Executive functions and intelligence- are there genetic difference?

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EXECUTIVE FUNCTIONS AND INTELLIGENCE - ARE THERE GENETIC DIFFERENCE?

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Abstract:
The aim of this study was to explore the aetiology of phenotypic relationships between different executive functions and sources of covariation between them, as well as 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 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, Trail–making Test–form B, Verbal Fluency Test. Raven’s Advanced Progressive Matrices were used as a measure of general cognitive ability in this study. In regard to the aetiology of mutual covariation of different executive measures and their covariation with the general cognitive ability construct, the study results suggest that their origin is primarily genetic. 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 the different executive measures, speaks in favour, at least partially, of the thesis about the unity of various executive measures and the existence of a certain common basic ability, while the specific genetic influence, together with the specific unshared environment, speaks in favour of the difference between each of the individual measures.

Keywords: behavioural genetics, cognitive abilities, executive functions, general cognitive ability
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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1. Introduction

The theoretical construct named “executive function” has been the subject of a great 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, a conceptual status to the term “executive function” (EF) is still unclear, mainly due to different strategies for assessment these phenomena and lack of unique empirical framework for their studying. Initial research of executive functions have been based on emphasizing the homogeneity of the construct and existence a single/common, central executive function (Baddeley, 2007; Norman & Shallice, 2000). Over time, the research findings began to indicate that the concept of executive functions is only an umbrella term that encompasses a set of interconnected processes, necessary for a purposeful, goal-oriented behaviour (Anderson, 2002; Anderson, Jacobs, & Anderson, 2008; Miyake & Friedman, 2012). This highly complex and integrated set of cognitive abilities, which is paramount for adaptive functioning, includes the processes of planning, goal setting, task initiation, task monitoring, ability to inhibit or delay responses, evaluation of responses, cognitive flexibility, and selection of efficient strategies necessary for problem solving (Anderson, 2002; Damasio & Anderson, 1993; 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, Tallei, Kej, & Curtiss, 1993), 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 long-established and strong tradition in neuropsychology and it is probably the most widely used measure of executive functions (Butler, Retzlaff, & Vanderploeg, 1991). This test engages different executive processes: strategic planning,
organized searching, utilizing environmental feedback to shift mental sets, maintaining mental sets, modulating impulsive responding, and goal-oriented behaviour (Demakis, 2003; Eling, Derckx, & Maes, 2008; Heaton, Chelune, Tallei, Kej, & Curtiss, 1993). Trail Making Test – TMT-A/TMT-B is the measure of simple (A) and complex (B) conceptual monitoring, i.e., divided attention. Baron (2004) pointed out that the achievement on this test, which evaluates higher levels of executive control or complex conceptual monitoring, primarily requires flexibility in shifting the mental set in conditions of rapid changes in concepts. While TMT-A is most often used as the measure of processing speed, the B form of this test is generally used as an index of executive function (Lezak, Howieson, & Loring, 2004). Verbal fluency tests assess the ability to generate verbal material (maximum number of words) according to set rules during a limited period of time and are often used in clinical practice when evaluating executive functions since they require planning, organized search and execution monitoring (Spreen & Strauss, 1998).

Other tests that are used as EF include 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, i.e., a specific task that is used to evaluate executive functioning usually encounter the problem of task impurity, and only their combination provides more reliable estimation (Suchy, 2009).

The second topic, related to the issue of discriminant validity, is the distinction between the concept of executive functions and the concept of general intellectual ability (Salthouse, 2005). The interconnection of these concepts can be illustrated by their definitions, since both of them refers to processes as primarily planning, problem-solving and comprehension, 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 at al., 2000; Boone, Ghafferian, Lesser, Hill–Gutierrez, & Berman, 1993; Welsh et al., 1991), others have found a correlation between general intellectual ability and almost all measures of executive functions (Salthouse, 2005; Salthouse, Atkinson, & Berish, 2003), or their certain aspects (Friedman et al., 2006). Previous studies, mostly conducted on clinical samples, have indicated that frontal lesions, resulting in the deficit of executive functions, do not lead to a significant decrease in general intellectual ability, suggesting relative independence of executive functions from general intellectual abilities (Damasio & Anderson, 1993; Hebb, 1939, 1945, according to Ardilla et al., 2000). However, some finding (Duncan, Burgess, & Emslie, 1995), have shown that the measures of fluid intelligence decline after frontal lesions, that are traditionally associated with EF deficit. It seems that correlation between EF measures and measures of general intellectual abilities depends on types of both intelligence tests and executive functions measures.

Great contributions in the process of determining an aetiology of phenomenon EF and specifying the nature of the relationship between EF and similar constructs provide behavioral genetic studies (Anokhin, Heath, & Ralano, 2003; Luciano et al., 2001; Friedman et al., 2008; Vasilopoulos et al., 2012; Swan & Carmelli, 2002). Generally, the results of behavioral genetic studies have shown that estimation of heritability of EF depends on type of assessment and the age of respondents (Anokhin et al., 2003, Friedman et al., 2008; Kremen et al., 2009; Taylor 2007; Vasilopoulos et al., 2012). Regarding the WCST, inconsistent results vary from evidence for no 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, Myake, & Hewitt, 2012). The heritability indices ranging from .23–.38 for TMT-A, to .39–.65 for TMT-B (Buyske et al., 2006; Swan & Carmelli, 2002; Vasilopoulos et al., 2012). and from .34 to .55
for the verbal fluency test (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) have shown that executive processes of inhibition, updating, and shifting are the cognitive traits are almost entirely genetic in origin, with heritability of up to 99%. Although there were three phenotypes (updating, inhibiting, and shifting) that comprised the entire variance of executive functions in this study, only one common/general genetic factor has been emerged in multivariate genetic analysis. This result has indicated that there are comprehensive genetic factors underlying different specific cognitive measures. Furthermore, Godinez et al. (2012) specified in their study that the covariance between different WCST indicators is best explained by a general/common genetic factor, whereas the differences between indicators are caused by specific genetic and environmental factors. Lee et al. (2012), have used the indicators of different executive functions (measure of working memory, verbal fluency, inhibition, and cognitive flexibility) and have found that there are a single common genetic factor for all measure, while each measure has its own specific factors of unshared environment.

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

The main objective of this research is to examine whether different aspects of executive functions have the same genetic basis. Since executive functions have a central role in cognitive processes, it seems 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 shifting, attention, and inhibition thorough WCST assessment, complex conceptual monitoring, thorough TMT assessment, and phonemic and categorical fluency thorough Verbal Fluency Test.

The second objective of the study was examination relations between different aspects of executive functions and general intellectual ability. More specifically, we have tried to determine whether executive functions share the same genetic basis with general intellectual ability. In this way, the results of this behavioral genetic study can contribute to the ongoing debate about whether executive functions are just one aspect of general intellectual ability or can be concerned as independent cognitive abilities.

2. Materials and Methods

2.1. Participants

The Twin Registry has data on 1654 participants. This study involved 468 twins, 154 pairs of monozygotic (75.3% female) and 80 pairs of dizygotic (61.3% female) twins of the same and different gender. Among the dizygotic twin pairs there were 35 mixed gender pairs and 45 same gender pairs. The age of the participants ranged from 18 to 60 years, and the average age was 24.7 years ($SD = 7.78$). The zygosity was determined for most of the participants (96.8%) using a DNA buccal swab analysis. Buccal swabs were 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 interpreted if at least 10 loci had results.
For a smaller sample fraction (3.2%) the zygosity was determined using the Twins Physical Resemblance Questionnaire (Oniszczenko, Angleitner, Strelau, & Angeri, 1993). This questionnaire includes a series of questions about similarities and dissimilarities between two twins, within twin pairs (e.g., eye colour, body weight, body height, etc.). Measures of this questionnaire 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).

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 ethical procedures of psychological research. The research has been approved by the Institutional Ethics Committee. The data was collected from 2011 until the end of 2018. Cognitive abilities and executive functions were examined by trained researchers.

2.3. Measures

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

*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 abilities. Longer completing test time indicates a lesser achievement.

*Verbal Fluency Test – phonemic and category* (Goodglass & Kaplan, 1983; Lezak, 1995). The test consists of three tasks of phonemic and one task of categorical fluency. Verbal fluency is measured by the number of words produced in the unit of time. Words are usually limited to certain categories. Phonemic fluency is assessed by a test of controlled oral associations, including phonemes S/K/L in Serbian language that is equivalent to the Verbal Fluency Test (FAS) in the English language. In the Category fluency test, the respondents were asked to generate exemplars from a given category. In this study the respondents were asked to indicate, within a minute, as many different animals as possible.

*Advanced Progressive Matrices* (APM: Raven, Raven, & Court, 1998). APM is a non-verbal type of 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 Spirman's g factor, which is often called general intelligence. Participants are instructed to complete each matrix, choosing one of eight response alternatives according to logical rules. Series II, which consists of 36 items, was applied in this study, and the time for solving tasks was limited to 40 minutes.

2.4. Statistical Analyses

2.4.1. Phenotypic analyses and Twin intraclass correlation analyses

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 effect by applying McGue and Bouchard (1984) regression technique, i.e., entering sex and age as predictors and taking each specific ability
test as criterion, retaining the residuals.

2.4.2. Factor analyses

The factor analytic procedures were applied to the seven measures of EF to determine their latent factor structure. In the first step, variables related to number of errors and reactions time were recoded, so that a higher value represents a better achievement. Next, using the “R environment” (R Core Team, 2016), exploratory factor analysis (EFA) was first performed on one of the twins in each pair (e.g., the Twin 1 subgroup). The results of the EFA were then cross-validated in the second subgroup (e.g., Twin 2) via confirmatory factor analysis (CFA) procedures. Analysis was run in “lavaan” R package (Rosseel, 2012).

2.4.3. Multivariate genetic analyses

Multivariate genetic analysis in behavioural genetics is used to examine the nature of relationships between different constructs by specifying to what extent they share genetic and environmental influences, and to what extent these influences are different. Multivariate structural equation modeling (SEM) was carried out in the "lavaan" R package (Rosseel, 2012).

Two multivariate, independent and common pathway models, were tested. Independent and common multivariate models (Rijswijk & Sham, 2002) were applied in order to estimate additive genetic factors (A); shared environmental (C), and non-shared environmental (E); and specific (s) and common (c) genetic and environmental sources of variance. These models represent different patterns by which genetic and environmental influences may explain the
observed phenotypic correlations among different cognitive measures. In both models there were specific (s) and common (c) genetic and environmental sources of variance.

The independent pathways model assumes that a single set of genetic and environmental factors influences covariation among different measures. In other words, this model allows for the covariation between different pairs of variables to be due to different genetic or environmental influences. In the case of the common pathway model, both genes and environment contribute to one latent variable that is responsible for the observed covariance between the outcome measures. In other words, it assumes that a single underlying latent phenotype is solely responsible for the covariation among different measures. This model also allows for residual genetic and environmental influences that are specific to each individual measure (genetic and environmental factors specific to each measure).

Additionally, genetic and environmental correlations between variables were calculated. Genetic and environmental mediation estimates, as well as genetic and environmental correlations, provide useful information for showing how and why two variables are etiologically related. Genetic and environmental correlations were calculated using multivariate Cholesky models.

A series of models (independent and common pathway) were fitted to multivariate covariance matrices. On the grounds of parsimony, the model with the least number of parameters that offered a fit not significantly worse than the full model was chosen. A comparison of the two groups of models, as well as the comparison between full (ACE) and reduced (AE, CE) models, was carried out by using several fit indicators for all plausible models. Analysis parameters were calculated by using the method of maximum likelihood. Model evaluation was conducted based on the Akaike Information Criterion (AIC; Akaike, 1973), Bayesian Information Criterion (BIC; Schwarz, 1978), comparative fit index and the Tucker–Lewis index (CFI and TLI – optimal values higher than .95, acceptable higher than .90), the
root mean square error of approximation (RMSEA - optimal values lower than .05, acceptable lower than .08), with acceptable value below .08 (Hu & Bentler, 1999).

3. Results

3.1. Descriptive statistics of Phenotypic Characteristics and Twin Intra-class Correlation

The values of skewness and kurtosis indicated that, except phonemic fluency, category fluency, and general cognitive ability, almost all cognitive measures were not normally distributed (Table 1). 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 the distributions reached normality. Means and standard deviations for the cognitive variables are provided in Table 1. For each of the phenotypes, similarities were compared between MZ and DZ twin pairs (Table 1).

<< INSERT TABLE 1 ABOUT HERE >>

Correlations between MZ twins were consistently higher than correlations between DZ twins for all measures. Correlations between MZ twins, on all eight measures, were positive, significant, and of low-to-moderate strength. High correlation coefficient was detected in 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, whereas 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)

Exploratory factor analysis (maximum likelihood method) was conducted on seven measures 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), Tucker-Lewis Index (TLI) values indicated that the one- and two-factor solution did not fit well ($\chi^2(14) = 168.48, p < .001$, RMSEA = .22, TLI = .55) and ($\chi^2(8) = 44.78, p < .001$, RMSEA = .14, TLI = .81). The 3-factor solution provided the best fit to the data, ($\chi^2(1) = 1.04, p = .79$, RMSEA = .00, TLI = 1.02). Factor loadings of this solution are given in Table 2. The pattern of loadings indicates that the seven measures form three separate domains. Factor 1 represents a WCST measure, consisting of the three different measures of this test (number of categories, perseverative errors and non-perseverative errors). Factor 2 represents a TMT measure (TMT-A and TMT-B), consisting of the two different measures of this test, and Factor 3 represents a measure of Verbal Fluency, consisting of two different measures (phonemic and category fluency).

The 3-factor solution that resulted from the EFA was subsequently tested via CFA in the Twin 2 subsample (see Table 2). It showed an adequate fit to the data; $\chi^2(11) = 8.23, p = .692$, RMSEA = .00, SRMR = .02, CFI = 1.00, TLI = 1.01. The second and third factors correlate .55, first and second .19, first and third yielded a correlation of .21. All loadings were significant. From these analyses, the 3-factor result suggests that the seven measures of EF can be taken to index 3 latent factors, a WCST factor, a TMT factor and a Fluency factor.

The results of EFA, as factors scores, have been used as the basis for behavioral genetic analyses.
3.3. Multivariate Genetic Analysis

The results of the multivariate genetic modelling are shown in Table 3. AE models fitted better than full ACE models in analyses. The most appropriate fit indices (Table 3) were for the AE independent pathways model. All the indices were within acceptable boundaries. The estimation of the parameters of the best fitting models is given in Table 4. In addition, the parameter estimates shown in Figure 1.

Results from the independent AE pathway model suggested that compared to the environment the genetic effects were higher in the case of General cognitive ability, while the environmental effects were stronger in case of WSCT, Verbal fluency, and TMT factor (Table 4). These genetic contributions ranged from low to high. The overall variance of heredity is better explained by common genetic factors in the case of APM (63%) and TMT (31%), while in the case of WCST and Verbal fluency are better explained by specific genetic factors. Unique genetic factors are most prominent in the Verbal fluency factor (28%). In all cases, specific environmental effects were stronger than common environmental effects. Common environmental impacts are low for TMT (18%) and Verbal fluency factor (20%), or non-existent (0%) for APM and WCST factor.
Phenotypic correlations between the WCST factor and the Verbal fluency factor, and WCST factor and TMT factor phenotypic correlations were low. While genetic correlations among WCST and TMT factors were moderate (.44), environmental correlations were low. In the case of the WCST and Verbal fluency factor, genetic correlations were moderate (.42), whereby the non-shared environmental correlations are non-significant (Table 5). On the other hand, moderate phenotypic correlation is recorded between TMT and Verbal fluency factors are the consequence of shared genes, which is illustrated by high genetic correlation (.62), while common nonshared environment factor explains a lower percentage of their covariance (low environmental correlation). Phenotypic correlations between the WCST factor and APM was moderate, but among these indicators, there are high genetic correlations (.65), and non-significant environmental correlations. Moderate phenotypic correlation between the TMT factor and APM is explained with a dominant genetic component (high genetic correlation), while common nonshared environment correlation non-significant. Concerning a moderate correlation between achievements on the Verbal fluency factor and APM, it is predominantly the result of shared genes, which is supported by the moderate to high genetic correlation (.53) that was obtained.
4. Discussion

The main objective of this study was to explore the genetic and environmental contribution to variance of executive functions, with a special focus on determination of the degree of genetic and environmental impact on covariation between general intellectual ability and executive functions. To cover the most important aspects of executive functions, we have applied various techniques to measure them - WCST for the assessment of shifting, attention, and inhibition, TMT for the assessment of complex conceptual monitoring, and Verbal Fluency Test for the assessment of phonemic and categorical fluency.

Structure of executive functions

Before the behavior genetic analyses, preliminary phenotypic factor analyses were performed on seven different measures of EF. This strategy allowed that extract factors representing variance common across selected tasks as 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 solution of three latent, method specific, EF factors the best fit the data. Consequently, they named as WCTS factor, TMT factor and Fluency factor.

The WCST factor encompasses three measures of WCST - Perseverative errors, Number of categories and Non-perseverative errors. These measures relate to use working memory capacity and the ability for self-regulation of responses. Also, the WCST measures include a component of conceptual or abstract reasoning, but this WCST latent factor dominant tapping executive function of cognitive flexibility.
The TMT factor involved two measures of Trail Making Test (TMT-A and TMT-B). Successful performance of this factor dependent on visuospatial ability, processing speed and capacity for set-shifting and, but performance on this factor is primarily related to the ability of complex conceptual monitoring and sequencing.

The Fluency factor consists of two measures Verbal Fluency-Phonemic and Category fluency tasks. This factor requires the ability to search semantic memory using phonological or categorical rules. The executive skills required parallel tracking prior responses (working memory) and block intrusions from other semantic categories. This factor primarily covers the capacity for response generation, initiation, and inhibition.

*Heritability of execution functions and general cognitive ability*

The results of multivariate biometric model indicate that moderate covariation of general intellectual ability and the executive functions can be explained by shared genes. This result is in line with previous findings (Lee at 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 with a common/general genetic factor.

In our research, the aetiology low to moderate covariation of general cognitive ability and achievement on the Fluency factor is almost fully explained by common additive genetic factor. Since the Raven’s Advanced Progressive Matrices represent a non-verbal test which requires almost no linguistic ability and engages visuospatial abilities, moderate to high genetic correlation with verbal fluency tests is controversial. Perhaps factors underlie achievement on APM and category and phonemic fluency are similar. For example, APM can assesses working memory capacity (Carpenter, Just & Schell, 1990; DeSchon, Chan, &
Weissbein, 1995) and processing speed, while category and phonemic fluency rely heavily on working memory capacity and the ability for response generation, initiation and process information quickly. It is, therefore, possible that these types of cognitive processes underlying both measures and have similar genetic basis.

The moderate phenotypic correlation of TMT factor and APM is mainly due to shared genetic variance among these constructs, as evidenced by the obtained high genetic correlations among these constructs and the existence of a common/general genetic factor in the multivariate model. It is possible that cognitive processes such as visual observation, visuospatial assessment, psychomotor speed and sequencing, represent the basis for overlapping between genetic influences and general cognitive ability measured with APM.

Raven’s Progressive Matrices use perceptual and figural material and, therefore, engage visuospatial abilities, but they also, to some extent, represent the measure of processing speed.

The obtained multivariate biometric model shows that low- to- moderate phenotypic correlation of WCST factor and APM is a consequence of solely shared genes among these constructs. Genetic correlations between these measures are high, suggesting that some aspects of these constructs share the same genes or the same set of genes. It is already clear by definition that these two tasks, in part, engage the same cognitive processes - such as the ability to abstract, form a concept (equivalent to problem solving), maintain a mental set (concerning the aspect of working memory), change a mental set (switching ability). All of these components are closely related to the function of the prefrontal lobe, which was assumed and later shown to be involved in performing these two tasks (Duncan et al., 1995; Gray, Chabris, & Braver, 2003). It is possible that a common set of genes - represented by a general gene factor - shapes precisely this brain structure. The existence of a specific genetic influence obtained in case od APM is more in favor of the model according to which the g-factor reflects a specific cognitive function, which contributes to successful performance in
different cognitive contexts, but which is not reducible to the components of executive functions measured in this research.

In case of EFs, genetic influences are expressed at both general and specific levels (Friedman et al., 2008). The common base of executive functions represents the ability to actively maintain the tasks and information regarding the goals, in order to exert influence on lower-level processes (Miyake & Friedman, 2012). Differences in pattern of heritability for various measures of executive functions are in line with the phenotypic correlations between EF measures, which imply that there is specificity of genetic basis for some aspects of executive control. These results are consistent with the established thesis of executive functions as a multi-domain construct (Duncan, Johnson, Swales, & Freer, 1997; Fisk & Sharp, 2004, Miyake et al., 2000). Also, this unitarity/particularity pattern has been replicated in numerous behavioural 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, covariation of general cognitive ability and executive functions can be explained by a shared genetic variance, with a small percentage of the general shared environmental factor. These results support the conception of the hierarchical structure of cognitive processes (Carroll, 1993). There is possibility that the common genetic factor reflects the general cognitive ability (g), which usually have the same genetic basis as more specific cognitive abilities (Bouchard & McGue, 2003; Johnson, Bouchard, Krueger, McGue, & Gottesman, 2004; Petrill et al., 1997). The consistent finding of various studies when have been used different cognitive measures, is that the g-factor accounts for 40% or more of total variance, whereas each of the individual cognitive tests
shows a significant amount of specific variance, ranging from 20 to 50%. According to Petrill (Petrill, 1997), the results of achievements on cognitive tests can be explained by gene molarity and environmental modularity, indicating possible pattern of cognitive hierarchy, with molar (g-factor) and modular (specific cognitive abilities) functions. Our results also indicate that genetic and central 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 measures of cognitive functioning, whereas the environment forms the basis of the difference between the different dimensions of cognition. However, the results of this research support the existence of independent dimensions of cognition formed, at least partly, by independent genetic influences.

The results of our study have important implications for future studies of phenotypic characteristics and genetic bases of general and specific cognitive abilities. While executive functions cannot be reduced to intellectual abilities, results indicate that part of the genetic variance is common to these two phenomena. Another important implication of this study is the additional evidence of the absence of executive functions as a single phenomenon. Executive functions include a series of specific abilities, each of them having a specific genetic basis.

Limitations

While the major strength of this study is the use of multiple measures of EF to explore its relationship with intelligence, there are several limitations. Specifically, the sample used in
our research encompasses, on average, upper-level education participants, so the consequence of such a sample structure would be reduced variability of ability - both intelligence and executive functions, which somewhat affects the mutual relationships of variables, thus reducing the height of the correlations of the different measures. This restriction resulted in a slightly higher assessment of heritability of general cognitive ability, compared to the estimates obtained on samples that more closely matched the general population (Bouchard & McGue, 2003; Neubauer, Spinath, Riemann, Angleitner, & Borkenau, 2000). The relatively small sample size would have reduced the statistical power in our analyses, and as such, we were unable to examine the genetic influences on sex difference. Also, although a wide age range of sample is present, the largest percentage of twins are into the young adult category (M = 24.5, and about 80% of twins in the sample are in the category up to 30 years).

Therefore, all cognitive measures were corrected for sex and age effect by applying McGue and Bouchard (1984) regression technique, i.e., entering sex and age as predictors and taking each specific ability test as criterion, retaining the residuals.

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


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Table 1

*Descriptive statistics and Twin intra-class correlation coefficients for the used measures with 95% Confidence Intervals*

<table>
<thead>
<tr>
<th>Measure</th>
<th>M (SD)</th>
<th>MZ</th>
<th>DZ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of WCST Categories</td>
<td>5.48 (1.27)</td>
<td>0.29** (0.17; 0.40)</td>
<td>-0.11 (-0.23; 0.02)</td>
</tr>
<tr>
<td>Perseverative Errors</td>
<td>12.22 (9.20)</td>
<td>0.21** (0.08; 0.33)</td>
<td>0.04 (-0.09; 0.17)</td>
</tr>
<tr>
<td>Non-perseverative Errors</td>
<td>10.63 (9.91)</td>
<td>0.28** (0.16; 0.39)</td>
<td>-0.17 (-0.29; -0.04)</td>
</tr>
<tr>
<td>TMT-A reaction time</td>
<td>29.95 (10.25)</td>
<td>0.42** (0.31; 0.52)</td>
<td>0.27** (0.15; 0.38)</td>
</tr>
<tr>
<td>TMT-B reaction time</td>
<td>44.48 (15.46)</td>
<td>0.39** (0.28; 0.49)</td>
<td>0.17 (0.04; 0.29)</td>
</tr>
<tr>
<td>Phonemic Fluency</td>
<td>11.45 (3.17)</td>
<td>0.50** (0.40; 0.59)</td>
<td>0.31** (0.19; 0.42)</td>
</tr>
<tr>
<td>Category Fluency</td>
<td>24.03 (5.56)</td>
<td>0.44** (0.33; 0.54)</td>
<td>0.28* (0.16; 0.39)</td>
</tr>
<tr>
<td>General Cognitive Ability (APM)</td>
<td>20.72 (6.18)</td>
<td>0.73** (0.65; 0.79)</td>
<td>0.43** (0.21; 0.60)</td>
</tr>
<tr>
<td>WCST factor</td>
<td></td>
<td>0.29** (0.14; 0.44)</td>
<td>-0.08 (-0.29; 0.14)</td>
</tr>
<tr>
<td>TMT factor</td>
<td></td>
<td>0.41** (0.27; 0.54)</td>
<td>0.18 (-0.03; 0.38)</td>
</tr>
<tr>
<td>Fluency factor</td>
<td></td>
<td>0.46** (0.32; 0.58)</td>
<td>0.28* (0.08; 0.48)</td>
</tr>
</tbody>
</table>

*Note.* M – mean, SD – standard deviation; MZ – monozygotic twins, DZ – dizygotic twins; *p < .05. **p < .01.
Table 2

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

<table>
<thead>
<tr>
<th>measures</th>
<th>Factor 1</th>
<th>Factor 2</th>
<th>Factor 3</th>
<th>Factor 1</th>
<th>Factor 2</th>
<th>Factor 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of WCST Categories</td>
<td>0.88</td>
<td></td>
<td></td>
<td>0.68</td>
<td>....</td>
<td>....</td>
</tr>
<tr>
<td>Perseverative Errors</td>
<td>0.86</td>
<td></td>
<td></td>
<td>0.89</td>
<td>....</td>
<td>....</td>
</tr>
<tr>
<td>Non-perseverative Errors</td>
<td>0.75</td>
<td></td>
<td></td>
<td>0.91</td>
<td>....</td>
<td>....</td>
</tr>
<tr>
<td>TMT-A reaction time</td>
<td>..</td>
<td>0.60</td>
<td></td>
<td>....</td>
<td>0.73</td>
<td>....</td>
</tr>
<tr>
<td>TMT-B reaction time</td>
<td>..</td>
<td>1.02</td>
<td></td>
<td>....</td>
<td>0.71</td>
<td>....</td>
</tr>
<tr>
<td>Phonemic Fluency</td>
<td>..</td>
<td></td>
<td>0.45</td>
<td>....</td>
<td>....</td>
<td>0.56</td>
</tr>
<tr>
<td>Category Fluency</td>
<td>..</td>
<td></td>
<td>1.03</td>
<td>....</td>
<td>....</td>
<td>0.88</td>
</tr>
</tbody>
</table>
Table 3

Fit indices for multivariate models

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

Notes. A – additive genetic variance, C – shared environmental variance, E – non-shared environmental variance and measurement error
Table 4

*Specific and common genetic and environmental contributions for AE multivariate models with 95% Confidence Intervals*

<table>
<thead>
<tr>
<th>measures</th>
<th>Ac</th>
<th>As</th>
<th>h²</th>
<th>Ec</th>
<th>Es</th>
<th>e²</th>
</tr>
</thead>
<tbody>
<tr>
<td>WCST factor</td>
<td>0.13 (0.10-0.15)</td>
<td>0.12 (0.06-0.17)</td>
<td>0.25</td>
<td>0.00 (0.00-0.01)</td>
<td>0.75 (0.72-0.82)</td>
<td>0.75</td>
</tr>
<tr>
<td>TMT factor</td>
<td>0.31 (0.27-0.35)</td>
<td>0.10 (0.06-0.15)</td>
<td>0.41</td>
<td>0.18 (0.07-0.43)</td>
<td>0.41 (0.18-0.52)</td>
<td>0.59</td>
</tr>
<tr>
<td>Fluency factor</td>
<td>0.19 (0.15-0.22)</td>
<td>0.28 (0.21-0.33)</td>
<td>0.47</td>
<td>0.20 (0.11-0.52)</td>
<td>0.33 (0.00-0.42)</td>
<td>0.53</td>
</tr>
<tr>
<td>APM</td>
<td>0.63 (0.55-0.70)</td>
<td>0.12 (0.06-0.20)</td>
<td>0.75</td>
<td>0.00 (0.00-0.00)</td>
<td>0.26 (0.23-0.27)</td>
<td>0.26</td>
</tr>
</tbody>
</table>

Table 5

*Phenotypic, genetic, and environmental correlations with 95% Confidence Intervals*

*Note. $r_g$ – genetic correlation, $r_e$ – environmental correlation, $r_f$ – phenotypic correlation.*

<table>
<thead>
<tr>
<th>measures</th>
<th>$r_f$</th>
<th>$r_g$</th>
<th>$r_e$</th>
</tr>
</thead>
<tbody>
<tr>
<td>WCST factor &amp; TMT factor</td>
<td>0.21**</td>
<td>0.44</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>(0.12; 0.29)</td>
<td>(0.33; 0.54)</td>
<td>(-0.02; 0.23)</td>
</tr>
<tr>
<td>WCST factor &amp; Fluency factor</td>
<td>0.19**</td>
<td>0.42</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>(0.10; 0.27)</td>
<td>(0.31; 0.52)</td>
<td>(-0.06; 0.20)</td>
</tr>
<tr>
<td>TMT factor &amp; Fluency- factor</td>
<td>0.44**</td>
<td>0.62</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>(0.36; 0.52)</td>
<td>(0.53; 0.69)</td>
<td>(0.17; 0.40)</td>
</tr>
<tr>
<td>WCST factor &amp; APM</td>
<td>0.30**</td>
<td>0.65</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>(0.21; 0.38)</td>
<td>(0.57; 0.72)</td>
<td>(-0.08; 0.18)</td>
</tr>
<tr>
<td>TMT factor &amp; APM</td>
<td>0.42**</td>
<td>0.79</td>
<td>-0.05</td>
</tr>
<tr>
<td></td>
<td>(0.35; 0.49)</td>
<td>(0.74; 0.83)</td>
<td>(-0.18; 0.08)</td>
</tr>
<tr>
<td>Fluency factor &amp; APM</td>
<td>0.32**</td>
<td>0.53</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>(0.24; 0.40)</td>
<td>(0.43; 0.62)</td>
<td>(-0.11; 0.15)</td>
</tr>
</tbody>
</table>

* $p < .05$. ** $p < .01$. 
Figure 1
Data availability statement:

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

Acknowledgements:

This study was supported by the Ministry of Education, Science and Technological Development of the Republic of Serbia [Grant ON179006].