Efficient hubs in the intelligent brain: Nodal efficiency of hub regions in the salience network is associated with general intelligence

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A R T I C L E   I N F O
Article history:
Received 6 April 2016
Received in revised form 30 September 2016
Accepted 7 November 2016
Available online xxxx

Keywords:
Intelligence
Functional magnetic resonance imaging (fMRI)
Graph theory
Efficiency
Salience network

A B S T R A C T
Intelligence-related differences in the intrinsic functional organization of the brain were studied with a graph-theoretical approach, comparing effects on nodal measures of brain network efficiency (concerning specific nodes of the network) and global measures (concerning the overall brain network). Functional imaging data acquired for 54 healthy adult participants during wakeful rest were modeled as graphs representing individual functional brain networks. Nodal and global measures of efficient network organization (i.e., nodal efficiency and global efficiency) were correlated with intelligence scores (IQ from the Wechsler Abbreviate Scale of Intelligence, WASI). While global efficiency showed no significant association with intelligence, the nodal efficiency was significantly associated with intelligence in three brain regions. Participants with higher IQ scores showed higher nodal efficiency in right anterior insula (AI) and dorsal anterior cingulate cortex (dACC), two hub regions of a functional brain network previously described as salience network. Furthermore, higher IQ was associated with lower nodal efficiency in the left temporoparietal junction area (TPJ). Distinct connectivity profiles were observed for brain regions showing a positive versus negative correlation between IQ and nodal efficiency. Our analyses suggest that intrinsic (i.e., task-independent) connectivity profiles of brain regions that have previously been associated with salience processing (AI and dACC) and the filtering of irrelevant information from higher-level processing (TPJ), play a role in explaining individual differences in intelligence. Based on these intelligence-related effects in resting-state fMRI data, we discuss the potential relevance of processing salient information for the explanation of differences in cognitive performance and intelligence.

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1. Introduction

Biological correlates of intelligence differences have been identified in structural and functional properties of the brain (Basten, Hilger, & Fiebach, 2015; Jung & Haier, 2007). Specifically, individual differences in intelligence have been linked to differences in the local amount of gray matter (e.g., Haier, Jung, Yeo, Head, & Alkire, 2004), the integrity of white matter (e.g., Penke et al., 2012), and the strength of brain activation during cognitive demands in circumscribed regions of the brain (Basten, Stelzel, & Fiebach, 2013; Gray, Chabris, & Braver, 2003). Recent investigations turned the focus from studying segregated correlates of intelligence in distinct regions of the brain, to the study of intelligence-related differences in functional interactions between brain regions (Song et al., 2009: Van den Heuvel, Stam, Kahn, & Hulshoff Pol, 2009). The latter approach accounts for the fact that the human brain is a complex network – characterized by interactions between functionally segregated regions – that continually integrates and processes information across various temporal and spatial scales (Achard, Salvador, Whitcher, Suckling, & Bullmore, 2006; Hagmann et al., 2008; Sporns, 2011). Fundamental properties of the intrinsic organization of functional brain networks can be observed even in the absence of cognitive demands, i.e., based on so-called resting state fMRI scans in which participants are awake but without a specific task (see, for example, van den Heuvel & Hulshoff Pol, 2010; Rosazza & Minati, 2011). The brain’s intrinsic functional organization during this resting state is suggested to influence the ability to form flexible and appropriate behavioral responses to cognitive demands (Sala-Llonch et al., 2012).

Recent research has begun to investigate whether patterns of intrinsic functional connectivity in the brain are also related to intelligence. Functional connectivity between brain regions during resting state can be inferred from temporal correlations between changes in functional magnetic resonance imaging (fMRI) blood-oxygen-level dependent (BOLD) signals in different regions of the brain (Friston, Frith, Liddle, & Frackowiak, 1993). Such resting state connectivity has been shown...
to be relatively stable over time (Shehzad et al., 2009; Zuo et al., 2010), to relate closely to underlying anatomical connections (Grecius, Supekar, Menon, & Dougherty, 2009; Hagmann et al., 2008; Honey, Kotter, Breakspear, & Sporns, 2007; for review, see Honey, Thivierge, & Sporns, 2010), and to represent fundamental topological principles of the functional networks in the brain (Biswal, Yetkin, Haughton, & Hyde, 1995; van den Heuvel & Hulshoff Pol, 2010). Furthermore, it has been reported that individual differences in the connectivity patterns of resting state data are associated with stable individual differences in personality traits (e.g., Adelstein et al., 2011; Beaty et al., 2015; Kim, Gee, Loucks, Davis, & Whalen, 2011) as well as cognitive functions (e.g., Song et al., 2008, 2009; van den Heuvel et al., 2009; Cole, Yarkoni, Repovs, Anticevic, & Braver, 2012; Langer et al., 2012; Xu et al., 2013; Markett et al., 2014; Santarnecci, Rossi, & Rossi, 2015). Many functional connectivity studies of the human brain have used seed-based correlation analyses or independent component analyses. Whereas seed-based approaches estimate the strength of associations between a circumscribed region of interest and all other voxels in the brain, independent component analyses enable the identification of distinct networks comprising brain regions that can be separated on the basis of statistical patterns in their time series dynamics (Beckmann, DeLuca, Devlin, & Smith, 2005; Damoiseaux et al., 2006). More recently, neuroimaging investigations have begun to apply graph theory to the analysis of large-scale functional dynamics in the brain. This method can take into account the entire pattern of correlations across the whole brain in an unbiased way (as opposed to seed-based analyses) and provides the opportunity to calculate metrics that characterize the interaction between brain regions and the information transfer in the brain.

Graph theory is a computational approach for the detailed modeling and characterization of large-scale networks (for overview, see Park & Friston, 2013; Rubinov & Sporns, 2010; Sporns, 2011; Wang, Zuo, & He, 2010). In contrast to seed-based approaches or independent component analyses, graph theory provides a set of measures that can be used to characterize the brain network as a whole (global level) as well as to characterize specific nodes or regions within the network (nodal level). To model the brain’s neural network as a graph, the brain is spatially parcellated into a set of homogeneous regions (i.e., voxels or anatomical regions of interest) that serve as network nodes. Functional connections between these nodes, called edges, are then defined by the correlations between the nodes’ BOLD activation time series, as measured with fMRI. The nodes and edges define a graph with a specific topology that reflects functional properties of the brain network. Different indices can be calculated for a graph that describe aspects of this topology, and thereby provide information about the brain’s functional organization (Rubinov & Sporns, 2010; Sporns, 2011). As a typical finding, for example, graph models of human brain networks show small-world organization, i.e., relatively high local clustering along with low average path lengths (Achard et al., 2006; Wang et al., 2009; for review, see Bassett & Bullmore, 2006). This small-world organization enables highly efficient information processing by ensuring high connectedness within as well as integration of information across different processing sites.

Recently, graph theoretical methods have also been applied to study intelligence-related differences in brain network organization. These studies differ in the types of connectivity that were studied (i.e., functional versus structural connectivity) and the neuroimaging techniques used to acquire the data for the network modeling. Intelligence-related differences in the efficiency of functional networks were studied with functional magnetic resonance imaging (fMRI; e.g., van den Heuvel et al., 2009; Song et al., 2009; Santarnecci, Galli, Polizotto, Rossi, & Rossi, 2014; Santarnecci et al., 2015; Pamplona, Santos Neto, Rosset, Rogers, & Salmon, 2015), electroencephalography (EEG; e.g., Langer et al., 2012; Smit, Stam, Posthuma, Boomsma, & De Geus, 2008), and magnetoencephalography (MEG; e.g., Duan et al., 2014). The efficiency of structural connectivity was investigated with diffusion tensor imaging (DTI; e.g., Li et al., 2009; Fischer, Wolf, Scheurich, & Fellgiebel, 2014; Pineda-Pardo, Martínez, Román, & Colom, 2016; Ryman et al., 2016). In the following, we focus on research that used fMRI to study efficiency of functional networks.

One of the pioneer studies of the association between intelligence and brain network topology suggested that higher IQ was associated with a brain network organization that renders information processing within the brain globally more efficient (van den Heuvel et al., 2009). In that study, higher global efficiency of brain networks in participants with higher IQ was inferred from a more pronounced small-world organization due to on average shorter path lengths in their functional brain networks. While some later studies also report significant associations between intelligence and global measures of efficient network organization (i.e., global efficiency, characteristic path length), these studies focused on different aspects of connectivity as they were based either on specific sub networks (DMN: Song et al., 2009), weak connections (Santarnecci et al., 2014), on groups of patients with altered network topology (Xu et al., 2013), used fundamentally different data (EEG: Langer et al., 2012), or relied on the investigation of structural connections (Li et al., 2009) – and thus did not provide a strict replication of the findings reported by van den Heuvel et al. (2009). In contrast, other studies did not observe a significant association between psychometric intelligence and global efficiency in functional networks (fMRI: Pamplona et al., 2015; MEG: Duan et al., 2014; EEG: Smit et al., 2008), structural networks (Fischer et al., 2014; Pineda-Pardo et al., 2016), or in specific populations (children: Wu et al., 2013; elderly: Fischer et al., 2014). While not concerning intelligence in a strict sense, global network efficiency has also been associated with intelligence-related factors, such as processing speed, visuospatial ability, and executive functioning (Wen et al., 2011). Taken together, empirical results concerning the relationship between intelligence and global network efficiency are heterogeneous, necessitating further research into the topological network properties underlying intelligence.

On the other hand, intelligence has also been associated with differences in local – i.e., node-specific – topological properties of brain networks. Rather than characterizing properties such as network efficiency for the entire brain, local (or nodal) graph theoretical measures describe the connectivity patterns of individual nodes (or regions) with the rest of the brain. While some researchers focused their analyses on the lateral prefrontal cortex (PFC) and reported that it was more closely connected to the rest of the brain in more intelligent individuals (Song et al., 2008; Cole et al., 2012, 2015), the above-mentioned study by van den Heuvel et al. (2009) suggests intelligence-related differences also in the functional connectivity of brain regions outside the lateral PFC. Specifically, in addition to their results for global efficiency, van den Heuvel et al. (2009) also tested for nodal topological differences in the entire brain and reported that the above-mentioned intelligence-related differences in global network efficiency came along with differences in the node-specific measure or efficiency (normalized path length) in medial PFC, posterior cingulate cortex (PCC), inferior parietal cortex (IPC), left superior temporal gyrus (STG), and left inferior frontal gyrus (IFG). Van den Heuvel et al. (2009) suggest that these regions are embedded within the network more efficiently, i.e., are characterized by shorter functional paths to other parts of the brain network in subjects with higher IQ scores. However, these findings were reported for a declaredly exploratory statistical threshold. With the current investigation, we extend the study of node-specific differences in the topological organization of brain networks, further investigating the idea that the connection efficiency of specific regions within the brain’s functional network varies with intelligence.

At the nodal level, we specifically expect an association between intelligence and nodal efficiency in so-called hub regions of the brain network, i.e., in regions that take a position of high centrality in the network. Centrality as a graph theoretical concept characterizes the importance of a node in relation to all other nodes of the network (van den Heuvel & Sporns, 2013) and is usually quantified as degree centrality by the number of direct edges connecting a given node to other nodes in the brain network.
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