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Development of the Default Mode and Central Executive Networks across early adolescence: A longitudinal study

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ABSTRACT

The mature brain is organized into distinct neural networks defined by regions demonstrating correlated activity during task performance as well as rest. While research has begun to examine differences in these networks between children and adults, little is known about developmental changes during early adolescence. Using functional magnetic resonance imaging (fMRI), we examined the Default Mode Network (DMN) and the Central Executive Network (CEN) at ages 10 and 13 in a longitudinal sample of 45 participants. In the DMN, participants showed increasing integration (i.e., stronger within-network correlations) between the posterior cingulate cortex (PCC) and the medial prefrontal cortex. During this time frame participants also showed increased segregation (i.e., weaker between-network correlations) between the PCC and the CEN. Similarly, from age 10 to 13, participants showed increased connectivity between the dorsolateral prefrontal cortex and other CEN nodes, as well as increasing DMN segregation. IQ was significantly positively related to CEN integration at age 10, and between-network segregation at both ages. These findings highlight early adolescence as a period of significant maturation for the brain's functional architecture and demonstrate the utility of longitudinal designs to investigate neural network development.

1. Introduction

Early adolescence is a period of substantial neural development, triggered in part by biological changes related to the onset of puberty as well as significant changes in youths' social sphere. Work in animals and neuroimaging studies in humans suggest that pubertal development corresponds with significant changes in the brains' structural and functional organization (e.g., Blakemore et al., 2010; Sato et al., 2008). This neural maturation is accompanied by developments in the social and cognitive domains. Adolescents experience a "social reorientation" (Nelson et al., 2005) whereby they become increasingly sensitive to social cues and peer relationships. Indeed, the emphasis on social learning and preparation for adult roles during adolescence occurs in cultures around the world (Schlegel and Barry, 1991; Schlegel, 1995). Youth also make important strides in executive functioning, including inhibitory control, planning for the future, metacognition, and hypothesizing about others' mental states (e.g., Dumontheil et al., 2010; Weil et al., 2013; Williams et al., 1999).

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Between childhood and adulthood, significant changes also occur in the functional architecture of the brain. The adult human brain is organized into functional networks, consisting of sets of distinct neural regions that demonstrate correlated blood oxygen level-dependent (BOLD) signal fluctuations both during specific tasks and while at rest (e.g., Fox and Raichle, 2007). Immature versions of these networks—i.e., significant but weaker connectivity between some or all "hub" regions of each network—have been documented in childhood and even, to some extent, in infancy (for a review, see Dennis and Thompson, 2013). Nonetheless, these immature networks tend to have weaker internal connectivity and are less functionally segregated (i.e., demonstrate stronger between-network correlation) than those in adulthood, with adolescence representing a period of intermediate connectivity (Jolles et al., 2011; Kelly et al., 2009; Fair et al., 2007a, 2009; Hwang et al., 2013). Despite our increasing understanding of the dramatic neural maturation that occurs during the second decade of life, relatively less is known about the development of functional networks *during* adolescence, particularly during the years when the most dramatic pubertal changes typically occur. Furthermore, the majority of research examining the maturation of functional networks has relied upon cross-sectional, rather than longitudinal data, with only a few exceptions in infant populations (e.g., Gao et al., 2014; Smyzer et al., 2010). The present study examines the development of two functional networks in early adolescence using a longitudinal sample of participants who were studied at ages 10 and 13. Specifically we examined the Default Mode Network (DMN) and the Central Executive Network (CEN), which have been implicated in social cognition and executive control, respectively.

Raichle and colleagues (2001) first observed that a network of neural regions, including the posterior cingulate cortex (PCC), the medial prefrontal cortex (mPFC), and the lateral parietal cortex showed increased activity during "baseline," or when an individual is at rest. This same network of regions has been shown to be deactivated during a variety of neuroimaging tasks requiring cognitive processing; indeed, it has also been labeled the "task-negative" network (Fox et al., 2005b; Greicius et al., 2003; Binder et al., 1999; Shulman et al., 1997). The past decade has seen a surge of scientific interest in the DMN, both in typical and clinical populations (for a review, see Broyd et al., 2009). In task-based fMRI designs, regions of the DMN are frequently activated during social cognition, including processing emotional stimuli, introspection, and thinking about others' mental states (e.g., Blakemore, 2008; Gusnard et al., 2001; Maddock, 1999). Given its involvement in social cognition, this network of regions is sometimes referred to as the "mentalizing network" in the social affective neuroscience literature (e.g., Atique et al., 2011).

The CEN, in contrast, is one of the two networks that frequently *activates* during typical fMRI tasks involving executive functions. Seeley and colleagues (2007) distinguished between the salience network, with main hubs in the dorsal anterior cingulate and orbitofrontal insular cortices, and the CEN, anchored in the dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (pPC), particularly the intraparietal sulcus (IPS). They reported that activity in the CEN, but not the salience network, correlated with performance on executive control tasks. Emerging evidence suggests the strength of within-network connectivity in the CEN, (also called the frontoparietal control system/network; Vincent et al., 2008) is associated with higher IQ in children, adolescents, and adults (e.g., Langeslag et al., 2013; Li and Tian, 2014; Song et al., 2008). CEN activity has been shown to be anticorrelated with activity in the DMN in healthy adults (Fox et al., 2005b; Menon and Uddin, 2010; Sridharan et al., 2008), and it has been proposed that it may even directly inhibit DMN activity under certain circumstances (Chen et al., 2013). Data from cross-sectional research suggests that increasing integration within each functional network and segregation between these and other networks occurs throughout childhood and adolescence (Fair et al., 2007a).

The present study aimed to investigate the integration and segregation of the CEN and DMN during a relatively narrow period of development—ages 10 to 13—wherein significant structural and functional brain maturation, as well as socioemotional and cognitive development, occur. The data were collected as part of a longitudinal study which did not involve a traditional resting-state scan. Instead, we used functional data from a passive listening task of meaningless speech (McNealy et al., 2006, 2010, 2011) and performed the analyses on a residual timeseries after the task-specific effects were statistically controlled for. While our fMRI scan does differ somewhat from a traditional "resting state" scan, it is worth noting that participants were not engaging in active semantic processing, as the auditory stimulus was composed of unbroken nonsense syllables. Previous research has found that the brain's functional networks are detectable during task-based studies as well as at rest (Fair et al., 2007b; Harris et al., 2014; Smith et al., 2009). Indeed, work by Fox et al. (2005a) suggests that spontaneous fluctuations of functional networks account for a significant portion of the BOLD signal response during task-based fMRI paradigms. Our present findings demonstrate that the hubs of the DMN and CEN do indeed demonstrate significant and strong functional connectivity during a passive listening task, after controlling for the effects of that task (note that while the present study does not examine functional networks *as they relate* to language tasks, a growing body of literature considers this question; see, for example, Regev et al., 2013; Honey et al., 2012). In using a longitudinal dataset, we were afforded the ability to detect changes in functional connectivity with more sensitivity, and to conclude with greater confidence that our findings indeed reflect changes over time rather than differences between two samples. To the best of our knowledge, the present study is the first to use longitudinal data to examine the development of the brain's functional architecture during adolescence.

2. Methods

2.1. Participants

A sample of 45 typically developing children (24 females) participated in a longitudinal study on brain and