



Tilts, developmental modules, and cognitive differentiation-integration effort: A multi-study response to Sorjonen et al. (2024)

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ABSTRACT

Sorjonen et al. (2024) critique a recently published finding that cognitive tilts are heritable, which was advanced as a line of evidence supporting their substantive (rather than artefactual) nature. These researchers claim: i) that the heritability of tilts is simply a function of the heritabilities of the specific cognitive dimensions used in their estimation, and ii) that spuriously heritable tilts can be recovered using difference scores between psychometric, anthropometric, and even random number variables. Here, multiple studies employing three behavior genetic datasets are used to test these claims. Even when cognitive tilts are residualized for their association with their constituent abilities, they still exhibit small, but non-zero heritabilities. *Shared* environmentality (C) accounts for the largest proportion of variance among these residuals. Tilts generated using random numbers are, by contrast, in all cases associated with AE models, exhibiting near 100 % E variance, corresponding to error. In the Swedish Twin Registry, the tilt residual is positively correlated with a measure of life history speed (Mini-K score), suggesting that tilts capture cognitive differentiation-integration effort conditioned developmentally by C variance. Distinct latent factors among psychometric and anthropometric variables in the Georgia Twin Study are also found. These indicate the presence of distinct developmental modules, meaning that tilts estimated using manifest variables associated with *different* modules lack theoretical credibility, as also evidenced by weak cross loadings.

1. Introduction

Debate surrounds the validity of cognitive ability tilts, which are within-subjects differences between two distinct abilities (e.g., verbal – spatial) or broad ability domains (e.g., academic – technical). Tilts are typically independent of general cognitive ability (GCA) and are said to capture tradeoffs favoring the cultivation of one ability, or cognitive domain, at the expense of another, by means of specific patterns of investment, such as time devoted to learning.

On the one hand it has been found that these tilts add incremental predictive validity to measurement models of certain criteria over and above general cognitive ability (GCA) (for reviews, see Coyle, 2018; Coyle & Greiff, 2021; see also Coyle, 2019, 2020, 2021, 2022a, 2022b). On the other it has been argued that tilts are spurious owing to their

correlations with the abilities or domains out of which they are constructed. This creates a theoretical objection to the idea that a tilt captures a *specific* tradeoff pattern between its two constituent abilities or domains, and that this is in turn the source of their apparent incremental validity in studies such as those produced by Coyle and co-workers. Instead, it may merely be the case that their seeming validity is entirely due to their being basically arbitrary pairings of non-GCA residuals, which exhibit variable levels across people for genetic and developmental reasons (unrelated to environmentally calibrated tradeoffs occurring in ontogenetic time, as the tilt model posits)—in which case, the constituent abilities are the true source of incremental validity in these sorts of studies (Sorjonen et al., 2022; Sorjonen et al., 2023).

Recently, tilts were investigated using behavior-genetic models in three large samples, two of which were sourced from US datasets (the

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Georgia Twin Study [GTS] and MIDlife in the United States II [MIDUS II]), and the third from a Swedish dataset (the Swedish Twin Registry Study of Twin Adults: Genes and Environment [STR STAGE]) (for full descriptions of these see Coyle et al., 2023). Tilts were estimated using broad cognitive abilities in each case. These included *Reasoning*, *Numeric*, *Verbal*, and *Spatial* primary mental abilities in the case of the GTS (yielding six tilts in total), *Executive functioning* and *Episodic memory* in the case of MIDUS II, and *Fluid reasoning* and a *Chronometric group factor*, capturing processing speed and accuracy, in the case of STR STAGE. AE (additive genetic, non-shared environmental, and error variance) models were found to fit the data in all but one instance (the *Verbal-Reasoning* tilt in the GTS, where a model incorporating a shared environmentality [C] component yielded the best fit). Estimates of tilt additive heritability were in line with those found in meta-analyses of general trait heritability (weighted mean $h^2 = 0.401$, 95 % CI = 0.375, 0.426, vs. 0.490 in Polderman et al., 2015). Moreover, a statistically significant Wilson-like effect (rising h^2) was found when the tilt heritabilities were compared based on the mean ages of their respective samples. Finally, a portion of the non-shared environmentality was speculated to reflect the action of “active” gene-by-environment correlations resulting from e.g., niche picking.

In a thoughtful response to Coyle et al. (2023), Sorjonen et al. (2024) argued that these heritability estimates are also spurious, as they likely merely reflect the heritability of the specific ability domains from which the tilts are constructed. They attempted to demonstrate this via the estimation of large numbers of tilts involving both cognitive and non-cognitive (anthropometric) variables sourced from the GTS, where correlations were found between the mean heritability of the constituent dimensions and the heritabilities of their associated tilts. This was reinforced with a simulation showing essentially the same pattern. Sorjonen et al. (2024) argue that the presence of apparently heritable tilts between counterintuitive domains (such as nose length and spatial ability), or among those estimated using a pseudo-variable composed of random numbers paired with phenotypes, further undercuts the case put forward in Coyle et al. (2023). They write that “[a]ccording to the logic of [Coyle et al.’s, 2023] argument ... this would suggest that the human genome codes for, for example, differences between height and nose length ($H^2 = 0.75$), between head circumference and verbal ability ($H^2 = 0.60$), and between spatial ability and a random number allocated to the person several decades after birth ($H^2 = 0.22$). We find it very unlikely that the human genome would code for such tilts. Instead, we propose ... that heritability of these, as well as other, tilts are spurious consequences of heritability of the constituent variables” (p. 3).

Sorjonen et al. (2024) raise some sound points. Nevertheless, one study that seemingly contradicts their broader criticism of the tilt paradigm is that of Kato and Scherbaum (2023). In this study of the criterion validity of tilts, it is noted that “[a]bility tilt related with job performance in the expected direction for 27 of the 36 tilt-job combinations examined, with a mean effect size of .04 when the tilt matched job requirements. The mean incremental validities for ability tilt were .007 over g and .003 over g and specific abilities, and, on average, tilt explained 7.1% of the total variance in job performance” (p. 1). Their findings therefore suggest that tilts add incremental validity to predictions of job performance, even when controlled for both GCA and its specific constituent abilities. Sorjonen et al. (2024) highlight a need to further develop the theoretical sophistication and specificity of predictions of the tilt research program, and the work of Kato and Scherbaum (2023) suggests that there may be a tilt residual that has substance net of its component abilities. In the remainder of this article, this possibility will be key to satisfactorily rebutting the criticisms that Sorjonen et al. (2024) offer.

1.1. Life history theory: a new approach to tilts

The literature on tilts tends to focus on their proximate causes. *Investment theory* (Cattell, 1987, pp. 138–146) is frequently used as a

causal framework for understanding the origins of these ability differences. Abilities, independently of GCA, are treated as effectively being in competition with one another, with the cultivation of one ability necessarily coming at the expense of another (so, e.g., time spent specializing in ability A is necessarily time not spent specializing in ability B). A more fundamental and distal (evolutionary), but complementary, framework within which tilts and related phenomena may be understood is *life history* (LH) theory (LHT). LHT describes the adaptive logic conditioning relationships among seemingly discrete physical, behavioral, and psychological aspects of phenotypes. Specifically, LHT posits that phenotypic traits covary along a continuum (though it is generally thought that there is more than one continuum of LH variation; see Ellis et al., 2009) of LH speed, with one end of the continuum called “slow” (or *K*-selected) and the other end called “fast” (or *r*-selected)¹. “Slow” life history traits, collectively called strategies, are adapted to the pursuit of fitness over a long time horizon, whereas “fast” life history traits/strategies are adapted to the pursuit of fitness over a short time horizon.

While originally developed to explain trait covariation across species, LH models have also been successfully applied to understanding the adaptive logic underlying correlations among seemingly distinct sources of individual differences in humans, and also other species (Ellis et al., 2009; Woodley of Menie et al., 2021). In humans, personality and other behavioral traits have been found to cohere into latent variables, such as the *general factor of personality* (GFP), the positive manifold among different personality traits such as extraversion, neuroticism, and agreeableness, which has been interpreted as capturing overall social effectiveness (Musek, 2017). The GFP in turn positively (phenotypically and genetically) correlates with measures of mental and physical health, and such health measures are correlated through a *Covitality* factor. Both the GFP and Covitality factor positively correlate with a cluster of behavioral traits paradigmatically associated with LH, such as low time preferences; low mating effort; and long-term sexual-romantic, familial, and communitarian attachments and investments. These behaviors all positively correlate through a psychometric “*K* factor.” A higher order “*Super-K*” factor emerges from the intercorrelations of the GFP, Covitality, and *K* factor, which is taken to be the most general factor of human LH (Figueredo et al., 2004; Figueredo et al., 2006; Figueredo & Rushton, 2009).

As with species-differences LHT, individual-differences LHT posits a “fast-slow” continuum capturing variation between people (or organisms within different species), with fast and slow poles corresponding to lower vs. higher levels of *Super-K* (all humans are highly *K* selected relative to other primates and mammals more broadly). Such models posit both genetically and environmentally conditioned individual differences in LH speed (Del Giudice, 2020; Ellis et al., 2009; Woodley of Menie et al., 2021).

Despite the considerable nomological breadth of the psychometric *Super-K* factor, measures of general cognitive ability (GCA) have been found to be at best only weakly, and also inconsistently, associated with psychometric measures of LH speed (Figueredo et al., 2014; Loehlin et al., 2015; Woodley, 2011; Woodley of Menie & Madison, 2015). This suggests that there might be distinct developmental modules that have

¹ The terms *r* and *K* selection originate from outdated forms of LH theory that “focused on population density-dependent causes for life history evolution ... whereas subsequent life history theory focused more on the role of age-dependent schedules of morbidity and mortality, attributable to factors such as environmental harshness and unpredictability” (Figueredo et al., 2017, p. 42). Contemporary models of LH evolution posit roles for density-dependent selection, but other selective factors tend to be emphasized. Although the *r-K* terminology is not quite current, “*K*-selected” and “slow” and “*r*-selected” and “fast” are still used interchangeably to refer to specific LH-related traits and trait clusters, and to organisms and species exhibiting such traits and trait clusters.

evolved in response to discrete selective pressures. Traits that are sensitive to the presence of deleterious mutations (for example) may have evolved to signal phenotypic condition in a way that would be expected to cut across LH variation owing to the globally negative effects of such mutations on condition, in contrast to LH adaptations that are more narrowly adapted to particular environmental contexts (therefore, high- and low-condition phenotypes should be found in both fast- and slow-LH individuals). GCA may be one such trait highly sensitive to genetic quality, which is subsumed under a broader “system integrity” factor that would occur at the same level of psychometric aggregation as Super-K (Woodley of Menie et al., 2021).

Although psychometric measures of LH speed, such as the GFP and K factor, are inconsistently and weakly associated with GCA, it has nevertheless been found that the positive manifold of GCA is weaker among those who on average exhibit slower LH speed. Woodley (2011) predicted the existence of this dimension of variation—stronger vs. weaker GCA manifold strength as a function of slower vs. faster LH speed. It has been demonstrated in both student and population-representative samples sourced from the US (Woodley et al., 2013). Weaker correlations among measures of cognitive ability are theorized to result from biased allocations of effort (investments of time, cortical real estate, and bioenergetic resources, such as calories) into the cultivation of specialized abilities (“differentiation effort”). Specialization is adaptive in environments that are stable enough to feature niches that can be exploited over a long time horizon, hence slow LH strategists cultivate specialized ability profiles to adapt to such niches in the stable environments that selectively favor such strategists. Stronger correlations among measures of cognitive ability, by contrast, are thought to result from fairly even allocations of effort (“integration effort”) to different ability domains—such even allocation is adaptively logical in unstable and harsh environments where only short-term pursuit of fitness is generally feasible (i.e. environments that favor fast LH strategists), and where the specific niches available for exploitation are not predictable, requiring fit organisms to be generalists. Consequently, the dynamic governing these LH-related investment patterns is termed cognitive differentiation-integration effort or CD-IE (Woodley, 2011).

1.2. Hypotheses

CD-IE is highly relevant to the etiology of tilts as it provides a distal framework within which they can be better understood. It enhances via *consilience* (the integration of proximate and distal theories), rather than replaces, Cattell’s (1987) investment model by providing an adaptationist account of the emergence of the investment process it describes (see Hertler et al., 2018, pp. 293–306 for discussion of this integration in relation to Cattell’s work). Based on the CD-IE model, tilts constitute true tradeoffs between abilities or ability domains as their development involves the devotion of finite bioenergetic resources to the cultivation of one ability or domain, at the expense of another. Moreover, CD-IE explicitly predicts that the overall cognitive profile of those with slower LH will exhibit a more uneven structure reflecting tilts among different abilities and therefore cognitive specialization (see Woodley, 2011, Fig. 3, p. 234). The overall ability to cultivate tilts should be a function of LH speed, even though the precise direction of the tilt (i.e., the degree to which the development of one arbitrary ability is being traded against another) will be conditioned by the immediate developmental requirements of the individual (as reflected in “active processes” such as niche picking; Coyle et al., 2023), and may vary substantially from individual to individual. This application of CD-IE to tilts leads to the following hypothesis:

Hypothesis 1. (H₁): When residualizing tilts for correlations with their component abilities (in addition to GCA and age as was done in Coyle et al., 2023), a more fundamental investment dimension will emerge.

The existence of this investment dimension may make sense of Kato and Scherbaum’s (2023) finding that even when their constituent

abilities are controlled, tilts still add incremental validity to models predicting job performance. Critically, this contrasts with a prediction based on Sorjonen et al.’s (2024) model, specifically that such tilt residuals should be *wholly* spurious. To differentiate between the two key predictions, behavior-genetic models can be used, leading to the following two sub-hypotheses:

Hypothesis 1a. (H_{1a}): Tilt residuals should be weakly heritable but also associated with substantial *shared environmentality* (C), with the ACE model best fitting the data.

H_{1a} emerges from the fact that a person’s level of cognitive differentiation effort should be strongly conditioned by factors associated with the shared environment: “active” effects such as familial and social pressures encouraging the picking of certain “cognitive niches” require stable environments to play out, and extant LHT research indicates that shared environmental effects related to stability of the home environment significantly predict the development of LH traits independently of genetic effects (Figueredo et al., 2020). This, it must be stressed, contrasts with our previous paper (Coyle et al., 2023), which did not proceed on the basis of LHT, and that anticipated that niche-picking should be driven by non-shared environmental factors.

Hypothesis 1b. (H_{1b}): AE models will fit tilts reflecting the differences between random number variables. These should be associated exclusively with E variance, as this captures measurement error.

Such pseudo-tilts should behave in line with predictions from Sorjonen et al. (2024), as these are spurious by design. This test allows for both the CD-IE and the “spurious origin” hypotheses to be directly competed with one another.

An obvious and major hypothesis stemming from the CD-IE model of tilts is as follows:

Hypothesis 2. (H₂): Tilt residuals will, if they do indeed significantly capture CD-IE, correlate positively with a psychometric measure of LH speed.

A final hypothesis is advanced given the predicted existence, in light of LHT, of largely separate developmental modules:

Hypothesis 3. (H₃): Distinct latent variables will exist among the psychometric and anthropometric traits included in the GTS data, indicating the presence of discrete developmental modules.

Confirmation of H₃ militates against the logic of constructing tilts using manifest variables sourced from *different* developmental modules (as Sorjonen et al., 2024 likely do), as these domains may not be in competition with one another for “common” sets of resources, and tradeoffs among the components of such modules may also be regulated by different sets of genetic and environmental factors.

Here these new hypotheses will be tested, not only to examine Sorjonen et al.’s (2024) criticisms in more detail, but to further the tilt research program.

2. Methods

2.1. Statistical analyses

GCA factor scores were computed using a unit-weighted estimation procedure for each set of cognitive indicators collected from the STR, MIDUS II, and GTS (as described in Coyle et al., 2023). Cognitive tilts were computed by subtracting the z-scores estimated for each cognitive ability for each pair of cognitive abilities. The resulting values were subsequently re-standardized. A General Linear Model (GLM) was then used to estimate the residuals (R1) of a model using z-GCA and z-age as predictors of the z-tilt. z-age was controlled as the heritability of tilts has been shown to exhibit a Wilson-like effect, specifically they increase significantly between samples as mean sample age increases (Coyle et al., 2023). This control reduces confounding due to potential *within-*

sample age dependent effects on the behavior genetic variance components. In a subsequent step, a GLM was conducted to estimate the models' residuals (R2) after including the standardized cognitive indicators (used to estimate GCA and the corresponding tilt) as predictors of the residuals (R1) computed in the previous stage. In the case of GTS, each of the six tilts were residualized for all four of the ability measures, yielding what could be termed "tilt super-residuals."

As with Coyle et al. (2023), the current study employed the *twinlm* function, associated with the *mets* package (Holst & Scheike, 2013) in R v. 4.3.1, to estimate ACE, ADE, and AE behavior-genetic models. Model comparisons were executed using AIC and BIC values estimated for each model. The function *akaike.weights*, found in the *qpcR* package (Ritz & Spiess, 2008), was used to estimate ΔAIC , ΔBIC , *AIC weights*, and *BIC weights* for each model. Although in the literature model selection is often based on positively signed AIC and BIC values, wherein lower values indicate a better model fit, it is not uncommon for certain models to feature negatively signed AIC and BIC values. For example, the addition of a constant can reverse the sign of the model fit parameters (Burnham & Anderson, 2004). Model selection based on negatively signed AIC and BIC values follows the heuristic wherein smaller values, hence more negative estimates, feature a better statistical fit. Variance component analyses were also employed to determine the proportion of phenotypic variance attributable to additive genetic, common environmental, and non-shared environmental factors in addition to error. Following Sorjonen et al. (2024), random number variables were generated for each subject and the resultant difference scores between pairs of these. These "pseudo-tilts" were then analyzed using the aforementioned behavior-genetic models.

A measurement model was estimated for the following GTS variables: reasoning, numerical, verbal, spatial, weight, height, head breadth, head circumference, head length, face length, and nose length, in order to identify latent variables among them. Horn's (1965) parallel analysis was used to determine the recommended number of underlying factors. Based on the suggested number of latent dimensions a Principal Axis Factor Analysis was computed. An inter-factor correlation was generated providing information on the association between these latent dimensions. These analyses were conducted using the packages *paran* (Dinno, 2009) and *psych* (Revelle, 2015). A reviewer suggested that these analyses should have been conducted using confirmatory as opposed to exploratory factor analysis, however for the purposes of the present study we note that confirmatory factor analysis is recommended when the factorial structure has been properly identified in previous studies and the goal of the study is to determine the model fit of the aforementioned latent structure (Orçan, 2018). In contrast, the use of exploratory factor analysis is appropriate when factor structure remains to be determined (Orçan, 2018). After reviewing the relevant literature, the present study is the first to examine a latent structure based on seven morphometric indicators (head circumference, head breadth, head length, face length, nose length, height, and weight), and four cognitive indicators (reason, number, verbal, and spatial). As no previous publications have used these variables to examine the factor pattern the present study therefore employed an exploratory factor analytic approach.

3. Results

3.1. Study 1: testing hypothesis 1

3.1.1. Hypothesis 1a: Heritability and shared environmentality in tilt residuals

3.1.1.1. *Swedish twin registry.* Tilts were computed using the score difference between *fluid ability* and a *chronometric factor*. These were residualized for i) associations with GCA (the average of the two factor scores for each subject) and age, and ii) associations with the two

abilities. The sample was composed of 711 monozygotic (MZ) and 665 dizygotic (DZ) twin pairs. The model comparison indicated that the ACE model statistically outperformed the ADE and AE ones. The variance component analysis indicated that common environmental factors explained most of the standardized residualized tilt variance. These results are further described in Table 1.

3.1.1.2. *MIDUS II.* Tilts were computed using the score difference between *Episodic memory* and *Executive functioning*. These were residualized for i) associations with GCA (the average of the two factor scores for each subject) and age, and ii) associations with the two abilities. The sample was composed of 164 monozygotic (MZ) and 228 dizygotic (DZ) twin pairs. As with the analysis involving STR STAGE, the model comparison revealed that the ACE model outperforms the others. A variance component analysis with the standardized residualized tilt indicated that, as with the STR STAGE tilt residual, common environmental factors accounted for most of the model's variance. Table 2 describes these results in further detail.

3.1.1.3. *Georgia twin study.* Tilts were computed using the score difference between each pairing involving *Reasoning*, *Numerical*, *Spatial*, and *Verbal* primary mental abilities, yielding six tilts. These were residualized for i) associations with GCA (estimated using exploratory factor analysis) and age, and ii) associations with each of the four abilities. The sample was composed of 82 monozygotic (MZ) and 108 dizygotic (DZ) twin pairs. The six tilt "super-residuals" (R2) estimated from the GLM were found to perfectly correlate with one another (Fig. 1).

This indicates the presence of a single prospectively CD-IE-like dimension among these tilt super-residuals. On this basis, the behavior-genetic analysis was conducted using just one of the tilt super-residuals (as they are all identical). Consistent with the previous two datasets, a model comparison showed that the ACE model statistically outperforms both the ADE and the AE models. As with STR and MIDUS II the variance component analysis found that common environmental factors explained most of the standardized super-residualized tilt variance in these data. The results are depicted in Table 3.

3.1.2. Hypothesis 1b: random variable tilts

Several model comparisons were conducted using five tilts composed of randomly generated values assigned to GTS subjects using the code from Sorjonen et al. (2024). The AE model was found to outperform both the ACE and the ADE models (Table 4). A set of variance component analyses on these standardized random tilts also indicated that E (which can only capture error in this model, as the tilts are based on differences between randomly generated numbers) explained virtually all of the models' variances. This is detailed in Table 5.

3.2. Study 2: testing hypothesis 2 – tilt residual and Life History Speed correlation

Two of the three datasets employed in the present analysis contain direct estimates of psychometric LHS; MIDUS II and the STR STAGE. The latter dataset (which contains a short-form measure of LH, the Mini-K) is the larger of the two, containing 6714 individuals, after including the large singleton subsample and excluding one monozygotic twin from each pair so as to reduce pseudo-repeated measures. If the tilt residual corresponds to a CD-IE tradeoff, then it is possible to estimate *a priori* the sample size necessary to detect it with a given level of power. Assuming a weighted *r* of -0.036 (this being the sample size weighted CD-IE effect size from Woodley et al., 2013), an α of 0.05, and a power of 0.80, the power calculation recommended a minimum sample size of 5918 (the power analysis was conducted with the statistical software *GPower 3.1*; Faul et al., 2009, the results of this are presented in Fig. 2).

Only the full STR STAGE sample exceeded the *a priori* power requirement, therefore this sample will be used in testing Hypothesis 2.

Table 1

Model comparison and variance component analysis on a standardized residualized tilt based on data collected from the STR STAGE. Bold indicates best fitting model and strongest behavior genetic variance component.

| Variable | Model | AIC | Δ AIC | AIC w | BIC | Δ BIC | BIC w |
|-------------------------|----------------------------|------------------|---------------|----------------|------------------|--------------|--------------|
| z Residualized Tilt STR | ACE | -9572.080 | 0.000 | 1.000 | -9556.400 | 0.000 | 1.000 |
| | ADE | -8107.449 | 1464.632 | 0.000 | -8091.768 | 1464.632 | 0.000 |
| | AE | -8109.449 | 1462.632 | 0.000 | -8098.995 | 1457.405 | 0.000 |
| Variable | Variance Components | Estimate | 2.50 % | 97.50 % | | | |
| | A | 0.016 | 0.010 | 0.021 | | | |
| | C | 0.971 | 0.966 | 0.976 | | | |
| | E | 0.013 | 0.012 | 0.015 | | | |

Table 2

Model comparison and variance component analysis on a standardized residualized tilt based on data collected from MIDUS II. Bold indicates best fitting model and strongest behavior genetic variance component.

| Variable | Model | AIC | Δ AIC | AIC w | BIC | Δ BIC | BIC w |
|------------------------------|----------------------------|-----------------|---------------|----------------|-----------------|--------------|--------------|
| z Residualized Tilt MIDUS II | ACE | 1742.173 | 0.000 | 1.000 | 1754.192 | 0.000 | 1.000 |
| | ADE | 1849.374 | 107.201 | 0.000 | 1861.393 | 107.201 | 0.000 |
| | AE | 1847.374 | 105.201 | 0.000 | 1855.386 | 101.195 | 0.000 |
| Variable | Variance Components | Estimate | 2.50 % | 97.50 % | | | |
| | A | 0.144 | 0.063 | 0.225 | | | |
| | C | 0.747 | 0.673 | 0.821 | | | |
| | E | 0.108 | 0.082 | 0.135 | | | |

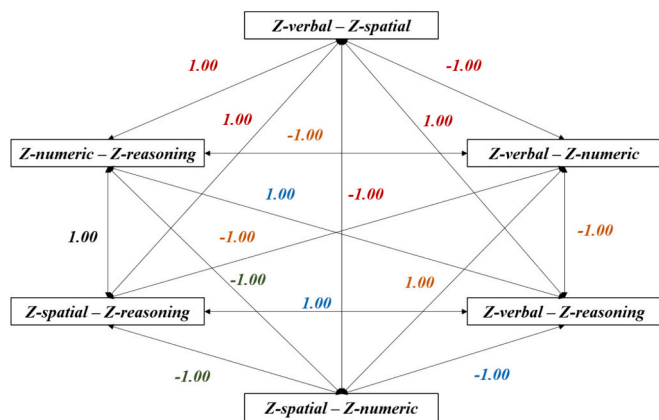


Fig. 1. Bivariate correlation constellation illustrating identical effect sizes among each standardized super-residualized tilt.

Table 3

Model comparison and variance component analysis on the standardized tilt super-residual based on data collected from GTS. Bold indicates best fitting model and strongest behavior genetic variance component.

| Variable | Model | AIC | Δ AIC | AIC w | BIC | Δ BIC | BIC w |
|---------------------------|----------------------------|-----------------|---------------|----------------|----------------|--------------|--------------|
| z Tilt Super Residual GTS | ACE | 535.823 | 0.000 | 1.000 | 545.548 | 0.000 | 1.000 |
| | ADE | 734.625 | 198.802 | 0.000 | 744.350 | 198.802 | 0.000 |
| | AE | 732.625 | 196.802 | 0.000 | 739.108 | 193.560 | 0.000 |
| Variable | Variance Components | Estimate | 2.50 % | 97.50 % | | | |
| | A | 0.007 | -0.016 | 0.030 | | | |
| | C | 0.966 | 0.947 | 0.986 | | | |
| | E | 0.027 | 0.017 | 0.037 | | | |

The STR STAGE data were winsorized using the *winsorize* function found in the *DescTools* package (Signorelli et al., 2017) in order to control for the effects of potential outliers. A General Linear Model, whose outputs were adjusted for the Mini-K's reliability via division by the square root of this parameter ($r_{xx} = 0.73$; Figueredo et al., 2014), yielded indications that higher levels of *K* (slower *LH*) are positively and significantly predictive of a larger tilt-residual above and beyond any influence of potential outliers ($r = 0.023, p = .0258$). A scatterplot of the tilt residual as a function of Mini-K is presented in Fig. 3.

3.3. Study 3: testing hypothesis 3 – latent variables in the Georgia Twin Study

Horn's parallel analysis recommended the extraction of four latent dimensions in the full GTS dataset. A principal axis factor analysis (assuming a four-factor solution) revealed that the first factor positively loaded onto *reasoning*, *numerical*, *verbal*, and *spatial* cognitive abilities, explaining 23.7 % of the variance, which clearly identifies this as GCA. The second latent dimension positively loaded onto *weight*, *height*, and *head breadth*, accounting for 14.6 % of the variance. This seems to represent a *general growth dimension*. The third factor positively loaded onto *head circumference* and *head length*, explaining 14.2 % of the variance, suggesting the existence of a *craniometric proportions dimension*.² The last latent dimension positively loaded onto *face length* and *nose length*, accounting for 11.2 % of the variance, suggesting the presence of a *facial proportions dimension*. Overall, the model explained 63.7 % of the variance. These results are further described in Table 6. The analysis also revealed that the GCA dimension featured statistically significant,

albeit weak, correlations with the various morphometric factors. In turn, the various morphometric dimensions featured weak-to-moderate inter-factor correlations (values given in Table 7). Due to the magnitude of the latter correlations it was not possible to explore alternative factor

² As this sample was composed of both black and white participants, it is possible that variation in craniometric index might be causing head circumference and length to load onto a different factor to head breadth.

Table 4

Model comparison involving standardized pseudo-tilts composed using randomly generated numbers. Bold indicates best fitting model.

| Variable | Model | AIC | Δ AIC | AIC w | BIC | Δ BIC | BIC w |
|----------------|--------------|-----------------|--------------------------------|--------------|-----------------|--------------------------------|--------------|
| z RandomTilt 1 | ACE | 1077.698 | 5.225 | 0.064 | 1087.424 | 5.225 | 0.064 |
| | ADE | 1077.715 | 5.242 | 0.063 | 1087.441 | 5.242 | 0.063 |
| | AE | 1075.715 | 0.000 | 0.873 | 1082.199 | 0.000 | 0.873 |
| Variable | Model | AIC | Δ AIC | AIC w | BIC | Δ BIC | BIC w |
| z RandomTilt 2 | ACE | 1076.940 | 1.615 | 0.246 | 1086.665 | 4.856 | 0.076 |
| | ADE | 1077.325 | 2.000 | 0.203 | 1087.050 | 5.242 | 0.063 |
| | AE | 1075.325 | 0.000 | 0.551 | 1081.809 | 0.000 | 0.861 |
| Variable | Model | AIC | Δ AIC | AIC w | BIC | Δ BIC | BIC w |
| z RandomTilt 3 | ACE | 1077.582 | 1.886 | 0.222 | 1087.307 | 5.128 | 0.067 |
| | ADE | 1077.695 | 2.000 | 0.209 | 1087.421 | 5.242 | 0.063 |
| | AE | 1075.695 | 0.000 | 0.569 | 1082.179 | 0.000 | 0.870 |
| Variable | Model | AIC | Δ AIC | AIC w | BIC | Δ BIC | BIC w |
| z RandomTilt 4 | ACE | 1077.716 | 2.000 | 0.212 | 1087.441 | 5.242 | 0.064 |
| | ADE | 1077.716 | 2.000 | 0.212 | 1087.441 | 5.242 | 0.064 |
| | AE | 1075.716 | 0.000 | 0.576 | 1082.200 | 0.000 | 0.873 |
| Variable | Model | AIC | Δ AIC | AIC w | BIC | Δ BIC | BIC w |
| z RandomTilt 5 | ACE | 1077.696 | 1.979 | 0.214 | 1087.421 | 5.221 | 0.064 |
| | ADE | 1077.716 | 2.000 | 0.211 | 1087.441 | 5.242 | 0.063 |
| | AE | 1075.716 | 0.000 | 0.575 | 1082.200 | 0.000 | 0.872 |

Table 5

Behavior-genetic variance component analyses using five pseudo-tilts composed using random variables. Bold indicates the strongest behavior genetic variance component.

| Variable | Variance Component | Estimate | 2.50 % | 97.50 % |
|-----------------|--------------------|--------------|--------------|--------------|
| z Random Tilt 1 | A | 0.003 | -0.185 | 0.191 |
| | E | 0.997 | 0.809 | 1.185 |
| z Random Tilt 2 | A | 0.063 | -0.133 | 0.258 |
| | E | 0.937 | 0.742 | 1.133 |
| z Random Tilt 3 | A | 0.015 | -0.185 | 0.214 |
| | E | 0.985 | 0.786 | 1.185 |
| z Random Tilt 4 | A | 0.000 | 0.000 | 0.000 |
| | E | 1.000 | 1.000 | 1.000 |
| z Random Tilt 5 | A | 0.000 | 0.000 | 0.000 |
| | E | 1.000 | 1.000 | 1.000 |

structures such as either a hierarchical organization, featuring a higher order factor, or alternative transformations, such as Schmid-Leiman.

A correlated factors model, based on Table 6 and Table 7, is illustrated in Fig. 4.

4. Discussion

The results of the three studies are broadly consistent with the hypotheses stated in the introduction. Consistent with H_{1a}, in all cases ACE models best fit the tilt residuals, with C variance being the dominant variance component, accounting for between 74.7 and 97.1 % of the variance across models. H_{1b} was also confirmed. The tilts constructed from the random number variables (assigned to GTS participants) were

associated with AE models in all cases, with E variance accounting for between 93.7 and 100 % of the variance across five runs. Confirmation of H_{1a} and H_{1b} corroborate H₁, as they indicate that even when tilts are residualized for their associations with their (and other) constituent variables, they are still substantive, being associated with C variance. This is consistent with the expectation that *irrespective* of how CD-IE is being allocated, the *degree* to which such effort is allocated should be strongly conditioned by factors associated with the shared environment, which would include “active” effects involving the identification of, and specialization with respect to, cognitive niches, driven by, among other things, perceptions of the stability of family, school, and neighborhood, as in the absence of perceived (and real) stability, mechanisms of specialization cannot function. Notably, the estimation of tilt super-residuals in the case of GTS (where each tilt could be residualized simultaneously for all four primary mental abilities, thus controlling for potential correlations between the tilt and seemingly uninvolved abilities) yielded clear indications of the existence of a single underlying super-residual (Fig. 1), which, as with the residuals estimated in the case of STR STAGE and MIDUS II, exhibited the highest affinity for ACE models. Another intriguing finding is the apparent persistence of C variance into late life. The mean ages of STR STAGE and MIDUS II participants were 40.7 and 60 years respectively. C variance for many traits tends toward zero among those in early adulthood (Horn & Loehlin, 2020), which makes these findings especially intriguing, as they very clearly violate this trend.

The tilt residuals also remain weakly heritable (statistically significantly so in the case of the two larger samples), with additive effects (A) accounting for between 0.7 and 14.4 % of the variance across samples.

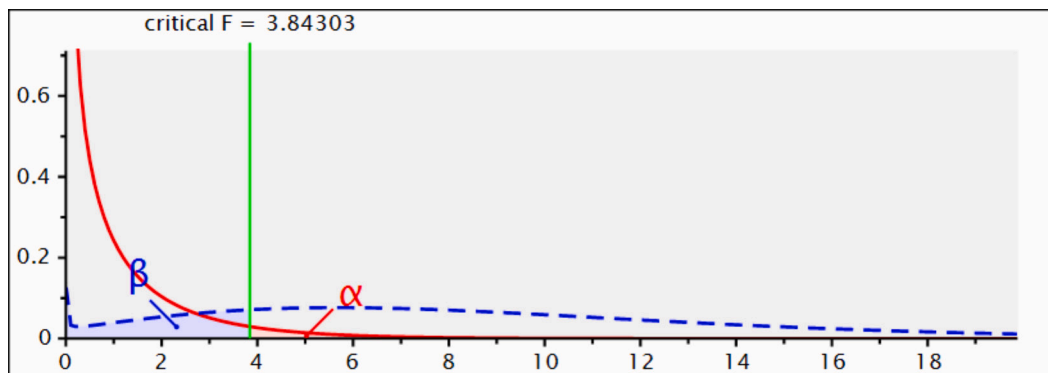


Fig. 2. A priori power analysis estimating minimum sample size based on weighted $r = -0.036$, $\alpha = 0.05$, and power = 0.80.

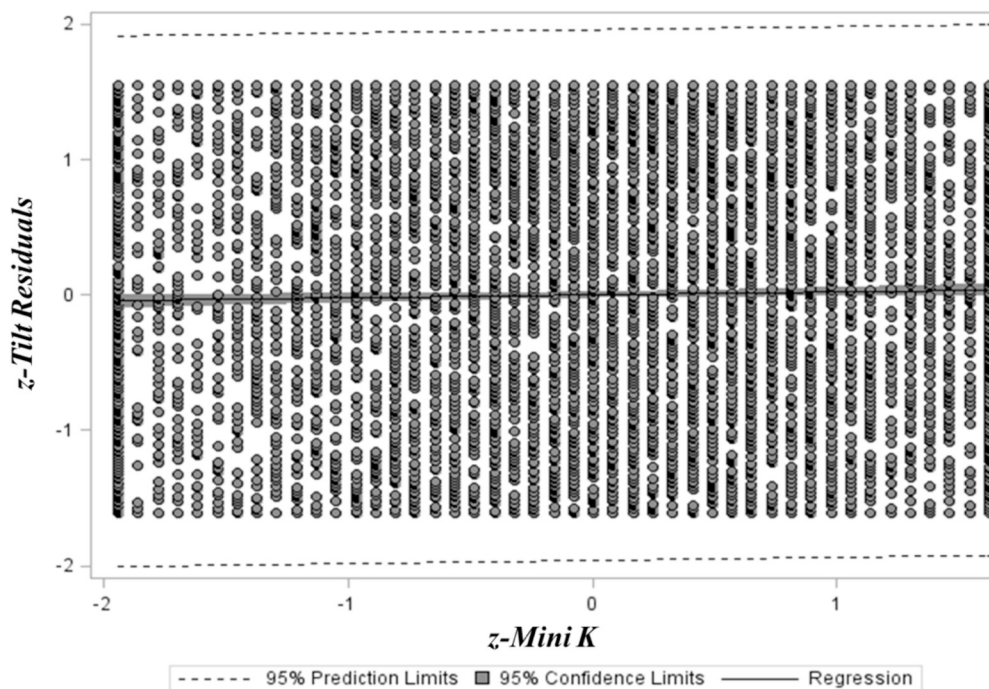


Fig. 3. Scatterplot of winsorized and standardized STR STAGE tilt residual vs. Mini-K scores.

Table 6

Principal axis factor analysis based on cognitive and morphometric indicators collected from the Georgia Twin Study. ML = Maximum Likelihood factor. Bold indicates which latent variables preferentially load onto which manifest variables

| Indicator | ML1 | ML2 | ML3 | ML4 | h^2 | u^2 | Communalities |
|--------------------|--------------|--------------|--------------|--------------|-------|-------|---------------|
| Reasoning | 0.925 | -0.026 | -0.021 | -0.075 | 0.835 | 0.165 | 1.020 |
| Numerical | 0.784 | 0.020 | 0.041 | 0.045 | 0.643 | 0.357 | 1.010 |
| Verbal | 0.771 | -0.002 | -0.088 | 0.079 | 0.601 | 0.399 | 1.050 |
| Spatial | 0.670 | 0.026 | 0.136 | -0.076 | 0.488 | 0.512 | 1.110 |
| Weight | -0.041 | 0.819 | 0.014 | -0.027 | 0.653 | 0.347 | 1.010 |
| Height | 0.055 | 0.604 | 0.029 | 0.232 | 0.557 | 0.443 | 1.310 |
| Head breadth | 0.057 | 0.580 | 0.216 | -0.153 | 0.472 | 0.528 | 1.450 |
| Head circumference | -0.018 | 0.089 | 0.951 | 0.006 | 0.995 | 0.005 | 1.020 |
| Head length | 0.203 | 0.045 | 0.554 | 0.342 | 0.652 | 0.348 | 1.990 |
| Face length | -0.086 | -0.026 | 0.208 | 0.760 | 0.683 | 0.317 | 1.180 |
| Nose length | 0.094 | 0.232 | -0.275 | 0.578 | 0.428 | 0.572 | 1.860 |

Table 7

Inter-factor correlation matrix estimated with a principal axis factor analysis based on cognitive and morphometric indicators collected from the Georgia Twin Study. Correlations below the diagonal, significances above. ML = Maximum Likelihood factor. CIs in parentheses.

| | ML1 | ML2 | ML3 | ML4 |
|-----|----------------------|----------------------|----------------------|-------|
| ML1 | 1.000 | <0.05 | <0.05 | <0.05 |
| ML2 | 0.243 (0.165, 0.318) | 1.000 | <0.05 | <0.05 |
| ML3 | 0.110 (0.029, 0.189) | 0.494 (0.430, 0.553) | 1.000 | <0.05 |
| ML4 | 0.101 (0.020, 0.181) | 0.340 (0.266, 0.410) | 0.280 (0.204, 0.353) | 1.000 |

Some non-zero additivity would also be predicted on the basis that cognitive plasticity might itself be to some extent heritable. This finding is consistent with theory and data presented in Woodley of Menie et al. (2015), in which the modest heritability of LH plasticity (estimated with respect to continuous parameter estimates of covariance among Super-K and its constituent LH subfactors) was demonstrated using Falconer’s-based heritability estimates. The finding of non-zero heritability for these tilt “super-residuals” further challenges the “spurious origin”

hypothesis, as they should have exactly zero heritability were this the case (precisely because spurious sources of heritability have been thoroughly controlled), in addition to being entirely associated with E variance, specifically capturing error.

Consistent with H₂ it was found that the tilt residual was positively correlated with Mini-K scores in the STR STAGE. The association is small by the standards of psychological science, however ($r = 0.023$ vs. $r \approx 0.20$; Gignac & Szodorai, 2016), indicating that H₂ is only weakly confirmed. Despite this, the presence of a positive and significant association between these two variables, using a large sample of singletons, DZ and MZ twins, provides at least some evidence supporting the identification of these tilt residuals with CD-IE, as the effect size is similar in magnitude to the sample size weighted CD-IE effect size reported in Woodley et al. (2013) (0.023 vs. -0.036). The association is consonant with the expectation that those exhibiting slower LH speeds should also have a greater general tendency to allocate effort to the cultivation of narrower abilities, irrespective of domain, which may in turn entail tradeoffs between abilities competing for common bioenergetic resources, yielding tilts. Future research should of course attempt to replicate this finding.

Consistent with H₃ it was found that the GTS data could be reduced to four latent variables. One of these corresponds clearly to GCA, the

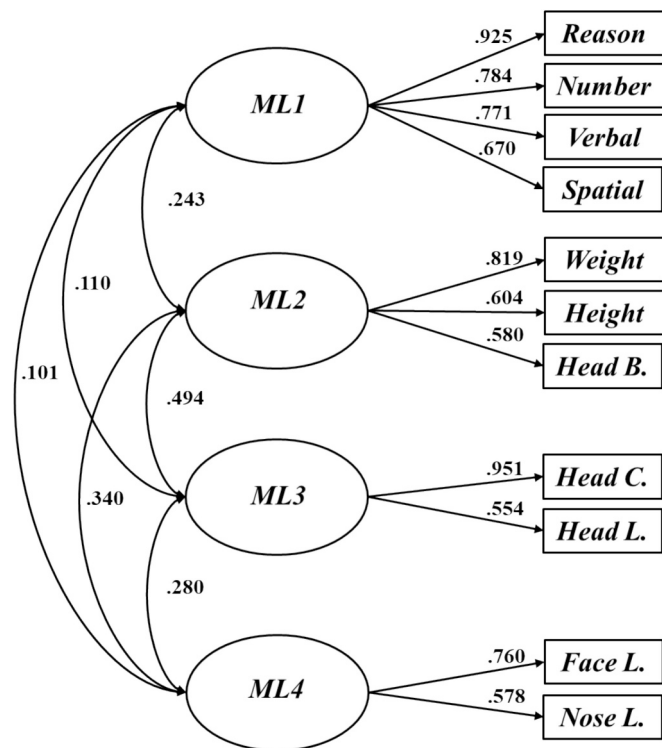


Fig. 4. Principal axis factor analysis demonstrating the presence of four latent dimensions corresponding to a general cognitive ability factor and three morphometric factors. Note: Head B: Head breadth; Head C: Head circumference; Head L: Head length; Face L: Face length; Nose L: Nose length. Cross loadings are not displayed.

others can be interpreted as dimensions of *general growth* (incorporating measures of weight, height, and head breadth), *craniometric proportions* (incorporating measures of head circumference and length), and *facial proportions* (incorporating face and nose length). These dimensions suggest the existence of distinct developmental modules that can accommodate tradeoffs among their constituent subdomains. Tradeoffs among subdomains associated with *different* developmental modules on the other hand lack validity. Sorjonen et al. (2024) give the example of an apparently heritable tilt between nose length and spatial ability (shorter noses go with greater spatial ability) by way of evidencing the spuriousness hypothesis, but based on Table 6, it is clear that nose length exhibits minimal cross-loading onto the GCA factor, to which spatial ability belongs (ML1; $\lambda = 0.094$). Similarly, spatial ability does not cross-load onto the *facial proportions* factor to which nose length belongs (ML4; $\lambda = -0.076$). These findings indicate that theoretical care must be taken when designating tilts, as these would only be expected to be meaningful when they involve specific measures that share a common latent source (suggesting affinity for a common developmental module).

It should be noted that there are significant (and positive) inter-factor correlations among these dimensions, but these do not cohere into a distinct superordinate latent variable. Such correlations may reflect the action of pleiotropic genetic variants (such as deleterious mutations), which cut across these developmental modules, yielding “global” variation in condition. Models positing the existence of global *fitness* or *system integrity* have been proposed as explanations for the existence of correlations between factors such as fluctuating asymmetry (the variance in positioning of ideally bilaterally symmetric anatomical markers), height, health outcomes, and GCA (Deary, 2012; Houle, 2000; Miller, 2000). The higher-order positive inter-factor correlations noted in GTS might therefore reflect general condition dependence. Alternatively, as was noted in the introduction, even though the psychometric Super-K factor is nomologically broad (incorporating general factors of

personality, covitality, and behavioral strategy) it seems to be (mostly) independent of GCA, suggesting the existence of developmental modules that may be partially or even wholly independent of one another. Associations between psychometric and biometric LH indicators seem also to be highly inconsistent, with self-reports of developmental milestones (such as pubertal timing) seeming to exhibit little association with psychometric measures of “high-K” or “slow” LH strategy (Copping et al., 2014; cf. Figueredo et al., 2015); but certain exceptions have been noted, such as a large-magnitude positive association between semen quality and Mini-K score ($r > 0.6$; Barbaro et al., 2018). Biometric and psychometric LH variables might be predicted to exhibit at least some degree of independence from one another in humans on the basis that slow LH is associated generally with weaker correlations among LH components, suggesting that LH is more modular in these cases (Figueredo et al., 2013; Woodley of Menie et al., 2015, 2021). The different morphometric investment domains identified in the GTS may therefore result from this process of modularization selection, with the higher-order inter-factor correlations reflecting the influence of another kind of genetic effect, specifically relational loci (which regulate the strength of the genetic correlations between traits via gene-by-gene and gene-by-environment interactions). The signature of these would be in the presence of positive inter-factor correlations *without* the existence of a higher-order unitary LH factor (see Woodley of Menie et al., 2021, p. 226). Future research should focus on the use of parallel analysis to explore the factor structure in the broader GTS database, as this includes numerous variables covering other domains (such as personality).

Sorjonen et al. (2024) identified potential flaws in the work of Coyle et al. (2023). They present a seemingly solid case to the effect that the apparent heritabilities of the reported tilts is spurious, reflecting the heritabilities of their constituent abilities. But their “spuriousness hypothesis” faced empirical anomalies (such as the findings of Kato & Scherbaum, 2023) and led to new predictions concerning the nature of tilts, and the specific factors that may generate them. By theoretically merging tilt research with LH theory a series of new hypotheses have now been advanced and confirmed, which in turn have offered new insights into the relationship between tilts, behavior-genetic variance components, and broader developmental modules. At its core, a tilt is simply the result of a tradeoff that takes place between two competing investment domains within the context of a broader developmental module. The “essence” of cognitive tilts (in particular) appears to be an LH dimension (CD-IE) which either enhances or inhibits (depending on the individual’s LH speed) the development of specialized abilities. Those with slower LH have a greater propensity toward the cultivation of narrow abilities, which necessitates tradeoffs among them, given finite bioenergetic resources. The CD-IE dimension is heavily conditioned by shared environmentality (consistent with models positing both active effects and adaptive calibration given perceptions of environmental stability). These may in fact be among the largest C variances ever reported in the behavior-genetic literature in adults. Remarkably, C is the dominant variance component among older participants, suggesting effects of development that endure throughout the life course. The tilt residuals also exhibit small heritabilities (up to 14 %), suggesting some degree of biological preparedness for developmental plasticity, again consistent with explicit predictions from LH theory (Woodley of Menie et al., 2015).

We thank Sorjonen et al. (2024) for their contribution to this debate, which has initiated a new and hopefully very productive phase of growth in the tilt research program.

Ethics statement

All analyses were based on publicly access databases and did not require an IRB review.

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CRedit authorship contribution statement

Michael A. Woodley of Menie: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization. **Matthew A. Sarraf:** Writing – review & editing, Conceptualization. **Mateo Peñaherrera-Aguirre:** Writing – original draft, Methodology, Formal analysis, Conceptualization. **Thomas R. Coyle:** Writing – review & editing. **Guy Madison:** Writing – review & editing.

Declaration of competing interest

The authors declare no financial interests in the outcome of this work.

Data availability

Data will be made available on request.

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