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Relationships between intrinsic functional connectivity, cognitive control, and reading achievement across development

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ABSTRACT

There are vast individual differences in reading achievement between students. Besides structural and functional variability in domain-specific brain regions, these differences may partially be explained by the organization of domain-general functional brain networks. In the current study we used resting-state functional MRI data from the Philadelphia Neurodevelopmental Cohort (PNC; N = 553; ages 8–22) to examine the relation between performance on a well-validated reading assessment task, the Wide Range Achievement Word Reading Test (WRAT-Reading) and patterns of functional connectivity. We focused specifically on functional connectivity within and between networks associated with cognitive control, and investigated whether the relationship with academic test performance was mediated by cognitive control abilities. We show that individuals with higher scores on the WRAT-Reading, have stronger lateralization in frontoparietal networks, increased functional connectivity between dorsal striatum and the dorsal attention network, and reduced functional connectivity between dorsal and ventral striatum. The relationship between functional connectivity and reading performance was mediated by cognitive control abilities (i.e., performance on a composite measure of executive function and complex cognition), but not by abilities in other domains, demonstrating the specificity of our findings. Finally, there were no significant interactions with age, suggesting that the observed brain-behavior relationships stay relatively stable over the course of development. Our findings provide important insights into the functional significance of interindividual variability in the network architecture of the developing brain, showing that functional connectivity in domain-general control networks is relevant to academic achievement in the reading domain.

1. Introduction

There are vast individual differences in reading achievement between students, which have major implications for future academic and socioeconomic success (Hernandez, 2011; Ritchie and Bates, 2013). In investigating the neurocognitive foundation of this variability, most prior studies have focused predominantly on regions associated with language, including occipito-temporal, temporo-parietal and inferior frontal cortex (e.g., Alcauter et al., 2017; Koyama et al., 2011). One other potentially relevant source of variation is the organization of *domain-general* functional brain networks (e.g., Chaddock-Heyman et al., 2018). To study the relationship between brain network organization and reading achievement, as well as potential changes across development, it is important to have a sufficiently large sample size to capture the diversity within the population. Here, we capitalized on data from a large community sample, the Philadelphia Neurodevelopmental Cohort (PNC; Gur et al., 2012; Satterthwaite et al., 2014), to study whether individual differences in functional connectivity contribute to performance on a widely used academic assessment task in the domain of reading: the Wide Range Achievement Word Reading Test (WRAT-Reading). Furthermore, because different neurocognitive systems might be involved during different developmental stages, we also examined whether brainbehavior relationships change across development.

Among the most powerful predictors of school achievement are domain-general cognitive abilities, including executive functions (e.g., Best et al., 2011; St Clair-Thompson and Gathercole, 2006) and complex cognitive abilities such as reasoning and problem solving, which are often assessed using intelligence tests (e.g., Deary et al., 2007;

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Abbreviations: cnb, penn computerized neurocognitive battery; EF-CC, executive function and complex cognition; LFP, left lateralized frontoparietal network; RFP, right lateralized frontoparietal network; STR, Striatum.

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Mayes et al., 2009). Within the domain of reading, this association is found most consistently for measures of reading comprehension (cf. Zelazo et al., 2016), but correlations with basic reading skills have been reported across childhood and adolescence as well. For example, in a large-scale representative sample of children between 5 and 17, performance on complex executive function tasks was correlated with both reading comprehension and basic reading skills, including reading isolated words and nonsense words (Best et al., 2011). This correlation may reflect a direct effect of executive functioning on reading skills, or be driven through more crystallized aspects of mental abilities (Zelazo et al., 2016). Interestingly, dynamic models of developmental changes from 1st to 12th grade suggest that there are bidirectional relationships between reading and cognition, suggesting that development of reading and domain general skills dynamically influence one another (Ferrer et al., 2007). This effect appears to be strongest during the early school years. Together, these findings suggest that executive functions and complex cognition are important factors to consider when examining individual differences in reading achievement. As such, studying brain networks associated with general cognitive ability may offer insights into the neurocognitive foundation of these individual differences (cf. Shanmugan and Satterthwaite, 2016).

It is well established that there is a common set of brain regions engaged during different kinds of cognitive challenges, contributing to the organization, maintenance and/or adjustment of goal-directed behavior. These so-called control regions are recruited independent of task or modality and involve a widespread network including lateral prefrontal cortex (PFC), anterior insula/frontal operculum, posterior parietal cortex, and dorsal anterior cingulate cortex/ pre-supplementary motor area (Dosenbach et al., 2008; Duncan, 2010; Jung and Haier, 2007; Power and Petersen, 2013). This distributed account of cognitive control signifies the importance of efficient communication across the brain. Using resting state functional connectivity measures, several studies have demonstrated that regions associated with cognitive control tend to show high levels of connectivity, even in the absence of a task (Smith et al., 2009). Yet, connectivity among these regions is not uniform; the pattern of connectivity seems to reflect a family of subnetworks contributing to different aspects of control. Although there is considerable ambiguity in the literature regarding the division of labor between different control systems (e.g., Corbetta et al., 2008; Dosenbach et al., 2008; Gratton et al., 2018; Seeley et al., 2007), a distinction is often made between a frontoparietal network (FP), with key nodes in dorsolateral PFC and inferior parietal cortex, a cinguloopercular or "salience" network (SN) with key nodes in anterior insula and dorsal anterior cingulate cortex, and a dorsal attention network (DAN) with key nodes in superior parietal cortex and the frontal eye fields. These networks are thought to be involved in adaptive task control, task-set maintenance and/or saliency detection, and goal-driven attention respectively (Gratton et al., 2018; Vaidya and Gordon, 2013), functions that are highly relevant in an academic context.

Importantly, there is large variability between individuals' patterns of connectivity, particularly in the control networks (Mueller et al., 2013). This individual variability is preserved during task performance (Finn et al., 2015; Shah et al., 2016), suggesting that individual differences in intrinsic connectivity underlie differences in cognition and behavior. A number of studies have already provided support for this hypothesis, demonstrating a relationship between intrinsic functional connectivity within and between frontal and parietal association areas and measures of general intelligence (Cole et al., 2012, 2015; Finn et al., 2015; Smith et al., 2015; Song et al., 2008), as well as executive functioning (Hampson et al., 2006a; Reineberg et al., 2015; Seeley et al., 2007). Moreover, recent evidence suggests that functional connectivity between these regions is also relevant to academic achievement. For example, in elementary school children (aged 7-9 years) a relationship was found between functional connectivity in domain general control networks and scholastic achievement (Chaddock-Heyman et al., 2018). Furthermore, using Multivariate Distance Matrix Regression, a novel analysis technique that examines inter-individual differences in whole-brain functional connectivity of each voxel, Koyama et al. (2017) showed that reading ability was specifically related to connectivity of the left middle frontal gyrus – and not connectivity of core language areas such as the fusiform gyrus.

Individual differences in cognition have also been linked to a network that is typically deactivated during demanding cognitive tasks, the default mode network (DMN) (e.g., Sala-Llonch et al., 2012; van den Heuvel et al., 2009). Furthermore, individuals who perform better on complex cognitive and academic tasks generally show greater functional segregation between the control networks and the DMN (Hampson et al., 2010; Keller et al., 2015; Kelly et al., 2008; Koyama et al., 2017, but see Hearne et al., 2016). For optimal cognitive performance it appears important to strike the right balance between the control networks, supporting externally-guided goal-oriented processing, and the DMN, supporting internally-driven reflective and predictive mechanisms (Immordino-Yang et al., 2012; Raichle, 2015). It is likely that efficiency of the control networks and their interaction with the DMN are also a key factor in explaining individual and developmental differences in learning and academic performance, including reading achievement.

Finally, besides connectivity between cortical regions, corticostriatal loops may also play a role in mediating individual differences in reading achievement. Although the striatum has traditionally been regarded as a motor region, current models of striatal function describe its involvement in a wide range of higher cognitive functions, including working memory, complex goal-directed behavior, and language (e.g., Haber, 2016; Pauli et al., 2016). In agreement with this conceptualization of striatal function, functional connectivity studies have demonstrated that the majority of the striatum is connected with frontal and parietal association cortices, including regions of the control networks and DMN (Choi et al., 2012; Di Martino et al., 2008). Furthermore, it appears that these connectivity patterns are associated with better executive functions and reduced impulsivity (Davis et al., 2013; Gordon et al., 2015), as well as increased reading speed (Alcauter et al., 2017). However, a reverse relationship with reading has also been observed (Achal et al., 2016).

Finally, when examining individual differences in functional connectivity in relation to cognitive and academic achievement, it is important to consider developmental changes in brain network configuration. Several studies have shown that the basic architecture of the control networks and DMN can be detected even in very young children, but there are still marked changes in functional network organization across childhood and adolescence (for recent reviews, see Ernst et al., 2015; Stevens, 2016). Overall, these changes in functional connectivity are thought to reflect more efficient and specialized processing over the course of development. Yet the behavioral significance of developmental and individual differences in connectivity has only recently become a topic of investigation. It has been demonstrated that the relationship between frontoparietal connectivity and intelligence exists even in young children (Langeslag et al., 2013) and that certain age-related changes in cognitive performance may be mediated by changes in functional connectivity (Gu et al., 2015; van Duijvenvoorde et al., 2016). Yet, it is important to acknowledge that brain-behavior relationships may change across development (Barber et al., 2013; Wendelken et al., 2016). For example, it has been shown that the relationship between reasoning ability and functional connectivity differs between children, adolescents, and adults (Wendelken et al., 2016). Similarly, in the context of reading, Koyama et al. (2011) report interactions between reading competence and age group, indicative of a shift in brain-behavior relationships across development. These findings suggest that different neurocognitive systems may be important during different stages of development, and underscore the importance of taking a developmental perspective.

The goal of the current study was to examine the extent to which individual differences on a standardized test of reading achievement can be explained by differences in intrinsic functional connectivity. We focused specifically on functional connectivity within and between brain circuits associated with general cognitive ability, which has been largely overlooked in prior studies of achievement in the reading domain (e.g., Alcauter et al., 2017; Koyama et al., 2011). Furthermore, because individual differences in neurocognitive functioning may interact with developmental processes, we also investigated whether brain-behavior relationships change across development. Finally, to examine the specificity of our findings, we investigated whether the relationship between brain function and reading achievement was mediated by cognitive test performance.

We used PNC resting-state fMRI data from 553 children and adolescents between 8 and 22 years in age. Functional connectivity was examined using a group independent component analysis (ICA)-based approach, focusing specifically on frontal and parietal association areas, as well as the striatum. Reading achievement was assessed using the WRAT-Reading, a well-validated measure of academic performance in the reading domain (Wilkinson and Robertson, 2006). In addition, we included data from the Penn Computerized Neurocognitive Battery (CNB), including tests of executive function and complex cognition (i.e., reasoning), as well as tasks measuring social cognition, memory, and sensorimotor speed (Gur et al., 2012, 2010). We hypothesized that individuals with better reading achievement would have better executive functions and complex cognition (e.g., Best et al., 2011; Mayes et al., 2009; Zelazo et al., 2016), and that this would be reflected in the connectivity of functional networks known to contribute to executive functioning and complex cognition (e.g., Vaidya and Gordon, 2013). More specifically, we hypothesized that better performance on the WRAT-Reading would be associated with increased functional connectivity within the control networks, greater segregation between control networks and the DMN and/or altered functional connectivity between control networks and the striatum. Furthermore, we hypothesized that the relation between control network connectivity and reading achievement would be mediated by executive function and complex cognition, but not by abilities in the other domains.

2. Materials & methods

2.1. Participants

The PNC involves a community sample of more than 9000 children and adolescents (8-22 years old), drawn from a pool of approximately 50,000 subjects who had previously taken part in research of the Children's Hospital of Philadelphia (CHOP) and had provided informed consent (or assent) to be contacted again for further studies (Gur et al., 2012; Satterthwaite et al., 2014). All participants took part in a detailed behavioral assessment, including multiple tasks of cognitive ability. In a subsample of 1445 participants multimodal magnetic resonance imaging (MRI) was acquired including a resting-state functional MRI (rs-fMRI) scan. For detailed information regarding participant recruitment and general inclusion criteria for neuroimaging, see Satterthwaite et al. (2014). For the present study, we used data from the first public data release, which included resting-state fMRI data from 799 participants (Database of Genotypes and Phenotypes (dbGap) platform, Project #6984, Karlsgodt). Of this subgroup, 201 participants were excluded because of excessive head movement (see Section 2.2.2. below), 3 participants were excluded because of poor fMRI data quality, and 26 participants were excluded because they did not have valid WRAT-Reading data (as indicated in the database). In the case of related individuals (siblings), only the youngest sibling was included, which resulted in exclusion of another 16 participants (Jalbrzikowski et al., 2019). The remaining sample for analysis consisted of 553 participants. Demographics for the 553 participants are reported in Table 1. All study procedures were approved by the institutional review boards of both the University of Pennsylvania and the Children's Hospital of Philadelphia.

1	fable 1
	Sample demographics

	Range	Mean (SD)	Ν
Age at scan	8.6-22.6	15.7 (3.1)	553
WRAT-Reading (Standard Score)	70-145	103.0 (15.8)	553
Father education (years)*	7-20	14.0 (2.7)	509
Mother education (years)*	9-20	14.3 (2.4)	543
Sex	55% Females		553
Ethnicity	49% AA, 40% EA, 11% other		553
Handedness 87% Right-handed		552	

Note: WRAT-Reading = age-normed score on the reading subtest of the Wide Range Achievement Test–Fourth Edition, AA = African American, EA = European American, Other – includes other ethnicities and mixed ethnicities. *Participants who reported < 3 years of education were excluded from analysis (one father, one mother).

2.2. Cognitive measures

2.2.1. WRAT-Reading

The Wide Range Achievement Test–Fourth Edition (WRAT-4) is widely used as a "a quick, simple, psychometrically sound assessment of academic skills" (cf. Wilkinson and Robertson, 2006, p.3). Here, we used the reading subtest of the WRAT, which measures participants' ability to recognize and pronounce increasingly complex words from various fields (e.g., mathematics, science, and social science). There are 55 words in total, but the test is discontinued if the participant pronounces 10 consecutive words incorrectly. Raw scores are converted to age-normed standard scores based on a mean of 100 and a standard deviation of 15. As can be seen in Table 1, the mean and standard deviation in the current sample were very similar to those in the normative sample. Performance in the subsample with imaging data was also similar to that in a prior behavioral study on the PNC cohort (Gur et al., 2012). All analyses in the current manuscript were performed using the age-normed scores.

Word recognition and pronunciation, as measured by the WRAT-Reading subtest likely involves a combination of basic reading skills and crystallized knowledge, such as vocabulary (Rohde and Thompson, 2007). WRAT-Reading performance has previously been related to parental education (Gur et al., 2012) and self-reported quality of education (Sayegh et al., 2014), but also with measures of intellectual functioning (Arffa, 2007; Mayes et al., 2009). Together, these findings suggest that WRAT-Reading performance relies on knowledge that is acquired through education and other cultural influences, but that this knowledge is obtained more easily by those with better cognitive abilities. Importantly, despite its correlation with intellectual abilities, WRAT-Reading generally does not show a decline in individuals with cognitive impairment related to cerebral injury or disease (e.g., Johnstone and Wilhelm, 1996). This suggests that WRAT-Reading does not directly measure cognitive control and reasoning, although these cognitive domains may be important for acquiring the skills and vocabulary to perform the task.

2.2.2. Computerized neurocognitive battery

A one-hour computerized neurocognitive battery (CNB) was administered to measure cognitive performance in 5 domains: executive function (EF), complex cognition (CC), memory, social cognition, and sensorimotor speed (Gur et al., 2012, 2010; Moore et al., 2015). In the current study, EF and CC were combined into one domain (EF-CC), as has been recommended by Moore et al. (2015) because of the high correlation between the two domains. Furthermore, from a neuropsychological perspective, EF and CC tasks likely involve similar cognitive abilities and overlapping frontoparietal brain networks (cf. Moore et al., 2015). Table 2 provides an overview of the tasks in each domain. For more details we refer to prior publications with this dataset (Gur et al., 2012, 2010; Moore et al., 2015).

Table 2

	Computerize	l neurocognitive	batterv	subtests.
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Domain	Test	Cognitive ability
Executive function		
	Penn Conditional Exclusion Test	Abstraction and mental flexibility
	Penn Continuous Performance Test	Sustained attention
	Letter N-back	Working memory
Complex cognition		
	Penn Verbal Reasoning Test (child version)	Analogical reasoning
	Penn Matrix Reasoning Test	Nonverbal reasoning
	Penn Line Orientation Test	Spatial ability
Memory		
	Penn Word Memory test	Memory for words
	Penn Face Memory Test	Memory for faces
	Visual Object Learning Test	Memory for shapes
Social cognition		
	Penn Emotion Identification Test	Identification of emotions
	Penn Emotion Differentiation Test	Differentiation between emotions
	Penn Age Differentiation Test	Differentiation between ages
Sensorimotor speed		
	Finger Tapping Test	Motor speed
	Motor Praxis Task	Sensorimotor processing speed

Scoring was performed as described in (Gur et al., 2012), with two exceptions: (1) accuracy for the Penn Continuous Performance Test and the Letter N-back test were calculated based on the percentage of correct trials rather than the number of true positive responses, thereby taking into account both hits and correct rejections, and (2) for the Letter N-back, we included performance on the 2-back task only because variability was higher as compared to 0- and 1-back (cf. Jaeggi et al., 2010). Accuracy and response time (RT) scores were standardized (ztransformed) based on the current sample. For each domain, we created an efficiency measure, averaging the mean z-scores for accuracy and the inverted z-scores for RT (Gur et al., 2012).

2.3. Brain imaging

2.3.1. Data acquisition & control for head motion

Data acquisition parameters are described in the Supplementary Material. For more information about data acquisition, including other scans that were acquired during the same imaging session, see Satterthwaite et al., 2014.

Head motion was computed using the FMRIB software library (FSL) MCFLIRT routine (Jenkinson et al., 2002). Participants with maximum displacement > 3 mm, mean relative displacement > 0.2 mm, or > 20 volumes with relative displacement of > 0.2 mm were excluded. In the remaining sample, average maximum displacement was 0.72 mm (SD 0.6) and average mean relative displacement was 0.06 mm (SD 0.03). Importantly, head motion was not correlated with our main outcome measure, WRAT-Reading (maximum displacement: r = -0.029, p = .492; mean relative displacement: r = -0.047, p = .270, N = 553). However, as in most prior developmental samples, we did find a correlation with age (maximum displacement: r = -0.214, p < .001; mean relative displacement: r = -0.217, p < .001, N = 553). There was also a correlation with EF-CC performance (maximum displacement: r = -0.106, p = .028; mean relative displacement r = -0.124, p = .010, N = 431), but this correlation was likely driven by age as it was no longer significant when controlling for age (maximum displacement: r = -0.004, p = .939; mean relative displacement r = -0.023, p = .629, df = 428). The correlation with parental education was not significant either (maximum displacement: r = -0.039, p = .387; mean relative displacement: r = -0.057, p = .201, N = 503).

Potential effects of motion on functional connectivity were first addressed by the high model order group independent component analysis (ICA), which separates motion artifacts from the networks of interest. To further address motion-related noise, variance associated with the six motion parameters (x, y, z, pitch, roll, and yaw), including their temporal derivatives and squares, was regressed from time courses of components after running the group ICA (see below). Moreover, spikes in the time courses (i.e., time-points with a root mean square of the frame-wise displacement > 0.5 mm) were interpolated using 3dDespike, applying a 3rd order spline fit to uncompromised neighboring data.

2.3.2. fMRI data preprocessing

FMRI data were preprocessed using FSL (fsl.fmrib.ox.ac.uk/) and AFNI (.nimh.nih.gov/afni/) commands. The first 3 volumes were discarded to allow for signal equilibration effects, resulting in 121 remaining volumes. Preprocessing procedures included motion correction, skull stripping, slice time correction, spatial smoothing using a Gaussian kernel of 6 mm full-width at half-maximum, grand mean scaling, co-registration to the individual's structural data, and normalization to the standard Montreal Neurological Institute (MNI) T1 template.

2.3.3. Group-ICA

Group-ICA analyses were performed using the Group Independent Component Analysis of fMRI Toolbox (GIFT; http://mialab.mrn.org/ software/gift). In short, we performed a high model order group ICA to decompose the multiple-subject fMRI data into 100 spatially independent components (ICs) (Allen et al., 2011; Calhoun et al., 2001), and then used group information guided ICA (GIG-ICA) to back-reconstruct subject-specific ICs with associated spatial maps and time courses, using the group ICs as guidance (Du and Fan, 2013). More details about the ICA procedures are provided in the Supplementary Material.

2.3.4. Component selection and network assignment

We restricted our analyses to components associated with the control networks (FP, DAN, and SN), as well as the DMN and the striatum. The striatum was included as a separate 'network' because it is usually not referred to as a core region of the control networks or DMN (Vaidya and Gordon, 2013). First, all 100 components were visually inspected by two viewers (D.D.J. and E.M.) and classified as noise versus non-noise based on the peak of activation (grey matter versus white matter and cerebral spinal fluid [CSF]), the power spectrum, and resemblance to motion- and other type of artifacts. This resulted in 55 components being classified as non-noise. Next, we performed a template-matching procedure to assign each non-noise component to a functional network template. The templates were obtained from Van Duijvenvoorde et al. (2016), who performed a 25-component group ICA in an age range similar to the current study (8-25 years). Van Duijvenvoorde et al. identified 12 functional networks, including 4 control networks - the left lateralized frontoparietal network (LFP), the right lateralized frontoparietal



Fig. 1. Components associated with the left lateralized frontoparietal network (LFP), the right lateralized frontoparietal network (RFP), the dorsal attention network (DAN), the salience network (SN), the striatum (STR), and the default mode network (DMN). To create this figure, participant-level components were averaged across participants and thresholded at Z = 2.3.

network (RFP), the DAN, and the SN — as well as anterior and posterior DMN. For each component, we calculated the number of voxels that overlapped with each of the 12 functional network templates. For this step, the subject-level components were averaged across participants and thresholded at Z > 2.3. If the first and second match were close (i.e., difference in number of overlapping voxels < 25%), network assignment was guided by prior literature. Because detection of the striatum as a separate component requires higher model order estimation (cf. Abou-Elseoud et al., 2010), assignment to the striatal network was based on anatomy. Twenty-two components were selected that matched one of the networks of interest (Fig. 1 and Supplementary Table 1). The components matching the anterior and posterior sections of the DMN were combined into one network, as the DMN is generally considered a single network (or multiple interwoven networks) comprising both anterior and posterior regions (Buckner and DiNicola, 2019; Raichle, 2015).

2.3.5. Postprocessing of time courses

After the Group-ICA, time courses underwent postprocessing in order to further account for motion-related noise. As implemented in GIFT, time-courses were detrended and despiked using 3dDespike (AFNI), then filtered using a fifth-order Butterworth low-pass filter with a high frequency cutoff of 0.15 Hz (Allen et al., 2011), and variance associated with the motion parameters was regressed out.

2.3.6. Mancovan with age, sex, and WRAT-Reading

To examine the effects of age, sex, WRAT-Reading, and their interactions on functional connectivity within and between networks we used the Mancovan toolbox in GIFT (Allen et al., 2011). A multivariate analysis of covariance (MANCOVA) was performed on the standardized connectivity matrix of the 22 identified components to determine which of the six predictors (age, sex, WRAT-Reading, and their interactions) explained the most variance. Backward model selection was performed as described in Allen et al. (2011). Finally, univariate tests were performed, including all predictors that were significant at p <.01 in the multivariate model (Allen et al., 2011). Univariate tests were performed at the component-level as well as the network-level. To examine within-network functional connectivity, pairwise Z-transformed



Fig. 2. Mediation model, testing whether the relation between functional connectivity and WRAT-Reading is mediated by cognitive control ability (i.e., performance on a composite measure of executive function and complex cognition). EF-CC = executive function and complex cognition, WRAT-Reading = agenormed performance on the wide-range achievement test, *a* = relation between functional connectivity and EF-CC, *b* = relation between EF-CC and WRAT-Reading, controlling for functional connectivity, *c* = relation between functional connectivity and WRAT-Reading, c' = relation between functional connectivity and WRAT-Reading for EF-CC. The indirect effect (ab) is the relation between functional connectivity and WRAT-Reading via EF-CC.

correlations were averaged for each network (LFP, RFP, DAN, STR, and DMN) within each participant. The same was done for between-network connectivity. Univariate results were FDR-corrected for multiple comparisons at p < .01.

2.4. Mediation by CNB measures

To investigate whether potential relations between functional network architecture and WRAT-Reading performance were mediated by EF-CC (Fig. 2), we performed mediation analyses using the Process procedure for SPSS (Hayes, 2017). Age and sex were included as covariates in the model. Indirect effects were tested by calculating 95% confidence intervals (CI) using bootstrapping with 5000 iterations. To test for the specificity of the effect, mediation analyses were also performed with social cognition, memory, and sensorimotor speed as mediators.





Fig. 3. Motion-corrected connectivity matrices across all participants (irrespective of age, sex, and WRAT-Reading score). (A) Network-averaged connectivity matrix. (B) Component-to-component connectivity matrix.

Table 3

Partial correlations between WRAT-Reading and CNB efficiency scores.

Domain	Correlation: r (df)	Domain-specific correlation: r (df)
EF-CC	0.468**** (427)	0.359**** (406)
Social cognition	0.345**** (518)	0.139* (406)
Memory	0.203**** (505)	-0.015 (406)
Sensorimotor speed	0.106 (524)	0.122 (406)

Note: correlations are corrected for age and sex; domain-specific correlations are corrected for age, sex, and the other CNB efficiency scores; EF-CC = executive function and complex cognition; Bonferroni-corrected p-values: **** p < .001/5 = 0.00025, *** p < .005/4 = 0.00125, *** p < .01/4 = 0.0025, *p < .05/4 = 0.0125.

3. Results

3.1. Behavior

As expected, the raw WRAT-Reading scores increased with age (r = 0.561, p < .001, N = 553), but there was no significant correlation between normalized (age-adjusted) WRAT-Reading and age (r = -0.056, p = .187, N = 553). Moreover, WRAT-Reading did not differ between males and females (t(551) = -1.33, p = .341, d = 0.11). Table 3 presents partial correlations between WRAT-Reading and CNB performance, corrected for age and sex. WRAT-Reading was correlated with performance in all four domains, but the correlation with sensorimotor speed did not survive Bonferroni correction for the four tests performed. Critically, the correlation between WRAT-Reading and EF-CC was significantly higher than the correlations with the other three domains (p's < 0.05), and the correlation remained significant when correcting for the other domains using partial correlations. Follow-up analyses on the EF-CC subtests showed that WRAT-Reading was highly correlated with all six subtests (Bonferroni-corrected p's < 0.001; Supplementary Table 2).

3.2. Within- and between-network connectivity

Motion-corrected connectivity matrices are presented in Fig. 3. As expected, within-network functional connectivity was generally higher than between-network connectivity (Fig. 3A). Furthermore, connectivity between cognitive control networks was positive, particularly between LFP and RFP, whereas connectivity between the control networks and the DMN was low or negative. The striatal network showed positive connectivity with the SN, but it was inversely correlated with all other networks. The high model order ICA further allowed examination of these connectivity patterns in more detail (Fig. 3B), which will be discussed in the Supplementary Results. In general, our observations are in line with the literature and set the stage for examining the relation between functional connectivity and WRAT-Reading.

3.3. Relation with age, sex, and WRAT-reading

MANCOVA results indicated that age, sex, and WRAT-Reading each explained a significant amount of variance in the multivariate model (p < .01), but their interactions did not. Therefore, univariate tests were only performed for the main effects.

3.3.1. Age

Functional connectivity increased with age within LFP, RFP, DAN, and DMN (Fig. 4A and B) as well as between LFP and RFP and between DAN and SN. Functional connectivity decreased with age between DMN and most other networks (LFP, RFP, SN, and STR) and between STR and LFP/ SN.

3.3.2. Sex

There were no significant effects of sex on functional connectivity at the network level. At the component level, there were only six connections that differed significantly between males and females (see Supplementary Figure 2).

3.3.3. WRAT-reading

On a network-level, individuals with higher WRAT-Reading scores, showed reduced functional connectivity between LFP and RFP, increased functional connectivity between DAN and STR, and reduced functional connectivity within STR (Fig. 5A and B). Component-to-component connectivity revealed that the reduced functional connectivity between LFP and RFP was particularly driven by two connections that were mirror images of each other: connectivity between left and right intraparietal lobule (IPL-I and IPL-III), and connectivity between left and right inferior frontal gyrus (IFG-I and IFG-III) (Fig. 5C). Importantly, follow-up analyses indicated that the reduced interhemispheric connectivity effects were not driven by handedness (see Supplementary Results). Furthermore, both putamen components were more strongly connected with all DAN components, and with a number of LFP, RFP,



Fig. 4. Connectivity matrices showing main effects of age, corrected for sex and WRAT-Reading. (A) Within and between network connectivity changes with age. (B) Component-to-component connectivity matrix for the effects of age. Increases with age are displayed in red, decreases are displayed in blue. Correlations surviving FDR-correction at p < .01 are indicated with an asterisk (*). For exact *r*-values, see Supplementary Fig. 1.

<u>∎</u>-9 PL-IV SPL-I PL-V SPL-II

MFG

IPL-I Ģ 5 **IACC**

SMA

al-l

al-II Put-l Put-II nAcc Prec

ACC PFC PL-VI



Fig. 5. Connectivity matrices showing main effects of WRAT-Reading performance, corrected for age and sex. (A) Within and between network connectivity related to WRAT-Reading score. (B) Component-to-component connectivity matrix for the effects of WRAT-Reading score. Positive correlations are displayed in red, negative correlations are displayed in blue. Correlations surviving FDR-correction at p < .01 are indicated with an asterisk (*). For exact r-values, see Supplementary Fig. 3. (C) Components that showed reduced interhemispheric connectivity (at x = -50 and x = 50; thresholded at Z = 1 for illustration purposes).

and SN components in individuals with higher WRAT-Reading scores. Within the STR, higher WRAT-Reading scores were associated with reduced functional connectivity between putamen and nucleus accumbens. We also found that higher WRAT-Reading scores were negatively associated with connectivity between DMN and DAN, SN, and STR components.

3.4. Mediation by cognitive control

To examine whether the relationship between functional connectivity and WRAT-Reading was mediated by cognitive control abilities, we performed mediation analyses in SPSS with EF-CC performance as mediator (Hayes, 2017). We focused specifically on relationships that

Table 4

Mediation of relationship between functional connectivity and WRAT-reading by EF-CC efficiency.

Direct and total effects				
	b	SE	t	р
LFP-RFP				
a	-0.476	0.155	-3.075	0.002
b	19.069	1.705	11.185	< 0.001
с	-19.750	6.194	-3.189	0.002
c'	-10.674	5.512	-1.937	0.053
DAN-STR				
a	0.354	0.098	3.619	< 0.001
b	19.066	1.714	11.124	< 0.001
с	12.583	3.935	3.197	0.001
c'	5.826	3.521	1.655	0.099
STR-STR				
a	-0.329	0.081	-4.090	< 0.001
b	19.384	1.726	11.230	< 0.001
с	-7.886	3.267	-2.414	0.016
c'	-1.499	2.929	-0.512	0.609
Indirect effects (ab)				
	Effect	SE-Boot	95% CI lower	95% CI upper
Unstandardized				
LFP-RFP	-9.076	2.924	-14.804	-3.341
DAN-STR	6.757	1.898	3.088	10.569
STR-STR	-6.387	1.587	-9.568	-3.308
Completely standardized				
LFP-RFP	-0.071	0.023	-0.115	-0.025
DAN-STR	0.082	0.023	0.038	0.127
STR-STR	-0.094	0.024	-0139	-0.048

Note: DAN = dorsal attention network, EF-CC = executive function and complex cognition, <math>LFP = left lateralized frontoparietal network, RFP = right lateralized frontoparietal network, STR = striatum. Age and sex were included in the model as covariates.

were significant on the network level, i.e., LFP-RFP, DAN-STR, and STR-STR.

Results are reported in Table 4. In short, for all three connections, we found that functional connectivity was a significant predictor of EF-CC performance (path *a*) and that EF-CC performance was a significant predictor of WRAT-Reading (path *b*). Furthermore, the relation between functional connectivity and WRAT-Reading was no longer significant when EF-CC performance was included in the model (path *c*'), suggesting that there was full mediation. Bootstrapping analyses with a 95% CI indicated that the indirect effect (*ab*) was significant for all three connections. Correlations with specific EF-CC subtests were also examined, as this may further elucidate the functional role of particular brain networks. Results are reported in the Supplementary Results and Supplementary Table 3. In short, results from these analyses suggest that the EF-CC mediation effect was driven largely through verbal reasoning.

Finally, to examine the specificity of the mediation effect, we also performed analyses with the other CNB performance measures, i.e., social cognition, memory, and sensorimotor speed. We found that performance on these tests was not significantly correlated with functional connectivity (Supplementary Table 4). Therefore, we conclude that the relationship between functional connectivity and WRAT-Reading was not mediated by social cognition, memory, and sensorimotor speed.

4. Discussion

There are marked changes in functional network organization across development, but it has become increasingly clear that there are also large differences between individuals of a certain age. Here, we examined how individual differences in brain networks associated with general cognitive ability contribute to differences in reading achievement, and how this changes across development. We show that individuals with higher scores on a widely used reading achievement test, i.e., WRAT-Reading, have stronger lateralization in frontoparietal networks, increased functional connectivity between dorsal striatum and control networks, and reduced functional connectivity within the striatum.

4.1. Lateralization in frontoparietal networks

Brain-behavior correlations revealed three major findings that were significant at the network level. First, individuals with higher reading performance showed reduced interhemispheric connectivity between LFP and RFP. This effect was driven by two sets of frontal and parietal components that were mirror images of each other. Although corresponding regions in opposite hemispheres generally show high functional connectivity, homotopic functional connectivity appears to be lowest for multimodal association areas, suggesting that these regions operate more independently from one another than primary sensory-motor and unimodal association areas (Santarnecchi et al., 2015; Stark et al., 2008; Zuo et al., 2010). In line with these findings, low model-order ICA usually identifies left and right lateralized FP networks as separate components, whereas other networks are commonly represented in bilateral components (e.g., Beckmann et al., 2005; Damoiseaux et al., 2006; Jolles et al., 2011; van Duijvenvoorde et al., 2016).

Different frameworks have been proposed regarding the significance of hemispheric lateralization. Some emphasize the importance of integration between hemispheres, especially when task complexity exceeds the processing resources of one hemisphere (Banich and Brown, 2000), whereas others underscore that lateralization is important for functional specialization, pointing to the left hemispheric dominance for language functions. According to the second perspective, neural asymmetry helps to avoid competition between the hemispheres and allows more efficient intra-hemisphere information processing (Toga and Thompson, 2003). Notably, the two regions that exhibited lower inter-hemispheric connectivity in better readers, IFG and IPL, lie at the intersection of different functional networks, and besides domain-general cognitive abilities they play an important role in reading and language. The peak of the IPL component is close to a parietal cortex region reported in a meta-analysis of reading in children (Houdé et al., 2010), and at a lower threshold it also includes a region in the fusiform gyrus that overlaps with the Visual Word Form Area (Fig. 5C). Furthermore, the left IFG component overlaps with Broca's area, and at a lower threshold it also shows other language areas including regions in left temporal cortex and temporal parietal junction (Fig. 5C). In prior studies, reading ability has consistently been related to connectivity between the left IFG and other regions of the language network, the left temporoparietal junction in particular (Achal et al., 2016; Alcauter et al., 2017; Hampson et al., 2006b; Koyama et al., 2011). Here, we extent these findings, showing that children with better reading abilities have reduced connectivity between left IFG / IPL, and their right hemisphere homologues. In line with our findings, it has been demonstrated that individuals with reading disabilities have reduced lateralization within the reading circuit (Finn et al., 2014). Moreover, the transition towards asymmetry in language regions, which begins at the end of the first year, occurs earlier in children with better language outcomes at age four (Emerson et al., 2016). Together these and our findings suggest that increased lateralization benefits reading performance by allowing greater hemispheric specialization (Toga and Thompson, 2003). Alternatively, reduced lateralization may be a hallmark of lower ability because intra-hemispheric resources are taxed more readily, requiring students to split processing demands between the hemispheres (Banich and Brown, 2000).

4.2. Cortico-striatal loops and connectivity within striatum

The second major finding was that individuals with higher scores on the WRAT-Reading test showed higher functional connectivity between the dorsal striatum and a number of frontal and parietal components, predominantly in the DAN. This finding is consistent with the proposed role of the striatum in mediating higher order cognition, including working memory and cognitive flexibility (e.g., Darki and Klingberg, 2018; Mestres-Missé et al., 2012; Monchi et al., 2006; Pauli et al., 2016). More specifically, it has been argued that the basal ganglia provide a dynamic gating mechanism that controls maintenance versus updating of working memory representations (Frank et al., 2001; Hazy et al., 2006). The peak of both striatal components was in the putamen, which plays an important role in language-related functions (Pauli et al., 2016). Moreover, prior work in school-age children has demonstrated an association between cortico-striatal connectivity and reading ability (Alcauter et al., 2017). Yet even in the context of language and reading, it has been argued that striatal involvement is likely related to higher-order cognitive abilities, rather than primary language or semantic functions per se (cf. Crosson et al., 2007).

It is important to note that most models of basal ganglia function focus on fronto-striatal interactions, as the frontal cortex is - via the thalamus — the main locus of output from the basal ganglia (e.g., Haber, 2016). However, primate histological research (Choi et al., 2017; Selemon and Goldman-Rakic, 1985; Yeterian and Pandya, 1993), as well as structural and functional connectivity studies in humans (Choi et al., 2012, 2017; Jarbo and Verstynen, 2015), show the striatum is also connected with the inferior and superior parietal cortex. Moreover, there are areas of convergence that receive projections from both frontal and parietal association areas. The present findings suggest that it is particularly the connectivity with the posterior parietal regions, including bilateral IPL and SPL, that is relevant to reading performance. Interestingly, opposite findings have been reported in 30-54 year old adults. Achal et al. (2016) showed that connectivity between striatum and left IPL was associated with weaker reading performance, which the authors interpreted as compensatory or inefficient overintegration of the striatum into attention networks. Together, these and our findings suggest that increased cortico-striatal connectivity is beneficial for children and adolescents, but that the reverse is true for adults. Koyama et al. (2011) reached a similar conclusion regarding the connectivity between intraparietal sulcus and thalamus, which showed a positive relation with reading competence in children, but a negative relation with reading competence in adults.

The third major finding was that individuals with higher reading achievement showed reduced functional connectivity between dorsal striatum (putamen¹) and ventral striatum (nucleus accumbens). Connectivity between dorsal striatum and ventral anterior cingulate cortex, a DMN region, was also reduced. These findings are in line with the different functional roles of dorsal and ventral striatum and diverging striatal connectivity patterns. Whereas the dorsal striatum is generally connected with lateral PFC and posterior parietal areas and involved with cognitive processes, the ventral striatum is connected with ventromedial PFC and orbitofrontal cortex and involved with emotion and motivational processes (Choi et al., 2012; Di Martino et al., 2008; Haber, 2016; Pauli et al., 2016; Porter et al., 2015). Post-hoc analyses indicated that the connectivity between dorsal and ventral striatum was inversely correlated with the connectivity between dorsal striatum and DAN (r = -0.625, p < .001), suggesting that the functional segregation within the striatum is paralleled by cortico-striatal integration.

4.3. Specialization of functional networks

Taken together, both the lateralization and the striatal findings suggest that individuals with higher reading abilities show increased specialization of functional brain networks. Component-to-component connectivity findings largely confirmed this interpretation, showing reduced functional connectivity between components that were assigned to different functional networks. Besides the findings reported above, it is noteworthy that higher reading abilities were associated with reduced connectivity between control network components and components of the DMN. Specifically, reduced connectivity was found between the anterior insula and both anterior DMN components, and between the SPL and both posterior DMN components. These findings are in line with a number of studies implicating anticorrelations between control networks and the DMN in higher-order cognitive abilities (Barber et al., 2013; Hampson et al., 2010; Keller et al., 2015; Kelly et al., 2008; Sala-Llonch et al., 2012) and may reflect antagonistic relationships between these systems during task performance. For example, it has been demonstrated that high-performing individuals show higher activation of control regions and larger deactivation of DMN regions during cognitive task performance (Anticevic et al., 2010; Satterthwaite et al., 2013). This suggests that suppression of the internally-focused DMN may facilitate attention to external task demands. How exactly the DMN and control networks are modulated to provide a good balance between internal and externally-driven processes remains to be further defined (Buckner and DiNicola, 2019).

4.4. Mediation by executive functioning and complex cognition

To further assess the functional roles of the connections that showed a correlation with reading performance, we performed additional correlation analyses with performance on a cognitive test battery. Behaviorally, the correlation between WRAT-Reading and EF-CC was stronger than its correlation with the other functional domains. These findings are in line with prior research showing that executive functioning and complex cognition (including reasoning) are important contributors to reading achievement (Best et al., 2011; Mayes et al., 2009; St Clair-Thompson and Gathercole, 2006). Importantly, EF-CC performance fully mediated the relation between functional connectivity and

¹ Note that there was no separate component of the caudate. Therefore, it is unclear whether the present findings are specific to the putamen, or whether they involve caudate as well. To differentiate between different subregions within dorsal striatum, future studies should examine striatal connectivity and its relation to reading achievement using more fine-grained methods (e.g., Di Martino et al., 2008; Choi et al., 2012).

WRAT-Reading, showing that the association between functional connectivity and WRAT-Reading was related to general cognitive ability, which was one of the main assumptions of our study. Follow-up analyses indicated that this effect was largely driven by the verbal reasoning subtest, illustrating the importance of verbal competence for performance on the WRAT-Reading. Finally, there were no correlations between functional connectivity and performance in the other domains, illustrating the functional specificity of the effect. In other words, despite the fact that social cognition and memory performance each strongly correlated with both EF-CC and WRAT-Reading, neither of these explained the relationship between functional connectivity and WRAT-Reading. This rules out an alternative explanation that the brain-behavior correlations were driven by an even more general underlying cognitive factor.

4.5. Changes with development

We found that functional connectivity within and between control networks increased with age, whereas functional connectivity between DMN and the control networks decreased, which is largely in line with prior work (e.g., Ernst et al., 2015; Stevens, 2016). Furthermore, our findings show that these age-related changes in functional connectivity hold when controlling for individual differences in achievement levels. However, in contrast to our expectations, we did not find a significant interaction between age and WRAT-Reading performance, suggesting that the observed relation between functional connectivity and reading achievement is relatively stable across development. These findings are at odds with prior work showing that the development of reasoning ability is driven by different neurocognitive networks in different stages of development (Wendelken et al., 2016). The reason for the discrepancy between findings might be related to the nature of assessment that was used. WRAT-Reading is a relatively simple task and, although it is correlated with reasoning, it does not measure reasoning itself. Thus, the neurocognitive processes contributing to individual differences in WRAT-Reading performance may not change as much over the course of development as the processes that allow for the acquisition of complex reasoning skills. Alternatively, the relation between age and reading achievement might be more complex than could be captured by the linear regression model that was used (Best et al., 2011). A group comparison or longitudinal design might be more sensitive to age differences in the neurocognitive systems that support reading achievement across development (Koyama et al., 2011; Wendelken et al., 2016). Finally, it is important to take into account that about 25% of participants were excluded based on motion, a factor highly correlated with age. Moreover, in the remaining sample, younger children showed greater motion than older children. Therefore, brain-behavior correlations specific to the youngest children might be harder to detect due to motion-related noise in the data.

4.6. Limitations and future directions

The current study provides important insights into the functional significance of inter-individual variability in the intrinsic network architecture of the brain, showing that functional connectivity in domaingeneral control networks is relevant to individual differences in reading achievement. Yet, there are a number of important points to be made regarding the potential impact of our findings. First, reading achievement is a complex construct, which is influenced by a number of different cognitive factors including orthographic and phonological processing, higher cognitive abilities, as well as crystallized knowledge. Despite its widespread use, the WRAT-Reading assessment provides only a rough approximation of reading proficiency. To get a more complete representation of the neurocognitive foundation of students' reading abilities it is important to characterize commonalities and differences in brain network involvement across different reading skills, including decoding, word recognition, and reading comprehension. Notably, it has been demonstrated that the influence of cognition on reading in children is more apparent for reading comprehension and word recognition than for decoding (Ferrer et al., 2007), suggesting that domain general networks might contribute differently to different subskills.

Furthermore, it is important to study the contribution of cognitive factors alongside socioeconomic and cultural factors. WRAT-Reading performance has been associated with self-reported quality of education (Sayegh et al., 2014) and parental education (Gur et al., 2012). Moreover, neuroimaging findings suggest that socioeconomic factors may influence brain development, which in turn could affect academic achievement (Hackman et al., 2010; Hair et al., 2015; Noble et al., 2015). In the Supplementary Material, we present post-hoc analyses suggesting that parental education may play a role in the observed brain-behavior correlations. Future studies should further examine the mechanisms though which parental education could influence brain function and behavior, by investigating genetic factors, parental educational behavior, and the role of a safe and stimulating developmental environment (cf. Rindermann and Baumeister, 2015).

A final point of consideration involves the sample that was used. We investigated a large community sample to capture the variability in the population in terms of reading achievement and general cognitive ability. This approach allows estimation of the 'true' correlation in the population with more precision than a smaller but better controlled sample. The flipside of this approach is that there is also other variability related to factors (both known and unknown) that are not pertinent to the current question, which increases noise in the data. Therefore, the fact that effect sizes were relatively low should be evaluated within the context of the broader causal system in which these variables operate (Fraley and Marks, 2007). Moreover, even subtle differences between individuals may provide important insights into the mechanisms contributing to reading achievement across development. Future studies with better controlled samples should follow-up on the current findings and investigate factors that moderate the relationship between brain network architecture and reading achievement. A complementary approach to advance our understanding of inter-individual variability is predictive modeling, which defines brain-based biomarkers predicting behavioral outcomes in novel individuals (Rosenberg et al., 2018).

5. Conclusion

The current study provides new insights into the role of intrinsic network organization to reading achievement across development, signifying the importance of lateralization in control circuits, involvement of the striatum through cortico-striatal loops, and segregation between dorsal and ventral striatum. Together, these findings suggest that individual differences in reading achievement are associated with increased specialization in cortical and striatal networks and provide an important step towards a more comprehensive investigation of brain-behavior correlations in reading achievement across development.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2020.117202.

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