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Asymmetric development of dorsal and ventral attention networks in the human brain

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ABSTRACT

Two neural systems for goal-directed and stimulus-driven attention have been described in the adult human brain; the dorsal attention network (DAN) centered in the frontal eye fields (FEF) and intraparietal sulcus (IPS), and the ventral attention network (VAN) anchored in the temporoparietal junction (TPJ) and ventral frontal cortex (VFC). Little is known regarding the processes governing typical development of these attention networks in the brain. Here we use resting state functional MRI data collected from thirty 7 to 12 year-old children and thirty 18 to 31 year-old adults to examine two key regions of interest from the dorsal and ventral attention networks. We found that for the DAN nodes (IPS and FEF), children showed greater functional connectivity with regions within the network compared with adults, whereas adults showed greater functional connectivity between the FEF and extra-network regions including the posterior cingulate cortex. For the VAN nodes (TPJ and VFC), adults showed greater functional connectivity with regions within the network compared with children. Children showed greater functional connectivity between VFC and nodes of the salience network. This asymmetric pattern of development of attention networks may be a neural signature of the shift from over-representation of bottom-up attention mechanisms to greater top-down attentional capacities with development.

1. Introduction

It is well established that there are two partially segregated attention networks in the human brain; the so-called dorsal and ventral attention networks (Corbetta and Shulman, 2002). The dorsal attention network (DAN) includes bilateral intraparietal sulcus (IPS) and the frontal eye fields (FEF), and is concerned with orientating ones focus on a particular task. Previous work has demonstrated that the FEF and IPS exert top-down influences on visual areas during visual orienting of attention (Bressler et al., 2008). The DAN shows sustained activation when focusing attention on an object (Corbetta et al., 2008), and is thought to be responsible for goal-directed, top-down processing (Corbetta and Shulman, 2002). The second network, the ventral attention network (VAN), is comprised of the temporoparietal junction (TPJ) and ventral frontal cortex (VFC), and responds to relevant external environmental stimuli. The VAN is dominant in the right hemisphere, and is generally activated when an unexpected event occurs and breaks ones attention from the current task (i.e. bottom-up processing) (for a full review of the DAN & VAN see Corbetta et al., 2008). This network's key function is to direct attention to stimuli outside of the current focus of processing and is referred to as the 'circuit breaking' section of the two attention networks (Shulman et al., 2002). Corbetta and colleagues argue that only behaviorally relevant

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environmental stimuli trigger the VAN, and that the response of the VAN is suppressed when irrelevant information is presented (Corbetta et al., 2008). The VFC has been identified to be mainly active when reorienting is unexpected and requires cognitive control or is coupled to a response (Corbetta and Shulman, 2002). The two core regions of the VAN are typically co-activated, as well as functionally connected (Fox et al., 2006; He et al., 2007).

Another brain system termed the 'salience network' has also been linked with functions that partially overlap with functions ascribed to the VAN, including responding to behaviorally relevant stimuli (Seeley et al., 2007). The salience network is comprised of dorsal anterior cingulate, subcortical, and limbic structures, as well as bilateral anterior insular cortices adjacent to or overlapping the VFC node of the VAN (Uddin, 2015), and has been demonstrated to show within- and between-network developmental changes including increases in functional and structural connectivity with age (Uddin et al., 2011). While some investigators see the high degree of functional and anatomical overlap between the VAN and salience network as evidence that they are part of the same system (Kucyi et al., 2012), the majority have conceptualized these networks as distinct entities (Cole et al., 2013; Power et al., 2011).

Resting state fMRI (R-fMRI) studies capitalize on the fact that large-scale neurocognitive networks can be reliably identified in the absence of task-related processing (Biswal et al., 1995; Damoiseaux et al., 2006; Smith et al., 2009). Fox et al. (2006) were the first to use R-fMRI to examine attention networks in the human brain. They identified a bilateral DAN and right lateralized VAN solely on the basis of seed-based functional connectivity analyses of resting state fMRI data, thus providing evidence that these attention networks are intrinsically coupled in the brain.

The use of R-fMRI to address developmental questions allows us to avoid many of the issues related to task performance that can confound interpretation of developmental neuroimaging findings (Casey et al., 2005; Uddin et al., 2010). R-fMRI studies have demonstrated that over the lifespan, the long-range connections within the DAN become more dominant until around the age of ~30 years (Cao et al., 2014). Cao and colleagues found inverted U-shaped trajectories mainly within the DAN and language regions, which are argued to be amongst the last regions to mature (Casey et al., 2000). This research is in line with previous studies which suggest that short-distance functional connectivity is greater in children than it is in adults (Dosenbach et al., 2010; Fair et al., 2009; Supekar et al., 2009) and that the long-range connections observed in adults are enhanced throughout development (Fair et al., 2009; Kelly et al., 2009; Supekar et al., 2009). It is argued that the process of synaptic "pruning" in which the abundance of short-range connections in typically developing children are eliminated, generally in the pubertal stage of development, contributes to the prominence of long-range connectivity in adults (Huttenlocher, 1990).

Though there is an abundance of literature surrounding human attention networks, there is surprisingly little research that focuses on the typical development of these networks (Konrad et al., 2005). A previous independent component analysis (ICA) study examining developmental differences in the dorsal attention network found stronger within-network connectivity in the DAN in 11–13 year-old children compared with 19–25 year old adults (Jolles et al., 2011). Seed-based approaches can offer complementary information to that derived from ICA, namely allowing for hypothesis-driven analyses of specific functional networks of interest (Uddin et al., 2010). To the best of our knowledge, no previous studies have used seed-based approaches to explore developmental differences in functional connectivity of DAN and VAN nodes, or inter-network relationships.

Here we use R-fMRI to explore the typical development of the DAN and VAN in the human brain. We aimed to test the following hypotheses: (1) R-fMRI can be used to identify the DAN and VAN in children, and these networks have a similar topological organization to that observed in adults; (2) long-range functional connectivity of DAN and VAN nodes will be more predominant in adults than in children; and (3) between- and within-network functional connectivity patterns will show developmental changes.

2. Materials and methods

2.1. Participants and data acquisition

The present study included a total of 60 healthy, right-handed neurotypical individuals from the publically available Autism Brain Imaging Data Exchange (ABIDE; http://fcon_1000.projects.nitrc.org/indi/abide/) (Di Martino et al., 2014). We examined only data collected from the New York University Langone Medical Center (NYU) for consistency. All participants had a full-scale IQ score of >80, and the groups did not differ significantly on IQ. The group of 60 was split into two groups of children (mean age: 10.2, range 7–12, 11 females) and adults (mean age: 24.2, range 18–31, 6 females) consisting of 30 participants each (Table 1). Participants were also carefully selected based on motion parameters. No participant was selected with absolute displacement > 1.95 mm. The range of motion parameters for the child group was 0.09–1.95 mm mean absolute displacement (0.27 ± 0.33). The range of motion parameters for the adult group was 0.15–0.89 mm mean absolute displacement (0.30 ± 0.18). No group differences in absolute displacement were observed ($p = 0.7$). The NYU institutional review board approved all procedures for data collection and sharing. Written informed consent was obtained from each participant.

Table 1
Participant characteristics.

Characteristic	Children ($n = 30$) (standard deviation) [range]	Adults ($n = 30$) (standard deviation) [range]
Age (years)	10.2 (1.74) [7.19–12.97]	24.2 (3.34) [18.59–31.78]
Sex (No.)		
Male	19	24
Female	11	6
Full-Scale IQ	116.17 (13.89) [80–142]	114.93 (10.09) [91–139]