



The Nature and Nurture of HEXACO Personality Trait Differences

An Extended Twin Family Study

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Abstract: This study was designed to provide detailed estimates of genetic and environmental sources of variance in the HEXACO personality traits. For this purpose, we analyzed data from a German extended twin family study including 573 pairs of twins as well as 208 mothers, 119 fathers, 228 spouses, and 143 offspring of twins. All participants provided self-reports on the HEXACO-60. Extended twin family analyses using structural equation modeling (SEM) yielded that additive and nonadditive genetic influences accounted for about 50% of the variance in personality traits. The remaining variance was primarily due to individual-specific environmental sources and random measurement error. Spousal similarity in Openness was attributable to assortative mating, whereas spousal similarity in Honesty-Humility was attributable to environmental circumstances, partly due to a shared social background and spouse-specific effects. Our analyses yielded specifics for different personality traits. However, transmission of trait similarity from one generation to the next was primarily genetic.

Keywords: personality, nuclear twin family model, spouses-of-twins model, genetic, environmental

Almost 200 behavior genetic studies on personality traits have robustly shown that about 40–50% of the variance in complex personality characteristics is attributable to genetic differences, with the remaining variance primarily due to environmental influences that act to increase differences among biologically related family members (see Johnson, Vernon, & Feiler, 2008; Vukasović & Bratko, 2015, for meta-analyses). After correction for variance due to measurement error, genetic sources account for about 50–60% of reliable personality trait variance (Kandler & Papendick, 2017). Based on these findings, within-familial socialization (i.e., shared environmental influences) contributes only marginally to the similarity of family members' personality traits and to personality differences between families. Rather, individualizing (i.e., nonshared) environmental influences matter, accounting for the remaining 40–50% of the variance in personality traits (after correction for random error variance).

These findings show strong evidence for the heritability of (i.e., the genetic contribution to the variance in) personality traits as conceptualized by the five-factor model (FFM) framework of personality (McCrae & John, 1992), or conceptually and empirically related personality models, as for example, Eysenck's three-dimensional Psychoticism-

Extraversion-Neuroticism model (Eysenck & Eysenck, 1985) or Tellegen's hierarchical personality model (Tellegen & Waller, 2008). Less is known about the nature and nurture of individual differences in the HEXACO personality traits. Though there is substantial construct-related and structural overlap between the broad dimensions Neuroticism, Extraversion, Openness, Agreeableness, and Conscientiousness of the FFM framework and the six-dimensional HEXACO framework, the inclusion of a sixth personality dimension Honesty-Humility alters the architecture of Agreeableness and Neuroticism (referred to as Emotionality in the HEXACO framework; Ashton & Lee, 2007; Lee, Ogunfowora, & Ashton, 2005). More specifically, some facets of Agreeableness as proposed and described within the FFM framework, such as Modesty, move to define Honesty-Humility, whereas facets of Neuroticism, such as Hostility, move to alter Agreeableness as proposed and described within the HEXACO framework.

Only one genetically informative (or environmentally sensitive) study, so far, examined the genetic and environmental architecture of the HEXACO facet-structure (Lewis & Bates, 2014). However, this study was based on data from mostly middle-aged and older female twins, and did not focus on the sources of individual differences in the

HEXACO trait dimensions per se. The authors investigated the genetic coherence of the six personality trait dimensions through analyses of the genetic covariation between facets of a personality trait dimension. They found that each of the (implied) six personality trait dimensions was adequately represented by a single common genetic factor, indicating that the six basic HEXACO dimensions of personality reflect a coherent underlying genetic architecture that mirrors the observable trait structure. The findings are largely comparable to those of twin studies on the FFM structure (Briley & Tucker-Drob, 2012; Kandler, Riemann, Spinath, & Angleitner, 2010).

As shown by Lewis and Bates (2014), most genetically informative studies on personality traits relied on the classical twin design (CTD). From the comparison of similarities in monozygotic (MZ) and dizygotic (DZ) pairs of twins, this design infers to what extent genetic and environmental sources act to increase or decrease the intrapair similarity and interindividual differences. MZ twins are genetically identical siblings who share all (i.e., 100%) of their genetic makeup, including all genetic influences that can vary among humans. Thus, all potential genetic influences on the variance in a specific trait contribute to MZ twins' trait similarity, and as a second consequence, only environmental sources can act to increase MZ twins' trait dissimilarity. While DZ twins are also same-aged, they are as genetically similar as other biological first-degree siblings. That is, they share 50% of segregating genes on average. If environmental sources contribute to DZ twins' resemblance to the same degree they contribute to the similarity of MZ twins (i.e., equal environments assumption), the difference between MZ and DZ twins' trait similarity could only be due to genetic sources. It thus informs about the heritability of a trait: The larger the difference between MZ and DZ twin correlations, the larger the contribution of genetic influences to the variance. The other way round, the lower the difference between these twin correlations, the larger the contribution of environmental factors that are shared between twin siblings, and act to increase the similarity within families and differences between families. Almost all twin studies on personality traits have shown substantial differences between MZ and DZ twin correlations, demonstrating the contribution of nature rather than nurture to family resemblance in personality traits.

Genetic effects can be additive and nonadditive. Additive genetic effects refer to the combined effects of genetic variants at two or more gene loci on observable trait differences. Nonadditive genetic sources include interaction effects between two genetic variants within gene loci (i.e., allelic dominance, with the dominant allele suppressing the effect of the recessive one) and between two or more genetic variants across different gene loci (i.e., emergensis;

Lykken, 2006). Whereas MZ twins completely share additive and nonadditive genetic sources, DZ twins share 50% of additive genetic effects on average, 25% of allelic dominance effects, and no effects due to emergensis. Thus, if nonadditive genetic factors were present, MZ twins would correlate more than twice as much as DZ twins. Indeed, twin studies on personality traits have reported those differences in MZ and DZ twin correlations, indicating that nonadditive genetic sources contribute to personality trait variance (Vukasović & Bratko, 2015).

Although CTDs allow estimations of nonadditive in addition to additive genetic effects, they rely on the assumption that shared environmental influences do not play any role. This is due to the limitation that only either nonadditive genetic or shared environmental factors can be estimated in the presence of additive genetic sources. However, if this assumption is wrong and both nonadditive genetic and shared environmental factors matter, additive genetic influences will be overestimated and the other two sources of variance will be underestimated in such a design. A recent extended twin-pedigree study on Neuroticism not limited to this problematic assumption found that 47% of this trait's variance was almost equally attributable to additive and nonadditive genetic factors, whereas shared environmental factors explained 13% of its variance (Boomsma et al., 2018). Similar results have been reported for self-esteem based on a nuclear twin family study including parents of twins and further siblings (Bleidorn, Hufer, Kandler, Hopwood, & Riemann, 2018). These nuclear twin family studies suggest that previous twin studies obscured significant shared environmental influences and tended to overestimate the heritability of personality traits.

CTDs have further limitations. They cannot control for the contribution of twin parents' assortative mating (i.e., mates choose similar mates) regarding the trait(s) of interest, the presence of which would lead to an overestimation of shared environmental influences and an underestimation of genetic factors. This is because spouses who are similar in their traits tend to also share genetic factors, creating a genetic covariance between them and increasing the genetic similarity of their offspring. As a consequence, siblings (except MZ twins) are genetically more similar than would be expected without assortative mating, leading to smaller differences between MZ and DZ twins regarding their similarity. Furthermore, CTDs cannot consider specific forms of gene-environment interplay. For example, *passive nature-nurture covariance* results from a nonrandom association between genetic and environmental influences transmitted from parents to their offspring. This association cannot be addressed by CTDs as they do not consider parental information. Extending twin designs by including information on the similarity among other relatives further reduces the indeterminacy and distortion of parameter

estimates (see Coventry & Keller, 2005; Keller & Coventry, 2005, for overviews).

The current study added to existing knowledge in two respects. First, we estimated the etiology of individual differences in HEXACO personality traits using a sample with a broad age range. Second, we used data from an extended twin family design (ETFD) across three generations (twins plus parents, offspring, and spouses of twins) to overcome many limitations of the CTD. This design allows more detailed information and less biased estimates of genetic and environmental sources of variance in HEXACO personality traits. Since this is the first extended twin family study on HEXACO personality traits, we did not formulate specific hypotheses and let the data speak.

Method

Participants

We used data from the twin family study of the Study of Personality Architecture and Dynamics (SPeADy; see <http://www.speady.de/studies/?lang=en>). SPeADy is a longitudinal, genetically informative research project. It aims to develop a comprehensive model suitable to sufficiently describe the differing personalities of human beings including core and surface traits, strivings, and value orientations (Kandler, Zimmermann, & McAdams, 2014), and to understand the sources of differences in personality development throughout the lifespan (Kandler & Zapko-Willmes, 2017). The twin family study includes data from 171 female and 50 male MZ pairs of twins as well as from 197 female, 57 male, and 98 female-male DZ pairs of twins. For some (rather younger) twins, data from their parents (208 mothers and 119 fathers) were available. From those twins who were married or in a committed relationship, 228 spouses provided data. Additionally, we had access to data from 143 offspring of (rather older) twins. The complete sample

($N = 1,844$) cannot be treated as representative for the general population, but it can be seen as heterogeneous regarding age, sex (see Table 1), family status (42% unwed, 48% married, 7% divorced, 3% widowed), and educational level (12% at school, 8% school-leaving qualification, 18% secondary school certificate, 9% polytechnic degree, 20% high school graduation, 5% bachelor's degree, 22% master's degree/diploma/state examination, 4% PhD, and 2% others).

Personality Measures

To capture the six HEXACO personality dimensions, we used the German version of the 60-item HEXACO Personality Inventory – Revised (Ashton & Lee, 2009; Moshagen, Hilbig, & Zettler, 2014). The internal consistency for the six personality trait measures and for each subsample is shown in Table 1 [see also Figure S1 in the Electronic Supplementary Material (ESM 1) for correlations between HEXACO traits across subsamples]. The reliability can be treated as acceptable. Although age and sex differences were out of the scope of the current study, they can inflate trait variance and bias family members' similarity. Thus, we corrected all trait scores for age and sex differences using a regression procedure (McGue & Bouchard, 1984). Standardized residual scores were used in the following analyses.

Statistical Analyses and Software

We first estimated intra-class correlations (ICCs) to get an insight into the family similarity of selective dyads. These initial and all preparatory data analyses were completed using the statistical software IBM SPSS 25. Because of the limited number of certain family dyads ($n < 30$; see Table S1 in ESM 1), the SPeADy twin family sample provided insufficient statistical power to estimate sources of

Table 1. Sample statistics and internal consistency of HEXACO-60 scores

Subsample	<i>n</i>	Female (%)	Age		Cronbach's α of HEXACO trait scores					
			Average	Range	HH	Em	eX	Ag	Co	Op
Twin <i>a</i>	573	73	38.98	14–88	.72	.77	.80	.74	.77	.71
Twin <i>b</i>	573	72	38.98	14–88	.71	.78	.80	.72	.75	.72
Twins' mother	208	100	57.40	37–87	.67	.66	.79	.63	.73	.67
Twins' father	119	0	59.23	35–85	.74	.65	.62	.72	.71	.79
Twin <i>a</i> 's spouse	115	25	51.05	19–89	.68	.71	.73	.75	.75	.74
Twin <i>b</i> 's spouse	113	28	52.34	16–94	.72	.75	.81	.65	.75	.73
Twin <i>a</i> 's offspring	77	66	29.97	14–59	.77	.74	.79	.77	.79	.72
Twin <i>b</i> 's offspring	66	58	30.68	14–59	.82	.75	.82	.76	.75	.78

Note. HH = Honesty-Humility; Em = Emotionality; eX = Extraversion; Ag = Agreeableness; Co = Conscientiousness; Op = Openness.

Table 2. SEM-based robust correlation estimates for specific twin family dyads

Family dyads	Genetic relation (%)	n Dyads	HEXACO personality traits											
			HH		Em		eX		Ag		Co		Op	
			r	P	r	p	r	p	r	p	r	p	r	p
MZ pairs of twins	100	221	.464	< .001	.581	< .001	.583	< .001	.468	< .001	.529	< .001	.662	< .001
First-degree relatives	50	1,277	.173	< .001	.138	< .001	.250	< .001	.080	.009	.149	< .001	.251	< .001
DZ pairs of twins	50	352	.229	< .001	.163	.002	.250	< .001	.155	.003	.166	.001	.270	< .001
Others	50	925	.147	< .001	.125	< .001	.258	< .001	.050	.184	.148	< .001	.248	< .001
Second-degree relatives	25	121	.077	.392	.028	.756	.052	.541	.018	.842	.040	.652	.091	.263
Spouses	0	328	.225	< .001	.082	.127	.056	.298	.012	.825	-.053	.324	.277	< .001
Sisters-/brothers-in-law	0	315	.146	.015	.008	.887	.111	.054	-.014	.820	.056	.327	.136	.018

Note. HH = Honesty-Humility; Em = Emotionality; eX = Extraversion; Ag = Agreeableness; Co = Conscientiousness; Op = Openness. First-degree relatives: DZ pairs of twins, parent-offspring, and MZ twin-co-twin's offspring. Second-degree relatives: uncle/aunt-nephew/niece, grandparent-grandchild, and MZ twins' offspring (cousins). Significant estimates ($p \leq .01$) are shown in bold. See Table S1 in ESM 1 for intra-class correlations and 95% confidence intervals for more specific twin family relations.

variance based on data from all three generations in one structural equation model (SEM), such as the so-called Stealth or Cascade models (see Keller et al., 2009; Medland & Keller, 2009, for more details). Therefore, we separately analyzed family constellations using SEMs based on more specific ETFDs to examine robust family correlations for different kinships and estimate the genetic and environmental sources of variance in HEXACO personality traits. For the latter, we used a Nuclear Twin Family Model (NTFM; Keller, Medland, & Duncan, 2010) and a Spouses-of-Twins Model (SoTM; Kandler, Lewis, Feldhaus, & Riemann, 2015). SEM analyses were run using the statistical software package Mx (<https://mx.vcu.edu/>).

Analyses and Results

Family Correlations

After correction for age and sex differences, ICCs (Table S1) and SEM-based robust correlation estimates (see Table 2) suggested substantial trait similarity for genetically identical twin siblings. For all six personality dimensions, twin correlations were statistically significant and significantly lower for fraternal pairs of twins (see Table S1 for the non-overlapping confidence intervals between MZ and DZ ICCs). Constraining the SEM-estimated MZ twin correlation and DZ twin correlation to be equal led to a significant decline in model fit for each trait, indicated by a significant likelihood-ratio test based on -2 times the logarithmized Likelihood difference ($\Delta -2\log L > 12$; $\Delta df = 1$; $\Delta p < .001$). For all HEXACO personality traits, MZ correlations were substantially higher and more than twice as high as DZ correlations, indicating substantial additive and nonadditive genetic factors contributing to the variance in all traits.

ICCs for all other first-degree relatives tended to be lower compared to those of the DZ twins (average ICC = .165 vs. ICC = .206 across traits). However, all correlations between first-degree relatives (excluding MZ twins) could be constrained to be equal without significant reduction of model fit ($\Delta -2\log L < 12$; $\Delta df = 7$; $\Delta p > .10$). These correlations were statistically significant for all personality traits (Table 2). Negligible differences across first-degree relatives' similarity indicated two things. First, there were negligible contributions of shared environmental influences that acted to increase the resemblance of siblings. Second, nonadditive genetic factors due to allelic dominance effects, which acted to increase the resemblance of siblings but not the similarity between parents and offspring, could also be assumed to be negligible. As a consequence, nonadditive genetic sources due to emergence (Lykken, 2006) may account for the substantial difference between genetically identical MZ twins and first-degree relatives regarding personality trait correlation.

There were no statistically significant correlations (beyond chance due to multiple testing) within second- or third-degree relatives, such as between DZ twins and their co-twins' offspring, twins' parents and their grandchildren, or between cousins (see also Table S1). This again indicated substantial nonadditive genetic factors contributing to the variance in HEXACO personality traits, but also suggested some shared environmental influences, which may act to increase the similarity of first-degree relatives compared to other relatives.

The spouse correlations within twins' parents and between twins and their spouses were not statistically significant, except for Openness. There was a significant spouse correlation regarding Honesty-Humility between twins and their spouses, whereas the latter was not replicable for parents of twins in terms of statistical significance (see Table S1 for specific ICCs). However, both correlations were not significantly different from each other

($\Delta -2\log L = 0.557$; $\Delta df = 1$; $\Delta p = .456$). Thus, a first inspection of spouse correlations suggested assortative mating for Openness and Honesty-Humility.

The hints on potential contributions of assortative mating and shared environmental influences in the presence of nonadditive genetic sources underscore the importance to extend CTDs by including additional family constellations. This allows to adequately estimate the genetic and environmental sources, which otherwise would be biased. In addition, NTFM and SoTM analyses offer further advantages. One advantage is the consideration of passive nature-nurture covariance. Another advantage refers to the question whether spouse similarity is really due to phenotypic – and thus in part genetically driven – assortment, or rather attributable to shared social, economic, and cultural circumstances (i.e., social homogamy; Morton, 1973).

Nuclear Twin Family Modeling

The SPeADy twins-plus-parents subsample ($n = 1,473$) provided adequate statistical power for NTFM analyses because information on at least $n = 100$ were available for each family dyad. The path diagram for the NTFM is presented in Figure 1. The black squares represent measured trait variables for twins and their parents. Upper case letters in the circles denote latent variables (genetic factors in gray and environmental factors in white) that account for the variance in the measured trait variables. Lower case letters reflect path coefficients with single-headed arrows signifying effects from one variable to another, and

double-headed arrows representing covariations between variables. Using a so-called path coefficient approach, variances of all latent variables are fixed to 1 (except for the additive genetic component A and the familial environmental component FE, which equal q and x , respectively). This allows the estimation of genetic and environmental components by multiplying squared path coefficients (except for A and FE): $V_A = a^2q$, $V_{NA} = d^2$, $V_{FE} = x$, $V_S = s^2$, and $V_E = e^2$. Note that there is also a covariance between A and FE: $COV_{A-FE} = w$. The non-arrow line connecting the mother and the father of twins is a co-path (μ), reflecting assortative mating (see Keller et al., 2009, for more details on the nuclear twin family modeling algebra and path analytic rules).

All latent variables can account for the observed variance (σ^2) in trait scores, which is assumed to be equal across twin siblings and parents, and can be set at 1 in case of z-standardized scores. It follows that the model-implied trait variance is: $\sigma^2 = a^2q + d^2 + 2aw + x + s^2 + e^2 = 1$. Note that trait variance due to the covariance between A and FE is entered twice: $2aCOV_{A-FE} = 2aw$. All individual differences in the parental and in the offspring's generation are attributable to the same latent sources of variance. For example, variance in parents' trait scores may be attributable to sibling-specific shared environmental influences (s^2). However, these influences are only shared by siblings and can act to increase similarity between siblings, but not between parents and offspring or between mothers and fathers, as shown in Figure 1.

The assortative mating co-path μ has consequences for the variances of the latent additive genetic factors A(q)

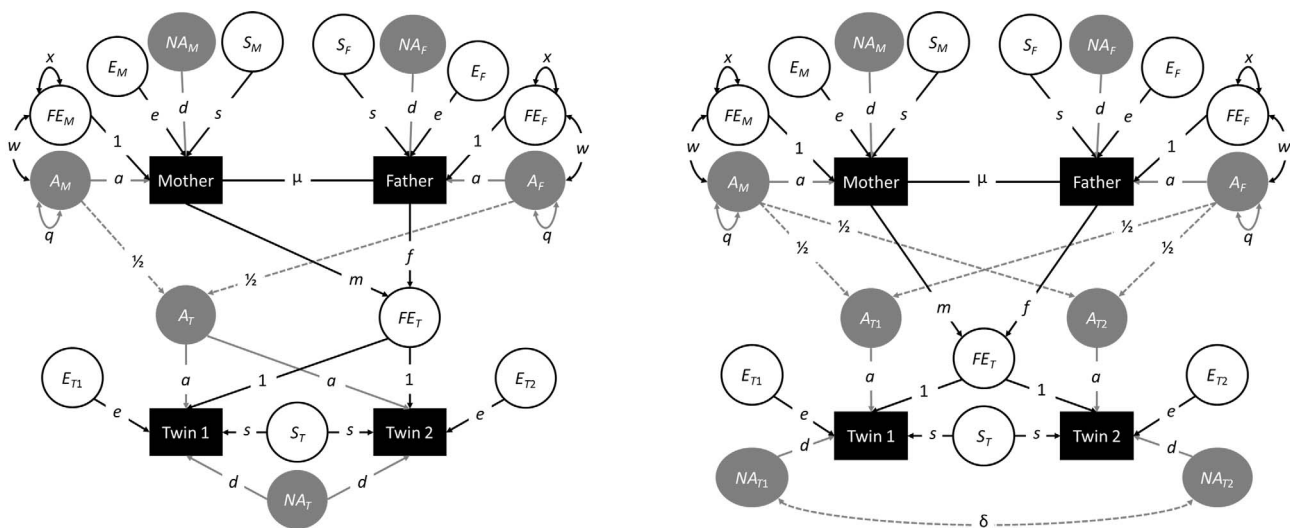


Figure 1. Path model of nuclear twin family design (adapted from Keller et al., 2009): MZ twin family (left) and DZ twin family (right); Black boxes represent measured variance in twins' and their parents' traits, whereas circles reflect latent sources of variance; gray circles reflect additive (A) and nonadditive (NA) genetic factors; white circles represent environmental factors due to sibling-specific shared environmental influences (S), shared family environments (FE) provided by parents (m , f), and individual-specific (nonshared) environmental influences (E); the model also allows for the estimation of the contribution of assortative mating (μ) and nature-nurture covariance (w). See text for more details.

and family environmental factors $FE(x)$, and for their covariance (w). Assuming equal variance components across parental and offspring generations, x is equal to all pathways that can be traced from and back to the same latent variable FE in offspring: $x = m^2\sigma^2 + f^2\sigma^2 + 2m\sigma^2\mu f\sigma^2 = m^2 + f^2 + 2mf\mu$ (because $\sigma^2 = 1$). As a consequence, x is not truly estimated but fully determined by m , f , σ^2 and μ . Since σ^2 is a function of x , and x is a function of σ^2 , these model parameters “comprise a set of *nonlinear constraints* [...]” that “describe, and constrain, the inter-relationships between estimated parameters in a way that keeps the entire model internally and logically consistent. Their values are not estimated, strictly speaking, but instead are determined by (and help to determine) estimated parameters and other non-linear constraints” (Keller et al., 2009, p. 11). Since assortative mating enhances additive genetic variance, it follows that $q > 1$ in case of a significant μ : $q = 1 + \mu (qa + w)^2$. Thus, q is a nonlinear constraint if $\mu \neq 0$ (see Keller et al., 2009, for details).

When both genetic and environmental transmissions from parents to offspring are significant, this will create a significant covariance between additive genetic factors and familial environmental influences (w). This covariance can be interpreted as passive nature-nurture covariance because the link is a function of the parental trait, which is genetically linked to the offspring's trait and associated with fitting family environments provided to the offspring and reinforcing the offspring's trait. This covariance is the third nonlinear constraint and estimated as follows: $w = \frac{1}{2}(qa + w)m + \frac{1}{2}(qa + w)f + \frac{1}{2}(qa + w)\mu m + \frac{1}{2}(qa + w)\mu f$. If maternal and paternal effects are equal, the covariance can be simplified as: $w = (qa + w)m + (qa + w)\mu m$ or $w = (qa + w)f + (qa + w)\mu f$.

The NTFM implies potential differences in the five observable covariances of the five types of family dyads (MZ twins, DZ twins, parents, mother-twin, and father-twin). The MZ twin covariance is: $COV_{MZ} = a^2q + d^2 + 2aw + x + s^2$. That is, all factors contribute to MZ twins' similarity, except nonshared environmental influences (e^2). The DZ twin covariance is: $COV_{DZ} = a^2(q - \frac{1}{2}) + \delta d^2 + 2aw + x + s^2$ ($\delta = 0\%^{1.25em}pt505\%/ .25em_4$ in case of allelic dominance effects and $\delta = 0$ in case of emergences). As a consequence, if DZ twins are less similar than MZ twins, the model implies that this would be attributable to the lower genetic resemblance between them. The mother-father covariance is: $COV_{MoFa} = \mu$. The mother-twin covariance is: $COV_{MoTw} = \frac{1}{2}a(qa + w) + \frac{1}{2}a(qa + w)\mu + m + f\mu$, whereas the father-twin covariance is: $COV_{FaTw} = \frac{1}{2}a(qa + w) + \frac{1}{2}a(qa + w)\mu + f + m\mu$. If mothers are more similar to their offspring than fathers, then $m > f$, and vice versa.

As initial SEM-based family correlation analyses yielded that correlations did not differ significantly among several first-degree relatives (excluding MZ twins) for all personal-

ity traits, we could assume that parents do not differ in their influences on their offspring: $m = f$. The same finding implied that DZ twin correlations were not significantly higher than correlations among other first-degree relatives (excluding MZ twins). Thus, we could assume that neither sibling-specific shared environmental effects nor allelic dominance effects can account for siblings' similarity: $s = 0$ and $\delta = 0$. The resulting NTFM allowed for estimates of additive genetic influences and nonadditive genetic effects due to emergences (perfectly correlated between MZ twins but $\delta = 0$ for DZ twins), assortative mating, shared environmental effects provided by parents, and passive nature-nurture covariance. We estimated 95% confidence intervals for each model parameter and tested whether the exclusion of insignificant parameters led to a significant decline in model fit using the $-2\log L$ -ratio test. We additionally used the sample-size-adjusted Bayesian Information Criterion (BIC). The smallest BIC indicates the best fitting model. To avoid implausible solutions in the model fitting procedure, we bounded each single-headed arrow path coefficient in the model to take positive values.

The model fit statistics of the different model variants tested for each HEXACO trait are provided in Table S2 in ESM 1. For Emotionality, Agreeableness, and Conscientiousness, a model implying additive and nonadditive genetic influences along with individual-specific (non-shared) environmental influences provided the best model fit. For Honesty-Humility and Extraversion, a model allowing for additive genetic and nonshared environmental sources of variance was sufficiently parsimonious. And for Openness, a model including significant assortative mating, additive and nonadditive genetic factors, and individual-specific environmental influences provided the best fit.

Allowing a better comparability across traits, we reported model parameter estimates derived from the initial NTFM for all traits (Table 3). Across all HEXACO traits, genetic sources accounted for 54% of trait variance with contributions of additive ($a^2q = .32$) and nonadditive genetic factors ($i^2 = .22$). The estimates ranged from 46% for Honesty-Humility to 63% for Openness. The non-genetic variance was primarily due to nonshared environmental sources (incl. variance due to error of measurement) that generally act to increase individuality within and between families. The model analyses also yielded significant assortative mating with respect to Openness as indicated by the significant spouse correlation. The consideration of μ allowed for model parameter estimates that otherwise would have been biased. However, a potential limitation of the NTFM is that it relies on the assumption that spouse correlations reflect phenotypic assortment. At least two other possibilities are conceivable. One possibility is social homogamy: Spouses are similar because of their shared social background that

Table 3. Nuclear twin family model analyses: Parameter estimates

Model parameters	HEXACO personality traits					
	Honesty-Humility	Emotionality	Extraversion	Agreeableness	Conscientiousness	Openness
<i>Path coefficients</i>						
a	0.564 [0.423, 0.655]	0.526 [0.319, 0.626]	0.643 [0.282, 0.766]	0.415 [0.264, 0.528]	0.534 [0.283, 0.640]	0.586 [0.442, 0.682]
q	1.055 [0.987, 1.127]	1.036 [0.977, 1.100]	1.074 [0.963, 1.189]	1.025 [0.988, 1.069]	1.014 [0.956, 1.072]	1.163 [1.068, 1.260]
d	0.337 [0.000, 0.492]	0.544 [0.421, 0.669]	0.360 [0.000, 0.601]	0.544 [0.412, 0.653]	0.483 [0.331, 0.636]	0.480 [0.366, 0.602]
$m = f$	0.000 [0.000, 0.082]	0.000 [0.000, 0.112]	0.013 [0.000, 0.224]	0.000 [0.000, 0.048]	0.000 [0.000, 0.136]	0.037 [0.000, 0.246]
e	0.735 [0.690, 0.783]	0.645 [0.606, 0.688]	0.646 [0.606, 0.691]	0.728 [0.683, 0.777]	0.688 [0.646, 0.734]	0.582 [0.546, 0.607]
w	0.000 [0.000, 0.048]	0.000 [0.000, 0.053]	0.010 [0.000, 0.117]	0.000 [0.000, 0.021]	0.000 [0.000, 0.000]	0.000 [0.000, 0.085]
μ	0.154 [−0.037, 0.328]	0.121 [−0.076, 0.303]	0.151 [−0.075, 0.346]	0.135 [−0.061, 0.315]	0.046 [−0.142, 0.229]	0.328 [0.142, 0.479]
<i>Standardized variance components</i>						
<i>Genetic components</i>						
a^2q	.339 [.188, .442]	.287 [.104, .395]	.442 [.081, .574]	.176 [.070, .281]	.290 [.081, .401]	.400 [.216, .629]
d^2	.116 [.000, .244]	.296 [.177, .445]	.129 [.000, .357]	.295 [.170, .420]	.234 [.110, .404]	.231 [.134, .361]
<i>Variance due to passive nature-nurture covariance and shared environmental influences</i>						
$2aw + x$.000 [.000, .045]	.013 [.000, .099]	.001 [.000, .114]	.000 [.000, .016]	.000 [.000, .045]	.030 [.000, .159]
<i>Variance due to individual-specific environmental influences (and error of measurement)</i>						
e^2	.545 [.480, .621]	.417 [.366, .476]	.416 [.363, .477]	.529 [.464, .603]	.475 [.417, .543]	.339 [.296, .390]

Notes. a = additive genetic parameter; q = variance of latent additive genetic factors; d = nonadditive genetic parameter; m = maternal shared environmental effects; f = paternal shared environmental effects; e = nonshared environmental effects; w = covariance between additive genetic and family environmental factors; μ = assortative mating. Estimates in boldface are statistically significant based on the 95% confidence interval (in brackets); note that model parameters a , d , m , f , and e were bounded to take positive values bounding the lower confidence limit at zero.

influences their traits. Another possibility is spouse-specific interaction, which would act to increase spousal similarity over time. If at least one of both sources is present but not taken into account, the contribution of phenotypic assortment and thus the genetic component would be overestimated.

Spouses-of-Twins Modeling

Although our sample contains relatively few dyads of twins' spouses (see Table S1), we decided to conduct SoTM as a way of exploring this technique in the current dataset. The SoTM allows for tests of the three sources of spouse correlations (Kandler et al., 2015). The full model is shown in Figure 2. Using z -standardized trait scores and the path coefficient approach (i.e., variances of all latent variables were fixed to 1 in order to estimate genetic and environmental components by multiplying squared path coefficients), the model implied trait variance as: $\sigma^2 = a^2 + i^2 + c^2 + u^2 + e^2 = 1$. This model could be reduced by fixing $c = 0$ because neither twin-family correlations (see Table 2) nor NTFM analyses (see Table 3) had suggested environmental influences shared by twins contributing to the variance in any of the HEXACO traits. In this case, the MZ twin covariance is: $COV_{MZ} = a^2 + d^2 + u^2$. The DZ twin covariance is: $COV_{DZ} = \frac{1}{2}a^2(1 + \mu a^2) + \delta d^2 + u^2$. The covariance between twins' traits and their spouses' traits can be decomposed as follows: $COV_{Sp-Tw} = \mu + u^2 + ve^2$. Thus, in contrast to the NTFM, the spousal similarity is potentially attributable to three different sources: phenotypic assortment (μ), social homogamy (u^2), and spouse-specific interaction (ve^2).

If phenotypic assortment acts to increase spousal similarity, the correlation between twins and their co-twins' spouse will be larger for MZ compared to DZ twins as follows: $\mu(a^2 + u^2)$ versus $\mu(\frac{1}{2}a^2[1 + \mu a^2] + u^2)$ (see Kandler et al., 2015). In addition, the correlations between spouses of twins would be larger for MZ twins' spouses compared to DZ twins' spouses: $\mu^2(a^2 + u^2)$ versus $\mu^2(\frac{1}{2}a^2[1 + \mu a^2] + u^2)$. If social homogamy explains spousal similarity, then the underlying shared environmental background will act to increase twins' similarity, similarity between twins and their co-twins' spouses, and similarity between twins' spouses each to the same degree, regardless of zygosity (u^2). Finally, spouse-specific interactions contribute exclusively to spousal similarity and cannot act to increase the similarity of twins or between twins and their co-twins' spouses, or between spouses of twins.

The SPeADy twins-plus-spouses subsample ($n = 1,374$) provided sufficient statistical power for the SoTM analyses because most information was based on $n = 100$ dyads, except for the comparison between the covariance of MZ twins' spouses ($n = 52$) and DZ twins' spouses ($n = 40$).

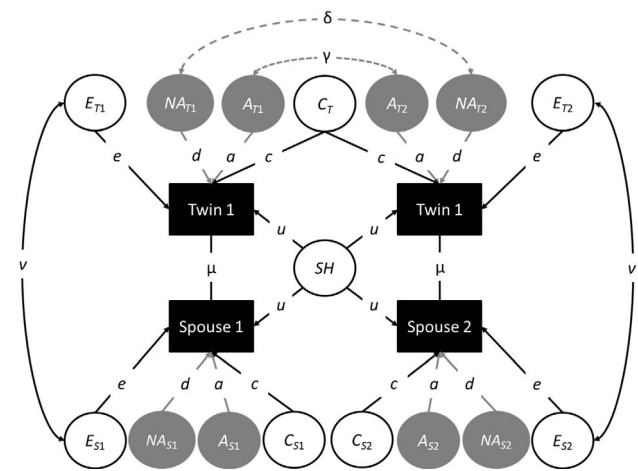


Figure 2. Path model of spouses-of-twins design (adapted from Kandler et al., 2015): Black boxes represent measured variance in twins' and their spouses' traits, whereas circles reflect source factors of variance; gray circles represent additive (A) and nonadditive (NA) genetic factors; white circles represent environmental factors due to social homogamy (SH), environmental influences shared by twins/siblings reared together (C), and individual-specific (nonshared) environmental factors (E); the model also considers phenotypic assortment (μ) and spouse-specific interactions (v) as sources of spousal similarity; $\gamma = 1$ for MZ twins and $\gamma = \frac{1}{2}(1 + \mu a^2)$ for DZ twins; $\delta = 1$ for MZ twins and $\delta = \frac{1}{4}$ (in case of allelic dominance effects) or $\delta = 0$ (in case of emergence) for DZ twins. See text for more details.

Since correlations between twins and their spouses were only significant for Openness and Honesty-Humility, we ran SoTM analyses for these two traits only. Following the results of the NTFM analyses, we started with the full ADE model implying that additive and nonadditive genetic factors as well as nonshared environmental factors sufficiently account for individual differences in personality traits. Then, we tested whether the exclusion of any of the additional parameters potentially accounting for spousal similarity (μ , u , or v) led to a significant decline in model fit using the $-2\log L$ -ratio test. We also looked at the smallest sample-size-adjusted BIC indicating the best-fitting model.

The SoTM analyses yielded different models for Honesty-Humility and Openness (see Table 4 for model parameter estimates and Table S3 in ESM 1 for model fit statistics of all model variants tested). The similarity between twins and their spouses with respect to Honesty-Humility was due to environmental sources: (1) social homogamy, which acts to increase the similarity of spouses and twins through a shared social background, and (2) spouse-specific interactions, where spouses reflect environmental factors not shared by twins. Our analysis suggested a significant contribution of social homogamy to variance in Honesty-Humility, accounting for about 16%. Spouse-specific interactions were estimated to account for about 10% of the variance in Honesty-Humility (95% CIs, however, suggested statistical insignificance).

Table 4. Spouses-of-twins modelanalyses: Parameter estimates

Model parameters	HEXACO personality traits	
	Honesty-Humility	Openness
Standardized variance components		
σ^2	.115 [.000, .359]	.473 [.223, .591]
d^2	.183 [.004, .338]	.179 [.063, .327]
u^2	.160 [.044, .249]	.008 [.000, .147]
$v \times e^2$.097 [.000, .215]	.017 [.000, .175]
$e^2 - (c^2 + v \times e^2)$.445 [.312, .604]	.328 [.159, .389]
Spouse correlation (r_s)	.254 [.161, .344]	.274 [.184, .361]
Standardized components of spouse correlation		
μ/r_s	.000 [.000, .823]	.928 [.049, 1.000]
u^2/r_s	.623 [.176, 1.000]	.030 [.000, .556]
$(v \times e^2)/r_s$.377 [.000, .760]	.042 [.000, .675]

Notes. Estimates in boldface are statistically significant based on the 95% confidence interval (in brackets); σ^2 = additive genetic component; d^2 = nonadditive genetic component; u^2 = variance due to social homogamy; v = latent correlation (or factor weight) due to spouse-specific interactions; e^2 = variance due to nonshared environmental effects (and error of measurement); μ = assortative mating.

Thus, the non-consideration of social homogamy could have led to an overestimation of the contribution of assortative mating and, thus, to an overestimation of additive genetic factors, alongside with an underestimation of non-additive genetic and environmental factors shared by twins (and spouses of twins). SoTM estimates suggested that 30% of individual differences in Honesty-Humility were attributable to genetic factors. For Openness, analyses painted a different picture and primarily confirmed the NTFM results, indicating that phenotypic assortment accounted for the spousal similarity. However, all of these SoTM results, and in particular the differences between Honesty-Humility and Openness, must be regarded as very tentative (see Table 4 for overlapping 95% CIs), given the relatively small numbers of specific dyads involved.

Discussion

The current investigation went beyond previous twin studies on personality traits by estimating the sources of variance in HEXACO personality traits using data from an ETFD across three generations. On the one hand, the findings confirmed previous studies on related personality trait concepts, indicating substantial contributions of genetic factors to within-family similarity and between-family differences in personality traits. In other words, environmental influences shared by siblings reared together in the same family and passive nature-nurture covariation were largely negligible. On the other hand, the estimates of different

genetic and environmental sources of variance based on the NTFM and SoTM analyses revealed new insights into the sources of HEXACO trait differences (see Figure 3 for a summary of results).

After exclusion of random error of measurement ($1 - \alpha$), at least 40% of individual differences in HEXACO personality dimensions were attributable to genetic sources, including both additive and nonadditive genetic components. The latter finding is in line with the meta-analysis by Vukasović and Bratko (2015), who reported almost balanced additive and nonadditive genetic contributions to the trait variance across several personality trait models. Thus, the finding on strong sources of nonadditive genetic components is not specific to HEXACO personality traits. The pattern of results is quite comparable to findings for other personality models, such as reliable measures of Big Five trait scores (e.g., Kandler, Waaktaar, Mõttus, Riemann, & Torgersen, 2019; Spengler, Gottschling, & Spinath, 2012). Our analyses also suggest some differences between traits regarding the amount of genetic influences (see Figure 3). We found the smallest genetic components for Honesty-Humility and Agreeableness. The highest genetic contribution, with assortative mating acting to increase additive genetic variance, could be established for Openness.

We found that family resemblance in complex personality traits was entirely due to genetic sources, except for Honesty-Humility. Our results tentatively suggest that environmental sources might contribute to the similarity of twins and spouses regarding this trait. This is noteworthy because Honesty-Humility largely represents the tendency to be fair and genuine in dealing with others (Ashton & Lee, 2007). In other words, priorities for fairness and modesty shared by twins and spouses may be partly based on similar social, economic, or cultural backgrounds, such as has been found to be true for values shared by twins and their spouses. Honesty-Humility has been shown to be linked with core value and socio-political orientations deeply anchored in humans: Individualism-Collectivism, Social Dominance Orientation versus Egalitarianism, or Self-Enhancement versus Self-Transcendence (Lee, Ashton, & Edmonds, 2018; Lee, Ashton, Ogunfowora, Bourdage, & Shin, 2010). Since previous studies also found family correlations in those characteristics partly attributable to social homogamy (Kandler, Bleidorn, & Riemann, 2012; Kandler et al., 2015), the link between Honesty-Humility and core value orientations could be due to those environmental sources. Future studies should address this suggestion.

Even after controlling for error of measurement, environmental factors accounted for twin differences in HEXACO personality traits (ranging from 10% for Openness to 37% for Honesty-Humility). That is, environmental influences became primarily manifest at the level of the individual. On the one hand, this may reflect socialization influences

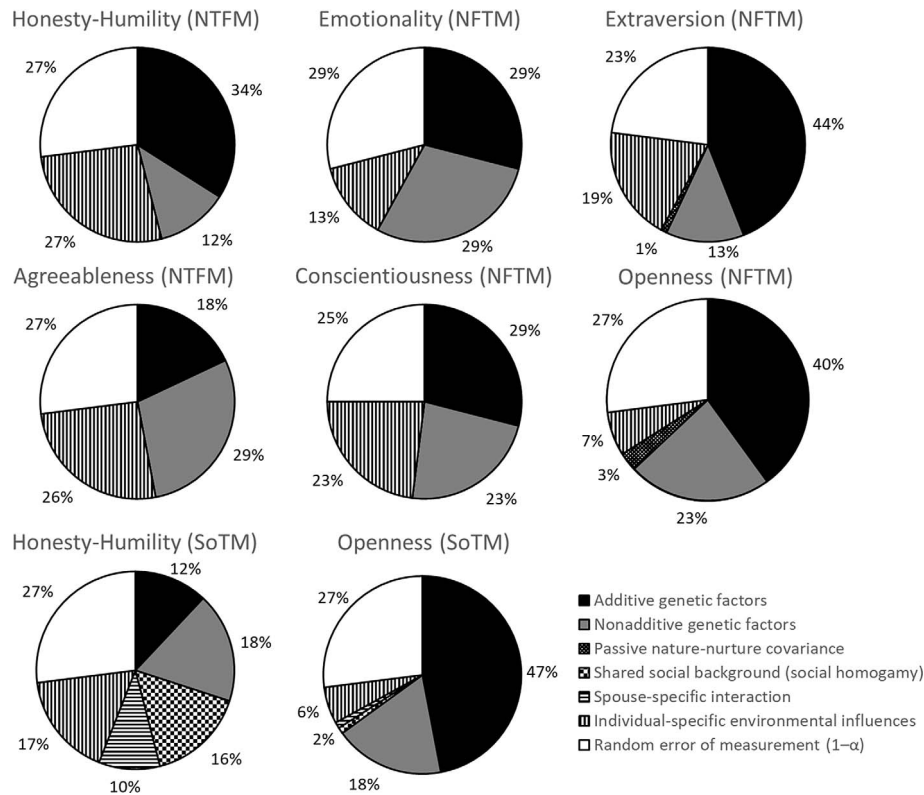


Figure 3. Summary of results on the sources of variance in HEXACO personality traits based on the Nuclear Twin Family Modeling (NTFM) and the Spouses-of-Twins Model (SoTM).

beyond those from the family of origin, such as peer influences. In case of Honesty-Humility, our findings suggest that spouses might reflect an important source of individual differences, in this sample accounting for more than a third of environmental differences between twin siblings. On the other hand, the insignificance of maternal and paternal influences does not necessarily mean that familial or other environmental influences objectively shared by twins are not important for the socialization and development of their personality traits. Our findings only suggest that, if familial nurture is important, then it would primarily act to increase differences between twins. For example, children's behavior related to their heritable traits may evoke different responses from their parents. The parental responses then are more or less shared by siblings depending on their offspring's genetic relatedness. As a consequence, MZ twins would evoke more similar responses than DZ twins. That is, this type of reactive nature-nurture covariation would be confounded with estimates of genetic influences.

In sum, our study provided new insights into the nature and nurture of individual differences in personality traits. Since this is the first extended twin family study without any hypotheses on specific sources of individual differences in HEXACO personality traits (e.g., a priori expectation of social homogamy for Honesty-Humility), the current study is only a first step of unraveling the sources of trait variance

and its transmission from one generation to the next. Our findings have to be considered tentative and must be replicated by further studies based on a larger sample and, at best, across different cultures and languages. A larger sample size is necessary as it allows to test for sex differences and provides sufficient statistical power for more sophisticated approaches of analyzing all three generations in one model – the so-called Cascade model (Keller et al., 2009).

Electronic Supplementary Material

The electronic supplementary material is available with the online version of the article at <https://doi.org/10.1027/2151-2604/a000378>

ESM 1. Additional statistics (Tables S1-S3) and robust correlation estimates for HEXACO personality traits (Figure S1)

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History

Received November 9, 2018

Revision received February 21, 2019

Accepted February 21, 2019

Published online August 2, 2019

Funding

This research based on the SPeADy project (www.speady.de/?lang=en) is supported by grants from the German Research Foundation awarded to Christian Kandler (KA-4088/2-1 and KA-4088/2-2).

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