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Review article

Linking brain network reconfiguration and intelligence: Are we there yet?

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ABSTRACT

Recent applications of dynamic network analyses to functional neuroimaging data have revealed relationships between a number of cognition conditions and the dynamic reconfiguration of brain networks. Here we critically review such applications of network neuroscience to intelligence. After providing an overview of network neuroscience, we center our discussion around the recently proposed Network Neuroscience Theory of Intelligence (Barbey, 2017). We evaluate and review existing empirical support for the theses made by this theory and argue that while studies strongly suggest their plausibility, evidence to date has largely been indirect. We propose avenues for future research to directly evaluate these theses by overcoming the methodological and analytical shortcomings of previous studies. In doing so, our goal is to stimulate future empirical investigations and present valuable ways forward in the network neuroscience of intelligence.

1. Introduction

Contemporary functional neuroimaging investigations conceive of the brain as functioning by means of dynamic interactions within and between distributed networks of brain regions at multiple spatial and temporal scales [1]. Accordingly, much research has investigated the functional network organization of the brain both during the so-called 'resting state' and during task conditions. This body of work has demonstrated that the resting brain can be consistently parcellated into sets of distinct and reliable functional networks [2–5], which reconfigure their interrelationships based on task demands [6–10]. Network organization has primarily been examined by averaging functional connectivity (FC) over resting or task periods on the order multiple minutes (typically, 6–12 min). However, recent research has also emphasized the temporal dynamics of brain network interactions on shorter time scales [6,11,7]. In this line of work, the brain is seen as a dynamic system that is continually reorganizing across a landscape of different functional network configurations both within particular cognitive conditions and in the transitions between them [12–25]. Critically, analyses with finer temporal sensitivity (typically on the order of tens of seconds) allow a window into behaviorally-relevant information that is obscured by relatively static approaches that average over multiple minutes [12,26,22,23].

Analyses that focus on brain network reconfiguration have now been applied to a number of mental phenomena, including task-unrelated thought and daydreaming [26], visuospatial attention [23], executive cognition [13], and learning [27,12]. Of note for the present context, research has also begun to apply such analyses to the investigation of intelligence [28,22]. The movement towards brain network dynamics in intelligence research is notable given that the majority of investigations over the past decade have primarily employed relatively static approaches, which e.g., relate intelligence to averaged structural or functional brain network connectivity with little emphasis on dynamics [29–32].

Before discussing more on the network neuroscience of intelligence, however, it is important to denote what this term actually refers to scientifically. For example, what is meant by 'general intelligence'? And what is its relationship to the related construct of 'g'? A great deal of intelligence research has been focused on g, also referred to as 'Spearman's g', little 'g', or the 'general factor of intelligence' [33]. Spearman's g, as traditionally conceived, refers to a domain-general intelligence factor that influences performance on various domain-specific cognitive abilities [33]. This construct was motivated by the fact that individuals' scores on cognitive tasks that tap into distinct domains (e.g., verbal vs. visuospatial) are highly correlated; a finding termed the 'positive manifold'. Thus, g is a statistically derived factor that accounts for unexplained variance between domain-specific cognitive abilities. It should be noted, however, that this view of g exerting

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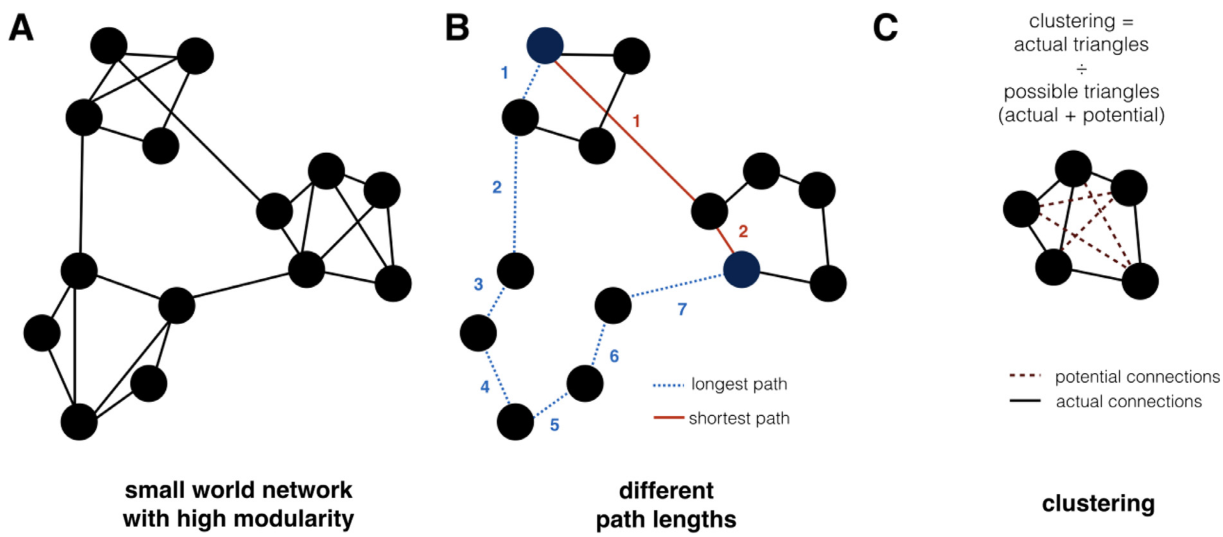

Fig. 1. Some basic graph theory concepts of relevance to network neuroscience. (a) Example of a small world network with high modularity (three different modules). There is a co-occurrence of high clustering (as exhibited by triangles within each of the modules) with low characteristic path length (mediated by long-range connections between modules). The modules are defined based on sets of nodes having greater intra-network than inter-network connectivity. (b) Example of differing path lengths in a network. The blue dotted path requires seven edges to connect targets α and β, compared to the solid red path which only requires two edges. Information transfer through the red path would be more efficient. The characteristic path length of a network is the average number of interim nodes in the shortest paths between each pair of nodes in the network, and global efficiency is defined as the inverse of the characteristic path length. (c) Example of clustering within a network. Dashed lines represent possible connections. Solid lines represent actual connections. When three nodes are fully connected, a triangle is formed. Clustering is computed based on the number of actual triangles divided by the number of possible triangles in a network. Here only one triangle is actually formed out of all possible triangles. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a top-down influence on domain-specific abilities is not without controversy and disagreement (e.g., see [34]). General intelligence, on the other hand, is a related but conceptually distinct construct which can be taken as synonymous with full-scale IQ [35,36]. Rather than specifically representing the correlations between domain-specific abilities, general intelligence pertains to one's composite score on a battery of intelligence measures (such as the Weschler Adult Intelligence Scale; [37,36]. Bearing this distinction in mind, in what follows we use ‘intelligence’ when referring to intelligence in a general sense and use either ‘g’ or ‘general intelligence’ as appropriate when discussing the findings of specific studies.

Offering a notable step forward in linking brain network reconfiguration to intelligence, Barbey [38] recently proposed a novel framework for understanding the neural basis of g based on findings in the network neuroscience of intelligence. Specifically, he proposed that “g depends on the dynamic reorganization of [brain networks] - modifying their topology and community structure in the service of system-wide flexibility and adaptation” ([38], p. 10). Adding to this, a recent empirical study claimed to provide empirical support for a relationship between brain network reconfiguration efficiency and general intelligence [22]. Thus, these two early papers in the dynamic network neuroscience of intelligence propose a central role for the adaptive, flexible, and efficient reconfiguration of brain networks in the neural basis of intelligence.

In the present paper, we first offer an overview of network neuroscience approaches to brain function, followed by a review of recent research exploring the role of brain network reconfiguration in the neural basis of cognition. We then outline and discuss the Network Neuroscience Theory of Intelligence in light of network neuroscience research preceding and following the publication of this framework [38]. Based on our review of the existing literature, we argue that this view is plausible, yet suggest that it has not yet been directly empirically tested to date; the few existing studies related to the framework do not currently provide substantive support for its claims. We end by suggesting avenues of research that can move past previous methodological and analytical shortcomings and offer a direct test of the hypothesis that general intelligence is mediated by the adaptive flexibility of brain network reconfiguration.

2. Network neuroscience

Network neuroscience has as its primary goal the mathematical characterization of the network properties of brain networks and the regions that comprise them [1]. In order to achieve its goals, network neuroscience employs the resources of network science, itself a subfield of complex systems science that draws on tools from mathematics, physics, computer science, and engineering. Very broadly, the tools drawn from network science can be divided into those that seek to characterize the static topological characteristics of brain networks, and those that are more concerned with the dynamic patterns of connectivity within and between networks. In this section we will provide a general overview of these tools and of primary findings from their application to the brain, so as to orient the reader and provide theoretical background for what follows.

2.1. Functional connectivity at multi-minute time scales

A large body of work has now applied metrics from graph theory, a subfield of mathematics concerned with the quantification of the topological properties of networks of interconnected elements [39], to neuroimaging data. In this context, a network can be seen as a formalized representation of a complex system, which is composed of a set of nodes (e.g., brain regions) connected by links (e.g., white matter pathways). Graph theory-based analyses of brain networks [40] have revealed a number of consistent topographical characteristics in the patterns of connections between brain regions. These analyses are typically done on ‘static’ functional connectivity; that is, connectivity averaged over an entire rest or task session.

Notably, the brain has been revealed to have a modular small-world organization at multiple spatial scales [41,42,3,43]. *Modularity* refers to the fact that the brain can be parcellated into functionally specialized modules (i.e., functional networks), each of which represents a set of regions that display greater intra-modular connectivity relative to inter-modular connectivity (Fig. 1A; [43]). A highly modular functional configuration is also often referred to as a state of (relative) segregation, while a configuration with less modularity (i.e., that has modules lower in number and larger in size) is referred to as a state of (relative) integration. *Small-worldness* refers to the observation that, although the brain can be separated into modules, it also features long-range connections that enable efficient communication between these modules (Fig. 1A; [41,44]). Formally, high small-worldness specifically pertains to the topological situation in which there is a combination of high *clustering* with relatively small *characteristic path length* (Fig. 1B and C; [39]). *Clustering* is a measure of local connectivity and indexes the fraction of directly connected node pairs that share a common neighbor (formally, the number of actual topological triangles relative to possible topological triangles). *Characteristic path length* refers to the average number of interim nodes in the shortest paths between each node in the network. The balance between local functional specialization and global functional integration enabled by small-worldness is thought to allow for greater complexity and flexibility of brain dynamics [45,41]. An important additional metric is *global efficiency,* which simply refers to the inverse of characteristic path length. Readers are directed to Rubinov and Sporns [40] for further discussion and formal definitions of graph theoretic concepts as applied to brain data.

2.2. Functional connectivity at sub-minute time scales

The above graph theoretic metrics have typically been applied to data averaged over an entire fMRI scan session. While providing a summary of the relevant topological characteristics over an extended period of time (e.g., 10 min), such metrics overlook the dynamic activity occurring at much shorter timescales (seconds). This obscures valuable information, given the rapid, time-varying nature of activity underlying cognition. Thus, recent work has adapted the tools of network science to the study of dynamic brain networks; an approach referred to as ‘dynamic functional connectivity’ (dFC; [46,7]).

One popular method in dFC research is to separate the neuroimaging scan session into shorter windows of a certain length, and to apply graph theoretic metrics to the network configurations of each window [46,7]. This sliding-window approach reveals how network properties evolve through time, and can give insight into the manner in which networks dynamically reconfigure at rest and during tasks [6,25]. By comparing the topological characteristics of brain networks across windows, one can determine, for example, dynamic changes in the overall integration and segregation of the brain and the particular brain networks instantiating such changes. Measures of dFC allow for the characterization of temporally-dependent properties such as FC variability and flexibility at both the regional and network level. FC variability, often computed as the standard deviation of inter-regional FC across windows, has been demonstrated to significantly differ across rest and task states, and has been related to response time variability and task performance in a number of domains [47,6]. dFC studies have defined and measured (regional) flexibility as the variability of a given region's network affiliation over time or across distinct cognitive conditions. This metric provides information on the degree to which a region can dynamically interact with and facilitate communication between multiple networks, and has notably been linked to cognitive phenomena such as learning [12] and executive cognition [13]. Relevant for the dynamic network basis of intelligence as proposed by Barbey, such dynamic metrics may be used to pinpoint and characterize the specific regions (and, by extension, networks) that play a preeminent role in driving the flexible reconfiguration of brain networks at the sub-minute level.

2.3. ‘Dynamic' versus ‘static’ functional connectivity: accounting for different time scale

As mentioned, multiple studies have demonstrated that dFC analyses allow access to behaviorally-relevant information that fails to be captured by the multi-minute averaging of static approaches [12,48,26,49,20,22,23]. At the psychological level, static approaches are concerned with temporally-extended cognitive conditions (i.e., rest or a task) taken as a whole, and are often aimed at illuminating trait-level properties. In contrast, dynamic approaches may allow greater sensitivity to the current mental state of the subject and of the dynamic shifts between mental states [50]. It is also possible that certain traits and abilities may be encoded *within* the dynamics of connectivity underlying mental state shifts; such as is being proposed in the Network Neuroscience Theory of Intelligence (see Section 4 below; [38]).

It is important to note that, depending on the timescale (static vs. dynamic), the notion of ‘functional brain network reconfiguration’ (FBNR) may have different meanings. One meaning is that FBNR refers to changes in brain network topology and community organization occurring on the sub-minute scale – such as examined by sliding-window dFC analyses. This conception of FBNR views it as more closely approximating dynamic shifts in cognitive processing and of providing fine-grained information on brain state transitions. Another meaning of FBNR employed in certain studies is that it refers to changes in brain network organization across cognitive conditions (e.g., [51,22]). Under this meaning, static analyses are employed on data averaged across distinct conditions, and then these are subsequently compared. This approach does not seek to examine transient mental state shifts but seeks to characterize each cognitive condition as a whole and the brain network differences between them. The distinction between these two approaches is important in the network neuroscience of intelligence, and we hold that empirical investigations employing the dynamic conception are what are required to substantively evaluate Barbey's Network Neuroscience Theory of Intelligence.

3. Brain network reconfiguration

In this section we provide an overview of empirical research on the relationship between brain network reconfiguration and cognition, so as to provide further background for the tenets of the Network Neuroscience Theory of Intelligence and our subsequent empirical suggestions. As detailed above, the brain can be parcellated into functionally specialized networks (synonymous with ‘modules’) which feature dense intra-network connectivity, and which are connected to each other via relatively sparse inter-network connections [3,43,4]. Early research on the network organization of the brain typically concerned itself with networks derived from the resting-state [52,43], motivated by a view of the resting-state as a task-free baseline which revealed the ‘intrinsic’/context-independent functional organization of the brain [53,52,54,55]. Recent research, however, has supported the notion that the brain's network organization dynamically changes both within particular cognitive conditions (including rest) and in the transitions between them [12–16,6,17–21,7,22,9,23–25]. Consequently, cognitive condition-dependent functional reconfiguration of brain networks has emerged as a likely mechanism that allows the brain to flexibly employ its anatomical connections to dynamically adjust to current cognitive demands [6–9].

Underscoring this view, brain network changes elicited by particular tasks have been directly related to behavioral and cognitive performance [12,56,13,57,47,58,28,59,17,10,23]. For example, dynamic brain network reconfiguration at the sub-minute level has been associated with individual differences in learning capacity, working memory, memory recall accuracy, cognitive flexibility, and executive function [56,13,57–59,24].

Specific regions of the brain significantly vary in their propensity to dynamically change their network affiliation (and therefore drive network reconfiguration) [20,60]. Empirical work, for example, has successfully separated areas of the brain into a set of regions that constitute a ‘core’ or ‘task-general’ structure, as well as a smaller set of regions (the ‘periphery’) associated with greater task-dependent dynamic change [61,14,62,51,19,63]. The ‘core network’ remains relatively stable across different cognitive conditions. For example, one study measured the connectivity structure common across 64 different task domains and revealed an organization with very high similarity to the resting-state (r = 0.90) [62]. Further support came from a study examining the similarity of functional organization across 14 distinct task states, all of which featured strong correlations, ranging from 0.69 to 0.82 [19]. Similar evidence of stable global network connectivity comes from additional graph theoretic measures: clustering and path length/global efficiency remains largely stable across tasks, while local changes selectively occur in particular regions/networks [21].

Certain regions are more likely to undergo dynamic change in network affiliation. Research suggests such regions often (but not always, e.g., [64]) consist of multimodal association 'hub' regions [28,6,49,8]. These flexible regions, which can be characterized by their high centrality and interconnectivity within the entire brain network, are thought to facilitate the selective and flexible integration of networks based on particular task demands [65,66,28,8,60]. Importantly, it should be emphasized that the flexibility of a particular region can vary across cognitive conditions, and that hub regions flexibly employ different subsets of their diverse connections depending on the level and type of current cognitive demands [20].

Research on brain network reconfiguration has also provided evidence that the brain's functional network organization continually oscillates, at the sub-minute level, between states of relative integration and segregation [67,58,9]. Research on task-dependent reconfiguration has revealed that most task-states elicit a more integrated (i.e., less modular) brain network organization than rest [8], and that the degree of task-dependent integration can track behavioral/cognitive performance [13,58,15,16,22,8]. This is likely driven by a tendency towards increased inter-network connectivity with concurrent decreases in intra-network connectivity during task states [6]. Studies also suggest that the degree of integration may track task difficulty and/or cognitive effort [18,8]. For example, the degree of inter-network integration for an n-back task is much higher than a simple motor task [8]. However, it should be noted that task-based integration is not universally associated with better performance [56,58]. For example, better performance on a simple motor task was associated with greater segregation of relevant networks [56,58]. Relatedly, an additional study found that greater working memory capacity was associated with greater modularity during rest (i.e., less whole-brain integration), suggesting that segregation might sometimes serve to inhibit noise propagation [68]. It is possible that cognitive tasks vary with respect to the degree to which they demand network cross-talk vs. functional modularity and to the degree to which they can become automatized (i.e., requiring less cognitive control and relying more heavily on skilled behavior), which may be represented in the competition between brain network integration and segregation. Collectively, this research suggests, in line with Barbey [38], that the brain's ability to flexibly reconfigure into either an integrated or segregated functional organization as required for particular cognitive demands is important for cognitive and behavioral performance.

4. Barbey's network neuroscience theory of intelligence

Although network neuroscience approaches have been gaining popularity in psychologically-relevant domains over the last decade, such approaches have only recently been applied to intelligence in empirical and theoretical work. A novel theoretical framework was recently proposed by Barbey (2018), which suggests that network neuroscience measures may help explain Spearman's *g*. According to Barbey's framework, *g* originates from individual differences in system-wide topology and the dynamic reorganization of intrinsic connectivity networks in the brain. It therefore holds that *g* is a global brain property specifically embodied by the properties of functional brain network dynamics. Moreover, Barbey's Network Neuroscience Theory of Intelligence proposes that the facility with which intrinsically connected networks can flexibly transition between network states is dependent on their small-world topology. This is to say that individual differences in *g* are related to the ability of one's brain to exhibit a functional network topology that facilitates an optimal balance between local (modular) and global (integrative) processing. In this model, the capacity to flexibly transition between two types of network states is critical to underlying individual differences in g: 1) easy-to-reach states that are achieved through strongly connected hubs requiring minimal transitions – driving crystallized intelligence (i.e. performance on tasks requiring prior knowledge and experience) and 2) difficult-to-reach states that are achieved through weak connections – driving fluid intelligence (i.e. performance on tasks requiring the capacity to reason and adapt in novel situations). Barbey refers to crystallized and fluid intelligence as broad cognitive abilities, and proposes that they emerge as domain specific (locally efficient) modules which are hierarchically embedded within other domain specific modules to give rise to greater global efficiency. Accordingly, he holds that, whereas transitions towards states that maximize local efficiency are associated with the engagement of domain specific cognitive abilities, transitions towards states that maximize global efficiency are associated with the engagement of broad or general abilities.

In addition, Barbey notes that intrinsically connected networks differ in terms of the variability of their inter-network connections over time. This means that differences will arise in the degree to which networks support dynamic flexibility. For example, the frontoparietal control network – which is most strongly associated with fluid intelligence – has been found to have the greatest dynamic flexibility across task states of any network [28,20], and is thus thought to also play a key role in general abilities.

In sum, Barbey's Network Neuroscience Theory of Intelligence offers a new way of thinking about general intelligence: it is the ability to leverage small-world topologies to flexibly shift between network states, ultimately promoting rapid information exchange at a global level. As such, it offers two main theses: (1) individual differences in *g* are based on the flexibility with which one's system-wide network organization can adaptively reorganize its topology and community structure in service of a task, and (2) that this flexibility depends on the small-worldness of one's brain network. The first thesis pertains to dynamics - specifically, the flexibility of transitions between states over time. The second thesis pertains to the underlying (static) topological organization of one's brain network. In what follows, we offer a discussion of empirical research related to each.

4.1. Thesis (1): flexibility of brain network reconfiguration

A number of empirical studies have explored how the brain dynamically reconfigures in the service of executive cognition and high-level reasoning. Given that intelligence tasks require similar processes for completion, we find such studies informative for understanding the role of brain network reorganization in relation to the neural basis of intelligence. In this section, we review these studies and evaluate the degree to which they provide initial evidence in support of Barbey's first thesis (1): individual differences in *g* are based on the flexibility of system-wide network reconfiguration.

In a notable study, Braun and colleagues [13] employed sliding-window dFC analyses to characterize the brain network reconfiguration underlying executive function as indexed via performance on the n-back task. They measured regional flexibility (the tendency of a region to change its modular affiliation across windows) and found preferentially greater network reorganization in frontal regions when cognitive load was higher, and, further, that this reorganization was significantly correlated with task performance [13]. Consistent with past results suggesting that greater network flexibility predicts greater learning ability [12], this study provided evidence that network flexibility may also facilitate stronger executive function. A related study employed resting-state dFC analyses and examined the length of time two region pairs remained connected or disconnected with each other (based on a connectivity threshold) prior to switching to the opposite state [48]. They interpreted lower average time spent in a particular connectivity state as indicating greater flexibility. The authors found that, averaged across all regions of the brain, lower average time spent in a particular connectivity state (across the whole brain) was positively correlated with executive performance, and explained significantly more variance relative to static multi-minute analyses [48]. This result was primarily driven by frontal-parietal executive control regions which featured significant flexibility over time as indicated by their measure [48].

An additional noteworthy study in this area built on the above-mentioned investigations by examining the relationship between neural flexibility and executive function [69]. This is particularly relevant for the present discussion given Barbey's claim that the brain's ability to flexibly reconfigure is central to intelligence. This study applied *k*-means clustering on sliding-windows to identify clusters of similar windows ('brain states'), each of which represented a whole-brain network connectivity pattern. They found that cognitive flexibility (NIH Card Sort) and processing speed (NIH Processing Speed) were higher in individuals who spent a greater fraction of time in brain states with greater variability relative to brain states with lower variability [69]. Interestingly, however, fluid intelligence (which is typically highly correlated with *g*) did not show this relationship, nor did it show any relationship with any other dFC measured used in this study. This suggests a non-trivial relationship between putative subcomponents of intelligence and brain function, with notable dissociations between them.

In combination, these studies offer support for the role of flexible brain network reorganization in cognitive processes that are often taken to be related to intelligence. However, the relationship between intelligence and its putative component processes is far from clear, and these studies provide indirect support at best. The question of the relationship between distinct executive functions (e.g., working memory, response inhibition, task switching, processing speed, etc.), and between them and intelligence, has been a source of continual controversy in the field [70–73]. This is motivated by the fact that executive functions differentially correlate amongst themselves, and not all functions correlate with measures of intelligence (e.g., as measured by full-scale IQ or fluid intelligence) [71,72]. Thus, the need to clarify the relationship between intelligence and executive function should be borne in mind in network neuroscience investigations of intelligence moving forward (see Section 5.1 for further discussion and suggestions on this point).

Two additional relevant studies, which examined brain network configuration but did not employ dFC analyses, also warrant discussion. A recent study by Hearne et al. [51] investigated how flexibility arises out of relatively stable brain networks, and how it changes over time. Their goal was to examine changes in functional connectivity (FC) across five different fMRI scans: a pre-task "resting state" scan, followed by three different levels of complexity on a relational reasoning task, and finally a post-task 'resting-state' scan. Each level of the reasoning task was then compared to FC values in both the pre- and post-task resting state scans in order to assess changes over time.

Four networks emerged during the pre-task resting state scan: sensory, default network, visual, and FPCN. In contrast, a transitory frontoparietal-visual (FPV) module emerged during task scans but switched back to its original configuration again during the post-task scan. They also found that the FPCN displayed the greatest amount of reconfiguration during task-scans compared to the other three networks found at rest. In addition, the authors assessed changes in each module's global efficiency across conditions and how this related to performance on the reasoning task. The FPV module not only demonstrated changes in efficiency across conditions, but its efficiency was also significantly correlated with better performance on the reasoning task.

Although the results of this study serve as a step towards understanding the network neuroscience of intelligence by underscoring the importance of flexible brain network reconfiguration and network efficiency, they do so only through potential inferences and inconclusive evidence. For example, the relationship between FPV efficiency and cognitive performance was maintained even with fluid intelligence scores partialled out, and the authors did not report the correlation between changes in efficiency and fluid intelligence. In addition, the authors critically did not employ dynamic measures of FC at the sub-minute level.

A final study, Schultz and Cole [22], also did not directly test Barbey's framework, but their results nevertheless demonstrated initial evidence that higher-performing individuals have more efficient network reconfiguration when switching from resting-state to three different cognitive conditions (language task, working memory task, and reasoning task). They assessed reconfiguration efficiency by measuring the similarity of FC patterns between rest and each of these conditions. This was based on the inference that greater similarity in FC patterns between two cognitive conditions indicates that a shorter distance in state-space is required to travel from one to the other. Employing this metric, they found that reconfiguration efficiency from rest to a given cognitive condition was positively related to performance for all three conditions. Further, they found that 1) individuals with greater similarity between task-general FC and resting-state FC exhibited stronger task performance, and 2) reconfiguration efficiency was correlated with general intelligence. This led the authors to suggest that individuals with greater intelligence have an intrinsic (resting-state) brain network configuration that is already closer to the type of configuration needed to perform well on demanding cognitive tasks.

Despite ostensibly providing support for Barbey's framework, this study also features limitations that preclude its ability to do so in a substantive manner. Notably, this study did not employ dFC analyses and used cognitive condition-averaged characterizations of FC. While examining the FC configuration similarity of two temporally adjacent cognitive conditions may be suggestive, without directly measuring the dynamics of the FC state transitions between and within them strong conclusions cannot be made with respect to Barbey's thesis (1).

Collectively, these studies offer indirect support for aspects of Barbey's theory. They offer evidence for intelligence and cognitive performance-related brain network reorganization, but do not represent substantive evidence for thesis (1) because they either did not employ dynamic analyses which examine connectivity at the sub-minute level, or they only observed relationships for executive cognition. In Section 5 below we provide suggestions for the kinds of empirical investigations that can build on these past studies and serve to directly evaluate the Network Neuroscience Theory of Intelligence.

4.2. Thesis (2): small-worldness and brain network flexibility

There is no empirical research to date directly assessing the relationship between small-worldness and the dynamic flexibility of brain network reconfiguration. There is, however, research investigating global brain network efficiency and intelligence. As described above, small-worldness is a measurement of the ratio of clustering to characteristic path length, and global efficiency is the inverse of characteristic path length. Thus, given that high global efficiency directly contributes to high small-worldness, the relationship between global efficiency and intelligence may be informative. The relationship between functional network global efficiency and intelligence was first suggested by a study by Van Den Heuval and colleagues [32]. This study analyzed the characteristic path length of functionally connected voxels across the brain during the resting-state, and found that overall characteristic path length was negatively correlated with full-scale IQ [32]. That is, individuals whose voxels, on average, featured greater topological proximity to each other scored higher on the IQ tests. In an attempt to further elucidate this finding, Santarnecchi et al. [74] sought to precisely characterize the nature of the connections that support the putative greater network efficiency of high intelligence individuals. Specifically, they noted that functional connections vary widely in their strength, yet many graph theoretic investigations of functional network organization (including [32], mentioned above) binarize connections between nodes based on a threshold. In their study, they separately analyzed the relationship between brain network efficiency and intelligence for weakly connected and strongly connected nodes. In addition to replicating the results of van den Heuval et al. [32], they found that weakly connected nodes (nodes connected via long-range connections) accounted for greater variance in intelligence scores than strongly connected nodes [74]. These were largely instantiated by functional connections involving regions of superior frontal gyrus, anterior cingulate cortex, the temporal pole, and the hippocampus [74]. These studies were taken to display a link between efficiency of functional brain network organization and general intelligence, for which weak connections (which typically mediate inter-network connections and are a critical component of small-worldness) play a large role. Of note, support for a relationship between global efficiency (as measured via small-worldness) and intelligence was also provided with functional networks derived using EEG [75]

Recent research, however, has called into question the intuitive relationship between brain network efficiency and intelligence. Pamplona et al. [99] related full-IQ scores to particular graph theoretic properties of functional brain networks and failed to replicate a statistically significant relationship between either characteristic path length or global efficiency with intelligence. An additional study found no relationship between global efficiency of functional networks and full-scale IQ [76]. Providing strong further evidence against this relationship, a study explicitly attempting to replicate the van den Heuval et al. [32] study with data from ~1000 subjects from the Human Connectome Project 1200 dataset, also found no significant relationships between global efficiency or characteristic path length with intelligence [30]. Thus, the jury is still out on whether a clear positive relationship exists between whole-brain functional network efficiency and intelligence.

Although the literature on whole brain connectivity has been mixed, the global connectivity of nodes in the FPCN – which we described above as having a strong role in both fluid intelligence and *g* – has been specifically linked to intelligence. One study measured the 'global brain connectivity' (GBC; which corresponds to the average connectivity of a region with every other region of the brain) of a set of cognitive control regions and found that the left lateral prefrontal cortex (LPFC) featured a significant positive correlation between its GBC and fluid intelligence [77,78]. This was in line with a previous study that found a relationship between general intelligence and the functional connectivity strength between bilateral dorsolateral prefrontal cortex and regions distributed across the frontal, parietal, temporal, and occipital lobes [79].

Thus, potentially notwithstanding findings specifically involving the FPCN, existing research does not unequivocally support a relationship between global efficiency and intelligence. This is suggestive with respect to the relationship between small-worldness and intelligence, but, again, does not constitute a direct test of Barbey's thesis (2). Although it has been approached through computational modeling [80], the relationship between small-worldness and the dynamic flexibility of brain networks has, to our knowledge, yet to be directly investigated empirically. It is worthwhile to note, however, that computational models have demonstrated that networks with greater small-worldness exhibit more complex dynamics and feature greater flexibility in response to perturbations/external inputs [45,41,80]. Empirical tests of the relationship between small-worldness and intelligence-related brain network reconfiguration flexibility should involve measures of small-worldness and analyses aimed at characterizing brain network dynamics, in addition to measures of intelligence.

One first step could be to compute small-worldness and dFC metrics of brain network flexibility (e.g., such as regional flexibility as mentioned above) on the Human Connectome Project data used by Kruschwitz et al. [30] and to examine relationships between them and measures of executive function and intelligence. An additional potentially worthwhile avenue would be to draw on research applying measures of the controllability of brain networks derived from network science [81]. Such measures are aimed at characterizing the manner in which certain regions play disproportionate roles in the propagation of activity in networks and could be employed to determine the particular neuroanatomical properties that are most facilitative of brain network flexibility [82]. This could, for example, facilitate evaluations of the importance of nodes that are deemed to play central roles in upholding the small-world organization of brain networks and could also reveal organizational properties (e.g., at different spatial scales) in addition to small-worldness that facilitate brain network flexibility.

5. Suggestions on moving forward

Despite the fact that the few studies highlighted above do not explicitly test the Network Neuroscience Theory of Intelligence, they provide evidence that network neuroscience approaches can be valuable tools in this domain and support the plausibility of Barbey's theses. Barbey's theory provides an important theoretical framework that can help spark research in this area, and we believe that empirically testing its claims constitutes a valuable way forward. Below we pose questions that have not been addressed to date but that will facilitate the empirical evaluation of Barbey's claims. Specifically, we focus on Barbey's thesis that *g* is underpinned by "dynamic reorganization of [networks] – modifying their topology and community structure in the service of system-wide flexibility and adaptation" ([38], p. 10).

5.1. How do different executive functions relate to intelligence and brain network reconfiguration?

Research has suggested non-uniform relationships between different components of executive function, and only a subset of executive functions appear to be highly associated with intelligence [71,72]. This has been taken to suggest that specific executive functions (such as working memory updating; [71]) may play a generalized role that disproportionately contributes to intelligence scores. This points to the question of whether *g* pertains to an actual higher-order cognitive capacity that plays a top-down causal role, or whether it is a bottom-up result of multiple cognitive tests featuring overlap in their component processes [34].

Barbey's Network Neuroscience Theory of Intelligence assumes the former and views *g* as a whole-brain phenomenon, but this view of *g* as a generalized, unitary construct with a causal role is far from consensual [83–85,34,86]. Thus, in empirically evaluating the claims of Barbey's theories, investigations will ideally explicitly examine how different executive functions relate to *g*/intelligence, and how intelligence and executive function relate to brain network reconfiguration at different spatial scales. Investigations could do this by examining both local (e.g., FC flexibility and efficiency of specific intra-network and inter-network relationships, such as between frontoparietal or executive regions) and global (e.g., whole-brain network reconfiguration or efficiency) neural measures in relation to distinct executive functions as well as intelligence. Such comprehensive studies would greatly facilitate a clearer picture of the brain network basis of *g*/intelligence and have potential to contribute to ongoing theoretical debates regarding the relationship between intelligence and executive function. As a specific example, an initial study could measure the dynamic flexibility of regions, networks, and the whole brain in relation to a cognitive flexibility task [87] and to Raven's Progressive Matrices (a fluid intelligence measure often used as a proxy for *g*) and determine the relationships between them. This would provide information on the degree to which neural flexibility relates to a specific function vs. fluid intelligence, and on what spatial scales.

5.2. How does the brain dynamically reconfigure in relation to engaging in an intelligence task, and how do these reconfigurations predict performance?

Intelligence studies so far [28,22] have not fully utilized measurements of dynamic changes of connectivity at shorter timescales as a means of investigating brain network reconfiguration. For example, Schultz and Cole [22] measured brain network reconfiguration efficiency via the relationship between the averaged FC patterns of entire cognitive conditions. Barbey's claim specifically refers to the dynamic flexible transitions between brain states and, given the rapid time-varying nature of neural activity, analyses should ideally seek to examine sub-minute time scales. Further, while past research has primarily retroactively related intelligence scores to independently collected brain data, we emphasize the importance of dynamic connectivity *during* intelligence task performance in testing Barbey's thesis (1). Thus, in order to investigate thesis (1), investigations should seek to directly assess the relationship between the dynamics of brain state transitions and intelligence task performance. This would also entail a closer characterization of changes in mental state both during and between tasks. Of interest are the mental and brain state space trajectories that lead e.g., from rest to a particular cognitive condition, and that lead from problem initialization to solution within a cognitive condition. Are there similar brain state trajectories followed by individuals of varying intelligence during a given cognitive condition? What general properties of brain state transitions into and during cognitive conditions can be ascertained? How do individual differences in cognitive strategy change this? Sub-minute analyses that more closely approximate the time scale of cognitive processing, in combination with phenomenological self-reports [88], may allow insight into these questions, and therefore enable a more fine-grained characterization of the dynamics underlying intelligence. As a means of doing this, investigations could draw from the methods employed in the burgeoning research on dynamic functional connectivity [6,11,7] as well as methods adapted from network science (e.g., [81,89,90]). For example, a study can use a dFC sliding-window 'brain state' protocol [91] or a Hidden Markov Model-based approach [92] on task-based fMRI with a continuous trial structure, with each condition featuring a distinct intelligence/executive cognition task. One may then evaluate relationships between particular states and performance on particular tasks and examine the transition probabilities between particular states around the boundaries between conditions.

5.3. How do easy-to-reach versus difficult-to-reach states, as discussed in the Network Neuroscience Theory of Intelligence, relate to intelligence?

Barbey's framework proposes that general intelligence is the ability to leverage small-world topologies to flexibly shift into easy-to-reach and difficult-to-reach states. Although there is evidence for the existence of these two types of states [89], they have not yet been reliably related to intelligence through empirical work. This may potentially be done using recent dynamic brain state-based analyses, which cluster connectivity or coactivation patterns into distinct states and map out their properties [91,93,94,69]. Future work could focus on addressing this gap in the literature by examining the regularity with which people transition into easy or difficult to reach states during specific intelligence tasks (e.g., fluid vs. crystallized) or at rest. The latter, if related to measurements of general intelligence or *g*, can notably be employed to explore the relationship between cognitive traits (e.g., tendency to engage in deliberate thinking), intelligence, and brain dynamics. This may also be helpful in interpreting Schultz et al.'s finding (2016) that more intelligent individuals have greater rest-task FC similarity. For example, it could be the case that individuals with greater intelligence engage in more deliberate thinking during rest, which translates to greater readiness to engage in cognitive tasks as embodied by greater task-related FC patterns during the resting state. A study aimed at this question could have individuals separately carry out tasks that (1) require past knowledge for completion and therefore depend primarily on easy-to-reach states as defined by Barbey, and (2) require adaptive, flexible problem solving and therefore depend on hard-to-reach states. Dynamic brain states could be assessed in each of these conditions, related to behavioral scores, and projected onto their resting-state timecourse to determine their frequency of occurrence independent of a task. Such a study could also incorporate subjective reports on mind-wandering tendencies and typical cognitive strategies to bolster psychological interpretation of the results.

5.4. Can accounting for individual differences in the brain's network organization help us refine our understanding of intelligence?

Much of the work being done currently focuses on generalizable findings based on group averages. While this work is crucial, accounting for between-subject variability in network measures may be equally useful as we refine our understanding further [95]. This suggestion is supported by the finding that within-subject similarity between individuals' resting-state and task-state organization correlated with behavior [22]. Their study indicated that, regardless of the exact organization of each of these states, what was significant was that for a given individual these two states were similar. Thus, intelligence as scientifically measured may be instantiated in an individual-specific manner (e.g., contingent on cognitive tendencies and problem-solving strategies). For example, how do network dynamics during the resting state for a given individual relate to scores on cognitive traits (e.g., tendency to engage deliberate thinking, conscientiousness, openness, etc.), and how does this relate to their performance on intelligence tasks and corresponding task-related network dynamics?

As mentioned before, the incorporation of subjective reports aimed at gaining information on the potentially idiosyncratic cognitive underpinnings of a given task state may provide valuable insight. Research in this vein may seek to systematically relate cognitive traits to resting-state brain dynamics and, for example, examine whether such cognitive traits explain the presence of brain-behavior correlations in some subjects but not others. An additional important factor to consider here is with respect to developmental changes and their relationship to particular cognitive tendencies and brain network dynamics [96,97]. Indeed, investigations have provided evidence of cognitively-relevant changes in brain network dynamics that occur over development (e.g., [94,98]). In light of this and research showing both stabilities and instabilities of aspects of intelligence over the life span [96], a comprehensive examination of the relationship between neurodevelopmental changes in brain network dynamics, cognitive traits, and intelligence measures represents an important line of research. Longitudinal studies which incorporate a comprehensive suite of psychological (including phenomenological reports of cognitive strategies), cognitive, and neural measures would provide invaluable insights in this domain.

6. Final conclusions

The burgeoning field of network neuroscience has provided a suite of novel theoretical and analytical tools that are increasingly applied to various cognitive domains. The application of these tools to the neuroscience of intelligence has just begun and offers the potential to significantly advance our understanding of the neural basis of intelligence. The Network Neuroscience Theory of Intelligence of [38] provides an important theoretical grounding that motivates specific future research directions that could provide important empirical tests for this theory. Here we have outlined a number of avenues for future research that could advance our understanding of the network neuroscientific basis of intelligence by directly testing the predictions of this theory. We believe that doing so will prove central to our understanding of intelligence and the neural basis of cognition more generally.

Declaration of interest

None.

Conflict of interest

We have no conflicts of interest to declare as part of this submission.

Ethics

No data was collected from humans or non-human animals as part of the work done for this paper. All research activities were compliant with university policies.

Financial disclosure

We certify that we have no financial disclosures to declare.

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