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Executive functions and intelligence- are there genetic difference?

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ABSTRACT

The first aim of this study was to explore the aetiology of phenotypic relationships between different measures of executive functions. The second objective was to examine sources of the covariation between different measures of executive functions and the measure of general cognitive ability. The study sample consisted of 468 twins (154 pairs of monozygotic twins and 80 pairs of dizygotic twins) of the same and different gender who grew up together. Executive functions were evaluated by the Wisconsin Card Sorting Test, the Trail Making Test – form B, and verbal fluency tests. Raven's Advanced Progressive Matrices were used as a measure of general cognitive ability. The study results suggest a primarily genetic origin of the mutual covariation of different executive measures and their covariation with the general cognitive ability construct. While the shared genetic variance primarily lies in the bases of similarity/unity of the used cognitive measures, their particularity/difference is determined by a specific unshared environment. The obtained result on the presence of a single general genetic factor, which can be singled out in the case of different executive measures, at least partially speaks in favor of the thesis about the unity of various executive measures and the existence of a common basic ability. Together with the specific unshared environment, the specific genetic influence speaks in favor of a difference between each of the individual measures.

1. Introduction

The theoretical construct of "executive function" has been the subject of a large number of studies in the past decades (Anderson, 2002; Barkley, 1997; Craig et al., 2016; Friedman et al., 2008; Lezak, 1982; Miyake et al., 2000; Puente, Lindbergh, & Miller, 2015; Salthouse, 2005; Zelazo & Carlson, 2012). However, the conceptual status of the term "executive function" (EF) is still unclear, mainly due to different strategies for assessing this phenomenon and the lack of a unique empirical framework for its study. Initial research emphasized the homogeneity of the construct and the existence of a single, central, executive function (Baddeley, 2007; Norman & Shallice, 2000). Over time, research findings have started to suggest that the concept of executive function is only an umbrella term that encompasses a set of interconnected processes necessary for purposeful, goal-oriented behavior (Anderson, 2002; Anderson, Jacobs, & Anderson, 2008; Hughes & Graham, 2002; Miyake & Friedman, 2012a). This highly complex and integrated set of cognitive abilities is paramount for adaptive functioning and includes the processes of planning, goal setting, task initiation, and task monitoring, ability to inhibit or delay responses, response evaluation, cognitive flexibility, as well as the selection of efficient strategies necessary for problem solving (Anderson, 2002; Damasio & Anderson, 1993; Diamond, 2013; Luria, 1966; Welsh, Pennington, & Groisser, 1991; Zelazo, Carter, Reznick, & Frye, 1997).

Some of the most frequently used EF measures are the Wisconsin Card Sorting Test (WCST; Heaton, Chelune, Talley, Kay, & Curtiss, 1993), the Trail Making Test – TMT-A/TMT-B (TMT: Reitan, 1955; Spreen & Strauss, 1991), and verbal fluency tests (Goodglass & Kaplan, 1983; Lezak, 1995). The WCST has a strong, long-established tradition in neuropsychology and it is probably the most widely used measure of executive functions (Butler, Retzlaff, & Vanderploeg, 1991). It engages different executive processes: strategic planning, organized searching, utilizing environmental feedback to shift mental sets, maintaining mental sets, modulating impulsive responding, and goal-oriented

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behavior (Demakis, 2003; Eling, Derckx, & Maes, 2008; Heaton et al., 1993). The Trail Making Test (TMT-A/TMT-B) is a measure of simple (A) and complex (B) conceptual monitoring, i.e., divided attention. Having in mind that this test evaluates higher levels of executive control or complex conceptual monitoring, Baron (2004) pointed out that high achievement on the test primarily requires flexibility in shifting the mental set in conditions of rapid changes in concepts. While TMT-A is most often used as a measure of processing speed, TMT-B is generally used as an index of executive function (Lezak, Howieson, & Loring, 2004). Tests of verbal fluency (Phonemic and Category fluency) assess the ability to generate verbal material, according to set rules during a limited time period. They are often used in clinical practice when evaluating executive functions, since they require planning, organized search, and execution monitoring (Spreen & Strauss, 1991).

Other tests that are used as EF measures involve language or visuospatial processing, components of short- and long-term memory, and motor and/or verbal reactions (Burgess & Shallice, 1997; Shallice, 1982; Stroop, 1935). Since executive functions are meta-processes that operate above other processes, a specific task used to assess executive function usually encounters the problem of impurity. Thus, only a combination of tasks and measures provides a more reliable estimation (Suchy, 2009).

The next topic is related to the issue of discriminant validity and concerns the distinction between the concept of executive functions and the concept of general cognitive ability (Salthouse, 2005). The interconnection of these concepts can be illustrated by their definitions, since both refer to planning, problem-solving, and comprehension, all of which are core components of "intelligent behavior" (Ardila, Pineda, & Rosselli, 2000; Arffa, 2007). While some authors have found no significant correlation between these concepts (Ardila et al., 2000; Boone, Ghaffarian, Lesser, & Hill–Gutierrez, E., 1993; Welsh et al., 1991), others have found a correlation between general cognitive ability and almost all measures of executive functions (Salthouse, 2005; Salthouse, Atkinson, & Berish, 2003) or certain aspects thereof (Friedman et al., 2006). Previous studies were mostly conducted on clinical samples. Their results have indicated that frontal lesions resulting in the deficit of executive functions do not lead to a significant decrease in general cognitive ability, suggesting their relative independency (Damasio & Anderson, 1993; Hebb, 1939, 1945). However, some findings (Duncan, Burgess, & Emslie, 1995) have shown that measures of fluid intelligence decline after frontal lesions, which are traditionally associated with EF deficits. It seems that the correlation between EF and general cognitive ability depends on both intelligence type and the EF measures used.

Behavioral genetic studies (Anokhin, Heath, & Ralano, 2003; Friedman et al., 2008; Swan & Carmelli, 2002; Vasilopoulos et al., 2012) have greatly contributed to determining the aetiology of the EF phenomenon and specifying the nature of the relationship between EF and similar constructs. The results of behavioral genetic studies have generally indicated that the estimation of EF heritability depends on the type of assessment and sample age (Anokhin et al., 2003; Friedman et al., 2008; Kremen et al., 2009; Taylor, 2007; Vasilopoulos et al., 2012). Regarding the WCST, inconsistent results have varied from no evidence of influence (Campana, Macciardi, Gambini, & Scarone, 1996; Chou, Kuo, Lin, & Chen, 2010; Kremen, Eisen, Tsuang, & Lyons, 2007; Taylor, 2007) to a modest-to-moderate influence of genetic factors on indicators of EF (Anokhin et al., 2003; Anokhin, Golosheykin, Grant, & Heath, 2010; Godinez, Friedman, Rhee, Miyake, & Hewitt, 2012). Heritability indices have ranged from 0.23–0.38 for TMT-A to 0.39–0.65 for TMT-B (Buyske et al., 2006; Swan & Carmelli, 2002; Vasilopoulos et al., 2012), and from 0.34 to 0.55 for verbal fluency tests (Phonemic and Category) (Hoekstra, Bartels, van Leeuwen, & Boomsma, 2009; Swan & Carmelli, 2002; Volk, McDermott, Roediger, & Todd, 2006).

On the other hand, on a sample of adolescent twins, Friedman et al. (2008) showed that the executive processes of inhibition, updating, and shifting are cognitive abilities that are almost entirely genetic in origin, with a heritability of up to 99%. Although the entire variance of EF in this study comprised three phenotypes (updating, inhibiting, and shifting), multivariate genetic analysis revealed only one common/general genetic factor. This result indicated that there were comprehensive genetic factors underlying different cognitive measures. Furthermore, Godinez et al. (2012) specified that the covariance between different WCST indicators is best explained by a general/common genetic factor, whereas differences between indicators are caused by specific genetic and environmental factors. Lee et al. (2012) used indicators of different executive functions (a measure of working memory, verbal fluency, inhibition, and cognitive flexibility) and found a single common genetic factor for all measures, while each measure had its own specific factors of unshared environment.

Multivariate genetic analysis of general cognitive ability and different executive processes suggests that these two cognitive constructs often have a high correlation, but cannot be reduced to one another. Findings indicate that there is a significant portion of specific genetic variance. This explains for the variance in executive functions, which is independent of general cognitive ability (Friedman et al., 2006; Friedman et al., 2008; Rabbitt, Lowe, & Shilling, 2001).

The main objective of this research was to examine whether different aspects of executive functions have the same genetic basis. Since executive functions have a central role in cognitive processes, it is important to determine whether the sources of individual differences in this domain are general or specific. As representative measures of executive functions in this study, we used the following: shifting, attention, and inhibition through WCST assessment, complex conceptual monitoring through TMT assessment and response generation and initiation through verbal fluency tests (Phonemic and Category fluency).

The second objective of the study was to examine relations between different aspects of executive functions and general cognitive ability. More specifically, we tried to determine whether executive functions share the same genetic basis with general cognitive ability. The results of this behavioral genetic study could contribute to the ongoing debate on whether executive functions constitute an aspect of general cognitive ability or could be considered as independent cognitive abilities.

2. Material and methods

2.1. Participants

The Twin Registry contains data from 1654 participants. This study covered 468 twins; 154 pairs of monozygotic (75.3% female) twins and 80 pairs of dizygotic (61.3% female) twins of the same and different gender. Dizygotic twin pairs included 35 mixed-gender pairs and 45 same-gender pairs. The age of participants ranged from 18 to 60, the average age being 24.7 (SD = 7.78). For most of the participants (96.8%), zygosity was determined by analyzing DNA material obtained by buccal swabs. DNA material was tested using short tandem repeat (STR) megaplex kits: either Investigator 24plex GO! (Qiagen, Valencia, CA, USA) or GlobalFiler (Applied Biosystems, Thermofisher Scientific, Waltham, MA, USA). Both kits detect 21 autosomal STRs. Samples with partial profiles were only interpreted if at least 10 loci were present.

For a smaller sample fraction (3.2%), zygosity was determined using the Twins Physical Resemblance Questionnaire (Oniszczenko, Angleitner, Strelau, & Angert, 1993). This questionnaire includes a series of questions about similarities and dissimilarities between twins in a twin pair (e.g. eye color, body weight, body height, etc.). Measures of this questionnaire have proved to be a reliable indicator of *zygosity* (accuracy of 90–95%) in a large number of studies (e.g., Reed et al., 2005; Spitz et al., 1996). Only participants who had all the results were included in our analysis.

2.2. Procedure

The entire procedure for testing and collecting data is described

elsewhere (Smederevac et al., 2019). Each respondent gave written informed consent for participation in accordance with the ethical procedures of psychological research. The research was approved by the Institutional Ethics Committee. Data were collected in the period between 2011 and the end of 2018. Cognitive abilities and executive functions were examined by trained researchers.

2.3. Measures

The Wisconsin Card Sorting Test – WCST (Heaton et al., 1993). The WCST is the most prominent test for assessing set-shifting, attention, and inhibition. The test assesses the possibility of creating and changing the principles of categorization. It uses the task of classifying a series of cards according to one of the three classification criteria (color, form, and number of elements). The variables used in this study were: the number of completed categories, the number of perseverative errors, and the number of non-perseverative errors.

The Trail Making Test – form A and B (TMT: Reitan, 1955; Spreen & Strauss, 1991). This test consists of two parts, each with a specific aim. The first part aims to measure attention, concentration, visual observation, visuospatial estimation, and visuomotor abilities. In addition to the above, the second part of the test assesses complex conceptual monitoring, which is also a type of executive ability. Longer completion time indicates lower achievement.

Verbal fluency tests– Phonemic fluency test and Category fluency test (Goodglass & Kaplan, 1983; Lezak, 1995). Verbal fluency is measured by the number of words produced in the unit of time. Words are usually limited to certain categories. Phonemic fluency test is assessed by testing controlled oral associations, including phonemes S/K/L in the Serbian language, which is equivalent to the Verbal Fluency Test (FAS) in the English language. In the Category fluency test, respondents are asked to generate exemplars from a given category. In this study, respondents were asked to indicate as many different animals as possible within a one-minute ("Animals" subtest from the Boston Diagnostic Aphasia Exam).

Advanced Progressive Matrices (APM: Raven, Raven, & Court, 1998). APM is a non-verbal test that measures fluid intelligence. It consists of 48 multi-choice questions, listed in the order of difficulty. This format is designed to measure the ability of reasoning; a component of Spearman's g factor that is often called general intelligence. Participants were instructed to complete each matrix, choosing one of eight response alternatives in accordance with logical rules. Series II, which consists of 36 items, was applied in this study. Task solving time was limited to 40 min.

Before starting the analysis, variables related to the number of errors and reaction time were recoded, with higher value representing better achievement (TMT-A reaction time, TMT-B reaction time, WCST-number of perseverative errors, and WCST-number of non-perseverative errors).

2.4. Statistical analysis

2.4.1. Phenotypic analysis and twin intraclass correlation analysis

Descriptive statistical parameters and correlations (phenotype and intraclass) were calculated in the SPSS v.21 software (IBM Corp, 2012). Prior to genetic model-fitting, all cognitive measures were corrected for age and sex effects by applying McGue and Bouchard's (1984) regression technique, i.e., entering sex and age as predictors and taking each specific ability test as a criterion, while retaining the residuals.

2.4.2. Factor analysis

The latent structure of the seven phenotypic EF measures was examined using both exploratory factor analysis (EFA) and confirmatory factor analysis (CFA), with a maximum likelihood estimator (ML). Therefore, the twin sample was split into two subsamples. The Twin 1 subsample was composed of all the first twins from the pairs, while the Twin 2 subsample was composed of all the second twins from the pairs. To determine the minimum number of latent factors that can account for the shared covariance among EF measures, we conducted EFAs using "R environment" (R Core Team, 2016) on the Twin 1 subsample. Since we expected high intercorrelations between EF variables, the Promax rotations were chosen, which allow for a correlation between factors. The series of EFA considered one-, two- and three-factor solutions. After comparing various fit indices among different models, the most appropriate EFA factor solution was chosen. The results of the EFA were then cross-validated in the Twin 2 subsample, via CFA, which was run in the "lavaan" R package (Rosseel, 2012). In line with recommendations made by Hu and Bentler (1999), several fit indices were used for determining model fit: χ^2, Comparative fit index—CFI, Tucker-Lewis index—TLI, Root mean square error of approximation—RMSEA, and Standardized root mean residual—SRMR. The results of the phenotypic factor analyses, as regression-based factor scores, were used as the basis for multivariate quantitative genetic models.

2.4.3. Multivariate genetic analysis

Multivariate genetic analysis was used to examine the nature of relationships between EF factors and general cognitive ability, by specifying to what extent they share genetic and environmental influences and how their influences differ. Multivariate structural equation modeling (SEM) was conducted in the "lavaan" R package (Rosseel, 2012).

Two multivariates, independent and common pathway models, were tested (Rijsdijk & Sham, 2002) in order to estimate additive genetic factors (A), shared environmental (C) and nonshared environmental (E) factors, specific (s) and common (c) genetic and environmental sources of variance. These models represent different patterns of genetic and environmental influences, which can explain for the observed phenotypic correlations between different cognitive measures. In both models, there were specific (s) and common (c) genetic and environmental sources of variance.

The independent pathway model specifies that genetic and environmental factors that are common to the variables have their own, independent pathways to each of the phenotypic variables. In the common pathway model, both genes and the environment contribute to one latent variable that is responsible for the observed covariance between the outcome measures. In other words, the common pathway model assumes that a single underlying latent phenotype is solely responsible for the covariation among different measures. Both the independent and common pathway models specify that each phenotypic variable may also be influenced by specific environmental or genetic factors that are not shared with the other variables.

A series of independent and common pathway models were fitted into multivariate covariance matrices. In accordance with parsimony criteria, we selected the model with the least number of parameters and a fit not significantly worse than the full model. Plausible solutions were chosen using several fit indicators to compare the independent and common pathways, full (ACE) and reduced (AE, CE) models. Analysis parameters were calculated using an ML estimator. Model evaluation was based on the Akaike Information Criterion (AIC; Akaike, 1973), the Bayesian Information Criterion (BIC; Schwarz, 1978), comparative fit index, the Tucker–Lewis index (CFI and TLI – optimal values higher than 0.95, acceptable higher than 0.90), and the root mean square error of approximation (RMSEA – optimal values lower than 0.05, acceptable lower than.08), with acceptable value below.08 (Hu & Bentler, 1999).

Additionally, genetic and environmental correlations between EF and general cognitive ability variables were calculated using multivariate Cholesky decomposition models, which provided useful information on aetiological relations between variables.

Table 1
Descriptive statistics and Twin intra-class correlation coefficients for the used measures with 95% confidence intervals.

	M (SD)	MZ	DZ
Number of categories (WCST)	5.48 (1.27)	0.29** (0.17; 0.40)	−0.11 (−0.23; 0.02)
Perseverative errors (WCST)	12.22 (9.20)	0.21** (0.08; 0.33)	0.04 (−0.09; 0.17)
Non-perseverative Errors (WCST)	10.63 (9.91)	0.28** (0.16; 0.39)	−0.17 (−0.29; −0.04)
TMT-A reaction time	29.95 (10.25)	0.42** (0.31; 0.52)	0.27** (0.15; 0.38)
TMT-B reaction time	44.48 (15.46)	0.39** (0.28; 0.49)	0.17 (0.04; 0.29)
Phonemic fluency	11.45 (3.17)	0.50** (0.40; 0.59)	0.31** (0.19; 0.42)
Category fluency	24.03 (5.56)	0.44** (0.33; 0.54)	0.28* (0.16; 0.39)
General cognitive ability (APM)	20.72 (6.18)	0.73** (0.65; 0.79)	0.43** (0.21; 0.60)
WCST factor		0.29** (0.14; 0.44)	−0.08 (−0.29; 0.14)
TMT factor		0.41** (0.27; 0.54)	0.18 (−0.03; 0.38)
Verbal fluency factor		0.46**(0.32; 0.58)	0.28*(0.08; 0.48)

Note. M – mean, SD – standard deviation; MZ – monozygotic twins, DZ – dizygotic twins; * $p < .05$. ** $p < .01$. WCST- Wisconsin card sorting test; TMT-A, TMT-B - Trail Making Test – form A and B; Phonemic Fluency and Category Fluency – Tests of verbal fluency; APM- Advanced Progressive Matrices; WCST factor- Number of Categories, Perseverative Errors, Non-perseverative Errors; TMT factor- Trail Making Test – form A and B; Verbal fluency factor- Phonemic fluency and Category fluency.

3. Results

3.1. Descriptive statistics of phenotypic characteristics and twin intra-class correlation

The values of skewness and kurtosis indicated that almost all cognitive measures were non-normally distributed, except for phonemic fluency, category fluency, and general cognitive ability. Therefore, all measures were first normalized using the rank-based inverse normal (Rankit) transformation (Solomon & Sawilowsky, 2009). After the transformation, the magnitude of both skewness and kurtosis fell within the range of −1 to 1, indicating that all distributions reached normality. Means, standard deviations, and univariate cross-twin (intraclass) correlations for each zygosity group are provided in Table 1.

Correlations between MZ twins were consistently higher than correlations between DZ twins for all measures. On all eight measures, correlations between MZ twins were positive, significant, and of low-to-moderate strength. The high correlation coefficient was detected in the case of general cognitive ability for MZ twins. Correlations between DZ twins were positive, significant, and of low-to-moderate strength for TMT-A, phonemic fluency, category fluency, and general cognitive ability. They were not significant for the remaining cognitive measures. Correlations for DZ twin pairs were approximately half of those for MZ pairs, suggesting that the resemblance between twin pairs is attributable to genetic factors.

3.2. Exploratory factor analysis (EFA) and confirmatory factor analysis (CFA)

The EFA was conducted on seven EF measures (the number of categories, perseverative errors, non-perseverative errors, TMT – form A and B, phonemic fluency and category fluency), with oblique rotation. One-, two- and three-factor solutions were examined as possible structures. The Chi-square test, Root mean square error of approximation (RMSEA), and the Tucker-Lewis Index (TLI) values indicated that the one- and two- factor solutions did not fit well ($\chi2(14) = 168.48$, $p < .001$, RMSEA = 0.22, TLI = 0.55) and ($\chi2(8) = 44.78$, $p < .001$, RMSEA = 0.14, TLI = 0.81), respectively. The three-factor solution provided the best fit to the data, ($\chi2(1) = 1.04$, $p = .79$, RMSEA = 0.00, TLI = 1.02). Factor loadings of this solution are given in Table 2. The pattern of loadings indicated that the aforementioned seven measures formed three separate domains. Factor 1 consisted of three different measures of WCTS (number of categories, perseverative errors, and non-perseverative errors). Factor 2 included TMT-A and TMT-B measures, while Factor 3 consisted of measures of Phonemic and Category fluency. These three factors were recognized as method factors, since each of them covered a specific EF measure.

The three-factor solution resulting from the EFA was subsequently tested via CFA in the Twin 2 subsample (see Table 2), showing an adequate fit to the data; $\chi2(11) = 8.23$, $p = .69$, RMSEA = 0.00, SRMR = 0.02, CFI = 1.00, TLI = 1.01. The correlation between factors ranged from 0.55, for second and third, 0.19 for first and second, and 0.21 for first and third factors. All loadings were significant. This three-factor solution suggested that the seven measures of EF could be covered by three latent factors: the WCST factor, the TMT factor, and the Verbal fluency factor.

3.3. Multivariate genetic analysis

Based on the results of the EFA, regression-based factor scores were used as variables in multivariate genetic analyses. The WCST factor, the TMT factor, and the Verbal fluency factor were entered as factor scores, while general cognitive ability was used as a score on the APM. The results of multivariate genetic modeling showed that AE models fitted better than full ACE models in analyses (Table 3). The most appropriate fit indices were for the AE independent pathways model. All indices were within acceptable boundaries. The estimation of the parameters of the best fitting models is given in Table 4. Additionally, parameter estimates are shown in Fig. 1.

The results from the independent AE pathway model suggested that genetic effects were higher for APM, while environmental effects were stronger in the case of WSCT, Verbal fluency, and TMT factors (Table 4). The overall variance of heredity was better explained by common genetic factors in the case of APM (63%) and TMT (31%), and specific genetic factors in the case of WCST and Verbal fluency. Specific genetic factors were most prominent in the Verbal fluency factor (28%). In all cases, specific environmental effects were stronger than common environmental effects. Common environmental impacts were low for TMT (18%) and Verbal fluency factors (20%) and non-existent (0%) for APM and WCST factors.

Phenotypic correlations were low between WCST and Verbal fluency, and WCST and TMT (Table 5). Genetic correlations between WCST and TMT were moderate (0.44), while the environmental correlation was non-significant. In the case of WCST and Verbal fluency, the genetic correlation was moderate (0.42), while the nonshared environmental correlation was non-significant (Table 5). On the other hand, the moderate phenotypic correlation between TMT and Verbal fluency is followed by a high genetic correlation (0.62). The common nonshared environmental factor explained for the lower percentage of their covariance. Furthermore, the phenotypic correlation between WCST and APM was moderate, with a high genetic correlation (0.65) and a non-significant environmental correlation. A moderate phenotypic correlation and a high genetic correlation were found between TMT and APM, while common the nonshared environmental

Table 2
Factor loadings from the 3-factor result of the EFA and CFA on measures of executive functions.

	EFA			CFA		
Measures	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Number of WCST Categories	0.88			0.68	....	....
Perseverative Errors	0.86			0.89	....	....
Non-perseverative Errors	0.75			0.91	....	....
TMT-A reaction time	..	0.60		....	0.73	....
TMT-B reaction time	..	1.02		....	0.71	....
Phonemic Fluency	..		0.45	....	....	0.56
Category Fluency	..		1.03	....	....	0.88

correlation was non-significant. A moderate correlation between the Verbal fluency and APM was predominantly the result of shared genes, which was supported by a moderate-to-high genetic correlation (0.53).

4. Discussion

The main objective of this study was to explore genetic and environmental contributions to the variance of cognitive abilities, with a special focus on determining the degree of genetic and environmental impact on covariation between general cognitive ability and executive functions. In order to cover representative aspects of intellectual ability and executive functions, we used APM for the assessment of general cognitive ability; WCST for shifting, attention, and inhibition; TMT for complex conceptual monitoring; and verbal fluency tests for response generation and initiation.

4.1. Latent structure of executive functions

Since seven different EF measures were expected to have a common variance, factor analysis allowed for the extraction of factors that represented the variance common to EF tasks, separate from potentially non-executive variance (i.e., Engelhardt et al., 2016; Friedman et al., 2008; Salthouse et al., 2003). The results of the EFA and CFA suggested that the solution of three latent, method-specific EF factors best fit the data. These factors were the WCTS factor, the TMT factor, and the Verbal fluency factor.

The WCST factor encompassed three measures of WCST – perseverative errors, the number of categories, and non-perseverative errors. These measures are related to working memory capacity and the ability for self-regulation of responses. While these WCST measures include a component of conceptual or abstract reasoning, the WCST factor primarily covered cognitive flexibility.

The TMT factor involved two measures of the Trail Making Test (TMT-A and TMT−B) and depended on visuospatial abilities, processing speed, and the capacity for set-shifting. This factor primarily related to the ability of complex conceptual monitoring and sequencing.

The Verbal fluency factor consisted of Phonemic fluency test and Category fluency test requiring the ability to search semantic memory using phonological or categorical rules. The default executive skills include parallel tracking of prior responses, based on working memory, as well as block intrusions from other semantic categories. This factor primarily covered the capacity for response generation, initiation, and inhibition.

4.2. Heritability of executive functions and general cognitive ability

The results of the multivariate biometric model indicate that the covariation of general cognitive ability and executive functions could be explained by shared genes. This result is in line with previous findings (Lee et al., 2012), which have shown that the entire covariance between four executive measures (working memory, verbal fluency, inhibition, and cognitive flexibility) and general cognitive ability can be explained by a common/general genetic factor.

In our research, the aetiology of covariation of general cognitive ability and achievement on the Verbal fluency factor was almost fully explained by the common additive genetic factor. Although the APM represents a non-verbal test that does not require linguistic resources, primarily engaging visuospatial abilities, the genetic correlation with the Verbal fluency factor indicated the possibility that similar cognitive abilities could underlie achievement on both measures. Since APM assesses working memory capacity (Carpenter, Just, & Schell, 1990; DeSchon, Chan, & Weissbein, 1995) and processing speed, and the Verbal fluency factor relied on working memory capacity and the ability to generate a response and initiate and process information, it is possible that these types of cognitive processes underlie both measures and have a similar genetic basis.

Moderate phenotypic correlation, high genetic correlations, and a common genetic factor in the multivariate model between the TMT factor and APM indicate the existence of a shared genetic variance among these constructs. It is possible that cognitive processes like visual observation, visuospatial assessment, psychomotor speed, and sequencing represent the basis for the genetic overlap between general cognitive ability measured with APM. Although APM uses perceptual and figural material, engaging visuospatial abilities, it may represent a measure of processing speed.

Similar results were obtained with regard to the relations between APM and WCTS. Namely, low- to- moderate phenotypic correlation and high genetic correlations between the WCST factor and APM suggest

Table 3
Fit indices for multivariate models.

		Model	$\chi^2(df)$	*p-level*	AIC	BIC	CFI	TLI	RMSEA (95% CI)
Model	Independent	ACE	61.91 (48)	0.086	4870.2	5008.4	0.969	0.964	0.050 (0.000–0.083)
		AE	64.58 (56)	0.202	4856.8	4967.4	0.981	0.981	0.036 (0.000–0.071)
		CE	100.99 (56)	0.000	4893.2	5003.8	0.900	0.900	0.083 (0.056–0.108)
		E	265.90(64)	0.000	5042.2	5125.1	0.550	0.606	0.164 (0.144–0.185)
	Common	ACE	85.34(53)	0.003	4883.6	5004.5	0.928	0.924	0.072 (0.042–0.100)
		AE	86.04(58)	0.010	4874.3	4978.0	0.937	0.940	0.064 (0.032–0.092)
		CE	119.64(58)	0.000	4907.9	5011.6	0.863	0.867	0.095 (0.071–0.120)
		E	265.90(63)	0.000	5044.2	5130.5	/	/	/

Notes. A – additive genetic variance, C – shared environmental variance, E – nonshared environmental variance and measurement error.

Table 4
Specific and common genetic and environmental contributions for AE multivariate models with 95% confidence intervals.

	measures	Ac	As	*h2*	Ec	Es	*e2*
AE independent pathways model	WCST factor	0.13 (0.10–0.15)	0.12 (0.06–0.17)	0.25	0.00 (0.00–0.01)	0.75 (0.72–0.82)	0.75
	TMT factor	0.31 (0.27–0.35)	0.10 (0.06–0.15)	0.41	0.18 (0.07–0.43)	0.41 (0.18–0.52)	0.59
	Verbal fluency factor	0.19 (0.15–0.22)	0.28 (0.21–0.33)	0.47	0.20 (0.11–0.52)	0.33 (0.00–0.42)	0.53
	APM	0.63 (0.55–0.70)	0.12 (0.06–0.20)	0.75	0.00 (0.00–0.00)	0.25 (0.23–0.27)	0.25

Note. Ac – common genetic variance, As – specific genetic variance, *h*2 – hereditary variance, Ec – common environmental variance, Es – specific environmental variance, *e*2 – environmental variance.

that some aspects of these constructs share the same genes or the same set of genes. These two tasks, in part, engage the same cognitive processes, such as the ability to abstract, form a concept, and maintain and change a mental set. Since all of these components are closely related to the function of the prefrontal lobe (Duncan et al., 1995; Gray, Chabris, & Braver, 2003), it is possible that this brain structure is shaped by a common set of genes, represented by a general genetic factor. Although the high specific genetic variance of APM indicates the possibility that specific cognitive functions contribute to successful performance in different cognitive contexts, they cannot be reduced to the components of executive functions measured in this research.

Genetic influences on EF are significant at both general and specific levels (Friedman et al., 2008). This indicates that the ability to actively perform goal-oriented tasks and keep related information creates a common base of executive functions, which affects lower-level processes (Miyake & Friedman, 2012b). Differences in the pattern of heritability for various measures of executive functions imply that some aspects of executive control have specific genetic basis. These results are consistent with the established thesis of executive functions as a

Table 5
Phenotypic, genetic, and environmental correlations with 95% confidence intervals.

Measures	r_f	r_g	r_e
WCST factor & TMT factor	0.21**	0.44**	0.11
	(0.12; 0.29)	(0.33; 0.54)	(−0.02; 0.23)
WCST factor & Verbal fluency factor	0.19**	0.42**	0.07
	(0.10; 0.27)	(0.31; 0.52)	-(0.06; 0.20)
TMT factor & Verbal fluency factor	0.44**	0.62**	0.29**
	(0.36; 0.52)	(0.53; 0.69)	(0.17; 0.40)
WCST factor & APM	0.30**	0.65**	0.05
	(0.21; 0.38)	(0.57; 0.72)	(−0.08; 0.18)
TMT factor & APM	0.42**	0.79**	−0.05
	(0.35; 0.49)	(0.74; 0.83)	(−0.18; 0.08)
Verbal fluency factor & APM	0.32**	0.53**	0.02
	(0.24; 0.40)	(0.43; 0.62)	(−0.11; 0.15)

* $p < .05$. ** $p < .01$.
Note. r_g – genetic correlation, r_e – environmental correlation, r_f – phenotypic correlation.

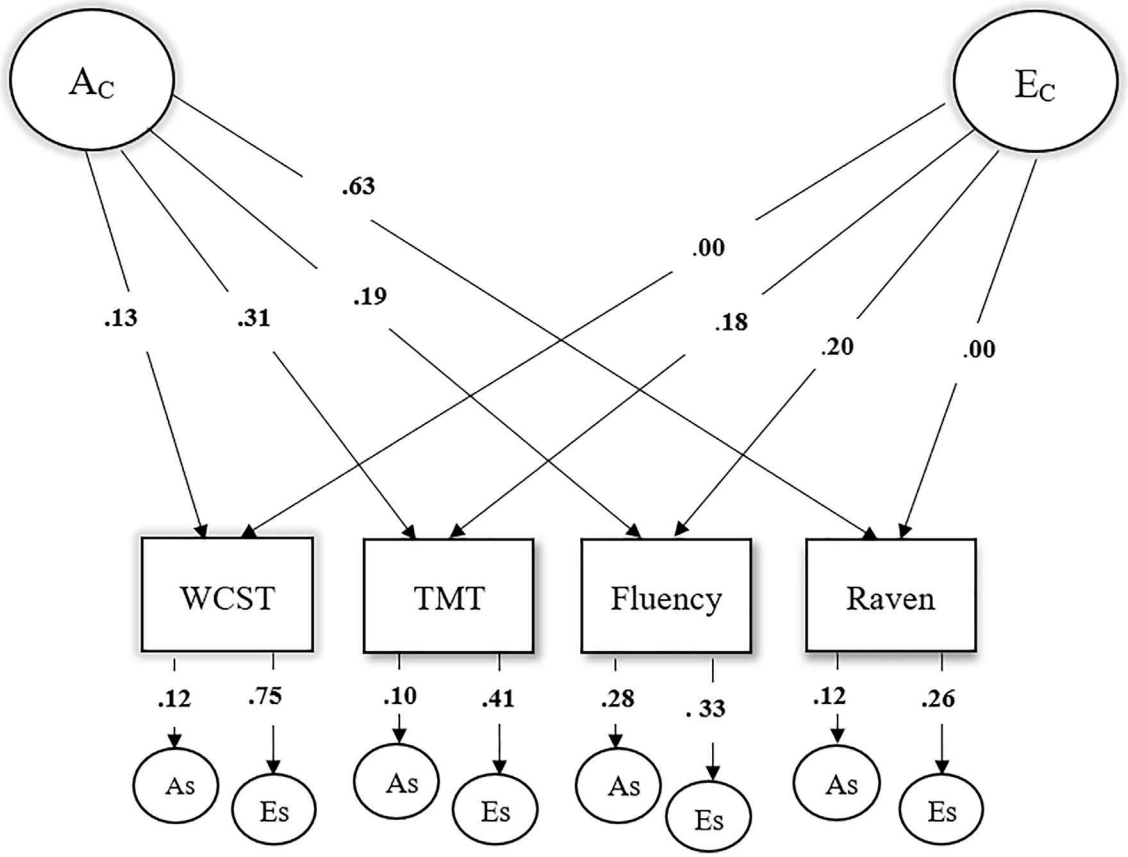

Fig. 1. Best-fitting (most parsimonious) genetic factor model (AE Independent pathway model).
Note. Standardized squared estimates from the best fitting independent pathway model are displayed. Ac – common genetic variance, As – specific genetic variance, Ec – common environmental variance, Es – specific environmental variance.

multi-domain construct (Duncan, Johnson, Swales, & Freer, 1997; Fisk & Sharp, 2004; Miyake et al., 2000). Moreover, this unitarity/particularity pattern has been replicated in numerous behavioral genetic studies (Friedman et al., 2006; Friedman, Miyake, Robinson, & Hewitt, 2011; Rose, Feldman, & Jankowski, 2011; Vaughan & Giovanello, 2010).

The most important result of our study is that general cognitive abilities and executive functions have a common genetic basis. Namely, the covariation of general cognitive ability and executive functions can only be explained by shared genetic variance. These results support the concept of the hierarchical structure of cognitive processes (Carroll, 1993). There is a possibility that a common genetic factor reflects general cognitive ability (g-factor), which usually has the same genetic basis as more specific cognitive abilities (Bouchard & McGue, 2003; Johnson, Bouchard, Krueger, McGue, & Gottesman, 2004; Petrill et al., 1997). Previous findings for different cognitive measures have shown that the g-factor accounted for 40% or more of the total variance, while each of the individual cognitive tests accounted for 20% to 50% of the specific variance. According to Petrill (1997)), the results of achievements in cognitive tests could be explained by gene molarity and environmental modularity, indicating a possible pattern of cognitive hierarchy with molar (g-factor) and modular (specific cognitive abilities) functions. Our results also indicate that genetic and environmental factors act on both levels – general and specific. Namely, most genetic effects are general, although there is evidence of the existence of independent genetic influences related to different cognitive processes.

It is important to emphasize that the environment has an effect on both levels of hierarchy. These results suggest that genetic influences form the basis of the unity of different cognitive functions, whereas the differences between specific dimensions of cognition are influenced by environmental factors and partly by independent genetic factors.

The results of our study have important implications for future studies of phenotypic characteristics and the genetic basis of both general and specific cognitive abilities. While executive functions cannot be reduced to intellectual abilities, the results indicate that part of genetic variance is common to these two phenomena. Another important implication of this study is the argument against considering executive functions as a unitary phenomenon. Executive functions include a series of specific abilities, with a specific genetic basis.

4.3. Limitations

While the real strength of this study lies in the use of multiple EF measures in exploring how EF relates to intelligence, there are several limitations. Specifically, the sample used in our research encompassed, on average, upper-level education participants. Such sample structure resulted in a reduced variability of both intelligence and executive functions, which somewhat affected the mutual relationships of variables, reducing the height of the correlations of different measures. Due to this, the calculated heritability of general cognitive ability was slightly higher than the one calculated on samples that more closely matched the general population (Bouchard & McGue, 2003; Neubauer, Spinath, Riemann, Borkenau, & Angleitner, 2000). The relatively small sample size may have reduced the statistical power of our analyses. Furthermore, we were unable to examine the genetic influences of sex differences. Although a wide age range of the sample was present, the largest percentage of twins belonged to the young adult category ($M = 24.5$, and about 80% of twins in the sample were up to 30 years of age). Therefore, all cognitive measures were corrected for sex and age effects by applying McGue and Bouchard's (1984) regression technique, i.e., entering sex and age as predictors and taking each specific ability test as a criterion, while retaining the residuals.

Future research should certainly replicate these results on different measures of executive functions and general cognitive ability. The generalization of these findings would be more successful if they were validated through experimental procedures for the assessment of executive functions and multidimensional assessment of intellectual abilities.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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