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PAPER

Higher education is an age-independent predictor of white matter integrity and cognitive control in late adolescence

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Abstract

Socioeconomic status is an important predictor of cognitive development and academic achievement. Late adolescence provides a unique opportunity to study how the attainment of socioeconomic status (in the form of years of education) relates to cognitive and neural development, during a time when age-related cognitive and neural development is ongoing. During late adolescence it is possible to disambiguate age- and education-related effects on the development of these processes. Here we assessed the degree to which higher educational attainment was related to performance on a cognitive control task, controlling for age. We then used diffusion tensor imaging (DTI) to assess the degree to which white matter microstructure might mediate this relationship. When covarying age, significant associations were found between educational attainment and fractional anisotropy (FA) in the superior longitudinal fasciculus (SLF) and cingulum bundle (CB). Further, when covarying age, FA in these regions was associated with cognitive control. Finally, mediation analyses revealed that the age-independent association between educational attainment and cognitive control was completely accounted for by FA in these regions. The uncinate fasciculus, a late-myelinated control region not implicated in cognitive control, did not mediate this effect.

Introduction

Socioeconomic disparities are important predictors of cognitive development and academic achievement (McLoyd, 1998). Methodologically, it is difficult to examine how socioeconomic status (SES) dynamically influences cognitive skill across the lifespan, from childhood through adulthood. Typical studies of SES in childhood measure the effects of parental factors, such as maternal education or family income, on child cognitive development (Bradley, Corwyn, Burchinal, McAdoo & Garcia Coll, 2001). Parental SES is an important indicator of family conditions, but is inherently a 'distal' factor used to account for children's experiences. In contrast, studies in adults commonly focus on the association between an individual's own educational or income attainment and cognitive performance (Gianaros, Horenstein, Cohen, Matthews, Brown, Flory, Critchley, Manuck & Hariri, 2007; Scarmeas, Albert, Manly & Stern, 2006; Stern, 2002). While this approach more proximally reflects the individual's experience, such studies commonly measure concurrent cognitive skill in adulthood, limiting conclusions about how SES influences cognitive and neural *development*. Although some studies of adults do include a measure of both childhood and adult SES (Gianaros, Manuck, Sheu, Kuan, Votruba-Drzal, Craig & Hariri, 2010; Singh-Manoux, Richards & Marmot, 2005; Turrell, Lynch, Kaplan, Everson, Helkala, Kauhanen & Salonen, 2002), this type of investigation typically relies on the

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adult participant's memory of childhood SES, which may be subject to recall bias.

Late adolescence provides a unique opportunity to study the effects of educational attainment within the individual, during a time when age-related cognitive and neural development is ongoing. During late adolescence it is possible to tease apart age- and education-related effects on the development of these processes, in a way that is difficult in childhood (when age and educational attainment are highly correlated) or adulthood (when cognitive performance tends to be stable or decline). This period thus provides the ideal window for studying how the attainment of one's own SES relates to cognitive and neural development.

Executive functioning (EF) may be influenced by higher educational attainment (Van der Elst, Van Boxtel, Van Breukelen & Jolles, 2006; Zafiri & Kosmidis, 2008). EF abilities continue to develop throughout childhood and adolescence (Casey, Trainor, Orendi, Schubert, Nystrom, Giedd, Castellanos, Haxby, Noll, Cohen, Forman, Dahl & Rapoport, 1997; Diamond, 2002; Hughes, 2002; Liston, Watts, Tottenham, Davidson, Niogi, Ulug & Casey, 2006b). Childhood EFs have been related to parental SES (Dilworth-Bart, Khurshid & Vandell, 2007; Mezzacappa, 2004; Noble, McCandliss & Farah, 2007; Noble, Norman & Farah, 2005), while in adults, EF has been linked both to one's own educational attainment (Ardila, Ostrosky-Solis, Rosselli & Gómez, 2000; Avila, Moscoso, Ribeiz, Arrais, Jaluul & Bottino, 2009; Van der Elst *et al*., 2006), and to parental SES (Evans & Schamberg, 2009).

The university experience – both within and outside the classroom – provides students with opportunities to develop 'cognitive control', or the skills necessary for inhibiting inappropriate thoughts and actions in favor of those more appropriate to the task at hand (Liston, Cohen, Teslovich, Levenson & Casey, 2011). Training with EF tasks has led to improvement in such abilities (Diamond, Barnett, Thomas & Munro, 2007; Klingberg, Fernell, Olesen, Johnson, Gustafsson, Dahlstrom, Gillberg, Forssberg & Westerberg, 2005; Rueda, Rothbart, McCandliss, Saccomanno & Posner, 2005).

The development of cognitive control is reflected in the protracted maturation of prefrontal and striatal circuits (Giedd, 2004; Gogtay, Giedd, Lusk, Hayashi, Greenstein, Vaituzis, Nugent, Herman, Clasen, Toga, Rapoport & Thompson, 2004; Huttenlocher, 1979; Klingberg, Vaidya, Gabrieli, Moseley & Hedehus, 1999; Liston *et al*., 2006b; Sowell, Peterson, Thompson, Welcome, Henkenius & Toga, 2003; Sowell, Thompson, Leonard, Welcome, Kan & Toga, 2004; Sowell, Thompson, Tessner & Toga, 2001). Diffusion tensor imaging (DTI) studies suggest that the development of white matter tracts in these regions is associated with various EFs during adolescence (Liston, Miller, Goldwater, Radley, Rocher, Hof, Morrison & McEwen, 2006a; Nagy, Westerberg & Klingberg, 2004), even when controlling for age (Liston *et al*., 2006a). Education may therefore lead to plasticity in prefrontal regions supporting these skills (Klingberg *et al*., 2005; Rueda *et al*., 2005; Springer, McIntosh, Winocur & Grady, 2005).

Structural characteristics of several white matter tracts have been linked with cognitive control. These include the **superior longitudinal fasiculus (SLF)** (Ashtari, Cottone, Ardekani, Cervellione, Szeszko, Wu, Chen & Kumra, 2007; Burzynska, Nagel, Preuschhof, Li, Lindenberger, Bäckman & Heekeren, 2011; Charlton, Barrick, Lawes, Markus & Morris, 2010; Karlsgodt, van Erp, Poldrack, Bearden, Nuechterlein & Cannon, 2008; Kennedy & Raz, 2009; Konrad, Dielentheis, El Masri, Bayerl, Fehr, Gesierich, Vucurevic, Stoeter & Winterer, 2010; Liston *et al*., 2011; Makris, Buka, Biederman, Papadimitriou, Hodge, Valera, Brown, Bush, Monuteaux, Caviness, Kennedy & Seidman, 2008; Olesen, Nagy, Westerberg & Klingberg, 2003; Pavuluri, Yang, Kaminen, Passarotti, Srinivasan, Harral, Sweeney & Zhou, 2009; Vestergaard, Madsen, Baaré, Skimminge, Ejersbo, Ramsøy, Gerlach, Akeson, Paulson & Jernigan, 2010); **cingulum bundle (CB)** (Kantarci, Senjem, Avula, Zhang, Samikoglu, Weigand, Przybelski, Edmonson, Vemuri, Knopman, Boeve, Ivnik, Smith, Petersen & Jack, 2011; Konrad *et al*., 2010; Liston *et al*., 2006b; Makris *et al*., 2008; Murphy, Gunning-Dixon, Hoptman, Lim, Ardekani, Shields,Hrabe, Kanellopoulos, Shanmugham & Alexopoulos, 2007; Pavuluri *et al*., 2009; Schermuly, Fellgiebel, Wagner, Yakushev, Stoeter, Schmitt, Knickenberg, Bleichner & Beutel, 2010; Skranes, Lohaugen, Martinussen, Indredavik, Dale, Haraldseth, Vangberg & Brubakk, 2009); and **anterior corona radiata (ACR)** (Liston *et al*., 2011; Niogi, Mukherjee, Ghajar, Johnson, Kolster, Lee, Suh, Zimmerman, Manley & McCandliss, 2008; Pavuluri *et al*., 2009). These fiber tracts have connections with the anterior cingulate gyrus (Makris *et al*., 2008; Niogi *et al*., 2008; Schermuly *et al*., 2010), a prefrontal region implicated in cognitive control (Adleman, Menon, Blasey, White, Warsofsky, Glover & Reiss, 2002; Botvinick, Braver, Barch, Carter & Cohen, 2001; Bush, Whalen, Rosen, Jenike, McInerney & Rauch, 1998; Casey, Thomas, Welsh, Badgaiyan, Eccard, Jennings & Crone, 2000).

These white matter tracts continue to develop through the teens and twenties, at which time briefly plateau and begin degenerating soon thereafter (Brickman, Meier, Korgaonkar, Provenzano, Grieve, Siedlecki, Wasserman, Williams & Zimmerman, 2012). Thus late adolescence – defined here as the late teens to early twenties – represents a period of ongoing cognitive and neural development in the context of wide variation in educational attainment. We hypothesized that higher educational attainment in this age group would be associated with better cognitive control, and that this would be mediated by structural differences in white matter tracts that support this skill.

Methods

Subjects

Subjects were recruited from the Brain Resource International Database, accessed via the independent BRAINnet Foundation (www.BRAINnet.net). This standardized database comprises demographic, psychometric, physiologic, and anatomic data collected on participants from six primary sites throughout the world (Grieve, Clark, Williams, Peduto & Gordon, 2005). For the current study, only participants from one site in Australia (Flinders University) were included, as this was the only site to collect DTI. The full DTI dataset from this site includes 282 healthy individuals, ranging in age from 7 to 87. Participants completed WebQ, a standardized computer-based battery of questionnaires that assess medical history, demographics, and psychological function, including current or lifetime diagnosis of neurological and psychiatric conditions (Williams, Gatt, Schofield, Olivieri, Peduto & Gordon, 2009). Participants were excluded from further participation if they had a history of brain injury, significant medical, neurological or psychiatric conditions, and/or drug or alcohol addiction. Individuals with first-degree family members with attention deficit hyperactivity disorder, schizophrenia, bipolar disorder, or genetic disorders were also excluded.

The present investigation included a sub-sample of 47 late adolescents (26 female). This sub-sample represents all individuals in the database ranging in age from 17 to 23 years old, and for whom education and DTI were available. Education ranged from 11 to 18 years (see Table 1).

Of note, in Australia, a range of educational attainment is fairly common in late adolescence. School is compulsory until age 16 (corresponding to approximately 10th grade in the US), at which time the decision is made whether to complete the 'senior years' (grades 11 or 12) or to seek employment (Pink, 2010). Approximately 75% of Australians complete high school, and approximately 30% complete some type of post-secondary education (Pink & Australian Bureau of Statistics, 2010). In addition, most universities have mechanisms for accepting talented youngsters to university early, around age 16–17, before the completion of grade 11–12 (Victorian Government Department of Education and Early Childhood Development, 2010). Thus, among 17–23-year-olds, some variation in educational attainment would be expected at each age (see Results).

Table 1 *Demographics of sample*

Demographic	Mean (*SD*)	Range
Age	20.1 (2.2)	17–23
Years of education	14.1 (1.8)	11–18

MRI scan acquisition

Magnetic resonance imaging was conducted on a 1.5 T Siemens Sonata system. The MRI protocol included a 3-D T1-weighted image (TR = 9.7 ms; TE = 4 ms; echo train: 7; flip angle = 12°; TI = 200 ms; NEX = 1) and a proton-density/T2-weighted dual echo sequence (TR: 7530 ms; TE: 15/105 ms; eEcho train: 7; flip angle: 180°; NEX: 1). DTI was acquired with an echo planar imaging sequence (TR: 160 ms; TE: 88 ms; fat saturation; NEX: 4; field of view: 22 cm × 22 cm), including a baseline image (b = 0) and 12 diffusion orientations with b-values of 1250. For DTI, 32 6.5-mm contiguous slices were obtained with an in-plane matrix of 128 × 128 and resolution of 1.72 mm^2.

DTI analysis

DTI analysis methodology in this cohort has been described in detail elsewhere (Grieve, Korgaonkar, Clark & Williams, 2011). Briefly, data were preprocessed and analyzed with the fMRIB Diffusion Toolbox and tract-based spatial statistics of the fMRI Software Library (FSL 4.1.3; www.fmrib.ox.ac.uk/fsl) (Smith, Jenkinson, Johansen-Berg, Rueckert, Nichols, Mackay, Watkins, Ciccarelli, Cader, Matthews & Behrens, 2006). Fractional anisotropy (FA) images generated for each participant were transformed into MNI152 1-mm^3 standard space using the nonlinear registration tool FNIRT (Andersson, Jenkinson & Smith, 2007). An average FA image was then generated and thinned to create a white matter skeleton representing the centers of all white matter tracts common to all subjects. A threshold of FA $\geq$ 0.2 was applied to include the major white matter pathways while avoiding peripheral tracts that are more vulnerable to intersubject variability and/or partial volume effects with gray matter. Each subject's aligned FA image was then projected onto the mean FA skeleton by assigning each skeleton voxel by the maximum FA value found in a direction perpendicular to the tract. This approach results in a standard space FA skeleton of the major white matter tracts for each subject accounting for any residual registration misalignments and variability in exact tract location between subjects (Smith *et al*., 2006). We used the JHU ICBM-DTI-81 white matter labels and tractography atlases (Hua, Zhang, Wakana, Jiang, Li, Reich, Calabresi, Pekar, van Zijl & Mori, 2008; Mori, Oishi, Jiang, Jiang, Li, Akhter, Hua, Faria, Mahmood, Woods, Toga, Pike, Neto, Evans, Zhang, Huang, Miller, van Zijl & Mazziotta, 2008) to label sections of the skeleton corresponding to the major tracts in both hemispheres.

Selection of regions of interest

The superior longitudinal fasciculus (SLF), cingulum bundle (CB), and anterior coronal radiata (ACR) were chosen as regions of interest (ROIs), based on their involvement in cognitive control broadly (Burzynska *et al*., 2011; Charlton *et al*., 2010; Kantarci *et al*., 2011; Karlsgodt *et al*., 2008; Konrad *et al*., 2010; Schermuly *et al*., 2010; Skranes *et al*., 2009; Vestergaard *et al*., 2010), and the Stroop task specifically (Kennedy & Raz, 2009; Murphy *et al*., 2007). Anomalies in these fiber tracts have been linked to attention-deficit hyperactivity disorder (ADHD), a disorder whose symptoms are closely related to deficits in cognitive control (Liston *et al*., 2011).

The uncinate fasciculus was selected as a control region with a similarly late-myelinating developmental trajectory (Brody, Kinney, Kloman & Gilles, 1987; Kinney, Brody, Kloman & Gilles, 1988; Yakovlev & Lecours, 1967), but which supports cognitive skills outside of EF (Niogi *et al*., 2008). Figure 1 displays the anatomical distribution of these ROIs. As we had no predictions concerning laterality, mean FA from each hemisphere was averaged to generate a mean value for each ROI.

Cognitive control

Participants were evaluated with IntegNeuro™, a standardized computerized neuropsychological battery that is valid and reliable (Brain Resource, 2010). A verbal interference task similar to the Stroop task (Golden, 1978) was used as an indicator of cognitive control. Subjects were presented with colored words with incongruent color-word combinations. In the first part of the task, the subject was required to identify the *name* of each word as quickly as possible. In the second part of the task, the subject was required to inhibit this prepotent response by identifying the *color* of each word

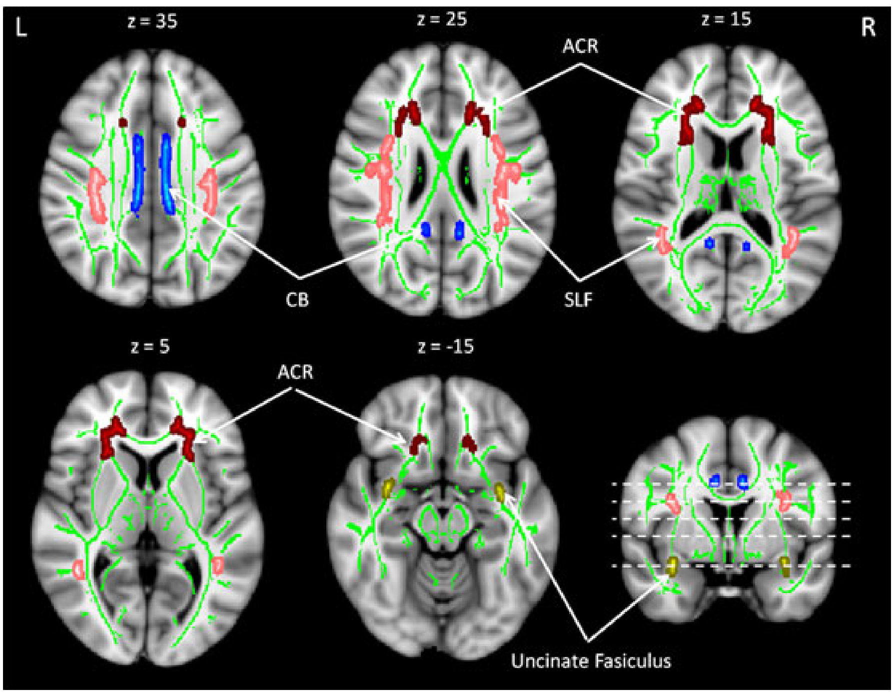

Figure 1 *Three regions of interest (ROIs). The superior longitudinal fasciculus (SLF) is represented in pink; the cingulum bundle (CB) is in blue; and the anterior corona radiata (ACR) is in red. The uncinate fasciculus, a late-myelinating control region, is depicted in yellow.*

as quickly as possible. The dependent variable of interest was the number of stimuli for which the font-color of the color-word was correctly selected (ignoring the name of the word) within 30 seconds (Williams, Simms, Clark, Paul, Rowe & Gordon, 2005).

This research was approved by local ethics committees and informed consent was obtained on all participants over age 18, or by parents or guardians after assent was established for individuals under age 18.

Statistical analyses

To assess whether higher educational attainment influences cognitive control performance, and the degree to which this relationship is mediated by white matter tract integrity, we conducted a mediation analysis, defined according to Baron and Kenny's (1986) criteria (though see Salthouse, 2011, for a discussion of limitations of this technique). These criteria require four separate regression analyses, which assess: (1) the degree to which educational attainment accounts for variation in cognitive control; (2) the degree to which educational attainment accounts for variation in FA; (3) the degree to which FA accounts for variation in cognitive control; and (4) the degree to which, when adjusting for FA, the association between educational attainment and cognitive control is reduced. All analyses included age as a covariate. We expected to find that FA in white matter tracts of interest would account for the effects of educational attainment on cognitive control.

Results

Educational attainment in this sample of late adolescents represented a span of secondary and higher education (see Table 1). Unsurprisingly, educational attainment was correlated with age ($R = 0.79$; $p < .000$), as older individuals have had more years to obtain education. Nonetheless, Table 2 shows that this sample also exhibits a range of educational attainment at each age, typical of the Australian population, as described above.

Table 2 *Education by age*

Age	Educational range
17	11–14
18	12–14
19	13–15
20	12–16
21	14–17
22	13–18
23	14–16

The first analysis investigated the degree to which educational attainment correlated with performance on the interference task, adjusting for age. Table 3 reveals that education, and not age, predicts task performance among this sample of late adolescents (R^2 change = 0.093, $p < .039$). Despite the high correlation between age and education, these two independent variables do not represent undue multicollinearity. A problem with multicollinearity exists if tolerance, or the proportion of variance in a predictor variable that is independent of any other predictor values, is low, defined conservatively as less than 0.1–0.2 (Pedhazur, 1997). As Table 3 shows, tolerance values for these variables are higher than this, lending confidence that age and education are not redundant predictors in this sample. There were no sex differences in educational attainment ($t(45) = 0.60$; $p = .55$), age ($t(45) = -0.41$; $p = .69$), or performance on the interference task ($t(45) = 0.04$; $p = .97$), and therefore analyses were not adjusted for sex.

Next, analyses investigated the degree to which educational attainment was correlated with FA in the hypothesized tracts of interest, namely the SLF, CB, and ACR. We also investigated the degree to which educational attainment was correlated with FA in the uncinate fasciculus, a control tract not typically associated with EF. To account for multiple comparisons of four tracts, alpha was set at 0.0125 (Bonferroni correction of 0.05/4). All analyses were adjusted for age. There were no sex differences in FA in these regions (all ps > .5), and therefore analyses were not adjusted for sex. Table 4 reveals that, when controlling for age, education was significantly associated with FA in the SLF (R^2 change = 0.189, $p < .002$), CB (R^2 change = 0.191, $p < .002$), and ACR (R^2 change = 0.182, $p < .003$), but not the uncinate (R^2 change = 0.016, $p = .178$).

Table 3 *Hierarchical regression of age and education predicting cognitive control performance*

Step		R^2 change	Sig F change	Beta	p	Tolerance
1	Age	0.000	0.948	−0.010	0.948	1
2	Age	0.093	0.039	−0.412	0.090	0.365
	Years of education			0.505	0.039	0.365

Note: A hierarchical regression was conducted with age and then years of education added as independent variables. Cognitive control, operationalized by performance on a Stroop-like task, was the dependent variable. Age did not account for variance in this cognitive control measure in this sample. When adjusting for age, years of education accounted for unique variance in this measure. Age and education did not exhibit undue multicollinearity, as evidenced by the tolerance value, suggesting that over one-third of the variance in each predictor variable is independent of the other predictor.

Table 4 *Hierarchical regressions of age and education predicting fractional anisotropy*

Dependent variable: Fractional anistropy	Step	Model	R^2 change	Sig F change	Beta	P
Superior longitudinal fasciculus	1	Age	0.027	0.271	0.164	.271
	2	Age			0.738	.002
		Years of education	0.189	0.002	−0.720	.002
Cingulum bundle	1	Age	0.029	0.252	0.171	.252
	2	Age			0.747	.002
		Years of education	0.191	0.002	−0.723	.002
Anterior corona radiata	1	Age	0.019	0.357	0.137	.357
	2	Age			0.700	.002
		Years of education	0.182	0.003	−0.706	.003
Uncinate fasiculus	1	Age	0.016	0.398	0.398	.398
	2	Age			0.572	.572
		Years of education	0.040	0.178	0.178	.178

Note: In each region of interest (ROI), hierarchical regressions were conducted with age and then years of education as independent variables. Fractional anisotropy (FA) values in each respective ROI were the dependent variables. When adjusting for age, educational attainment significantly predicted FA in the superior longitudinal fasiculus, the cingulum bundle, and the anterior corona radiata, three ROIs that have previously been linked with cognitive control. In contrast, years of education did not account for variance in FA in the uncinate fasiculus, a control region which has not been linked to cognitive control.

The next question concerned the degree to which FA in our ROIs accounted for variation in cognitive control. Again, alpha was set at 0.0125 to account for multiple comparisons. Table 5 shows that, when adjusting for age, FA in the SLF significantly predicted interference task performance (R^2 change = 0.136, p < .012). The CB showed a borderline effect (R^2 change = 0.107, p < .026). Neither the ACR (R^2 change = 0.054, p < .12) nor the uncinate (R^2 change = 0.028, p = .264) was a significant predictor of interference task performance.

To this point, the SLF meets preliminary criteria for mediation, and the CB nearly does so. The final criterion for mediation is that FA in these ROIs accounts for the link between educational attainment and cognitive control performance. Table 6 and Figure 2 reveal that, indeed, when FA in the SLF or CB is controlled, the association between education and performance on the interference task is no longer significant. The addition of years of education to these models did not account for unique variance, once age and FA are accounted for (R^2 change SLF = 0.025, p = .264; R^2 change CB = 0.032, p = .215).

Table 5 *Hierarchical regressions of age and fractional anisotropy predicting cognitive control*

Step	Model	R^2 change	Sig F change	Beta	p	Tolerance
Dependent variable: Cognitive control						
1	Age	0.000	0.948	−.010	.948	1
2	Age			.052	.718	0.973
	FA – SLF	0.136	0.012	−.374	.012	0.973
1	Age	0.000	0.948	−.010	.948	1
2	Age			.047	.746	0.971
	FA – CB	0.107	0.026	−.333	.026	0.971
1	Age	0.000	0.948	−.010	.948	1
2	Age			.023	.879	0.981
	FA – ACR	0.054	0.120	−.235	.12	0.981
1	Age	0.000	0.948	−.010	.948	1
2	Age			.031	.836	0.984
	FA – uncinate	0.028	0.264	−.170	.264	0.984

Note: Three hierarchical regressions were conducted, with age and then fractional anisotropy added as the independent variables. In each case, the dependent variable was performance on a Stroop-like task. When adjusting for age, fractional anisotropy in the superior longitudinal fasiculus significantly predicted cognitive control, and fractional anisotropy in the cingulum bundle showed a borderline effect when considering multiple comparisons (alpha set at 0.0125). In contrast, FA in the anterior corona radiata and uncinate fasiculus were not related to cognitive control. Age and FA do not exhibit multicollinearity. FA = fractional anisotropy. SLF = superior longitudinal fasciculus. CB = cingulum bundle. ACR = anterior corona radiata.

Table 6 *Fractional anisotropy in the superior longitudinal fasciculus and the cingulum bundle mediates the association between educational attainment and cognitive control*

Dependent variable: Cognitive control					
Model	R^2 change	Sig F change	Beta	p	Tolerance
Age			−.194	.458	.291
FA – SLF			−.295	.068	.784
Years of education	0.025	0.264	.292	.264	.294
Age			−.230	.387	.289
FA – CB			−.243	.136	.780
Years of education	0.032	0.215	.329	.215	.293

Note: Mediation analysis assessed the degree to which the significant effect of FA in the SLF and the cingulum accounted for the relation between educational attainment and cognitive control. Two hierarchical regression analyses were conducted, with age, regional FA, and years of education added as independent variables in a step-wise fashion. The dependent variable in each case was performance on a Stroop-like task. Steps 1 and 2 are shown in Table 5; Step 3 is shown above. When adjusting for age and fractional anisotropy in the superior longitudinal fasiculus and the cingulum bundle, years of education no longer significantly predicted cognitive control task performance. Thus, FA in these regions mediates the relation between educational attainment and cognitive control, as measured by this task. Age**,** FA and years of education do not exhibit multicollinearity in either model. FA = fractional anisotropy. SLF = superior longitudinal fasciculus. CB = cingulum bundle.

Discussion

Late adolescence is a time of transition from parental SES to the attainment of one's own socioeconomic position. Here we have shown that higher educational attainment in late adolescence is associated with cognitive control, independent of age. Further, this relation is statistically mediated by white matter microstructure in several regions that support cognitive control processes. One interpretation of these results is thus that higher educational attainment may lead to age-independent changes in white matter development, which in turn supports cognitive control.

Although cognitive control continues to develop through childhood and adolescence (Diamond, 2002; Hughes, 2002; Liston *et al.*, 2006b), it is difficult to disambiguate the effects of age and education, as these two factors tend to be extremely highly correlated in childhood (Reitan & Wolfson, 1995). Using a 'natural experiment' of school cut-off age, Morrison and colleagues have shown effects of early schooling on certain cognitive skills in early childhood, controlling for age (Morrison, Smith & Dow-Ehrensberger, 1995), though results have been mixed concerning the effect of schooling on EF (Burrage, Ponitz, McCready, Shah,

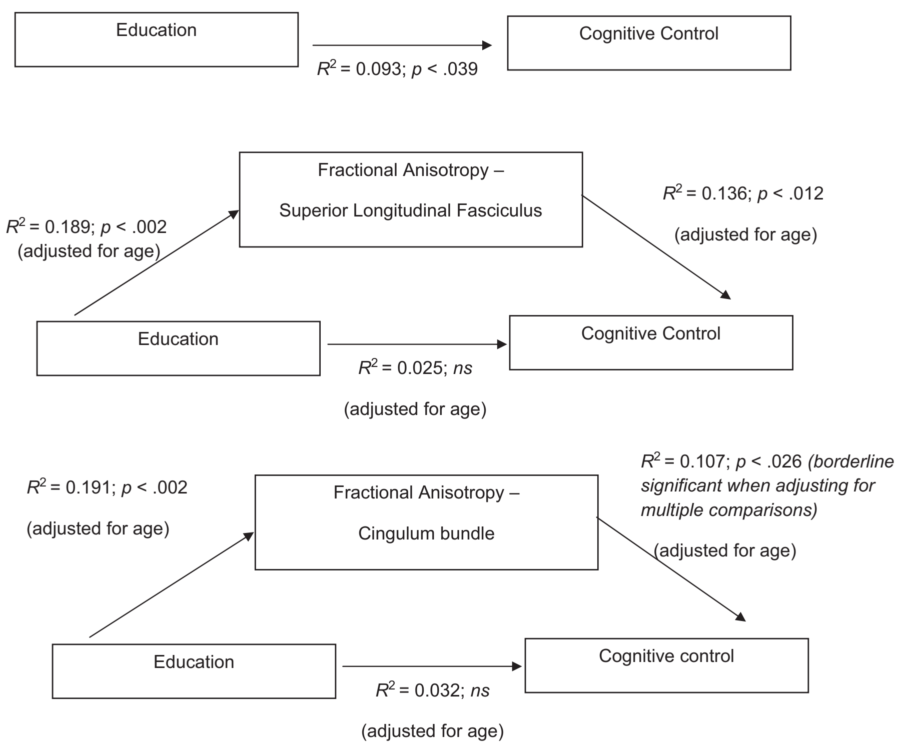

Figure 2 *The association between educational attainment and cognitive control is mediated by fractional anisotropy in the superior longitudinal fasciculus and the cingulum bundle. All analyses are adjusted for age.*

Sims, Jewkes & Morrison, 2008; Skibbe, Connor, Morrison & Jewkes, 2011). Although such studies support the role of education in cognitive development, there is little variation in whether children *ultimately* complete the early school years. In late adolescence, however, there is wide variation in educational attainment across similarly aged individuals, ranging from not completing high school to obtaining an advanced degree. Thus, by studying the effects of higher educational attainment in this age group, we are in effect studying SES-in-the-making. In the present sample of late adolescents, higher education was associated with improved cognitive control when controlling for differences in age.

The prefrontal and striatal circuits that underlie cognitive control exhibit protracted maturation (Giedd, 2004; Gogtay *et al*., 2004; Huttenlocher, 1979; Klingberg *et al*., 1999; Liston *et al*., 2006b; Sowell *et al*., 2003; Sowell *et al*., 2004; Sowell *et al*., 2001), in part accounted for by cognitive skill (Liston *et al*., 2006b). However, it is difficult to disambiguate the effects of age versus education. One study showed regionally specific changes in several fronto-striatal brain structures during the first year of college (Bennett & Baird, 2006). However, whether such changes occurred as a function of age or education was unclear. The present data suggest that, independent of age, higher education is associated with differences in white matter microstructure in several regions previously associated with cognitive control, including the SLF, CB, and ACR. Moreover, these differences in the SLF and, to a lesser extent, the CB, statistically mediate the relationship between education and cognitive control.

There are many pathways by which socioeconomic disparities might lead to differences in brain development (Noble, Houston, Kan & Sowell, 2012). For example, research suggests large differences in exposure to stress across SES (Evans, 2004). The experience of stress has important negative effects on prefrontal cortical structures, including the ACC (Liston, McEwen & Casey, 2009; McEwen & Gianaros, 2010). Future research is necessary to elucidate whether the white matter findings reported here result from differences in earlier childhood experiences which influence the likelihood of obtaining higher education, or conversely, whether findings are due to direct effects of higher education on brain development.

Of note, one previous report using a large sample of twins found that SES was not significantly associated with FA in white matter (although the authors did find that SES modifies the heritability of FA) (Chiang, McMahon, de Zubicaray, Martin, Hickie, Toga, Wright & Thompson, 2011). Interestingly, the study sample in that paper was also drawn from Australia. Possible causes for the disparate findings across the two studies may include differences in the age of participants (late adolescents versus adults) and/or differences in characterization of SES (educational attainment versus occupational status). Certainly, more research is needed to determine whether the findings presented here may be replicated in other samples.

This study suffers from several weaknesses. Notably, we did not have a measure of parental SES in this dataset. The present data are therefore unable to disambiguate whether an individual's own educational attainment directly improves cognitive control, or whether going to college is simply more likely among adolescents from higher socioeconomic backgrounds, and that it is childhood SES conditions which have a direct effect on cognition. Of note, some work suggests that adult SES may influence cognition across the lifecourse independently of childhood SES (Turrell *et al*., 2002), and that the effects of childhood SES may operate on adult cognitive achievement indirectly through adult socioeconomic position (Singh-Manoux *et al*., 2005). In contrast, other research suggests that childhood SES predicts adult brain structure whereas adult SES does not (Staff et al., 2012).

Secondly, this study used a cross-sectional design, which limits our ability to draw strong conclusions regarding development. In addition, all participants in this study were from Australia, potentially limiting generalizability to other populations.

We also note the unusual pattern that, in all cases, FA was negatively associated with both education and cognitive control (though not with age). Although this is not the typical pattern that would be expected, other studies have reported inverse correlations between FA and aspects of cognition, including processing speed (Tuch, Salat, Wisco, Zaleta, Hevelone & Rosas, 2005), creativity (Jung, Grazioplene, Caprihan, Chavez & Haier, 2010), and visuospatial skills (Hoeft, Barnea-Goraly, Haas, Golarai, Ng, Mills, Korenberg, Bellugi, Galaburda & Reiss, 2007). Inverse correlations between FA and mental health have also been reported (Abe, Yamasue, Kasai, Yamada, Aoki, Iwanami, Ohtani, Masutani, Kato & Ohtomo, 2006; Han, Renshaw, Dager, Chung, Hwang, Daniels, Lee & Lyoo, 2008; Yoo, Jang, Shin, Kim, Park, Moon, Chung, Lee, Kim, Kim & Kwon, 2007). Thus the picture of ''optimal'' white matter microstructure may not always be straightforward. Certainly this aspect of the data bears further investigation in future replications.

Finally, the small sample size in the present paper was powered to observe large effect sizes in mediation paths (Fritz & MacKinnon, 2007). It is possible that, in a larger sample, it would be possible to detect smaller (or even directionally opposite) effects in other white matter tracts.

Conclusions

In late adolescence, educational attainment is associated with cognitive control, independent of age. This association was statistically mediated by differences in white matter microstructure in several regions previously shown to support cognitive control. This has implications for how SES may influence cognition, at a time of transition from parental socioeconomic background to the attainment of one's own socioeconomic position. Future studies would benefit from longitudinal measures of neural and cognitive development in this age range, and from the simultaneous measurement of parental socioeconomic factors, to disentangle the effects of family SES and ongoing individual socioeconomic attainment as predictors of cognitive and neural development.

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