Title:

The neurocognitive architecture of fluid ability in children and adolescents

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Abstract

Fluid ability is the capacity to solve novel problems in the absence of task-specific knowledge, and is highly predictive of outcomes like educational attainment and psychopathology. Here, we modelled the neurocognitive architecture of fluid ability in two cohorts: CALM (N=551, aged 5-17) and NKI-RS (N=335, aged 6-17). We used multivariate Structural Equation Modelling to test a preregistered ‘watershed model’ of fluid ability. We found that the watershed model fit the data well for both samples: White matter contributed to working memory and processing speed, which, in turn, contributed to fluid ability ($R^2$(CALM)=51.2%, $R^2$(NKI-RS)=78.3%). The relationship between cognitive abilities and white matter differed with age and showed a dip in strength around ages 7-12 years. Speculatively, this age-effect may reflect a reorganization of the neurocognitive architecture around pre- and early puberty. Overall, these findings highlight that fluid ability is part of a complex hierarchical system of partially independent effects.
Fluid reasoning or fluid intelligence ($g_f$) is a core part of human cognition and refers to the capacity to solve novel problems in the absence of task-specific knowledge. It is highly predictive of a number of important life span outcomes, including educational attainment (Primi, Ferrão, & Almeida, 2010; Roth et al., 2015), psychopathology (Gale, Batty, Tynelius, Deary, & Rasmussen, 2010) and mortality (Batty, Deary, & Gottfredson, 2007; Calvin et al., 2011). However, our understanding of the neurocognitive architecture of $g_f$ remains limited. Longstanding debates have considered, for instance, how $g_f$ relates to more fundamental cognitive functions such as working memory and processing speed, and how all of these cognitive functions relate to brain structure and function (Chuderski, 2013; Ferrer et al., 2013; Fry & Hale, 2000; Kyllonen & Christal, 1990).

Working memory refers to the ability to hold and manipulate information in the mind short-term. It has been suggested that working memory is a key determinant of $g_f$ by limiting mental information processing capacity (Chuderski, 2013; Fukuda, Vogel, Mayr, & Awh, 2010). Proponents of this working memory account of $g_f$ cite high correlations between the two domains ranging from 0.5 to 0.9 in meta-analyses (Ackerman, Beier, & Boyle, 2005; Oberauer, Schulze, Wilhelm, & Süß, 2005). Such high correlations have led some to suggest that $g_f$ and working memory are, in fact, isomorphic (Kyllonen & Christal, 1990). However, more recent work has highlighted that this isomorphism only arises under conditions of high time constraints for $g_f$ tasks (Chuderski, 2013). This suggests that $g_f$ and working memory are, in fact, separable constructs and underlines the importance of processing speed for $g_f$.

Processing speed, the speed of mental computations, is thought to be rate-limiting to $g_f$ and is therefore often proposed to be a particularly good predictor of $g_f$ (Ferrer et al., 2013; Kail,
Lervåg, & Hulme, 2015; Kail & Salthouse, 1994; Salthouse, 1996; Schubert, Hagemann, & Frischkorn, 2017). Proponents of the processing speed account cite moderate but robust correlations between $g_f$ and processing speed of 0.2 in meta-analyses (Sheppard & Vernon, 2008) as well as longitudinal evidence, particularly from ageing populations (Coyle, Pillow, Snyder, & Kochunov, 2011; Finkel, Reynolds, McArdle, & Pedersen, 2005; Kail et al., 2015). Salthouse (1996) argued in the context of cognitive aging, that processing speed determines high-level cognitive performance because slow processing means that relevant sub-operations cannot be completed in a set amount of time or are not available for successful integration. A complementary explanation of individual differences in $g_f$ proposes that processing speed may be a direct reflection of fundamental neuroarchitectonic properties of the brain, such as myelination or white matter microstructure (Chevalier et al., 2015; Lu et al., 2011).

White matter shows protracted development throughout childhood and adolescence, which extends into the third decade of life (Mills et al., 2016). White matter tracts can be characterised in vivo using diffusion-tensor imaging (DTI), which is sensitive, but not necessarily specific, to white matter microstructural properties such as myelination or axonal density (Jones, Knösche, & Turner, 2013; Wandell, 2016). Fractional anisotropy (FA) is the most commonly investigated DTI measure and quantifies the directionality of water diffusion in different white matter tracts (Pfefferbaum et al., 2000; Wandell, 2016). Working memory, processing speed and $g_f$ have each been linked to individual differences in FA in several white matter tracts (Bathelt, Johnson, Zhang, & Astle, 2018; Kievit, Davis, Griffiths, Correia, CamCAN, et al., 2016; Vestergaard et al., 2011). Studies of FA have shown that $g_f$ is associated with FA in the cingulum (Bathelt et al., 2018), that working memory is linked to the superior longitudinal fasciculus (Vestergaard et al., 2011) and cingulum (Bathelt et al.,
2018), while processing speed has been associated mainly with the forceps minor (Kievit, Davis, Griffiths, Correia, CamCAN, et al., 2016), the anterior thalamic radiation, and the uncinate fasciculus (MacPherson et al., 2017).

The literature thus shows strong bivariate links between \( g \), working memory, processing speed and white matter. There are, however, several methodological and practical issues, which we seek to address here: First, there is limited systematic evidence on the concurrent relationships between \( g \), working memory, processing speed and white matter. This leaves the relative contributions of processing speed and working memory to \( g \) unclear, which, in turn, poses challenges for the design of effective interventions for populations with learning problems and disabilities. Second, studies usually use a single task as an indicator (i.e. observed variable) as a proxy for complex and abstract constructs (i.e. latent variables) such as processing speed, working memory, and \( g \). This raises questions about the generalizability of findings (Noack, Lövdén, & Schmiedek, 2014). Third, our understanding of how the relationships between relevant cognitive domains and between brain and cognition change with age remains limited (Achterberg, Peper, van Duijvenvoorde, Mandl, & Crone, 2016; Tamnes, Roalf, Goddings, & Lebel, 2017). Influential work by Garrett (1946) suggested that relationships between cognitive abilities may change with age such that cognitive abilities differentiate (i.e. decrease in covariance) over development (Garrett, 1946; Li et al., 2004), or, conversely, de-differentiate (i.e. increase in covariance) with age (Blum & Holling, 2017), while others still found no changes in covariance with age at all (de Mooij, Henson, Waldorp, & Kievit, 2018; Molenaar, Kő, Rózsa, & Mészáros, 2017; Tucker-Drob, 2009). Age-related changes in the relationship between brain and cognition is even less well understood. Johnson (Johnson, 2000, 2001, 2011) proposed the interactive specialization theory, which holds that brain maturation involves activity-dependent reorganization and specialization of
networks. Critically, interactive specialization predicts that the same cognitive function may be represented by different structures at different ages. Brain-cognition relationships may therefore change fundamentally and dynamically with age (Johnson, 2011). At present, however, there are very few empirical investigations of potential non-monotonic, dynamic changes in brain-cognition relationship in general and for the neurocognitive architecture of fluid ability in particular (de Mooij et al., 2018).

To address these issues, we here used structural equation modelling (SEM) to investigate the multivariate associations between latent variables of \( g_f \), working memory, processing speed, and observed variables of white matter microstructure (FA) and age in two large samples: the Centre for Attention, Learning and Memory sample (CALM, \( N = 551 \), aged 5 – 17 years (Holmes, Bryant, & Gathercole, 2018)), which consists of children referred to a clinic for having problems which attention, learning and memory, and the Enhanced Nathan Kline Institute – Rockland Sample (NKI-RS, \( N = 335 \), aged 6 – 17 years (Nooner et al., 2012)), a community-ascertained sample.

To investigate the neurocognitive architecture of \( g_f \) in a principled way, we used a watershed model of individual differences. This model was originally developed for understanding complex psychopathological phenotypes (Cannon & Keller, 2006) and then repurposed for the investigation of individual differences in \( g_f \) in an ageing sample (Kievit, Davis, Griffiths, Correia, CamCAN, et al., 2016). Based on the metaphor of a watershed, the model predicts a hierarchical many-to-one mapping of partially independent effects such that upstream tributaries (e.g. brain structure) contribute to intermediate cognitive phenomena (cognitive endophenotypes), which then contribute to downstream, complex cognitive phenomena (Cannon & Keller, 2006; Kievit, Davis, Griffiths, Correia, CamCAN, et al., 2016). Kievit et al.
(2016), for instance, showed that individual differences in white matter anatomy predicted individual differences in processing speed, which in turn predicted fluid intelligence scores and a cohort of participants aged 18 - 87 years. Here, we extend the watershed model to include working memory as well as processing speed as cognitive endophenotypes and tested this model in two heterogeneous developmental cohorts. See Figure 1 for a representation of the model. Using structural equation modeling trees (Brandmaier, von Oertzen, McArdle, & Lindenberger, 2013), a novel, decision-tree-based exploratory technique, we also investigated whether the associations in the watershed model change with age.

Based on the watershed model we made the following preregistered predictions (http://aspredicted.org/blind.php?x=u5pf6z):

1. Working memory, $g_f$ and processing speed are separable constructs.
2. Individual differences in $g_f$ are predicted by working memory and processing speed.
3. White matter microstructure is a multi-dimensional construct.
4. There is a hierarchical relationship between white matter microstructure, cognitive endophenotypes (working memory and processing speed) and $g_f$, such that white matter contributes to working memory and processing speed, which, in turn contribute to $g_f$.
5. The contribution of working memory and processing speed to $g_f$ changes with age.
Figure 1. The Watershed Model. Schematic representation of the watershed model developed by Cannon & Keller (2006) and adapted for the present study. Fluid ability is hypothesized to be the downstream product of working memory and processing speed, which are, in turn, the product of white matter contributions. Figure adapted from Kievit et al. (2016).

Results

Measurement Models of Cognition and White Matter

Cognition. To examine the neurocognitive architecture of $g_f$, we built up the watershed model in steps, starting with the measurement model of $g_f$, working memory and processing speed. We first examined whether these three cognitive skills are best described as three separate, two separate or a single cognitive factor (Figure 2).
Figure 2. Different Measurement Models of Cognition. Abbreviations: WM: working memory, PS: processing speed.

The Single-Factor Model (Figure 2) showed acceptable absolute fit (Table 1) but poor comparative fit: The Akaike weight (AIC$_{\text{weight}}$) of the Single-Factor Model was approximately 0% for both samples, indicating an extremely low probability that the Single-Factor Model was the data-generating model compared to more complex alternatives. Two-Factor Model A (Figure 2, treating processing speed and $g_f$ as a unitary factor) showed good absolute fit (Table 1) but also approximately 0% probability of being the data-generating model. Two-Factor Model B (Figure 2, treating working memory and $g_f$ as a unitary factor) fit the data well (Table 1). Two-Factor Model B showed low probability of being the data-generating model for NKI-RS (AIC$_{\text{weight}}$ = 3.40%) but a high probability of being the data-generating model for CALM (AIC$_{\text{weight}}$ = 72.85%). The Three-Factor Model (Figure 2) showed 96.60% probability of being the data-generating model for NKI-RS and 27.15% probability for CALM.
**Table 1. Model Fit of Competing Measurement Models**

| Model Fit | CALM | NKI-R |
|-----------|------|-------|
| **χ²** (20), p < .001 | **χ²** (19), p < .001 | **χ²** (35), p < .001 |
| RMSEA = .068 | RMSEA = .068 | RMSEA = .080 |
| [.051 -.085] | [.052 -.086] | [.064 -.097] |
| CFI = .963 | CFI = .964 | CFI = .936 |
| SRMR = .047 | SRMR = .043 | SRMR = .045 |
| AIC = 9697.18 | AIC = 9696.44 | AIC = 7155.64 |
| BIC = 9800.66 | BIC = 9776.37 | BIC = 7270.07 |

**Note.** See Figure 2 for the configuration of different models. Abbreviations: root mean square error of approximation (RMSEA), comparative fit index (CFI), standardized root mean square residual (SRMR), Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC)

Even though working memory, processing speed and *g*_f were highly correlated in both samples (Table 2), this pattern of results indicates that processing speed formed a clearly separable factor from working memory and *g*_f in both samples. Working memory and *g*_f were also clearly separable in NKI-RS, but not in CALM. To facilitate comparison across samples and in accordance with our preregistered analysis plan we used the Three-Factor Model (Table 2, Supplementary Table 1) in all subsequent analyses.

**Table 2. Covariance between Cognitive Measures in the Three-Factor Model**

| Sample | Path | Standardized Estimate |
|--------|------|-----------------------|
| CALM   | *g*_f <— memory | 0.71, *z* = 28.42, p < .001 |
|        | *g*_f <— speed  | 0.55, *z* = 12.20, p < .001 |
|        | memory <— speed | 0.79, *z* = 19.35, p < .001 |
| NKI-RS | *g*_f <— memory | 0.91, *z* = 19.51, p < .001 |
|        | *g*_f <— speed  | 0.81, *z* = 24.73, p < .001 |
|        | memory <— speed | 0.87, *z* = 17.43, p < .001 |

**Note.** See Supplementary Table 1 for factor loadings.
White matter. We examined whether white matter microstructure could be adequately captured by a single factor by examining model fit. The single-factor model of white matter microstructure did not fit the data well (CALM: $\chi^2(35) = 124.63, p < .001; \text{RMSEA} = .125 [.103 - .147]$; CFI = .933; SRMR = .039; NKI-RS: $\chi^2(35) = 132.33, p < .001; \text{RMSEA} = .204 [.167 - .242]$; CFI = .885; SRMR = .023). This indicates that white matter microstructure could not be reduced to a single ‘global FA’ dimension in our samples, in line with Lövdén et al. (2013) and Kievit et al. (2016). We therefore modelled each of the ten white matter tracts separately in all subsequent models.

The Relationship between Working Memory, Processing Speed and $g_f$

Using Multiple Indicators, Multiple Causes (MIMIC) models (Jöreskog & Goldberger, 1975; Kievit et al., 2012), we examined the relationship between proposed cognitive endophenotypes (processing speed and working memory) and $g_f$. The MIMIC model fit well for both samples (CALM: $\chi^2(18) = 41.74, p = .001; \text{RMSEA} = .049 [.030 - .068]; \text{CFI} = .983; \text{SRMR} = .032$, NKI-RS: $\chi^2(32) = 54.15, p = .009; \text{RMSEA} = .045 [.024 - .065]; \text{CFI} = .981; \text{SRMR} = .030$). To understand whether working memory and processing speed made significant joint and independent contributions to $g_f$, we compared a freely-estimated MIMIC model to one in which regression paths from processing speed and working memory to $g_f$ were constrained to zero. The freely-estimated MIMIC model fit better than a model in which these regression paths were constrained to zero (CALM: $\Delta \chi^2(2) = 250.20, p < .001$; NKI-RS: $\Delta \chi^2(2) = 199.67, p < .001$). This indicates that working memory and processing speed jointly contributed to $g_f$. In CALM ($\Delta \chi^2(1) = 15.53, p < .001$), but not NKI-RS ($\Delta \chi^2(1) = 3.25, p = .072$), the freely-estimated MIMIC model also fit better than a model in which paths from processing speed and working memory to $g_f$ were constrained to be equal. Working memory showed a greater effect (as
indicated by standardized path estimates) than processing speed in both samples, but the
difference was more pronounced in CALM (Table 3). Contrary to our prediction, therefore,
processing speed seemed to make a negligible contribution to $g_t$ above and beyond working
memory.

Table 3. Regression Paths in the MIMIC Model.

| Sample   | Path          | Standardized Estimate |
|----------|---------------|-----------------------|
| CALM     | speed $\rightarrow g_t$ | -0.01, $z = -0.16, p = .876$ |
|          | memory $\rightarrow g_t$  | 0.72, $z = 7.65, p < .001$ |
| NKI-RS   | speed $\rightarrow g_t$  | 0.06, $z = 0.21, p = .208$ |
|          | memory $\rightarrow g_t$  | 0.86, $z = 1.81, p = .070$ |

The Watershed Model: Relationships between Cognition and White Matter

Next, we built the full watershed model including white matter, working memory, processing
speed and $g_t$. We examined path estimates and alternative configurations of the model to
assess whether the main prediction from the watershed model holds, namely, that white
matter contributes to working memory capacity and processing speed, which, in turn,
contribute to $g_t$.

We found largely converging results across samples. The watershed model showed good fit in
CALM ($\chi^2(78) = 107.78, p = .014$; RMSEA = .026 [.012 - .038]; CFI = .981; SRMR = .043) and
acceptable fit in NKI-RS ($\chi^2(112) = 219.22, p < .001$; RMSEA = .053 [.043 - .064]; CFI = .928;
SRMR = .088). White matter explained large amounts of variance in working memory ($R^2_{\text{CALM}}$
= 32.3%; $R^2_{\text{NKI-RS}} = 46.1$%) and processing speed ($R^2_{\text{CALM}} = 38.2$%; $R^2_{\text{NKI-RS}} = 54.4$%), which, in turn, explained even more variance in $g_t$ ($R^2_{\text{CALM}} = 51.2$%; $R^2_{\text{NKI-RS}} = 78.3$%).

Comparing the freely estimated watershed model to alternative, constrained, models
showed that white matter contributed significantly to memory and processing speed.
Specifically, a model in which paths from white matter to processing speed were constrained to zero fit worse than the freely-estimated model (CALM: $\Delta \chi^2(10) = 50.26, \ p < .001$; NKI-RS: $\Delta \chi^2(10) = 27.19, \ p = .002$), as did a model in which paths from white matter to working memory were constrained to zero (CALM: $\Delta \chi^2(10) = 52.26, \ p < .001$; NKI-RS: $\Delta \chi^2(10) = 25.85, \ p = .004$).

White matter tracts differed in their relationship to cognition. A model in which paths from white matter to cognition were constrained to be equal, fit worse than the freely-estimated model for CALM ($\Delta \chi^2(18) = 47.76, \ p < .001$) and NKI-RS ($\Delta \chi^2(18) = 30.42, \ p = .034$), indicating that the role of white matter microstructure in supporting working memory and processing speed differed across tracts. For CALM, only the anterior thalamic radiation contributed significantly to processing speed while the superior longitudinal fasciculus, forceps major and cingulum were significantly and positively related to working memory (Figure 3). For NKI-RS, the superior longitudinal fasciculus was significantly and positively related to processing speed and working memory (Figure 4). Two tracts showed an unexpected, strongly negative (< -1), relationship: the forceps minor for CALM and the inferior fronto-occipital fasciculus for NKI-RS. We found that these negative estimates occurred only when all other brain to cognition pathways were also estimated: When estimated on their own, path estimates became positive (forceps minor to working memory: standardized estimate = 0.36, $z = 4.05, \ p < .001$; inferior fronto-occipital fasciculus to working memory: standardized estimate = 0.14, $z = 0.859, \ p = .390$; inferior fronto-occipital fasciculus to processing speed: standardized estimate = 0.26, $z = 1.41, \ p = .158$). This pattern of results suggests that the negative pathways were potentially due to modelling several, highly-correlated paths at the same time (Jöreskog, 1999).
Figure 3. The Watershed Model in CALM. See Supplementary Table 3 for regression estimates. Residual covariances between white matter tracts were allowed but are not shown for simplicity. Abbreviations: uncinate fasciculus (UNC), superior longitudinal fasciculus (SLF), inferior fronto-occipital fasciculus (IFOF), anterior thalamic radiations (ATR), cerebrospinal tract (CST), forceps major (FMaj), forceps minor (FMin), dorsal cingulate gyrus (CG), ventral cingulate gyrus (CH), inferior longitudinal fasciculus (ILF).

Testing alternative hierarchies in the model showed that the watershed model had a high probability of being the data-generating model for CALM (AIC weight = 49.64%) but not NKI-RS (AIC weight = 0.10%). For NKI-RS, a model with an additional level, such that $g_t$ was regressed on working memory, which was regressed on processing speed, which was then regressed on white matter showed the highest probability (AIC weight = 96.95%). This model showed a low probability for CALM, however (AIC weight = 0.19%). For CALM, reversing the hierarchy of levels of the watershed model such that white matter was regressed on processing speed and working memory, which are then regressed on $g_t$, showed as similarly high probability as the original watershed model (AIC weight = 49.64%). This was not the case for NKI-RS (AIC weight = 0.10%). A model, in which the hierarchy between cognitive endophenotypes and $g_t$ was
inverted, showed comparatively poor fit for CALM (AIC_weight = 0.00%) and NKI-RS (AIC_weight = 2.85%). Similarly, a model in which $g_f$ was directly regressed on white matter, working memory and processing speed, showed no clear advantage over the watershed model for CALM (AIC_weight = 0.53%) or NKI-RS (AIC_weight = 0.00%).

We carried out a series of supplementary and exploratory analyses to examine whether possible confounders influenced our models. These analyses showed that our findings were robust to the inclusion of covariates such as scanner motion or socio-economic status. They were also robust across genders and participants taking or not taking medication. There were no differences between participants with and without diagnosed disorders for CALM, while potential differences cannot be ruled out for NKI-RS, likely due to the low number of diagnosed participants ($N = 106$) (see Supplementary Analyses).
In summary, we found that the watershed model performed well for both cohorts and explained large amounts of variance in $g_f$. As predicted by the watershed model, white matter contributed to working memory and processing speed, which, in turn, contributed to $g_f$.

**Age-Related Differences in the Neurocognitive Architecture of $g_f$**

We investigated whether there were age-related differences in the neurocognitive architecture of $g_f$. An examination of cross-sectional age differences in $g_f$, working memory and processing speed showed that factor scores increased with age for all three cognitive phenotypes (Figure 5).

*Figure 5. Cognitive Factor Scores by Age.*
Using SEM trees, we investigated whether the associations among cognitive and neural dimensions varied with age. As per our preregistration, we investigated potential age-differences in the relationships between $g_0$, working memory and processing speed. In additional, exploratory, analyses we investigated potential age differences in significant watershed paths between white matter and cognitive endophenotypes (Figure 3 and 4).

SEM trees combine SEMs with decision tree methods, whereby separating a dataset into subgroups (in this case age groups) if SEM parameter estimates of interest differ sufficiently (Brandmaier et al., 2013). SEM trees allowed us to investigate age as a potential moderator without imposing a-priori categorical age splits. It is an inherently data-driven technique and the results obtained from SEM trees depend on parameters passed to the algorithm such as the minimum number of individuals allowed per group (here $N = 50$) or the number of levels per branch of the tree allowed, which determines the maximum number of possible subgroups. To counterbalance the inherently exploratory nature of SEM Trees and maximise the robustness of our results, we implemented cross-validated model selection and a conservative, Bonferroni-corrected alpha level of .001. We initially allowed for a maximum depth of one level per tree branch, which could result in no more than two age groups. This yielded inconsistent results for CALM and NKI-RS (Supplementary Table 4). To test whether these inconsistencies were an artefact of allowing for only two groups, we repeated our analysis and allowed for a maximum depth of two levels per branch, which could result in up to four age groups. This analysis yielded consistent results between CALM and NKI-RS (Table 4). This pattern of results indicates that the initial parameters of our analysis caused us to miss relevant age differences.
Table 4. SEM Tree Results for the Watershed Model. The table shows differences in parameter estimates for paths of interest (as shown in Figure 3 and 4) depending on participants’ age in years.

| Path                  | Est. Before | Age Split 1 | Est. Betw. | Age Split 2 | Est. Betw. | Age Split 3 | Est. After |
|-----------------------|-------------|-------------|------------|-------------|------------|-------------|------------|
| CALM                  |             |             |            |             |            |             |            |
| memory <- speed       | 0.85        | 8.46        | 0.97       | 9.46        | 0.74       | -           | -          |
| memory -> g<sub>t</sub> | 0.83       | 9.38        | 0.42       | 10.04       | 1.14       | 10.88       | 0.94       |
| speed -> g<sub>t</sub> | 0.04       | 6.88        | -0.19      | 11.21       | 0.17       | -           | -          |
| SLF -> memory         | 0.67        | 7.21        | 0.18       | 11.21       | 0.76       | -           | -          |
| FMaj -> memory        | 0.59        | 7.71        | 0.14       | 9.29        | 0.33       | 11.13       | 0.74       |
| CG -> memory<sup>1</sup> | 0.64      | 6.96        | 0.09       | 11.04       | 0.70       | -           | -          |
| ATR -> speed          | 0.96        | 7.13        | 0.68       | 7.96        | 0.17       | 11.96       | 0.65       |
| NKI-RS                |             |             |            |             |            |             |            |
| memory <- speed       | 0.90        | 9.82        | 0.48       | 14.72       | 1.11       | -           | -          |
| memory -> g<sub>t</sub> | 1.10       | 8.59        | 0.59       | 12.67       | 1.03       | -           | -          |
| speed -> g<sub>t</sub> | 0.53       | 8.59        | -0.12      | 12.96       | 0.52       | -           | -          |
| SLF -> memory         | 2.15        | 8.30        | 1.47       | 12.15       | 1.93       | -           | -          |
| SLF -> speed          | 3.12        | 8.63        | 1.83       | 15.09       | 2.31       | -           | -          |

As shown in Table 4, we observed age-related shifts in brain-behaviour associations throughout childhood and adolescence. For both samples and all but one path, there was an initially strong relationship between variables, then a dip around ages 7 - 9 for CALM and age 8 for NKI-RS, followed by an increase in path strength around ages 11 to 12. Speculatively, this pattern of results is consistent with an interpretation of a reorganization of neurocognitive faculties in late childhood, followed by a consolidation of neurocognitive pathways around the onset of adolescence.
Here we used multivariate statistical techniques to investigate the neurocognitive architecture of \( g_f \) in two large developmental cohorts and, for the first time, investigated how the neurocognitive architecture of \( g_f \) changes dynamically with age. We tested a preregistered watershed model of \( g_f \), which predicts a hierarchy of partially independent effects. We found that the watershed model performed well for both the atypical (CALM) and typical cohort (NKI-RS): White matter contributed to working memory and processing speed, which, in turn, contributed to \( g_f \) and explained 51% of variance therein for the CALM sample and 78% of variance for the NKI-RS. The watershed model performed well against most alternative models tested. Models were robust across genders, participants taking or not taking medication and when controlling for socio-economic status and scanner motion.

Investigations of age effects showed that the relationship between cognitive abilities and white matter dipped in strength around ages 7 - 12. Speculatively, this age-effect may reflect a reorganization of the neurocognitive architecture during pre-puberty and early puberty (Byrne et al., 2017). These findings have implications for understanding and targeting cognitive impairments in populations with learning difficulties.

Our watershed model consisted of three levels: \( g_f \) was conceptualized as the most downstream point, with working memory and processing speed as intermediate tributaries, and white matter microstructural tracts as upstream sources. Previous studies suggested that matter microstructure is best characterised by a single, ‘global FA’ factor (Penke et al., 2010) while others have contended that association patterns among different white matter tracts are more complex (Kievit, Davis, Griffiths, Correia, CamCAN, et al., 2016; Lövdén et al., 2013).

Here we found strong evidence for a multifactorial view of white matter tracts – for both
samples, a unidimensional model of white matter fit poorly, and for CALM multiple tracts also showed partially independent contributions to distal cognitive outcomes. In line with previous research (Bathelt et al., 2018; Kievit, Davis, Griffiths, Correia, Cam-CAN, et al., 2016; MacPherson et al., 2017), we found that the anterior thalamic radiation was related to processing speed, as were the forceps major, forceps minor and the cingulum to working memory. Of note, the superior longitudinal fasciculus was consistently associated with working memory in both samples. For NKI-RS, the superior longitudinal fasciculus was also associated with processing speed. The superior longitudinal fasciculus is a large, bilateral association fibre connecting temporal, occipital, parietal and frontal regions (Kamali, Flanders, Brody, Hunter, & Hasan, 2014). It may therefore be particularly suited to contributing to cognitive processes that rely on general multiple-demand systems such as $g_t$ (Parlatini et al., 2017).

The cognitive levels of the watershed model highlighted a close relationship between working memory and $g_t$. Previous studies had variably suggested that $g_t$ and working memory (Fukuda et al., 2010; Kyllonen & Christal, 1990), or $g_t$ and processing speed (Ferrer et al., 2013; Kail et al., 2015; Kail & Salthouse, 1994; Salthouse, 1996; Schubert et al., 2017) may be most closely related (but see Chuderski, 2013). We found that all three cognitive factors were highly correlated for both samples. Nonetheless, processing speed formed a cognitive factor clearly separable from working memory and $g_t$. Working memory and $g_t$, in turn, were separable in NKI-RS but not in the CALM sample. This close relationship between $g_t$ and working memory was also evident in other models where processing speed and working memory were used as predictors of $g_t$. Working memory showed a stronger relationship to $g_t$ than processing speed. Contrary to the predictions of the watershed model, processing speed became non-significant after controlling for working memory for CALM. This indicates
that working memory was more strongly related to $g_f$ than processing speed and supports the notion that mental information processing capacity is a key determinant of $g_f$ (Fukuda et al., 2010; Kyllonen & Christal, 1990).

The associations in the watershed model differed between ages in a complex, non-monotonic fashion. Previous research had suggested either a decrease in covariance among cognitive domains with age (age differentiation) (Garrett, 1946; Li et al., 2004), an increase in covariance with age (age de-differentiation) (Blum & Holling, 2017), or no changes with age (de Mooij et al., 2018; Molenaar et al., 2017; Tucker-Drob, 2009). These investigations have traditionally focussed on relations between cognitive domains, however, not on relationships between brain and cognition (although see de Mooij et al., 2018 for a recent example in an aging cohort). Possible linear and non-linear changes in brain-behaviour mapping with age have remained mostly unexplored (Tamnes et al., 2017). Using structural equation modelling trees, a novel decision-tree-based exploratory technique, we here found evidence of complex developmental differences that were consistent across samples and relationships in the watershed model: Initially strong path estimates showed a pronounced decrease in strength around ages 7 - 9, followed by a renewed increase in the strength, even surpassing initial levels, around ages 10 - 15. In line with the interactive specialization theory (Johnson, 2000, 2001, 2011), we speculate that this dip may reflect a remapping of the relationships between brain substrates and cognitive abilities during late childhood and early adolescence, manifesting in weaker covariance between cognitive domains and between brain and cognition.

On a physiological level, this effect could be driven by neuroendocrine changes during pre- and early puberty. Puberty is driven by a complex and only partially understood set of hormonal events including gonadarche and andrenarche (Blakemore, Burnett, S., & Dahl, R.
Gonadarche begins with the secretion of gonadotropin-releasing hormone from the hypothalamus around ages 10 - 11 and closely tracks the overt bodily changes of puberty (Dorn, 2006). Andrenarche, beginning with the maturation of the adrenal gland, starts as early as six years of age, and is increasingly recognized as a complimentary driver of puberty and brain development (Byrne et al., 2017). It is possible that the hormonal changes of andrenarche and early gonadarche may lead to a level of neural reorganization, which may initially weaken relationships in the watershed model. The sweeping bodily, social and cognitive changes happening in early adolescence may then drive a consolidation of the neurocognitive architecture of $g_f$.

On a more general level, this result highlights the existence of potential non-linear changes in brain-behaviour mapping during childhood and adolescence and underlines the value of modern statistical approaches, such as SEM Trees, for the study of age-related differences. Nonetheless, it is worth noting that this exploratory result will need to be replicated in future confirmatory studies with fine-grained data on puberty and larger sample sizes. The latter will also allow for detailed investigations of potential gender differences.

Testing our model in two different samples allowed us to address several critical questions: First, participants from both samples completed a small set of common and a larger set of different cognitive tasks. Therefore, the results obtained here are likely not task-specific, but rather can be expected to generalize to the domains of working memory, processing speed and $g_f$ (Noack et al., 2014). Second, by comparing an atypical (CALM) and a typical (NKI-RS) sample, we demonstrated that the watershed model performed well for different populations. We are not able to make general claims about potential differences between typical and atypical populations, however. CALM and NKI-RS were collected in countries with
different socio-economic conditions (United Kingdom and United States of America) and were of different sample sizes. It will therefore be necessary to replicate these findings in large typical and atypical cohorts collected in the same setting. Another limitation of our study is that our samples were cross-sectional, and not longitudinal. This means that were able to investigate individual differences in $g_t$, but we could not assess intra-individual changes during childhood and adolescence. Although the relatively narrow age range makes large cohort effects unlikely, it may still be that there were differences in recruitment and selection that varied across the age range. As such, the cross-sectional nature of our samples limits our ability to make inferences about developmental dynamics and causality. The watershed model predicts that white matter changes would precede changes in cognitive endophenotypes, which then precede changes in $g_t$, but this remains to be tested by future longitudinal studies such as ABCD (Volkow et al., 2018).

The findings from our study have implications understanding and targeting cognitive impairments in populations with learning difficulties. First, the close relationship between working memory and $g_t$ found here, and in other studies (Fukuda et al., 2010; Kyllonen & Christal, 1990), indicates that children and adolescents struggling with reasoning tasks in school are likely to also struggle in terms of working memory. Either reducing working memory load or training working memory and fluid ability capacity in such populations may therefore be promising lines of inquiry for intervention studies. It is worth highlighting, however, that cognitive training studies have so far shown little generalizability: Training abstract reasoning, a common measure of $g_t$, has not resulted in robust increases in working memory (Knoll et al., 2016) and working memory training has not been shown to transfer to reasoning skills or school performance (Dunning, Holmes, & Gathercole, 2013; Schwaighofer, Fischer, & Bühner, 2015). Similarly, transfer from processing speed to reasoning seems to be
limited (Mackey, Hill, Stone, & Bunge, 2011). The results obtained here suggest that interventions may increase their chance of success by implementing programs of sufficient complexity to affect the entire neurocognitive architecture of effects (see also Kievit et al., 2016). The level of intensity required to produce sustained benefits may also need to be similarly demanding as education itself, which shows robust effects in increasing general cognitive abilities over time (Ritchie & Tucker-Drob, 2018). This work and work by others (Noack et al., 2014) also highlights the value of assessing, modeling and potentially intervening on multiple tasks, rather than relying on a single task to capture complex cognitive domains such as $g$. Finally, the age-related differences in the relationships of the watershed model observed here also highlight that some interventions may work best at particular developmental phases.

### Materials and Methods

#### Samples

We analysed data from the CALM and NKI-RS sample, as described in detail by (Holmes et al., 2018) and (Nooner et al., 2012) respectively. We had also preregistered to analyse data from the ABCD cohort (Volkow et al., 2018). The latter cohort contains only data for 9- and 10-year olds at present, however, which limits comparability to CALM and NKI-RS, and makes it unsuitable for investigations of developmental differences. We therefore opted to not analyse ABCD data here and instead recommend a replication of the analyses presented here in ABCD once longitudinal data is available. The CALM sample consists of children and adolescents referred by health and educational professionals as having difficulties in attention, learning and/or memory. The NKI-RS is a community-ascertained, lifespan sample, and representative of the general population of Rockland, New York, and the United States as
a whole, in terms of ethnicity, socioeconomic status etc. For NKI-RS, we included data for participants under the age of 18 only to match the age range of CALM and excluded data that were completed more than half a year after enrolment. The latter was implemented to ensure that age at assessment did not differ substantively between cognitive measures. The final samples included 551 participants from CALM (30.85% female, aged 5.17 – 17.92, \(N_{\text{Neuroimaging}} = 165\)) and 335 participants from NKI-RS (43.48% female, aged 6.06 – 17.92, \(N_{\text{Neuroimaging}} = 67\)). See Table 5 for prevalence of relevant disorders and problems in the samples.

**Table 5. Prevalence of Relevant Disorders and Problems**

| Variable               | Percentage CALM | Percentage NKI-RS |
|------------------------|-----------------|-------------------|
| ADHD                   | 31.94           | 17.01             |
| Dyslexia               | 5.81            | 5.67              |
| Autism                 | 6.72            | 0.60              |
| Mood disorder          | 0.54            | 0.90              |
| Anxiety disorder       | 2.36            | 18.21             |
| Medicated\(^1\)        | 10.53           | 17.01             |
| Speech/language problems | 38.11          | 19.40             |

*Note.* \(^1\)unspecified medication for NKI-RS, ADHD-medication for CALM

**Cognitive Tasks**

We included cognitive tasks measuring the domains of \(g_i\), working memory or processing speed for CALM and NKI-RS. See Table 6 for the complete list of tasks used and the Supplementary Material for detailed task descriptions. See Supplementary Figure 1 and 2 for raw scores on all tasks. The tasks modelled here were preregistered for CALM but not NKI-RS.

**White Matter Microstructure**
We modelled mean FA for ten tracts of the Johns Hopkins University (JHU) white matter tractography atlas (Hua et al., 2008) averaged over the hemispheres (Figure 5). See Supplementary Methods for details of MRI data acquisition, quality control and DTI data processing.

Table 6. Cognitive Tasks Modelled

| CALM                      | NKI-RS                      |
|---------------------------|-----------------------------|
| Working memory            |                             |
| AWMA Digit Recall (forward digit span) | WISC-R Forward Digit Span  |
| AWMA Backward Digit Span  | WISC-R Backward Digit Span  |
| AWMA Dot Matrix           | -                           |
| AWMA Mr X                 | -                           |
| -                         | CNB N-back task             |
| g                        | WASI-II Matrix Reasoning    |
| -                         | WASI-II Block Design        |
| -                         | WASI-II Similarities        |
| -                         | CNB Verbal Reasoning        |
| Processing speed          |                             |
| DKEFS Trail-Making        | DKEFS Trail-Making          |
| PhAB Rapid Naming         | -                           |
| TEA-Ch RBBS               | -                           |
| -                         | CNB Motor Speed             |
| -                         | CNB Sensory Motor Speed     |

Note. Abbreviations: AWMA - Automated Working Memory Assessment (Alloway, 2007), CNB - Computerized Neurocognitive Battery (Gur et al., 2001), DKEF - Delis-Kaplan Executive Functioning System (Delis, Kramer, Kaplan, & Holdnack, 2004), PhAB – Phonological Assessment Battery (Gallahger & Frederickson, 1995), TEA-Ch RBBS - Test of Everyday Attention for Children, Red & Blues, Bags & Shoes subscale (Manly et al., 2001), WASI - Wechsler Abbreviated Scale of Intelligence - Second Edition (Wechsler, 2011), WISC-R - Wechsler Intelligence Scale for Children - Revised (Kaufman, 1975).

Data Processing and Structural Equation Modelling

Covariance matrices and scripts replicating key analyses can be obtained from: https://github.com/df1234/gf_development. We modelled raw scores for g and working memory tasks, as preregistered. Raw scores on processing speed tasks were transformed, which was not preregistered. First, we inverted response time scores to obtain more intuitive measures of speed for all but the CNB Motor Speed task, for which raw scores were already a measure of speed. To satisfy SEM assumptions of normality, we additionally applied a log-
transformation to reaction time tasks. For the CNB Motor Speed task only, we removed values $\pm 2 \, SD$ of the mean ($N = 6$) because of the presence of outliers.

We modelled the associations between cognition and white matter microstructure using Confirmatory Factor Analysis and SEM in R (R core team, 2015) using the package lavaan (Rosseel, 2012). All models were fit using maximum likelihood estimation with robust Huber-White standard errors and a scaled test statistic. Missing data was addressed using full information maximum likelihood estimation. Model fit was inspected using the chi-square test, RMSEA, CFI and SRMR. Good fit was defined as approximately RMSEA < 0.05, CFI > 0.97 and SRMR < 0.05; acceptable fit as approximately RMSEA = 0.08 - 0.05, CFI = 0.95 - 0.97, SRMR = 0.05 - 0.10 (Schermelleh-Engel, Moosbrugger, & Müller, 2003). Comparative model fit for nested models was assessed using the chi-square test. Non-nested models were compared using the $AIC_{weight}$, which indicates the probability of a model being the data-generating model compared to all other models tested (Wagenmakers & Farrell, 2004). Effect sizes were evaluated by inspecting $R^2$ and standardized parameter estimates manifest variables. Absolute standardized parameter estimates above 0.10 were defined as small effects, 0.20 as typical and 0.30 as large (Gignac & Szodorai, 2016).

We used SEM Tress to investigate whether the associations among cognitive and neural measures differed with age. SEM Trees use decision tree methods to hierarchically split a dataset into subgroups if parameter estimates differ significantly based on a covariate of interest - in this case age (Brandmaier et al., 2013). We first ran the watershed model in OpenMx (Boker et al., 2011) and then passed this model object to semtree to compute the SEM Trees. We ran one SEM Tree for each parameter of interest (e.g. the covariance between working memory and processing speed). All other parameters in each semtree
object were set to be invariant across groups to ensure that splits were specific to the
parameter of interest. We used a 10-fold cross-validation estimation method as recommend
by Brandmaier et al. (2013). For the path from the cingulate to working memory only we
used 5-fold cross-validation because the model did not converge using 10-fold cross-
validation. Minimum sample size in age group was set to $N = 50$ to ensure reliable estimation
of standard errors. Note that this choice effectively limited search space for potential splits to
ages 6.58 - 12.42 years for CALM and 8.08 - 15.49 years for NKI-RS

Figure 5. White Matter Tracts Modelled in the Analyses.

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Conflicting Interests

The authors report no conflict of interest.

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