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Development of large-scale functional networks from birth to adulthood: A guide to the neuroimaging literature

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ABSTRACT

The development of human cognition results from the emergence of coordinated activity between distant brain areas. Network science, combined with non-invasive functional imaging, has generated unprecedented insights regarding the adult brain's functional organization, and promises to help elucidate the development of functional architectures supporting complex behavior. Here we review what is known about functional network development from birth until adulthood, particularly as understood through the use of resting-state functional connectivity MRI (rs-fcMRI). We attempt to synthesize rs-fcMRI findings with other functional imaging techniques, with macro-scale structural connectivity, and with knowledge regarding the development of micro-scale structure. We highlight a number of outstanding conceptual and technical barriers that need to be addressed, as well as previous developmental findings that may need to be revisited. Finally, we discuss key areas ripe for future research in order to (1) better characterize normative developmental trajectories, (2) link these trajectories to biologic mechanistic events, as well as component behaviors and (3) better understand the clinical implications and pathophysiological basis of aberrant network development.

Introduction

The human brain is organized into multiple distributed functional brain networks that can be measured at multiple spatiotemporal scales

Coordinated neuronal activity between anatomically disparate regions is an essential feature of human brain function. Across all stages of postnatal development, brain activity to a large degree is consolidated within so-called "resting-state networks" (RSNs). RSNs are defined as distinct modules of regions that exhibit highly synchronized activity even in the absence of external stimuli. RSNs have proven to be highly reproducible in the adult brain (Doucet et al., 2011; Gordon et al., 2016; Power et al., 2011; Yeo et al., 2011) and have become an influential framework for interpreting functional and structural neuroimaging data. Patterns of functional connectivity (FC) within and between the major RSNs are increasingly understood as intrinsic properties of brain function, given that they strongly predict patterns of interregional co-activation across different tasks (Cole et al., 2014; Smith et al., 2009) and are associated with task-relevant behavioral performance (Cole et al., 2012; Lewis et al., 2009).

Interregional FC arises from anatomical projection strengths (Messe et al., 2014; Shen et al., 2012), correlated gene expression (Richiardi et al., 2015), and synaptic receptor densities (Turk et al., 2016; van den Heuvel et al., 2016b) – properties that, in turn, undergo experience-dependent and activity-dependent modulation over the lifespan (Huttenlocher, 2002; Markham and Greenough, 2004; Scholz et al., 2009). This intricate structural-functional interplay underscores that the ontogeny of functional networks likely reflects programmed neurodevelopmental events (e.g. neurogenesis, cell death, myelination, pruning, synaptic plasticity, and glial development) (Innocenti and Price, 2005; Stiles and Jernigan, 2010) and that FC aberrations may point towards the etiological bases of neuropsychiatric disorders (e.g. (Swartz and Monk, 2014; van den Heuvel et al., 2016a)). Thus, exploring the normal trajectory of functional network development and its relationships with these underlying biological processes should be a central mission of both basic and clinically relevant neurodevelopmental research.

Current views regarding network development have been heavily informed by resting-state functional connectivity MRI (rs-fcMRI),

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which measures the correlations in spontaneous, low-frequency activity between investigator-defined regions. This review will accordingly provide in-depth discussions of the developmental rs-fcMRI literature, its limitations, and unique insights gained from complementary approaches, especially electroencephalography and magnetoenceophalography (EEG/MEG). We will begin by discussing emerging themes in the analysis of functional network data. We will then synthesize current findings regarding FC changes from birth to adulthood, and place them within the context of co-occurring macro- and micro-scale structural modifications. Finally, we will discuss some of the implications with regard to neurodevelopmental disorders and highlight several crucial knowledge gaps that are likely to guide research efforts in the near future.

Analytic approaches to functional connectivity are evolving rapidly

Correlated resting-state activity was first identified in bilateral sensorimotor cortex by Biswal et al. (1995), followed soon after by similar findings of bilaterally correlated activity in early visual and early auditory cortex (Cordes et al., 2001; Kiviniemi et al., 2000; Lowe et al., 1998). These discoveries were made using "seed" regions outlined based on *a priori* anatomical boundaries. Correlations were then quantified between the seed region's fMRI timecourse and all other voxels of the brain, producing an FC map. More data-driven approaches were developed based on the concept of independent components analysis (Beckmann and Smith, 2004), which decomposes brain activity into a set of spatial maps (i.e. components) that minimally overlap. ICA maps reproducibly reveal early visual, early auditory, and primary sensory/motor components, as well as other components comprising distributed portions of the frontal, parietal, and temporal association cortices (Damoiseaux et al., 2006).

Building upon these advances, the neuroimaging community has increasingly focused on interrogating the brain as an integrated complex system. In this context, graph theory has emerged as a powerful new approach. A 'graph' is simply a network of things, referred to as nodes, and the connections between those things, referred to as edges. The network's behavior can thus be modeled as a set of properties that emerge from the network's unique global structure and local features (Sporns, 2014). Graph theoretic studies typically construct functional brain networks using regions as nodes and correlations in activity as edges. Past reviews have already written eloquently about the rationales for applying this approach to study development (Power et al., 2010; Vertes and Bullmore, 2015), which we will only briefly summarize and expand upon here.

First, most individual cognitive abilities arise not solely from a particular brain area, but from networks of activity spanning multiple distributed regions (Petersen and Sporns, 2015). From social cognition in infancy (Eggebrecht et al., 2017) to cognitive control and decision-making in adolescence (Dwyer et al., 2014; van Duijvenvoorde et al., 2015), specific cognitive capacities co-evolve with complex network effects within and between different RSNs, throughout postnatal development. Second, structural connectivity shapes and constrains functional networks across the lifespan (Betzel et al., 2014; Hagmann et al., 2012; Vertes and Bullmore, 2015). Cross-modal network analysis is therefore crucial for elucidating normative mechanisms of cognitive development and the pathophysiology of neurodevelopmental disturbances. As a proof-of-principle, recent studies have found that even purely local, experimentally induced perturbations (e.g. exogenous stimulation or inactivation) result in widespread, complex neurophysiological changes, which are at least partly explainable as local interactions with global network structure (Andoh et al., 2015; Grayson et al., 2016; Gu et al., 2015a; Misic et al., 2015). By extension, one could reason that developmental modifications in brain FC, whether normative or pathological, are also best understood via an emerging network science that merges structural and functional connectivity data. Third, graph-based methods are flexible and generalizable. Networks can be measured at various temporal scales depending on imaging methodology, at various conditions (during rest or task completion), and can be compared with corresponding networks of structural connectivity or gene co-expression. A graph theoretic approach is therefore well-suited for multimodal investigations linking brain function across temporal scales or examining structural drivers of functional development.

Graph theory techniques for defining network organization

Below we describe 3 broad themes that have emerged with regard to functional (and structural) network analysis in neuroimaging: the brain's community structure (i.e. the spatial and topological organization of specialized systems), the significance of hub regions that integrate information within and between these systems, and global network properties that facilitate efficient and integrated information transfer.

Community structure

A defining feature of human brain activity is "modularity," which refers to an unexpectedly high level of within-RSN FC relative to between-RSN FC (Lohse et al., 2014). "Community detection" algorithms partition the brain into distinct communities, or modules, by maximizing this modularity quotient. The adult brain has several modules at the coarsest level that are remarkably reproducible despite slight methodological differences across studies (Doucet et al., 2011; Gordon et al., 2016; Power et al., 2011; Yeo et al., 2011). These modules include (1) segregated, non-distributed modules for sensory/motor activity, such as in early visual cortex and in somatomotor cortex, (2) the default-mode network (DMN), comprising the medial prefrontal, posterior cingulate/precuneus, angular gyrus, and medial temporal cortex; the DMN is considered "task-negative" as it has been linked to internal mentation and is known to deactivate during processing of external stimuli (Buckner et al., 2008), and (3) three large, distributed modules for task-positive cognition: (a) dorsal attention, involved in eye movements and attentional orienting, (b) the cingulo-opercular salience module, involved primarily in attentional maintenance, and (c) the frontoparietal executive module, important for task-switching. At finer resolutions, several other modules can be identified (Doucet et al., 2011; Gordon et al., 2016; Power et al., 2011; Yeo et al., 2011), including hierarchical visual subdivisions, topographical somatomotor subdivisions, an auditory module, a limbic module, a ventral attention module, and other smaller subdivisions of the executive, salience, and default-mode modules. See Fig. 1A and B for a graphical summary.

The brain's modular composition is believed to help segregate information processing between distinct sensory modalities or cognitive architectures. It remains a fundamental challenge to understand what other network properties help integrate disparate data streams in order to meet complex task demands (Cohen and D'Esposito, 2016; Petersen and Sporns, 2015). As discussed throughout this review, the themes of segregation and integration are core concepts in understanding the brain's maturational processes. Thus, further analytic exploration is needed to isolate the critical network components that facilitate segregation, integration, or efficiency. Below we briefly describe some local network measures toward this end.

Node measures

The most straightforward nodal description is its *strength* (Rubinov and Sporns, 2010), defined as the sum of a node's connection weights. Other *centrality* measures quantify higher order measures of influence. For instance, *betweeness centrality* (Rubinov and Sporns, 2010) computes the frequency with which a node lies on the shortest paths that connect any other nodes, a property that theoretically enables

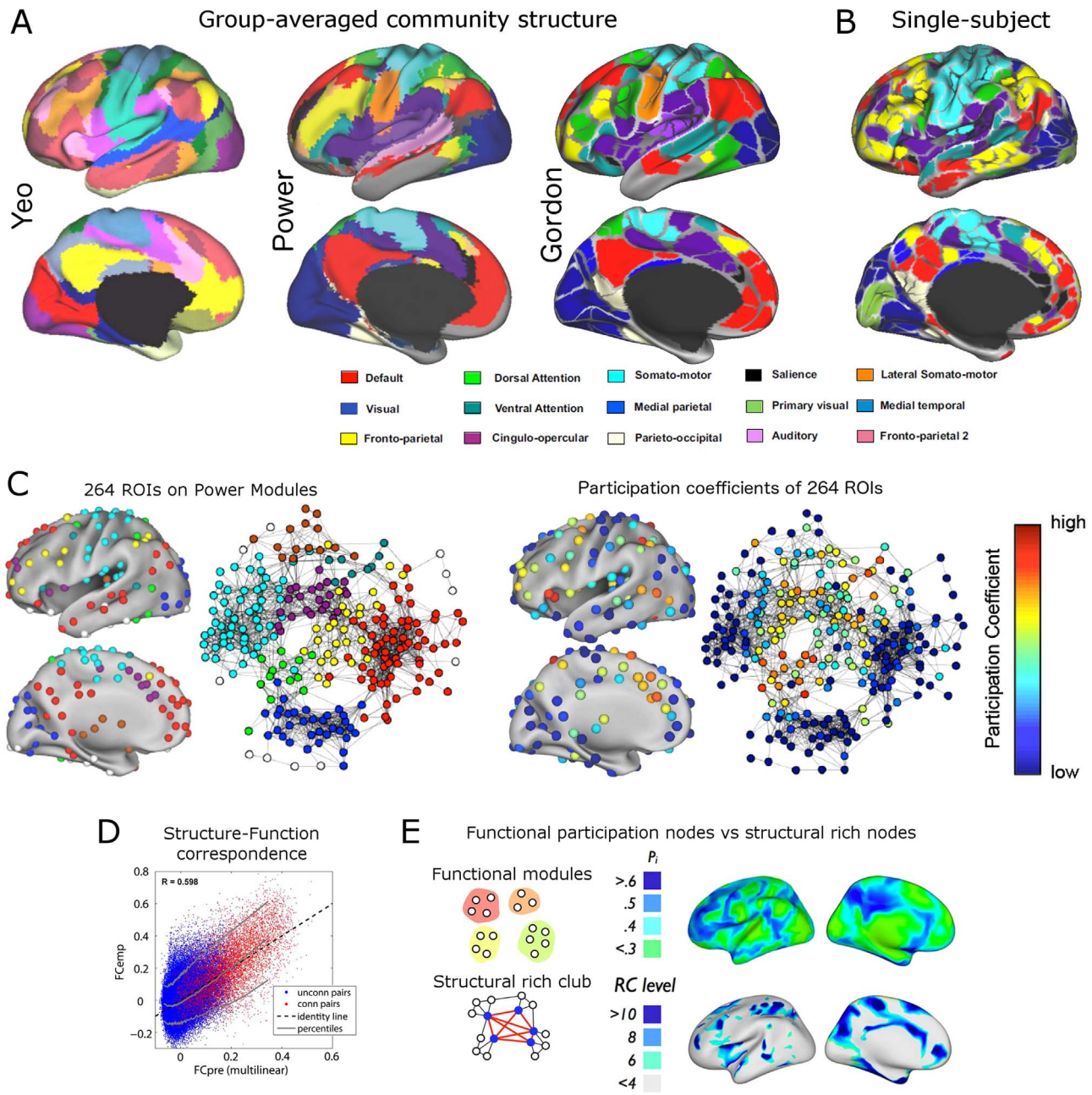

Fig. 1. Crucial network properties of resting-state activity in the normal adult brain. A) Group-averaged community structure of resting state brain activity, densely sampled across the cortical surface, in three independent studies (Gordon et al., 2016; Power et al., 2011; Yeo et al., 2011). Different colors correspond to different modules with highly correlated activity, i.e. functional connectivity (FC). Several canonical modules appear in all three studies, including early visual, early somatomotor, default mode, dorsal attention, frontoparietal, and cingulo-opercular modules. Community structure is highly reproducible across these studies. The color scheme in Power and Gordon matches the legend, but differs in Yeo. A novel areal parcellation is also defined in Gordon, as evidenced by interareal boundaries. **B)** Community structure and areal parcellation of an individual subject (Laumann et al., 2015), obtained via repeated scanning sessions in the same individual. Community structure strongly resembles that of the group, although idiosyncracies are also clearly observable (see (Laumann et al., 2015)). **C)** Group-average resting-state network organization defined using 264 spherical nodes situated within different functional modules. On the left, the location and modular assignment of these nodes are pictured on the brain, next to a spring-embedded layout of the thresholded functional matrix. The network layout depicts nodes with stronger links (i.e. stronger correlations in activity) as closer together. The layout illustrates that network organization is heterogeneous – some modules are highly segregated from the rest of the network, whereas others are more integrated. On the right, the participation coefficient is quantified for each node. The participation coefficient signifies the extent to which a node integrates activity across multiple modules. Comparing the network layouts, integrator nodes tend to exist within the modules reflecting task-positive cognition, i.e. the frontoparietal, cingulo-opercular, and dorsal attention modules. See Power et al. (2013). **D)** Structural connectivity shapes and constrains FC. As an example, this plot illustrates the correspondence between empirical FC (y-axis) and predicted FC (x-axis) based on modeling communication via the structural connectome. Dots represent region pairs that either are (blue) or are not (red) directly connected via fiber pathways. See Goni et al. (2014). **E)** Structural hubs tend to interlink to each other and across functional modules, providing an anatomical substrate for integration between otherwise segregated domains of information processing. The schematic on the left illustrates this hypothesis, where the modules on top are functionally defined and the connections shown on the bottom reflect neuroanatomical links. The "rich club" nodes (shown in blue) reflect structural hubs that disproportionately connect to each other. On the right, evidence that the rich club serves an integrative function, as functional network nodes with high participation coefficient (i.e. high between-module integration) overlap significantly with the brain's structural rich club. See van den Heuvel and Sporns (2013).

efficient global communication. By far, strength and betweenness have been the most popular hub metrics within neuroimaging, although others such as *eigenvector centrality* (Lohmann et al., 2010; Zuo et al., 2012) and node *communicability* (de Reus and van den Heuvel, 2014; Mantzaris et al., 2013) have seen useful application as well. These metrics, however, require careful consideration of what the network's

edge weights signify (see de Reus and van den Heuvel (2014), Grayson et al. (2016) and Misic et al. (2015)) for discussions about the neurobiological relevance of shortest paths). Investigators must especially consider whether connections are statistical or structural in nature. For example, a node with structural links to many different RSNs (and thus, high structural network centrality) may have weak statistical associations overall (and thus, low functional network centrality). It has therefore been proposed to consider functional hubs as nodes with integrative capacity across distinct modules (Power et al., 2013). This goal is accomplished in part by the *participation coefficient* (Guimera and Nunes Amaral, 2005), which computes the between-module connectivity and therefore is particularly useful for functional networks (see Fig. 1C).

Another way of identifying nodal integration is to compare functional against structural networks (see Fig. 1E). Structural networks in the mammalian brain exhibit an important phenomenon known as "rich-club" organization, whereby hubs (i.e. nodes with high strength) link disproportionately to other hubs. Rich-club nodes tend to span multiple RSNs, thereby facilitating integration between them (Sporns, 2013; van den Heuvel and Sporns, 2013). Similarly, structural hubness has been linked to integration of global brain activity (Grayson et al., 2016).

Finally, node *clustering coefficients* and *local efficiency* (Rubinov and Sporns, 2010) are popular ways of measuring node specialization – i.e., integration specifically within a node's local environment. The clustering coefficient quantifies the combined strength of connectivity between a given node's immediately connected neighbors, whereas the closely related local efficiency computes the average (inverse) path length between a node's neighbors.

Global network properties

A network's capacities for globally efficient communication and integration can be defined formally as properties. The *global efficiency* is measured by averaging the (inverse) shortest path length between all node pairs. Greater global efficiency in structural and functional networks has been linked to higher IQ, attentional capacity, and working memory in healthy young adults (Cohen and D'Esposito, 2016; Kitzbichler et al., 2011; Li et al., 2009; Stanley et al., 2015; van den Heuvel et al., 2009), supporting the notion that it confers advantages for complex cognitive processing. When networks exhibit both high global efficiency and high average clustering coefficients, they exhibit "small-world" organization (Watts and Strogatz, 1998). This property, which is ubiquitous across vastly different scales of investigation in the brain, is thought to emerge from a biological need to balance the benefits of integration against the costs of long-range wiring (Collin et al., 2013; Vertes and Bullmore, 2015). Furthermore, these distinct network effects, i.e. segregated versus integrated neural processing, are interwoven features of cognition. Both effects in tandem are crucially involved in cognitive control (Dwyer et al., 2014) and executive functioning (Reineberg et al., 2015), and are differentially associated with performance on simple motor tasks versus complex working memory tasks (Cohen and D'Esposito, 2016). This review will highlight extensively these competing network influences in the context of development. Finally, network *integration* can also be defined alternatively. Similar to the participation coefficient of a given node, one can compute the network's global integrative capacity by taking into account the network modules and the interdependencies between them (de Reus and van den Heuvel, 2014; Tononi et al., 1994).

Functional brain organization in infants and toddlers

Overall structural and functional organization

The human brain expands at an explosive rate during the first few years of life (see Fig. 2A), doubling in volume during the first year and reaching 80–90% of adult volume by age 3 (Courchesne et al., 2000; Knickmeyer et al., 2008). This same time period is marked by rapid and widespread cortical synaptogenesis, followed by a protracted period of synapse elimination and cell loss which carries into adulthood (Huttenlocher, 2002; Innocenti and Price, 2005). The brain's major fiber pathways become consolidated through myelination, though their presence is largely established prenatally (Stiles and Jernigan, 2010). It is also worth noting that both progressive and regressive changes in structure occur simultaneously during infancy (Gilmore et al., 2012; Scott et al., 2015), despite overall growth in volume and connectivity. These first few years of life, therefore, coincide with the formation of the brain's foundational anatomical circuitry, paralleling the genesis of an intricate functional architecture.

RSNs are already present during infancy, and potentially to some extent in utero (Thomason et al., 2013). Seed-based and component-based approaches demonstrate the existence of robust, bilateral segregated networks for somatomotor, primary auditory, primary visual, and extrastriate visual cortex (Fransson et al., 2007; Gao et al., 2015a; Kiviniemi et al., 2000; Lin et al., 2008; Liu et al., 2008; Smyser et al., 2010). These sensory networks undergo subtle refinements and strengthening over the first two years of life, and by age two bear substantial resemblance to their adult counterparts (Gao et al., 2015a; Lin et al., 2008). Distinct components throughout heteromodal association cortex have also been described in infants, and are believed to represent prototypical elements of distributed, higher-order cognitive networks identifiable in adults (Graham et al., 2015). For instance, in adults the DMN is a tightly integrated circuit comprising several distinct and distant areas of cortex (as described in *Community Structure*). In neonates and very young infants, these individual compartments demonstrate locally correlated activity, but fail to synchronize into a coherent network (Damaraju et al., 2014; Fransson et al., 2007; Gao et al., 2009; Smyser et al., 2010; Wylie et al., 2014). Over the course of the first two years of life, these regions undergo a precise evolution to gradually bring the network 'online' (Damaraju et al., 2014; Gao et al., 2009, 2013). By two years of age, the network bears adult-like qualities, although coupling between distant anterior and posterior nodes of the network remain relatively low. Similar spatial and temporal properties characterize the emergence of distributed connectivity in the dorsal attention (Gao et al., 2013), salience (Alcauter et al., 2015a; Gao et al., 2015a, 2015b) and frontoparietal executive (Gao et al., 2015a, 2015b) networks. Collectively, these findings suggest that sensory networks become established at a much earlier age relative to those implicated in higher-level cognition (Gao et al., 2016). These trends are consistent with the presence of basic somatosensory and visual functions at birth, and help contextualize findings that primary sensory regions are generally the first cortical areas to reach plateaus or peaks in growth (Geng et al., 2016; Gilmore et al., 2012; Lyall et al., 2015; Scott et al., 2015).

Development of community structure from birth

Despite these insights, network topology in early development remains poorly understood. What is the collective community structure of the brain at birth? How does it evolve during early and late infancy, and how is it distinguished from the now well-described adult community structure?

The current nascent literature on infant network topology (see Fig. 2B) suggests that a robust community structure does exist, albeit in a primitive form. In neonates, two independent rs-fcMRI studies found evidence for modules comprised largely of anatomically proximate areas (De Asis-Cruz et al., 2015; van den Heuvel et al., 2015b). One recent report compared community structure in adults against that in 1–2 year olds using closely matched methods (Eggebrecht et al., 2017), providing the first direct evidence for numerous anatomically localized modules in the infant brain and their relationship to adult functional

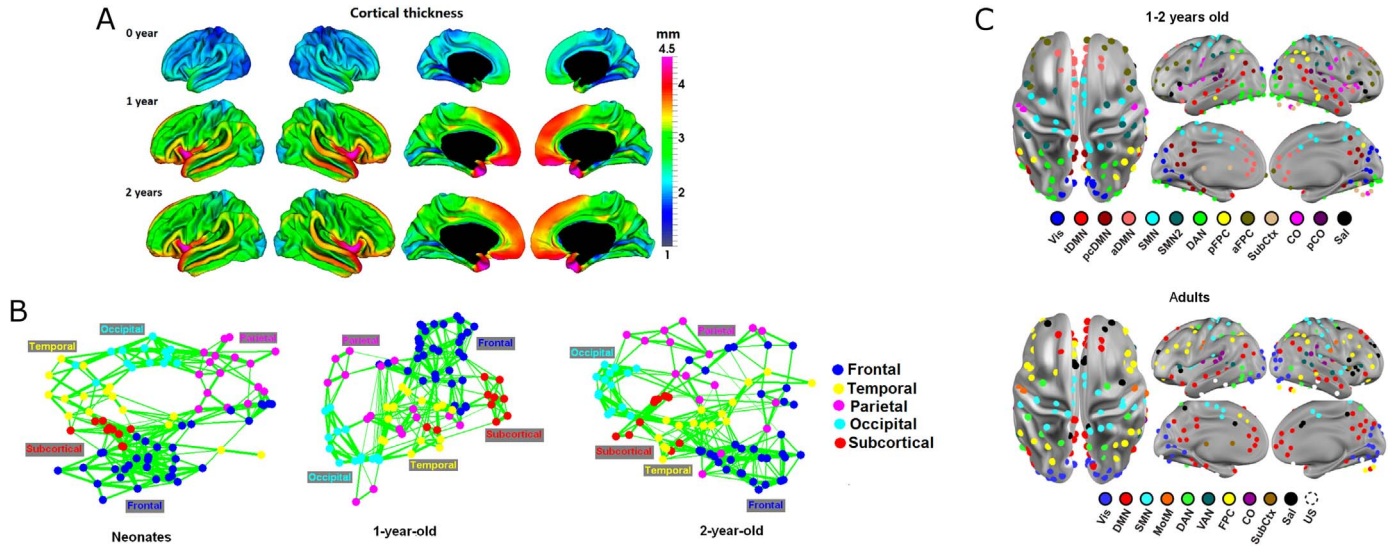

Fig. 2. Infant brain structural and functional development. A) Visualizations of infant brain cortical surfaces at birth, 1 year, and 2 years of age. Large growth is clearly visible in terms of total brain size, cortical surface area, and cortical thickness Adapted from Li et al. (2015). **B)** Resting-state functional connectivity network visualizations at birth, 1 year, and 2 years of age. The different lobes containing each region are labeled. Increasing separation of regions into functional modules spanning multiple lobes is apparent over this timespan. Adapted from Gao et al. (2011). **C)** Community structure of 230 functional ROIs in 1–2 year olds (top) and in adults (bottom) using closely matched methods. Labeling of infant modules was informed via the adult set: Vis (visual), tDMN (temporal default mode network), pcDMN (posterior cingulate DMN), aDMN (anterior DMN), SMN (somato-motor network), SMN2 (somato-motor network 2), DAN (dorsal attention network), pFPC (posterior frontal parietal control network), aFPC (anterior frontal parietal control network), SubCtx (subcortex), CO (cingulo-opercular), pCO (posterior CO), and Sal (salience). Adapted from Eggebrecht et al. (2017).

organization (Fig. 2C). Many of these modules clearly reflect anterior/posterior/temporal subdivisions of the adult salience, frontoparietal, DMN, dorsal attention, and ventral attention modules. Another distinction seen is that infant modules tend to group together anatomically proximate ROIs that have divergent roles in adulthood. Community structure assessed at two years of age (Alcauter et al., 2015b; Gao et al., 2015b) indicates the presence of distinct modules encompassing early auditory, early somatomotor, and early visual areas, and potentially, other prototypical modules similar to the canonical salience, frontoparietal, and DMN seen in adults. These latter modules also exhibit substantial growth of distributed synchronization and homotopic coupling from birth through the first two years of life (Gao et al., 2015b; Homae et al., 2010), concomitant with decreasing between-module connectivity (i.e. greater functional specialization). Taken together, these studies point towards several trends that corroborate seed and component based findings – (1) modular patterns at birth take a coarse, primitive form that is heavily influenced by local anatomy, (2) this structure undergoes rapid postnatal refinement, leading to progressively stronger coupling between distributed links that facilitate modular specialization, and (3) these enhancements result in the establishment of stable, primary sensory networks well before networks involved in higher-level cognition appear substantially adult-like.

Regional hub metrics

Hub configurations are robustly evident after birth (De Asis-Cruz et al., 2015; Fransson et al., 2011; Gao et al., 2011), but undergo substantial changes postnatally. Multiple reports have found that high strength and betweenness hubs in adulthood are largely located within the default mode, attentional, sensorimotor, and visual areas (Cao et al., 2014; Fransson et al., 2011; Grayson et al., 2014; Hwang et al., 2013), whereas neonatal hubs primarily involve early sensorimotor, visual, and limbic regions (De Asis-Cruz et al., 2015; Fransson et al., 2011; Gao et al., 2011). The first two years of life reflect a gradual decrease in the hubness of sensorimotor areas and increased involvement of various association cortical areas, especially the medial frontal and parietal portions of the default mode (Gao et al., 2011). This pattern of hub strengthening bears substantial spatial and temporal overlap with the pattern of increasing within-module synchronization. This is consistent with the notion that node strength and betweenness in functional networks may serve, at least to some extent, as proxies for modular size and synchronization (Power et al., 2013). Thus, there continues to be much less known regarding what regions become more involved in the integration of different information processing streams (e.g. sensory, cognitive, and emotional) over time. Such anatomical areas are likely critical for the development of complex cognitive and social abilities, and are potentially uniquely susceptible to early environmental influences (Graham et al., 2015). It is also clear that several prenatal factors (e.g. immune and endocrine systems) strongly affect postnatal network trajectories (Canetta et al., 2016; Scheinost et al., 2016b). Future work examining node participation coefficients in functional networks and other centrality measures in structural networks (see *network measures*) promises to shed greater light on the emergence of network integrators and their potential susceptibility to pre- and post-natal factors.

Global network metrics

Other important topological properties are also robustly evident at birth. Small-worldness (De Asis-Cruz et al., 2015; Fransson et al., 2011; Gao et al., 2011), as well as its constituent properties of global efficiency and average clustering coefficient, are already high in neonates. These properties only appear to marginally increase during the first year of life, plateauing thereafter until at least the end of the second year (Gao et al., 2011). Concomitantly, long-distance links are preferentially strengthened during the first year of life, leveling off thereafter (Gao et al., 2011). Rich clubs are also evident in both structural and functional networks in neonates along with both high functional modularity and integration capacity between modules (Ball et al., 2014; Scheinost et al., 2016a; van den Heuvel et al., 2015b). These findings suggest that the development of a small-world architecture, as well as the capacity for globally efficient communication and integration, largely occurs during the first year of life and prenatally, a finding that is supported by multimodal structural and functional network analysis in preterm infants (Ball et al., 2014; van den Heuvel et al., 2015b). This (very) early developmental trajectory stands in contrast to the more protracted progression towards increasingly

segregated and refined modular architecture which continues into early childhood and beyond.

Considerations in infant rs-fcMRI

A crucial caveat to the above observations is the potential for unidentified sources of artifact in infant studies (also see *Methodological challenges and recommendations*). In the case of identified networks in infants it is important to note that different community detection algorithms can provide unique results and all are not appropriate for any given experimental condition (Gates et al., 2016). Other considerations include early postnatal changes in cerebral vasculature, and altered state of consciousness when scanning very young participants. fMRI relies on hemodynamic measurements (usually BOLD), and there is good reason to suspect that infancy is accompanied by specific changes in neurovascular coupling (Hagmann et al., 2012). Human and animal studies indeed indicate differences in stimulus-evoked neurovascular coupling between infants and older individuals, but whether these differences impact rs-fcMRI measurements has yet to be determined (Graham et al., 2015). Infant imaging studies are also predominantly done during natural sleep (e.g. (Liu et al., 2008)) or sedation (e.g. (Fransson et al., 2007)). A natural benefit is the attenuation of micromovements and their attendant signal artifacts. However, altered state of arousal and consciousness might pose important confounds when comparing network findings to those seen in conscious children or adults. This concern is partly mitigated by findings of similar global functional network topology in conscious versus unconscious state in adults (Spoormaker et al., 2010), but key differences have been found in corticocortical (Heine et al., 2012; Horovitz et al., 2009; Spoormaker et al., 2010) and thalamocortical (Spoormaker et al., 2010) connectivity. Different sleep stages also correspond with different neurophysiological phenomena, which impact rs-fcMRI measurements (Laumann et al., 2016; Spoormaker et al., 2010). Until additional work can more definitively tease apart artifactual vs. neural contributions to the fMRI signal or awake versus sleep affects in these early postnatal years, developmental changes in modular partitions and other network changes must be viewed with at least some caution.

Developmental refinements of network structure into adulthood

General observations

Many of the network changes seen during infancy reflect long-term trajectories that extend into childhood and adolescence. As with the infant literature, much of the literature in children and adolescents has focused on the regions that define the adult DMN. Seed and component approaches have consistently found that connectivity between these areas (and indeed, connectivity within other cognitive RSNs) continues to strengthen from early childhood throughout development, especially with respect to long-range anterior-posterior links (de Bie et al., 2012; Fair et al., 2008; Sato et al., 2014; Sherman et al., 2014; Supekar et al., 2010).

More generally, one of the more reproducible findings of child and adolescent development (until very recently) had been an apparent shift from a local to global organization. Prior to 2012, multiple studies had found that functional connectivity between anatomically proximate ROIs gradually decreased, whereas long-range functional connections, especially anterior-posterior links, gradually increased until adulthood (Dosenbach et al., 2010; Fair et al., 2009; Kelly et al., 2009; Supekar et al., 2009). In addition, it appeared that the modular assignments of regions shifted. In childhood, regional assignments appeared to strongly depend on local anatomy. With age, regions gradually became more defined by their respective functional roles (Power et al., 2011; Power et al., 2010). These trends pointed to coherent changes that involved a dampening of non-specific local spread of activity and strengthening of long-range links, thereby facilitating cognitive development (Bunge and Wright, 2007; Fair et al., 2009; Uddin, 2011; Uddin et al., 2011). Distance-dependent effects were even strong enough to enable reasonably accurate predictions of an individual subject's age on the basis of a single resting-state scan (Dosenbach et al., 2010).

However, recent concerns about the influence of head-motion artifact have raised some doubts about the interpretability of such broad trends. In particular, it has been revealed that motion increases non-specific local coupling and decreases long-range coupling in ways that are similar to differences found between children and adults (Fair et al., 2012b; Power et al., 2012; Satterthwaite et al., 2012; Yan et al., 2013). When processing techniques intended to remove motion artifact are applied, developmental effects of this type – both in terms of overall local versus distributed coupling and in terms of changing modular assignments – are substantially attenuated, though still present to a limited extent (Fair et al., 2012b; Power et al., 2012; Satterthwaite et al., 2012). As motion-denoising strategies continue to evolve, such findings will need continual re-evaluation. It is likely, however, that functional network maturation follows more precise spatiotemporal trajectories than previously understood. Indeed, there are now at least 3 reports that suggest the network structure in children as defined by community detection (see Fig. 3) are largely similar to the adult (Fair et al., 2012b; Marek et al., 2015; Power et al., 2012). Despite this “adult like” level of organization, refinements within and between systems do appear to occur over time, although details to this end are still being worked out (Fair et al., 2012b; Gu et al., 2015b; Marek et al., 2015).

Much of this new work is finding that systems with different functional roles are characterized by substantially different trajectories (Gu et al., 2015b; Marek et al., 2015). For example, Gu et al. (2015b) found that sensorimotor systems, already well-segregated in childhood, displayed little change into adulthood. On the other hand, networks involved in task-positive cognitive function (e.g. salience, frontoparietal executive, and attentional networks), being generally well-connected with other systems, became increasingly segregated and exhibited increasingly variable spatial structure. The DMN was found to exhibit both increasingly synchronized within-network and between-network connections. The authors contend that these changes potentially support the ability to traverse through more diverse cognitive states in order to accomplish increasingly complex task demands (Bassett et al., 2011; Braun et al., 2015). Similar, albeit not identical developmental findings, are observed by Marek et al. (2015)), who found increased cross-network integration between the cingulo-opercular/salience and somatomotor modules over the age of 10–26, which they showed to be associated with the development of cognitive control. Two additional reports also suggested that functional restructuring over this timespan disproportionately involves the cingulo-opercular and somotomotor modules (Fair et al., 2012b; Grayson et al., 2014), and potentially specific links between them (Grayson et al., 2014) (see Fig. 4). Therefore, there is recent convergence of data suggesting that network structure continues to evolve after late childhood in ways that are not primarily distance-dependent; rather, complex but specific changes may coincide with the development of specific cognitive abilities. Additional follow-up work using up-to-date methods for artifact prevention and removal, and more sensitive longitudinal designs, will be crucial for expanding on these important new findings.

EEG/MEG findings

Resting-state networks obtained using electrophysiological recording (EEG or MEG) provide greater temporal resolution (< 100 Hz) relative to rs-fMRI (< 0.1 Hz) and therefore offer complementary insights about functional development. One of the classical and well-reproduced findings is that spectral power (i.e. amplitude of activity within different temporal frequency bands) decreases continually from

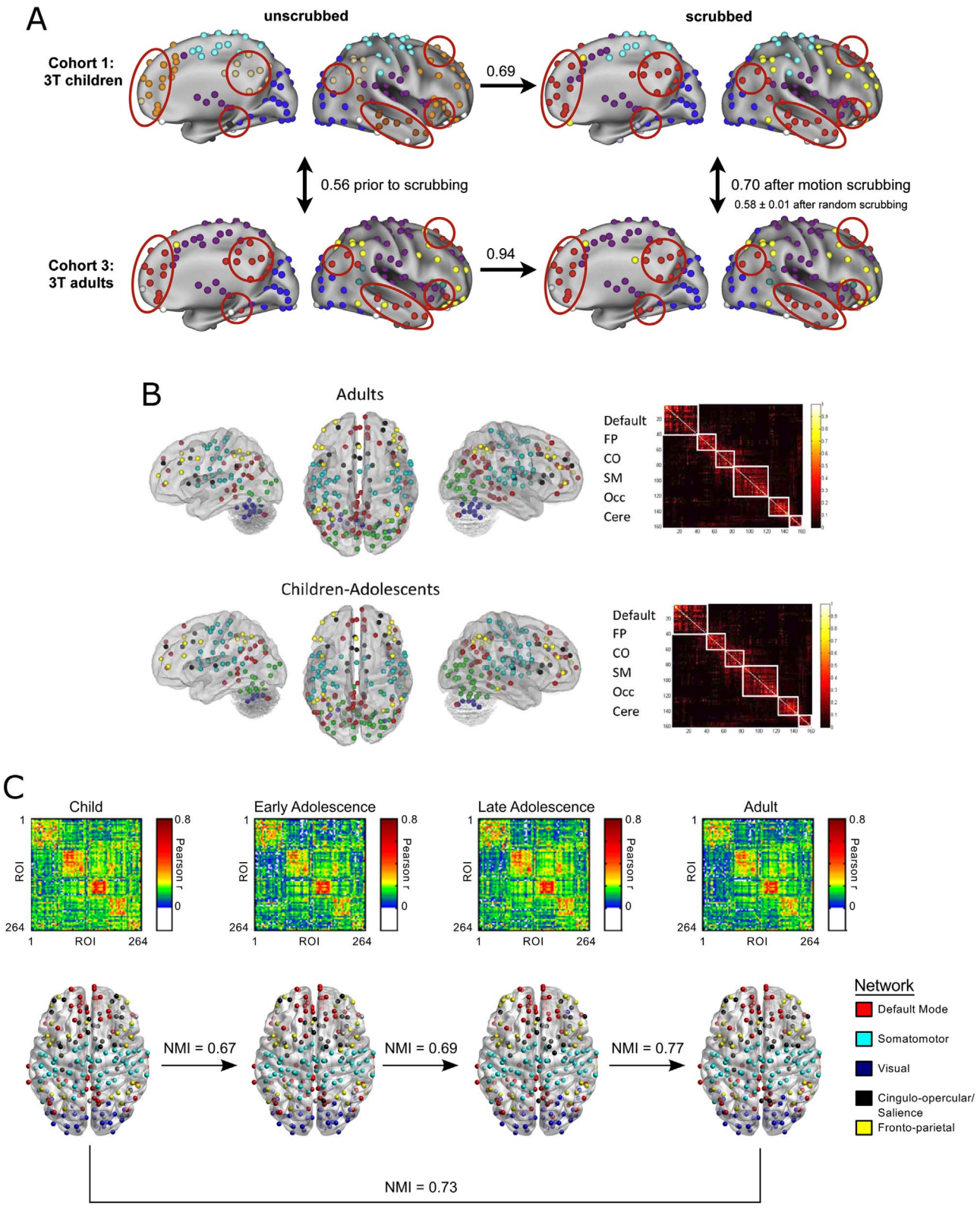

Fig. 3. Development of functional architecture from childhood to adulthood: similarities in community structure across age. A) Illustration shows community structure of functional networks in childhood (top) and adulthood (bottom), with (right) or without (left) denoising of scans via removal of high head-motion frames (i.e. "scrubbing"). Nodes are 264 spherical ROIs, colored according to community assignments. Circles illustrate areas that show apparent age-related differences prior to motion denoising, but which do not demonstrate age effects after denoising. Numbers next to arrows indicate the mutual information (a measure of similarity) in the two community structures. Motion exaggerates age-related differences in community structure. From Power et al. (2012). **B)** Similar community structure is obtained in adults and children when using strict criteria to minimize the influence of motion artifact. Overall network structure looks remarkably similar as well. From Fair et al. (2012b). **C)** Similar community structures are identified in late childhood, early adolescence, late adolescence, and adulthood. On the other hand, there is evidence for refinement within this modular framework (see Fig. 4). From Marek et al. (2015).

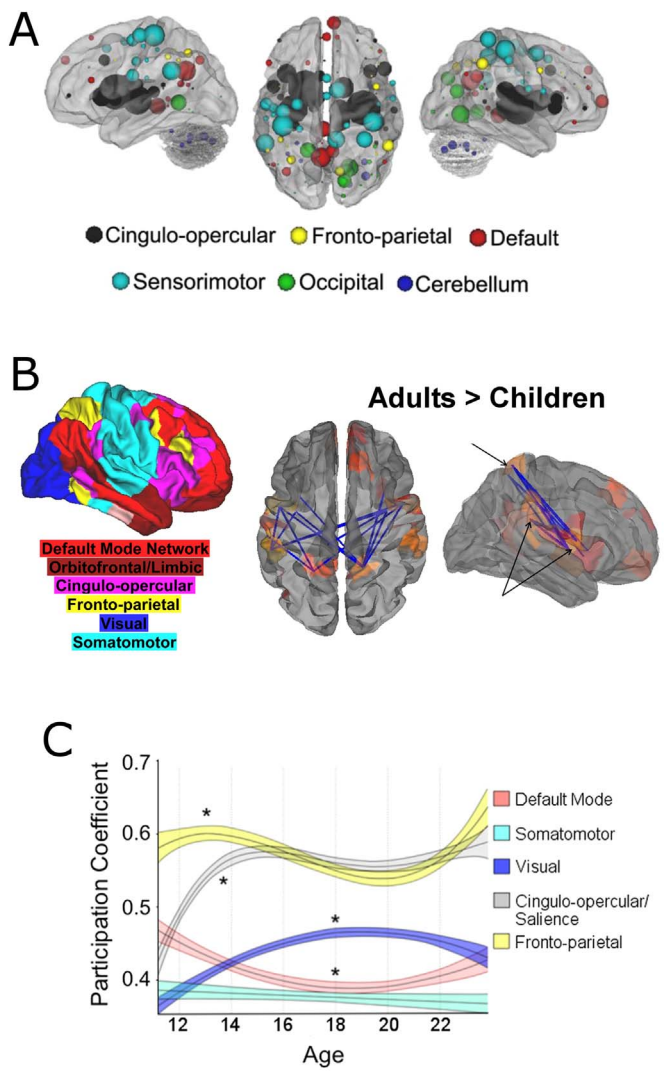

Fig. 4. Evidence for disproportionate involvement of the cingulo-opercular and somatomotor systems during development from late childhood into adulthood. A) Regions that are most predictive of age, from late childhood to young adulthood, via age-related changes in functional connectivity. Nodes are sized according to predictive strength in a support-vector machine. Adapted from Fair et al. (2012b). B) On the left, average functional community structure is shown for healthy young adults. On the right, differences in functional connectivity between adults and older children are shown. Adults have greater functional connectivity of selected links within and between the somoatomotor and cingulo-opercular modules. Regions on the cortical surface with high functional connectivity overall are highlighted in warm colors, illustrating that developmental differences also involve hub regions. Adapted from Grayson et al. (2014). C) Developmental trajectories are illustrated for five networks. Average participation coefficient for nodes within each network are plotted over age. The cingulo-opercular network exhibited the most substantial increase over development. These changes mediated age-related increases in cognitive control and were especially driven by increased connectivity between cingulo-opercular and somatomotor nodes. From Marek et al. (2015).

5–30 years of age across most frequency bands, but particularly in the slow-wave (0.5–7 Hz) (Miskovic et al., 2015; Rodriguez-Martinez et al., 2015; Smit et al., 2012; Whitford et al., 2007). There is also a progressive shift in peak amplitude towards higher frequency activity (Miskovic et al., 2015; Rodriguez-Martinez et al., 2015; Smit et al., 2012; Whitford et al., 2007). Interestingly, frontal and parietal cortical gray matter (but not white matter) volume decreases across this same age bracket, and exhibits curvilinear trajectories that are closely correlated to the loss of slow-wave power in these same areas (Buchmann et al., 2011; Smit et al., 2012; Whitford et al., 2007). These coincident trajectories have provided key support for the hypothesis that developmental changes in baseline electrophysiological signatures may primarily be subserved by reduction of neuropil and progressive synapse elimination (Buchmann et al., 2011; Smit et al., 2012; Whitford et al., 2007).

EEG/MEG functional connectivity networks can also be constructed from synchronized activity within different frequency bands. Reports of resting-state EEG/MEG networks in infancy are scant (although see later section on temporal dynamics), but a number of network studies have been conducted regarding later development. It is important to note that these studies are generally unable to map activity to precise brain areas due to challenges in source localization, and often treat the scalp sensors as the network nodes. Nonetheless, there are several noteworthy findings. From roughly 5 years of age until adulthood, theta (~4 Hz), alpha (~10 Hz), and beta (~20 Hz) oscillation networks exhibit concurrent increases in clustering coefficient (Boersma et al., 2011; Smit et al., 2012) and strength of long-range anterior-posterior and interhemispheric connections (Barry et al., 2004; Miskovic et al., 2015; Smit et al., 2012; Srinivasan, 1999). There is also consensus that network structure becomes increasingly non-random across this timespan (Boersma et al., 2011; Miskovic et al., 2015; Smit et al., 2012). Somewhat unexpectedly, two reports found path length to also increase with age (Boersma et al., 2011; Smit et al., 2012), although more recent work demonstrates age-related reductions (Miskovic et al., 2015). While this work is in its infancy, these studies thus far suggest some consensus between electrophysiological and MRI-based findings, implying that changes in brain organization are at least partially preserved across temporal scales of investigation.

Regional hub metrics

Returning to the MRI literature, there is convergent evidence that the locations of high-strength and high-betweenness hub regions appear to be stable after 5 years of age (Cao et al., 2014; Grayson et al., 2014; Hwang et al., 2013; Wang et al., 2012; Wu et al., 2013; Zuo et al., 2012). However, there is also evidence for regional refinement of hub properties. Node strength and centrality of subcortical regions have both been reported to decrease in late childhood and adolescence (Sato et al., 2015; Supekar et al., 2009). Among cortical areas, some have reported increasing hubness of frontal nodes (Cao et al., 2014; Wu et al., 2013) while in other lobes there have been mixed reports of increasing (Cao et al., 2014; Grayson et al., 2014) and decreasing (Wu et al., 2013; Zuo et al., 2012), or stable (Hwang et al., 2013) hubness. At first glance, these mixed or non-significant findings might suggest that regional properties of cortical hubs are largely established during very early development. However, given that different networks display varying trajectories for within-network and between-network connectivity (Gu et al., 2015b; Marek et al., 2015), renewed examination of nodal hub-like properties such as the participation coefficient (which quantifies within vs. between module strength) may be warranted (e.g. see Marek et al. (2015)). More detailed network analyses have revealed that specific connections to cortical hub regions increase during childhood and adolescence (Grayson et al., 2014; Hwang et al., 2013) resulting in increased rich club coefficients in adulthood (Cao et al., 2014; Grayson et al., 2014). Regional properties have also been found to exhibit nonlinear relationships with age (Wang et al., 2012), emphasizing the importance of mapping trajectories with more detailed temporal precision.

Development of temporal dynamics

Here we will briefly discuss the topic of temporal dynamics in brain function, a rapidly emerging theme in the functional neuroimaging literature. First, we will point out that brain functional dynamics can relate to changes that occur over decades (e.g., myelination) or over fractions of a second (e.g. receptor turnover). Thus far, network

changes in infancy, childhood, and adolescence have been discussed. This section discusses the growing literature of dynamics that occur over seconds and minutes measurable via rs-fcMRI.

Mounting evidence suggests that the functional connectome exhibits temporal instability that allows it to flexibly switch between multiple different configurations within a scanning session (Allen et al., 2014; Chang and Glover, 2010; Kang et al., 2011; Shen et al., 2015). There is evidence that this property is important for executive functioning, learning, and switching between challenging task demands (Bassett et al., 2011; Braun et al., 2015; Chen et al., 2016). Over development, rs-fcMRI networks show increased within-subject variability (Hutchison and Morton, 2015; Marusak et al., 2016; Qin et al., 2015), consistent with EEG studies showing that signal complexity increases over development (McIntosh et al., 2008; Vakorin et al., 2011). Recent simultaneous EEG-fMRI work (Fransson et al., 2013) links developmental differences (infants versus adults) in rs-fcmri network dynamics with differences in EEG power spectra. These data agree with notions that temporal variability in very low frequency correlations is an emergent, hidden property of higher frequency power spectra (Chang et al., 2013; Tagliazucchi et al., 2012), which is known to change continuously throughout development (Miskovic et al., 2015; Rodriguez-Martinez et al., 2015; Smit et al., 2012; Whitford et al., 2007). Given that different EEG frequency components have unique neurophysiological underpinnings (Miskovic et al., 2015), changing frequency spectra and temporal dynamics may point to clearer mechanistic substrates for network development.

Unfortunately, we have to repeat a recurring theme here and make yet another note of caution. Laumann et al. (Laumann et al., 2016) has recently provided strong evidence that much of the observed dynamics in rs-fcMRI networks primarily reflects noise (especially movement). The authors note that instability is not absent, but that it exists in the form of measurable state transitions (e.g. from awake to sleep, or eyes open versus closed), and that there is considerably less evidence for intrinsic dynamics otherwise. Other work has called into question some of the common statistical approaches to assessing dynamic FC (Hindriks et al., 2016; Leonardi and Van De Ville, 2015), which may not test against null models that properly account for random noise. It is also not clear whether the BOLD measurements are simply less sensitive to dynamic changes because of the sluggish nature of the signal. Altogether, these findings warrant more work, especially using simultaneous EEG-fMRI and animal models, to determine the potential role of network dynamics in development.

Structure-function relationships over development

What are the underlying substrates of functional network development? This question is informed, in part, by previous studies investigating the correspondence between structural connectivity (SC) and FC. In humans, SC networks can be estimated using diffusion-weighted imaging (DWI), which allows for virtual reconstructions of white-matter tracts (a method known as tractography). There is an abundance of research demonstrating a correlation between DWI-tractography connection weights and FC in adults (Hagmann et al., 2008; Hagmann et al., 2010; Honey et al., 2009). More generally, SC networks can be combined with various modeling approaches to predict FC networks, allowing for detailed exploration of how the structural connectome gives rise to complex neural interactions. Models can involve highly parameterized simulations of regional activity (Hansen et al., 2015; Messe et al., 2014; Sanz-Leon et al., 2015), or sparser analytic predictions of FC using graph metrics of mutual communication (Goni et al., 2014; Grayson et al., 2016) (although, both approaches appear to be comparably effective; see Fig. 1D). Predictive models have been extensively validated on both rs-fcMRI and EEG data (Chu et al., 2015), suggesting that SC strongly shapes and constrains activity across temporal scales.

A natural extension to this work would be to examine how structure-function correspondence develops, and whether optimized model parameters might evolve in tandem. Given that macroscale FC is modulated by both interregional connectivity strength as well as local population dynamics (Sanz-Leon et al., 2015), alterations in SC-FC coupling could potentially point to important shifts in the underlying drivers of various network phenomena. At least two reports have found abnormally low SC-FC correlation in epileptic patients (Chiang et al., 2015; Zhang et al., 2011), highlighting that aberrant SC-FC coupling may indeed indicate aberrations in neuronal physiology.

The first foray into developmental work was conducted in 2010, when Hagmann et al. (2010) reported that SC-FC correspondence was higher in older teens versus in young children. Although the cause remains unknown, this result is broadly consistent with the notion that large white-matter bundles increase their capacity for information transfer with age via mechanisms such as increased myelination and axon diameter (Hagmann et al., 2012). Unfortunately, follow-up work on this topic in humans has been relatively scant, and this work was prior to new information regarding tractography artifacts (Calabrese et al., 2015; Donahue et al., 2016; Reveley et al., 2015; Thomas et al., 2014), and prior to systematic motion artifacts being demonstrated in diffusion-weighted MRI (Kong, 2014; Yendiki et al., 2014). The possibility for confounding artifactual contributions should therefore not be ruled out. However, new findings by Van den heuvel (van den Heuvel et al., 2015b) show similar phenomena in preterm infants, such that neonates at 40 weeks gestational age have substantially greater SC-FC coupling than neonates born at 30 weeks. Another study found that age-related changes in FC disproportionately impacts polysynaptic connections (Betzel et al., 2014), although this study was performed across the lifespan and may reflect an effect of aging.

The role of animal models

The importance of animal work for understanding structure-function relationships over development, and developmental fMRI findings in general, cannot be understated. The non-invasive measurements used to examine human populations are now readily available in rodent and monkey models where rich methodologies for studying genetic and pharmacologic manipulations exist. While clearly several cognitive domains in humans (e.g. language) and their relation to connectivity profiles are unlikely to be measured directly in animal models, network properties and structure-function relationships supporting sensory and cognitive function (see Fig. 5) are attainable across species (Grayson et al., 2016; Miranda-Dominguez et al., 2014b; Stafford et al., 2014; Hutchison et al., 2015; Hutchison and Everling, 2012; Margulies et al., 2009).

Why is this important? As is oft repeated in the current review, a very large portion of the current human developmental literature is in dire need of re-examination in light of recent developments regarding systematic artifacts in the imaging signals. Even with the current approaches aimed at optimizing signal versus noise, the question remains: What other lurking land mines are hidden in our data?

For example, structure-function modeling using MRI data suffers from a number of inherent limitations in DWI-tractography that have not been overcome by state-of-the-art acquisition and processing approaches (Calabrese et al., 2015; Donahue et al., 2016; Reveley et al., 2015; Thomas et al., 2014). Invasive tract-tracer injections, a method that is only feasible in animal models, remains the “gold standard” for identifying and quantifying interareal connection weights. In the monkey, whole-brain tract-tracer connection networks and tractography networks demonstrate a significant, but only moderately high correspondence. Currently, the highest reported correlation stands at r=0.59 (Donahue et al., 2016), though it is often much lower (van den Heuvel et al., 2015a). Future work could probably improve these relationships substantially by imposing rigorous anatomical constraints in the tractography process (Smith et al., 2015), but such efforts have not seen extensive validation yet.

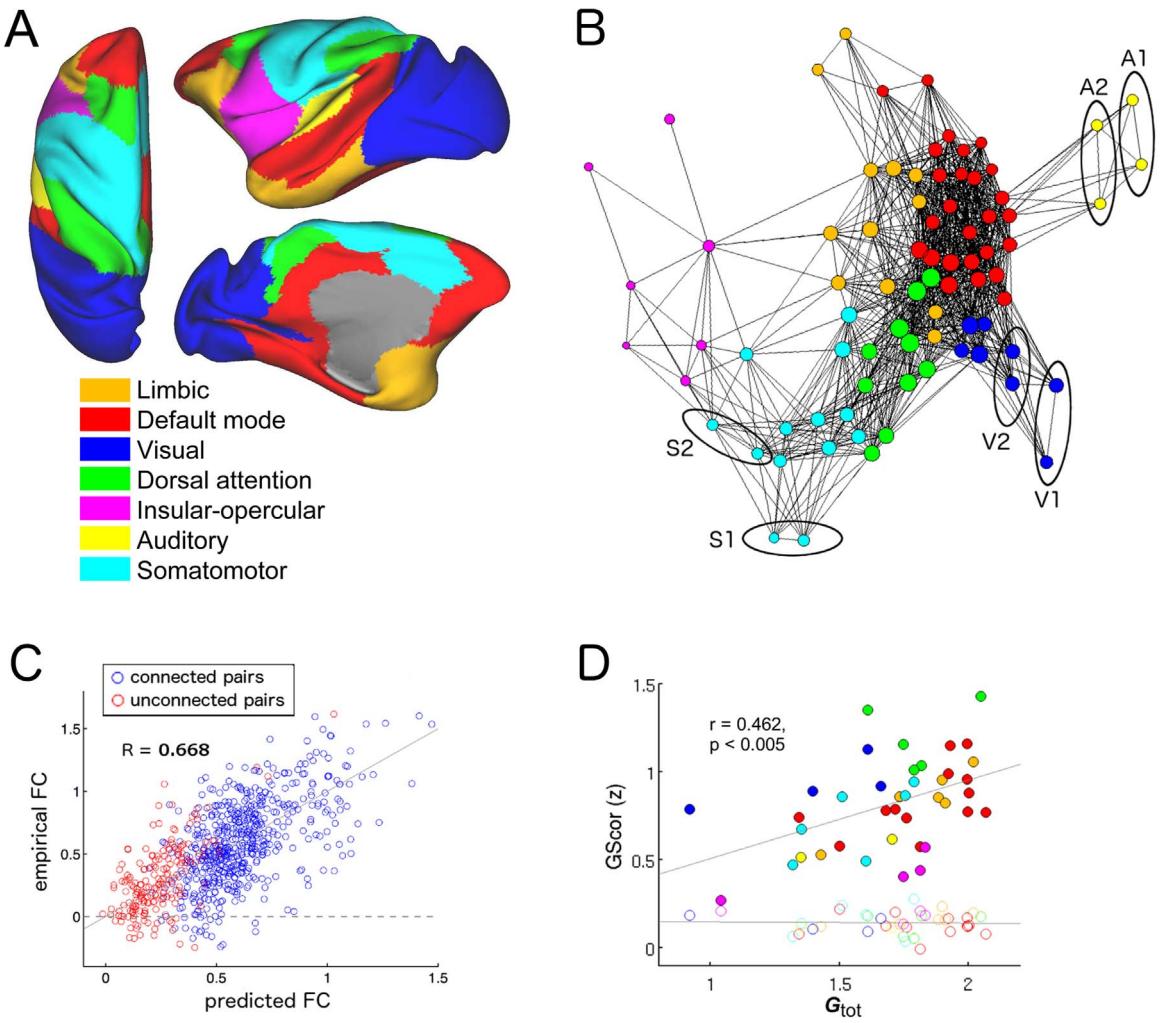

Fig. 5. Functional network organization, hierarchies, and structure-function relationships in the monkey brain gleaned through contrast-enhanced resting-state imaging. A) Community detection performed on an 80-region parcellation of the rhesus monkey brain. Resting-state networks were obtained under anesthesia using enhanced imaging methodologies that included exogenous contrast, a surface coil with high SNR, and head fixation. Reported modules show clear homology with those seen in the human literature. B) Spring-embedded graph layout visualizing correlations between regions. Integrated versus segregated activity is visible, as are hierarchies within different sensory modalities. For instance, dorsal attention nodes are situated centrally, suggesting globally integrated processing. In contradistinction, primary visual, auditory, and somatosensory cortex are the most peripheral nodes within their respective modules, followed by secondary sensory cortices, suggesting both segregation of sensory streams and hierarchical relationships within them. Nodes are sized by their correlation with the global signal, illustrating that more central nodes have higher global signal correlation. C) Plot illustrates the correspondence between empirical FC (y-axis) and predicted FC (x-axis) based on modeling communication in the structural connectome. Dots represent region pairs that either are (blue) or are not (red) directly connected via fiber pathways. D) Structure-function relationships are also observable at the node level. Regional correlation with the global signal (y-axis) is associated with total communication capacity to and from the rest of the brain (x-axis). Dots show global signal correlations before (closed) and after (open) regressing out the global signal from each region's timecourse. Adapted from Grayson et al. (2016).

In the meantime, animal models are proving to be an important and necessary “bridge” for identifying ground-truth structure-to-function principles (Deco et al., 2014; Grayson et al., 2016; Miranda-Dominguez et al., 2014b; Stafford et al., 2014). One interesting aspect of the work in Grayson et al. (2016), is how tightly functional imaging conditions had to be controlled in order to reveal novel structure-function relationships and in order to maximize model performance (see Supplementary materials of Grayson et al. (2016) for an extensive exposition). First, motion had to be reduced to undetectable levels with head fixation; second, the MR coil was specially optimized to enhance SNR; and third, a contrast agent was used to boost the functional signal. Without these efforts (which are not feasible in the large majority of human studies), critical structure-function relationships were much degraded.

Along the same lines, other factors outside of macro-anatomical connectivity likely affect FC measurements. Even the best-performing SC-FC models generally account for less than 50% of the variance in FC across the brain in both humans and non-human primates (Grayson et al., 2016; Messe et al., 2014; Misic et al., 2015). Identifying these other hidden factors will be of critical importance to understanding the drivers of FC development in a given age range and why FC networks may go awry in various developmental disorders. More to the point, macroscale FC is known to be modulated by interareal correlated gene expression, areal densities of excitatory and inhibitory receptors, and other features of microscale architecture that vary across brain structures (Richiardi et al., 2015; Scholtens et al., 2014; Turk et al., 2016; van den Heuvel et al., 2016b) and undoubtedly evolve with age. Thus, more empirical mapping of brain structure and integration into a coherent modeling framework is needed. Of course, probing cellular and molecular markers across the whole human brain at high-throughput is exceptionally difficult (Richiardi et al., 2015) and cannot be done under strict experimental conditions. Experimental animal models should therefore remain indispensable for this purpose the foreseeable future.

Clinical disorders of neurodevelopment

While this review has focused on studies of normative development, there is also a rich rs-fcMRI and EEG/MEG network literature in neurodevelopmental disorders. Complex, distributed disruptions in resting-state networks are consistently implicated in Schizophrenia (Baker et al., 2014; Khadka et al., 2013; Satterthwaite et al., 2015), ADHD (Castellanos and Aoki, 2016; Fair et al., 2012b), and Autism (Kessler et al., 2016; Moseley et al., 2015; Supekar et al., 2013) – though a thorough examination of this literature is beyond the scope of this review. Rather, we turn our attention here to two crucial challenges that are likely to dominate future research efforts into these conditions.

The first challenge is the ever-expanding evidence that Schizophrenia (Meda et al., 2014; Satterthwaite and Baker, 2015), ADHD (Costa Dias et al., 2015; Fair et al., 2012a; Gates et al., 2014; Karalunas et al., 2014), Autism (Jeste and Geschwind, 2014; Rudie et al., 2012), and potentially other DSM defined disorders, each constitutes a highly heterogeneous set of etiologies. Indeed, recent work suggests that Autism Spectrum Disorder is characterized by increased subject-to-subject variability relative to the general population (Hahamy et al., 2015). Such findings are consistent with the notion that different pathologies in brain function may lead to related clinical outcomes, and underscore the importance of identifying individualized abnormalities.

Some recent work has already aimed at addressing this by attempting to identify brain-based subtypes within a diagnostic category, mostly through the application of various analytic clustering methods to multivariate neuroimaging or behavioral data. For an excellent review of recent progress, as well as promises and pitfalls in this area, we direct the reader to Marquand et al. (2016). Another related approach to tackling heterogeneity would be to focus on deviations from typical brain organization at the individual-subject level, rather than performing classical between-group analyses. Cutting-edge work in resting-state fMRI acquisition and network analysis suggests that individual brains, even among typical subjects, are distinguishable via their functional connectomes (Finn et al., 2015; Laumann et al., 2015; Miranda-Dominguez et al., 2014b). Future work exploring the notion of the 'functional fingerprint' or 'connectotype' (Miranda-Dominguez et al., 2014a) may help to identify what deviations from the canonical functional connectome lead to atypical behavioral outcomes, versus what deviations may be considered to fall within the typical range. This would also be strongly in line with the National Institute of Health's new initiative for precision medicine (Collins and Varmus, 2015).

The second challenge is in understanding the pathophysiological basis of network-level disturbances that are distributed and complex. In other words, if one sees atypical functional profiles amongst a specific set of brain regions or connections, does that suggest that the substance of the pathology is co-located? There are several reasons from a theoretical standpoint (Pessoa, 2014), which are largely supported empirically, why this is not necessarily the case. As an example, simulation experiments using structure-function models have predicted that even purely focal and transient perturbations in activity should result in diffuse network reorganization that affects distant brain systems (Alstott et al., 2009; Honey and Sporns, 2008; Misic et al., 2015). In our recent paper, we presented experimental validation of these ideas through focal pharmacogenetic inactivation (Grayson et al., 2016), and similar findings were presented by Andoh et al. (2015) using cortical transcranial magnetic stimulation. Both works demonstrate a causal effect on distributed resting-state connectivity and other neurophysiological signatures, driven by cascading neuronal interactions. These data empirically suggest that in a broad context, disease processes localized to one part of the brain can cause widespread neurophysiological disturbances in areas distant and unconnected from the pathology. This work also provides evidence that site-specific pathology can be deduced from distributed functional network disturbances (Grayson et al., 2016). However, in the absence of strong hypotheses regarding a ground-truth, one must be mindful that multiple structural network configurations can theoretically give rise to the same apparent aberrations in function – this is essentially the 'many-to-many mappings' problem very nicely described in Pessoa (2014). In summary, reducing these sources of complexity in neuropsychiatric case-control studies is likely to require integrated multimodal imaging approaches, more widespread application of SC-FC modeling, and breakthrough innovations in imaging tissue structural and functional properties that relate to functional connectivity.

Methodological challenges and recommendations

FMRI signal artifacts

Rs-fcMRI investigators must be mindful that the fMRI signal is susceptible to a number of spurious sources of variance due to hardware instabilities, respiratory and cardiac signals, and head motion artifacts (Jo et al., 2010; Power et al., 2016). Effects of respiratory and cardiac activity can be attenuated through the use of temporal filtering, ICA-denoising, or directly acquiring these signals and removing them post-hoc. There is ongoing debate regarding the adequacy of these techniques (Jo et al., 2010; Power et al., 2016), and more work may be warranted to determine optimal ways to account for age-related physiological confounds. In addition, head motion has become a substantial concern since 2012 when a trio of papers pointed to systematic motion-related artifacts in rs-fcMRI (Power et al., 2012; Satterthwaite et al., 2012; Van Dijk et al., 2012). Chief among these findings was distance-dependent effects; head motion increases functional correlations between spatially proximal nodes and decreases correlations between distant nodes (Power et al., 2012). Motion tends to be greater in patient populations and younger children, posing a fundamentally important challenge for developmental research. Considerable work and debate is now ongoing to determine the optimal 'denoising' approaches during data processing (Patriat et al., 2016; Power et al., 2014). The most contentious debate probably concerns the use of global signal regression (GSR) – arguably the most effective motion-denoising technique currently available (Burgess et al., 2016; Power et al., 2015; Yan et al., 2013). Recent data reinforces concerns about artifactual contributions to the global signal in conventional 3 T rs-fcMRI acquisitions sensitive to BOLD contrast (Grayson et al., 2016; Power et al., 2016), but also partly substantiates concerns regarding GSR under less conventional, high signal-to-noise scenarios where motion can be physically restricted (Grayson et al., 2016). Thus, GSR is likely to be a useful tool in developmental rs-fcMRI studies, where good control of such artifact is exceptionally important, but this debate may need to be revisited as methodologies in acquisition continue to advance. Moving forward, there is strong consensus about the importance of preventing head motion during acquisition and rigorously quantifying motion effects in study data (Goto et al., 2016; Power et al., 2015; Siegel et al., 2016).

We also wish to emphasize that future work using strict artifact removal are an increasing need for neuroimaging studies quite broadly – well beyond functional connectivity studies. Strong artifacts due to motion, in addition to their relevance for fMRI, have been noted in diffusion weighted imaging (Roalf et al., 2016; Yendiki et al., 2014) and cortical thickness measurements (Reuter et al., 2015; Savalia et al., 2017). Motion artifacts appear to be tightly related to clinical factors (Fair et al., 2012b) and a whole host of behavioral phenotypes and metrics (Siegel et al., 2016). Some of the techniques currently being used to remove these artifacts are non-optimal (Burgess et al., 2016; Goto et al., 2016). Thus, close examination of many of the developmental MR imaging findings is still warranted.

Parcellation choice

Developmental network researchers also must make important decisions when defining the nodes (i.e. functional areas) under investigation. There is currently no consensus regarding an optimal set of criteria for defining an areal parcellation (Craddock et al., 2013; Glasser et al., 2016a; Gordon et al., 2016), and even less known about the stability of these parcellations at younger ages.

Parcellation density (i.e. number of regions) is a crucial consideration. Global topological metrics for structural and functional networks show stability across different parcellation schema of similar density, but vary considerably as a function of network size (de Reus and van den Heuvel, 2013; Fornito et al., 2010; Zalesky et al., 2010). In addition, with functional connectivity data some parcellation schemes can obscure known community structure. For example, regions or parcels that are overly large may encompass multiple distinct functional areas in ways that make community/network organization non-recognizable (Power et al., 2011). Functional network analyses that strongly relate to known network organization may therefore find signal homogeneity within parcels to be a useful optimization criterion for choosing a parcellation (e.g. see Gordon et al. (2016) and Glasser et al. (2016a)).

In our opinion, the primary guiding factors in choosing a parcellation are based in fundamental principles of neuroscience. The cerebral cortex is both anatomically and functionally organized at many physical scales - starting at the level of single neurons and extending up to functional systems (Churchland and Sejnowski, 1992). At one scale are discrete regions of the cortex, known as functional areas. Functional areas possess unique internal structure (e.g. architectonics and topography). They also contain distinct combinations of inputs and outputs, which in turn group related areas into specialized networks (Felleman and Van Essen, 1991). These areal boundaries appear very early in development (Kostovic et al., 1995) and each area is thought to make a distinct contribution to information processing (Cohen et al., 2008; Felleman and Van Essen, 1991; Fuster, 2002; O'Leary and Nakagawa, 2002; Sur and Rubenstein, 2005). Ideally, parcellations for functional connectivity studies would closely reflect these areal boundaries in order to more clearly link network effects to the brain's underlying information processing architecture. In animal studies (rodents and non-human primates), this is feasible through the use of comprehensive, histologically and functionally defined whole-brain areal parcellations (Bezgin et al., 2012; Lein et al., 2007; Paxinos et al., 2000; Saleem and Logothetis, 2007; Swanson, 2015; Van Essen et al., 2012). In humans, there is much less clarity regarding potential areal boundaries (outside of elementary cytoarchitectonic divisions described, for example, by Brodmann (1909) and Economo and Koskinas (1925)) since a comparable amount of comprehensive data has not been readily available in a common reference space. Several groups, however, are finding ways to utilize today's non-invasive imaging tools to bring us closer to realizing these goals (Behrens et al., 2003; Glasser et al., 2016a; Gordon et al., 2016; Wig et al., 2014a, 2014b; Zhang et al., 2010).

Atlas or template choice

A topic related to parcellation choice is how to spatially normalize individual subjects onto a common reference template. Cortical folding patterns change continually from birth into adulthood, and especially during infancy. Infancy is also a time during which the image contrasts in various MR acquisitions changes dramatically. These changes pose challenges during template-based data processing steps such as spatial normalization and image segmentation, and are particularly problematic in studies that use template brains derived from only one age group and therefore rely on assumptions regarding similarity in shape characteristics of the brain across participant groups. The use of high-contrast, age-specific and study-specific template brain images for image registration is a well-validated approach to help overcome some of these confounds (Avants et al., 2010; Fonov et al., 2011), and is increasingly adopted in both structural and functional studies of (especially early) development (Eggebrecht et al., 2017; Fonov et al., 2011; Gao et al., 2015a; Scott et al., 2015). Surface based registrations that take into account the sulcal and gyral anatomy also help mitigate these confounds, and may be the future direction of the field (Fischl, 2012; Van Essen, 2012).

On top of these issues, functional areal boundaries (see *Parcellation Choice*) of heteromodal association areas are variable with respect to sulcal and gyral anatomy (Fischl et al., 2008). New multimodal approaches that also anchor surface-based registrations to other structural or functional characteristics of an individual are likely to improve subject to subject registrations, and hence reduce intersubject variability, even more (e.g. (Glasser et al., 2016b; Robinson et al., 2014). Unfortunately, these advanced methods require more data acquisition time than is typically afforded for developmental studies. Nonetheless, a high quality anatomical image that is capable of being segmented properly into grey and white matter by itself is enough for the most basic surface-based registration tools.

Test-retest reliability

A final point regarding the use of rs-fcMRI for network mapping concerns its reliability as a measurement tool. Multiple studies have found evidence for limited test-retest reliability using a multitude of conventional rs-fcMRI network characteristics and analytic approaches (Braun et al., 2012; Wang et al., 2011; Wisner et al., 2013; Zuo et al., 2010; Zuo and Xing, 2014). Recent evidence suggests that these effects may largely result from insufficient data acquisition. For instance, FC networks in one highly sampled individual converged as a function of the timeseries length used to extract correlations and were extremely reproducible using approximately 1 hour of motion-free data (Laumann et al., 2015). However, this length of scan time for each individual is likely prohibitive in most developmental rs-fcMRI studies, underscoring the importance of internal study replication. In addition, more work could be done to develop analytic methods with both high sensitivity to individual variation and high test-retest reliability (see Miranda-Dominguez et al. (2014a)).

Conclusions

This review has surveyed the development of correlated, resting-state activity and the emergence of network organization from birth until adulthood. Across all stages of postnatal development, functional brain networks exhibit non-trivial properties such as community structure, hub organization, cross-module integration, and global efficiency. Community structure at birth is coarse and primitive, but gradually evolves into a denser, more spatially structured, and distributed organization. The most dramatic changes appear to occur in the first two years of life, though network refinement continues through childhood and adolescence, strengthening connections particularly among functional hubs. While the past decade has seen remarkable growth of network neuroscience and its application to development, there is still ample work that needs to be done. The field will benefit from resolving technical issues with acquisition and artifact removal, and from gaining a better understanding of the heterogeneity that exists across typical and atypical populations. Finally, we believe there is an urgent need to establish stronger links between different functional imaging modalities, between structural and functional connectivity, and between micro- and macro-scales of investigation via animal models.

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