



Trajectories of brain system maturation from childhood to older adulthood: Implications for lifespan cognitive functioning



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ABSTRACT

The human brain's intrinsic functional architecture reflects behavioural history and can help elucidate the neural mechanisms underlying age-related cognitive changes. To probe this issue, we used resting state ($N = 586$) and behavioural ($N = 255$) data from a lifespan sample and tested the interactions among ten intrinsic neural systems, derived from a well-established whole-brain parcellation. Our results revealed three distinguishable profiles, whose expression strengthened with increasing age and which characterized developmental differences in connectivity within the ten systems, between networks thought to underlie cognitive control and non-control systems, and among the non-control networks. The within-network connectivity profile was typified by decreased connectivity within two external processing networks (auditory/language and ventral attention). The non-control-to-non-control connectivity profile was typified by increased separation between networks involved in external processing, including language (dorsal attention, auditory) and those linked to internally generated cognitions and category learning (default mode, subcortical). Finally, the third connectivity profile was characterized by increased coupling of the three control networks (frontoparietal, salience, cingulo-opercular) with one another and with the remaining systems, particularly the subcortical and the two networks showing declining segregation with age. All three profiles showed significant associations with behavior during young adulthood, although these effects were less discernible during early development (before the age of 21) and degraded during late middle age and older adulthood. An exception to this trend was observed with respect to the within-network connectivity profile, whose "precocious" expression during early development predicted superior cognitive functioning. These findings thus help explain lifespan changes in the quality of mental processes, while also pointing to distinguishable mechanisms, which aid behavioural performance during different life stages.

1. Introduction

Substantial evidence suggests that the human brain is organized into dissociable anatomical networks (Fox and Raichle, 2007), which provide a latent functional architecture that is readily recruited during goal-directed cognition (Laird et al., 2011; Smith et al., 2009). Inter-individual variations in this intrinsic neural architecture carry significant implications for optimal functioning not only in adulthood (e.g., Alavash et al., 2015; Grady et al., 2016; Hampson et al., 2006; Li et al., 2009; Stevens et al., 2012; Van den Heuvel et al., 2009), but also during earlier development (e.g., Church et al., 2009; Fair et al., 2010; Graham et al., 2015; Vega et al., 2015).

The brain's intrinsic functional architecture is regarded as partly reflecting an individual's behavioural history, since it indicates the neural

configurations consistently recruited to manage specific cognitive demands, presumably both cumulatively and with respect to the more recent past (Wig et al., 2011). To the extent that this is indeed the case, a better understanding of shared developmental trajectories of intra- and internetwork connectivity at the whole-brain level may lead to valuable insights into the neural mechanisms underlying age-related differences in cognitive performance (Park and Reuter-Lorenz, 2009). Nonetheless, extant research on the inter-relationships among large-scale intrinsic networks, derived from whole-brain parcellations, has involved younger and older adults (e.g., Chan et al., 2014; Geerligs et al., 2015a,b). In contrast, most investigations of typical age-related functional connectivity differences during childhood and adolescence focused either on a small number of networks or on whole-brain (i.e., not network-specific) connectivity patterns (Fair et al., 2007, 2008; Sato et al., 2015; Song

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Table 1
Demographic characteristics of the three samples.

Variable	Sample 1	Sample 2	Sample 3	Years of Education	Total
N	171	113	302		586
Female/Male	66/105	60/53	201/101		327/259
Age: 5–11 years	76	N/A	30		106
Age: 12–21 years	56	7	45		108
Age: 22–34 years	15	53	66	15.36 ± 2.51	134
Age: 35–64 years	23	9	99	15.87 ± 2.32	131
Age: 65–85 years	1	44	62	16.36 ± 3.04	107
Right-hand dominant	150	113	259		522
Resting state instructions	Eyes open	Eyes closed	Eyes open		

Note. Years of education have been added for the adult group only, since all the child and adolescent participants were typically developing and enrolled at their age-appropriate educational level.

et al., 2015; van Duijvenvoorde et al., 2016; for exceptions, see Betzel et al., 2014; Jolles et al., 2011; Wang et al., 2012). Thus, relatively little is known about lifespan (i.e., childhood through older adulthood) differences in patterns of whole-brain network connectivity and their implications for cognitive functioning.

To probe this issue, we used resting state data from a large lifespan sample and tested the interactions among ten intrinsic neural systems, derived from a well-established whole-brain parcellation into functional networks (Power et al., 2011). The atlas included seven processing/non-control networks and three networks linked either to cognitive-behavioural control initiation (top-down: frontoparietal vs. bottom-up: salience) or its maintenance (i.e., cingulo-opercular) (Craig, 2002; Dosenbach et al., 2007; Eisenberger et al., 2003; Grinband et al., 2006; Seeley et al., 2007; Spreng et al., 2010). The seven processing networks have been previously associated with action/perception (somatomotor, visual, auditory), externally oriented attention (top-down: dorsal attention [DAN] vs. bottom-up: ventral attention [VAN]), internally oriented/generated representations (default mode [DMN]) and feedback-based learning or processing of personally relevant information (subcortical) (Andrews-Hanna et al., 2014a; Corbetta and Shulman, 2002; Fox et al., 2006; Grady et al., 2012; Power et al., 2011; van Duijvenvoorde et al., 2016).

Our main goal was to identify functional systems with common developmental trajectories of within- and/or between-network connectivity and, then, using data from a comprehensive behavioural battery, investigate their role in the expression of age-related differences in cognitive functioning. Recruitment of behavioural control-relevant networks to compensate for the structural and functional decline of perceptual processing systems, which can no longer meet environmental demands, is considered a hallmark of neurocognitive aging (for a review of relevant findings, see Park and Reuter-Lorenz, 2009). We thus reasoned that identifying lifespan patterns of control-to-processing system connections may provide important insights in the neural mechanisms supporting age-related compensatory processes. Complementarily, a characterization of the developmental trajectory of processing-to-processing network connections could offer a better understanding of the neural resources that are most malleable to change across the lifespan and, thus, potentially, most vulnerable to decline through aging.

2. Method

2.1. Participants

The present study included 586 participants (259 males) who were tested at the Hospital for Sick Children (Sample 1: N = 171) or Rotman Research Institute (Sample 2: N = 113) in Toronto (Canada), or who were

part of the enhanced Nathan Kline Institute-Rockland Sample (NKI-RS/ Sample 3: N = 302) (Nooner et al., 2012). Table 1 contains the relevant demographic details on all three samples.

The majority of participants (N = 522) were right-handed. All participants were screened for physical conditions or body implants that may render their participation unsafe. Past or current diagnosis with a mental health disorder was an exclusion criterion across all three samples. Participants provided informed consent in accordance with their study research ethics boards.

2.2. Behavioural measures

Of all three samples, only the NKI-RS sample completed an extensive behavioural battery in addition to the fMRI session. From the NKI-RS assessment package, we selected the following measures, which provide a comprehensive evaluation of cognitive functioning and, thus, could shed light on the behavioural relevance of the connectivity indices used in our present research.

2.2.1. Wechsler abbreviated scale of intelligence (WASI-II)

This measure of general intelligence (i.e., IQ) comprises four subtests, which assess verbal (i.e., the 31-item Vocabulary and 24-item Similarities subtests) and performance (i.e., the 13-item Block Design and 30-item Matrix Reasoning subtests) IQ (Wechsler, 1999). To avoid potential overlap with the verbal reasoning measure from the Penn Computerized Neurocognitive Battery, we used participants' scores on the Vocabulary, but not Similarities subtest. In all brain-behaviour analyses, we used the participants' independent estimates of verbal and performance IQ as existing evidence suggests that the two are dissociable traits that follow distinct developmental trajectories (Blair, 2006; McArdle et al., 2002).

2.2.2. Penn Computerized Neurocognitive Battery (CNB)

The CNB provides measures of accuracy and speed in the following neurocognitive domains: abstraction/flexibility, sustained attention, working memory, episodic memory, language, sensorimotor, motor, and emotion identification.

2.2.2.1. Abstraction/mental flexibility. Penn Conditional Exclusion Test (PCET; Kurtz et al., 2004) assesses abstraction and concept formation skills. Participants are asked to decide which of four presented objects does not belong with the other three based on one of three sorting principles (e.g., shape, size, line thickness). Sorting principles change after 10 successive correct responses, and feedback is provided to guide discovery of the principle and its subsequent change. An accuracy score is calculated by multiplying the proportion of correct responses by the number of categories attained (out of three possible). The median response time on correct trials is the measure of speed.

2.2.2.2. Sustained attention. Sustained attention is assessed with the Penn Continuous Performance (PCPT; Kurtz et al., 2001), in which participants are required to respond to a set of 7-segment displays presented 1/s, whenever they form a digit (NUMBERS, initial 3 min) or letter (LETTERS, next 3 min). The number of true positive responses is recorded as the accuracy score and the median response time for true positive responses is the measure of attention speed.

2.2.2.3. Working memory. Working memory capacity is assessed with the Letter N-Back task (LNB; Ragland et al., 2002), in which participants have to respond to letters presented in one of the three conditions: 0-Back - press the spacebar when the letter presented is an "X", 1-Back - press when the letter presented is the same as the previous letter or 2-Back - press when the letter presented is the same as the one just before the previous letter. Following a training period, the test presents three blocks of each condition in a pre-determined order, for a total of 135 trials. The number of correct responses is recorded as the measure of accuracy and

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