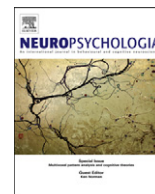




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Developmental changes in within- and between-network connectivity between late childhood and adulthood

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ABSTRACT

A number of behavioral changes occur between late childhood and adulthood, including maturation of social cognition, reward receptivity, impulsiveness, risk-taking and cognitive control. Although some of these abilities show linear improvements with age, some abilities may temporarily worsen, reflecting both the restructuring and/or strengthening of connections within some brain systems. The current study uses resting state functional connectivity to examine developmental differences between late childhood and adulthood in task positive (TP) regions, which play a role in cognitive control functions, and task negative (TN) regions, which play a role in social cognition, self-referential, and internally-directed thought. Within the TP network, developmental differences in connectivity were found with the left dorsolateral prefrontal cortex. Within the TN network, developmental differences in connectivity were found with a broad area of the medial prefrontal cortex and the right parahippocampal gyrus. Connections between the two networks also showed significant developmental differences. Stronger anticorrelations were found in the TN maps of the adult group for the right anterior insula/inferior frontal gyrus, bilateral anterior inferior parietal lobule, bilateral superior parietal lobule and an anterior portion of the right posterior cingulate cortex. There was a significant brain-behavior relationship between the strength of anticorrelation in these regions and inhibitory control performance on two Go/No-go tasks suggesting that the development of anticorrelations between late childhood and adulthood supports mature inhibitory control. Overall, maturation of these networks occurred in specific regions which are associated with cognitive control of goal-directed behavior, including those involved in working memory, social cognition, and inhibitory control.

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1. Introduction

Attention and control function undergoes marked development throughout childhood and adolescence. Developmental improvements occur in a number of goal-directed behaviors including: basic speed of processing and response variability, sustained attention, working memory, set shifting, and response inhibition (Bedard et al., 2002; Crone, Donohue, Honomichl, Wendelken, & Bunge, 2006; Crone, Wendelken, Donohue, van Leijenhorst, & Bunge, 2006; Geier, Garver, Terwilliger, & Luna, 2009; Geier, Terwilliger, Teslovich, Velanova, & Luna, 2010; Jazbec et al., 2006; Rueda et al., 2004; Williams, Ponsesse, Schachar, Logan, & Tannock, 1999). While some functions show relatively early maturation, many continue to improve through adolescence. For example, orienting and conflict scores do not change between childhood and

adulthood, however, overall RTs and alerting scores decrease during this period (Rueda et al., 2004). These findings suggest that brain systems supporting goal-directed behaviors may undergo specific changes.

Over the course of development, brain regions supporting cognitive control become more integrated within their networks and more segregated from other networks. Decreased connectivity between local, adjacent regions and increased connectivity between remote regions supporting distributed mature networks has been well-documented (Fair et al., 2008, 2009, 2007; Kelly et al., 2009). The angular gyrus, which forms part of the default mode network (DMN), and the adjacent inferior parietal lobule, which forms part of the fronto-parietal network, are more strongly connected with each other in children but are distinctly segregated into separate networks in adults (Fair et al., 2009; Vogel, Power, Petersen, & Schlaggar, 2010). Other long-range connections strengthen over the course of adolescence, such as the one between the posterior cingulate cortex (PCC) and the medial prefrontal cortex (MPFC), supporting integration of the anterior and posterior portions of the DMN in adulthood (Supekar et al., 2010; Uddin, Supekar, Ryali, & Menon, 2011).

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These developmental changes contribute to the formation of mature distributed networks seen in adults, and there is evidence that the basic topology of some of these networks exists early in development. Infants already have identifiable sensorimotor and visual networks within the first year of life, however cognitive systems such as the DMN and fronto-parietal network are at best only partially present (Fransson, Aden, Blennow, & Lagercrantz, 2011; Fransson et al., 2009; Fransson et al., 2007). Network maturation involves the strengthening of some preexisting connections, but the reshaping of other connections. Connectivity within task positive and DMN regions increase over the course of development (Anderson, Ferguson, Lopez-Larson, & Yurgelun-Todd, 2011; Fair et al., 2007) and the strength of voxel connectivity in childhood, predicts how strongly that voxel will affiliate with other voxels within its own network and how weakly that voxel will affiliate with other voxels outside of its network (Anderson et al., 2011). In addition to changes in the strength of network connectivity, there is evidence that specific restructuring also occurs.

Studies have found that task positive brain networks, which support goal-directed response to external stimuli, undergo reorganization during development. Fair and colleagues (2007), found that nodes of the dorsal attention network and the cingulo-opercular network change affiliation during adolescence. In addition, task-based studies have suggested that adolescents have less-developed prefrontal regions, which may reduce behavioral control and leave them more susceptible to risky behavior (Casey, Getz, & Galvan, 2008; Casey, Jones, & Hare, 2008; Somerville, Hare, & Casey, 2011). Both task-based and resting state functional connectivity studies have found that children and adolescents have immature medial prefrontal regions which may further affect their control processing (Blakemore, den Ouden, Choudhury, & Frith, 2007; Kelly et al., 2009).

Developmental changes in cognitive control are likely related to these maturational changes within task positive networks. They may also result from increased anti-correlations between task positive (TP) and task negative (TN) regions. Fox, Snyder, Barch, Gusnard, and Raichle (2005) first noted that these two networks, which show opposing activity during a variety of attentionally-demanding and working-memory tasks, also show opposing, anti-correlated time-courses at rest. Further examination has found that this opposing activity is behaviorally relevant (Hampson, Driesen, Skudlarski, Gore, & Constable, 2006; Kelly, Uddin, Biswal, Castellanos, & Milham, 2008; Mennes et al., 2010, 2011). In addition, the anti-correlations between these networks increase over the course of development (Anderson et al., 2011). However, it is not clear whether developmental behavioral improvements are specifically related to connectivity changes within TP network regions or whether they may also be related to connectivity changes between TP and TN regions.

For the current study, we examined group differences in TP and TN network connectivity between children (8–12 years old) and adults (20–47 years old) and the association of these changes with behavioral measures of cognitive control. We focused on changes in developmental connections with those seed regions of the TP and TN networks that are consistently (de-)activated during attentionally-demanding tasks (Fox et al., 2005). This allowed us to identify regions that are important for instantiating mature task control. We examined changes in both positive and negative connections to these two networks. In order to differentiate between those developmental changes that result in stronger connections within a network and those that result in stronger anti-correlations between networks, separate TP and TN network maps were compared between the two groups. Brain-behavior relationships between those connections that show developmental differences and cognitive control on two Go/No-go tasks were examined. One was a “Simple” Go/No-go task in which

working memory demands were minimized using a straightforward stimulus-response association (green=Go, red=No-go) and a second “Complex” Go/No-go task in which response selection was associated with higher working memory demand. We hypothesized that regions within the TP and TN networks would show increased connectivity with the seed regions in the adult group and that certain TP and TN regions would become more anti-correlated with the seed regions in the adult group. In addition, we hypothesized that connectivity with these developing regions would be related to cognitive control function as indexed by commission error rates on the two Go/No-go tasks.

2. Materials and methods

2.1. Participants

28 healthy adults (12 male, 16 female) and 63 typically-developing children (36 male, 24 female) participated in the study. All adults and 60 children were right-handed. Two children showed mixed handedness (Edinburgh handedness score between 0.5 and -0.5) and one child was left-handed. Adults were between 18 and 47 years old (mean=27.57, SD=6.22). All adults were screened for any history of mental health or neurological difficulties, including a history of developmental disabilities. Children were between 8 years 0 months and 12 years 11 months of age (mean=10.20, SD=1.06). All children had normal Full Scale IQ on the Wechsler Intelligence Scale for Children (mean=111.00, SD=10.54) with no history of intellectual disability, developmental language disorder, reading disability, pervasive developmental disorder, visual impairment, neurologic disorder nor psychiatric diagnosis, as confirmed using the DICA-IV (Sala, Granero, & Ezpeleta, 2006). Only subjects with movement of less than 3 mm translation and 3° rotation over the course of the resting scan were included in the current sample.

For the examination of network group-differences, all 28 adults (12 male, 16 female) and 42 gender-matched children (18 male, 24 female, all right-handed) were examined. For the brain-behavior correlations, 27 adults (12 male, 15 female) were included in the analysis. One adult was excluded for poor task performance. This adult had > 50% omission error rate on the Complex Go/No-go task and it was not clear whether the subject understood and/or was adequately attending to the task. 25 children had completed the behavioral tasks. Of these, one subject was excluded from further analyses for being left-handed. Twenty-four remaining children were included in the brain-behavior correlation analyses (11 male, 13 female). For this subgroup, mean age was 10.23 years (SD=1.07).

This study was approved by the Johns Hopkins Medical Institutional Review Board. Written consent was obtained for all participants. For children, written consent was obtained from a parent or legal guardian and verbal assent was obtained from the participating child.

2.2. fMRI acquisition and processing

Images were acquired on a Philips 3T scanner. A high-resolution anatomical scan (MPRAGE, 8-channel head coil, TR=7.99 ms, TE=3.76 ms, Flip angle=8°) was acquired for image co-registration, segmentation and normalization processing steps. Resting state scans were acquired in each participant for 5 min 20 s (D-SENSE EPI, 8-channel head coil, TR=2500 ms, TE=30 ms, Flip angle=70°). Participants were instructed to relax and fixate on a center cross. Preprocessing of functional images was performed using SPM5 and Matlab scripts. This included slice time correction, motion correction, co-registration, segmentation, and normalization. Nuisance variables were removed from each voxel, including cerebrospinal fluid and white matter signals identified using the CompCor method, global mean signal, and six motion parameters. Functional images were spatially smoothed using a 6 mm FWHM filter and then temporally filtered (bandpass 0.01–0.1 Hz).

2.3. Data analysis

6 mm-radius 3D seeds were centered at locations taken from a previous study (Fox et al., 2005). These seeds were originally centered at peak coordinates for regions showing consistent activation (task positive seeds) and deactivation (task negative seeds) from task-fMRI studies of attention-demanding and working memory tasks (Fox et al., 2005). Fox and colleagues had examined full-brain connectivity of task-derived seeds to show that the same regions that show opposing activation during task paradigms also form anti-correlated networks at rest. Those seeds included three task-positive (TP) seeds: intraparietal sulcus (IPS, talairach coordinates: $-25, -57, 46$), frontal eye field (FEF: $25, -13, 50$), and a middle temporal region (MT+; $-45, -69, -2$); and three task-negative (TN) seeds: medial prefrontal cortex (MPFC: $-1, 47, -4$), posterior cingulate cortex (PCC: $-5, -49, 40$), and lateral parietal cortex (LP: $-45, -67, 36$). The seed

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