, 2007; Kovacs and Conway, 2016, phenotypic (Kievit et al., 2016), and global (Euler, 2018)—theories of intelligence either draw either directly or indirectly from research into cognitive neuroscience, making overlapping predictions between the abilities and organization of the brain, and the structure of the cognitive abilities.

While current cognitive neuroscience theories of intelligence each propose to explain individual differences in *g* on the basis of neurobiological evidence, these theories are each pitched at different levels of resolution, are often built on the basis of different modalities of research evidence. Looking across these theories as a whole, two central themes emerge: the importance of specialized regions and connections that support flexible brain network reconfiguration, and the importance of global brain network topology and organization. Reconciling these regional and global levels of resolution can be difficult, in part due to the indirect nature of relationships between *g* and cognitive neuroscience evidence.

A key area for future research and theory development is the incorporation fine-grained mechanisms for network reconfiguration (e.g., Avena-Koenigsberger et al., 2019; Khambhati et al., 2018) into accounts of the emergence of *g* from large-scale brain networks (Bressler and Menon, 2010; Varoquaux et al., 2018). Current research in systems neuroscience suggests an explanation for *g* in which global principles of network topology organize connectivity into a modular and hierarchical structure, and that same modular structure (and the local topology it affords) further tunes and refine those global properties. This modular and dynamic hierarchy produces the adaptive and massively parallel nature of human cognition, facilitating topological reconfigurations of brain networks during cognition Cole et al., 2014 that depend critically on modifying the allegiance of hub nodes and network modules (Bolt et al., 2017). While the critical role of modules for organizing and maintaining brain network topology may be a general organizational principle across the connectome (Bertolero et al., 2018), the particular hub regions and modules that facilitate brain network reconfigurations display flexible membership with frontoparietal and multiple demand network (Camilleri et al., 2018; Cole et al., 2012; Power and Petersen, 2013), and appear to play

an important role coordinating network state transitions related to task-based cognitive performance (Cole et al., 2013; Duncan and Owen, 2000) and general intelligence in particular (Barbey et al., 2013a; Hilger et al., 2017). Adjustments to both long-range structural connectivity (Byrge et al., 2014; Gu et al., 2015), and intrinsic functional network representations (Yeo et al., 2011; Yeo et al., 2014), produce and maintain a connectome that can sit in a balanced, critical states (Beggs, 2008; E. Bullmore and Sporns, 2012; Fekete et al., 2021; Sporns et al., 2004). Mismatches between external task demands and internal representations (e.g.,Bubic et al., 2010; Ficco et al., 2021; Huang and Rao, 2011) appear to perturb this connectome, facilitating network reconfigurations through a pattern of excitatory and inhibitory functional signaling (Cole et al., 2012), leading to the top-down and bottom-up recruitment of a hierarchy of task-relevant functional modules (Bolt et al., 2017; Soreq et al., 2021).

A key challenge going forward is to develop theories that can account for these various resolutions of network mechanism while generating testable predictions. These network mechanisms involved in g will support the specialization and local efficiency of many segregated network communities, while simultaneously affording long-range integration and global efficiency between networks. A primary strength of Network Sampling and the Network Neuroscience Theory of general intelligence is that each can offer a parsimonious mapping of those neurobiological properties to cognitive abilities, such that segregated local communities and global network integration respectively underlie specific cognitive capacities and the recruitment of those operations to adaptively facilitate cognitive performance. These hierarchies of brain networks—either spatially hierarchical (as in processing overlap) or dynamically hierarchical (as in network neuroscience) may in fact mirror the factor structure of cognitive abilities, in which narrow cognitive abilities (e.g., induction, lexical knowledge) can be grouped into broad abilities (e.g., fluid intelligence, crystallized intelligence) that collectively reflect overall individual differences in intelligence (i.e., the positive manifold).

Two primary limitations currently beset cognitive neuroscience theories of general intelligence. A first weakness of cognitive neuroscience theories is the somewhat indirect nature of the evidence they assemble. Much neuroimaging evidence emerges from of an investigation into a particular modality of neuroscience data (structural, functional, metabolic) using a particular analytic technique. Further, only a subset of empirical evidence is focused particularly on the neurobiology of the positive manifold. Network neuroscience evidence shows a clear relationship between underlying brain networks and individual differences in cognitive ability - however, many of these network properties are studied at a single level of resolution in isolation, as opposed to investigated jointly, or with respect to general intel-

ligence explicitly. This lack of mechanistic and explanatory exclusivity compounds the indirect nature of network neuroscience evidence. Consider the well known relationship between intelligence and gray matter volume (Cole et al., 2012). How often do studies include and control for this relationship when investigating the contributions of other neurobiological properties to intelligence? Is it even appropriate to perform this control? Similarly, little work has been done to establish specificity in neuroimaging theories by distinguishing experimentally between existing cognitive neuroscience theories of general intelligence, or by attempting to replicate the corpus of results on which they base their evidential support (e.g., see Kruschwitz et al., 2018).

This leads to a second limitation of current theories: network neuroscience research makes limited interdisciplinary contact with psychology theories on the structure of intelligence and the positive manifold. While factor accounts of g and positive manifold remain predominant (Schneider and McGrew, 2018), growing reinterest in network models of intelligence has led to the reemergence of sampling theorem (Thomson, 1951), and newfound interest in network models (Savi et al., 2019; van Der Maas et al., 2017) for explaining the structure and development of cognitive abilities. While Processing Overlap (Kovacs and Conway, 2016) and Network Sampling (Soreq et al., 2021) take a sampling theorem perspective, their neuroimaging evidence is again primarily indirect, and does not provide a test of the predictions made by sampling theorem against the different predictions made by other formal explanations of g. Even the use of sampling theorem is novel, as most network neuroscience theories adopt a factor analytic perspective to g. To the extent that neuroscience theories parse the neurobiology of broad facets of intelligence, their focus is predominantly on the distinction between fluid and crystallized intelligence. The CHC account of the positive manifold and the factor structure of g identifies up to 14 broad intelligences beyond Gf and Gc that load onto g, identifying for example, facets as various as short-term memory (Gsm), processing speed (Gs), auditory processing (Ga), and domain-specific knowledge (Gkn). Of these broad facets, Neural Speed (Schubert et al., 2017) and the Watershed Model (Kievit et al., 2016) remain the only neuroscience theories which address individual differences in broad ability beyond Gf and Gc, namely processing speed—and not ways consistent with the well-supported factor structure of intelligence identified by CHC theory. Beyond factor and sampling theories on the positive manifold, more recent cognitive neuroscience theories of intelligence remain unexplored in neuroscience data. At present, little attention has been paid by neuroscience to theoretical predictions on the structure of intelligence, with a particular lack of within-subjects data from developmental and longitudinal studies. Building a more robust network neuroscience of intelligence may ultimately require a more precise mapping

between brain networks and cognitive abilities, reflecting the nuanced hierarchical relationships between cognitive operations and neurobiological substrates that facilitate the positive manifold.

To what extent can or should cognitive neuroscience theories of intelligence further integrate with findings on individual differences in the positive manifold from non-neuroscience fields? *g* is fundamentally a measure of individual differences, and characterizing the neurobiology that underlies individual differences in cognitive ability remains an open problem. In particular, understanding remarkable breadth of variation in human intellectual abilities will require accounting for intellectual performance at very high ends of the human population's distribution, either in terms of a more fundamental characterization of the nature of brain network dynamics, or a more fundamental reassessment of individual differences in the mapping between network topology and cognitive performance. Further, it remains an open question how generally to map levels of the hierarchy of intellectual abilities (general, broad, and narrow) onto levels of resolution in brain networks. What role might higher-order representations of network structure and dynamics, possibly beyond those currently assessed in connectomics, have to play in facilitating dynamic reconfiguration in brain networks? What unifying theories and modeling approaches could be applied to develop a more integrated and comprehensive understanding of the brain network dynamics, in order to better account for the network relationships between intelligence, neurobiological structures, and the information-processing capabilities they support (Savi et al., 2021)?

Finally, a full and comprehensive understanding of human intelligence may require characterizing the developmental timecourse cognition over the lifespan with respect to properties of brain networks and their topology. Cognitive abilities develop and decline at differing rates through the lifespan—how do these changes map onto the structure of the brain, and in what respects are they sensitive to genetic and environmental factors? As the scope of these issues suggest, fundamental questions about the nature and mechanisms of human intelligence remain. Cognitive neuroscience theories of intelligence will hopefully continue to provide a catalyst for contemporary network neuroscience research in this area, motivating important future work into neurobiological underpinnings of individual differences. Several key questions remain, promising to enhance our understanding of the fundamental nature of human intelligence and individual differences if they can be answered. Through further investigating the neurobiological foundations of general intelligence, network neuroscience will continue to make advances in our understanding of the remarkable breadth and variation of human abilities.

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