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How Genetic and Environmental Variance in Personality Traits Shift Across the Life Span: Evidence From a Cross-National Twin Study

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Decades of research have shown that about half of individual differences in personality traits is heritable. Recent studies have reported that heritability is not fixed, but instead decreases across the life span. However, findings are inconsistent and it is yet unclear whether these trends are because of a waning importance of heritable tendencies, attributable to cumulative experiential influences with age, or because of nonlinear patterns suggesting Gene × Environment interplay. We combined four twin samples (N = 7,026) from Croatia, Finland, Germany, and the United Kingdom, and we examined age trends in genetic and environmental variance in the six HEXACO personality traits: Honesty-Humility, Emotionality, Extraversion, Agreeableness, Conscientiousness, and Openness. The cross-national sample ranges in age from 14 to 90 years, allowing analyses of linear and nonlinear age differences in genetic and environmental components of trait variance, after controlling for gender and national differences. The amount of genetic variance in Extraversion, Agreeableness, and Openness followed a reversed U-shaped pattern across age, showed a declining trend for Honesty-Humility and Conscientiousness, and was stable for Emotionality. For most traits, findings provided evidence for an increasing relative importance of life experiences contributing to personality differences across the life span. The findings are discussed against the background of Gene × Environment transactions and interactions.

Keywords: HEXACO personality traits, life experiences, cross-national twin study, life span, heritability

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Behavioral genetic research has robustly shown that almost all traits that vary between humans are heritable. Indeed, a meta-analysis of twin studies on almost 18,000 human traits reported an average heritability of .49 (Polderman et al., 2015). Another meta-analysis specifically examining the heritability of personality traits on the basis of identical and nonidentical twin data yielded a comparable estimate of .47 (Vukasović & Bratko, 2015), meaning that about 47% of population variance in personality involve

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genetic contributions, with the remaining personality differences primarily attributable to individual life experiences and error of measurement. When taking random and nonrandom error of measurement into account, the heritability estimates typically exceed .50 (Kandler & Papendick, 2017; Kandler, Richter, & Zapko-Willmes, 2017; Riemann, Angleitner, & Strelau, 1997).

Substantial heritability, however, does not imply immutability across the life span. A sizable literature shows that genetic influences wax and wane across the life span depending on the trait in question (Plomin, DeFries, Knopik, & Neiderhiser, 2016) with different implications for underlying developmental processes (Briley et al., 2019). The existing evidence for personality traits is equivocal, with some work reporting less support for shifting genetic and environmental contributions across the life span (e.g., Loehlin & Martin, 2001), and more recent studies providing evidence for shifts, though the specific nature of these shifts is inconsistent across studies (Briley & Tucker-Drob, 2014; Kandler & Papendick, 2017). The current study was designed to clarify this inconsistency by estimating linear and nonlinear age trends in genetic and environmental contributions to the variance in personality traits across the life span in a large-scale cross-national twin sample.

Explanations for Genetic and Environmental Variance

Describing the potential explanations for estimates of genetic and environmental variance in traits can help us understand why genetic and environmental contributions might shift over the life span. Estimates of genetic variance could reflect individual differences in people's molecular genetic makeup. Despite substantial heritability estimates for personality traits based on quantitative genetic (e.g., twin) designs, large-scale genome-wide associations studies (GWAS) have struggled to identify any single gene that accounts for more than 1% of the variance in complex personality traits (de Moor et al., 2012; Lo et al., 2017). Several explanations for this so-called *missing heritability problem* have been discussed (Maher, 2008; Plomin, 2013), such as a small number of rare within-population genetic variants with large effects, a large number of multiple genetic variants with very small main effects, or multiple interactions across different gene loci (see online Supplement Material A for a more in-depth discussion). Analogously, only tiny main effects of specific environmental factors (e.g., work life, social experiences, life events, etc.) on personality have been identified (Bleidorn et al., 2020; Bleidorn, Hopwood, & Lucas, 2018; Turkheimer & Waldron, 2000), pointing to a comparable missing "environmentality" problem.

Solving the puzzle of very small main effects of specific genes and certain events on personality requires recognizing that genetic and environmental influences are intricately interwoven. As a result, contributions of genetic factors and life experiences—and, thus, estimates of genetic and environmental variance components—may vary across the life span (Bleidorn, Kandler, & Caspi, 2014; Briley, Livengood, & Derringer, 2018; Kandler & Zapko-Willmes, 2017). For example, different life stages and individual living conditions provide different opportunities for heritable individual tendencies to arise. Increasing opportunities allow more scope for unfolding, whereas narrow boundaries typically attenuate genetic contributions (Briley et al., 2019). Similarly, environmental influences are dependent on genetic sensitivities (Belsky & Pluess, 2009). Thus, environmental influences vary as a function of genetic differences and vice versa. Effects of these so-called Gene × Environment interactions can change across the life span with changing sensitivity toward experiences and changing environmental opportunities.

Age Trends in Genetic and Environmental Variance

Quantitative reviews have provided evidence for shifts in genetic and environmental contributions to personality differences across the life span (Briley & Tucker-Drob, 2014; Kandler, 2012): genetic contributions appear to decrease relative to environmental ones. Such patterns could result from the individual opportunities and life experiences that accumulate with personality maturation across the life span. Consequently, environmental variance is expected to increase, whereas genetic variance remains constant (Hypothesis 1). As a consequence, heritability estimates (i.e., the relative genetic contribution to the trait variance) would decline with age.

Environmental factors can reduce the unfolding of genetic differences by constraining an individual's opportunities for expression or prompting scripted behaviors or normative pressure to behave in a specific way within specific social roles (e.g., in family or at work). Environmental factors can even influence gene expression by switching on and off the genetic activity without altering the genome, a phenomenon known as environmentally modified epigenetic regulation (Shah et al., 2014). Such influences can be viewed as Gene × Environment interaction effects, because they regulate the genetic unfolding and sensitivity to environmental influences. Cumulative intraindividual epigenetic changes that arise during the human life course (*epigenetic drift*) have been found to be primarily driven by environmental factors not shared by twins reared together (Tan et al., 2016). Hence, increasing epigenetic differences between genetically identical individuals (monozygotic twins) must be environmental. As a consequence of those Gene × Environment interactions, genetic contributions to the variance are expected to decrease across the life span, whereas environmental variance is expected to increase (Hypothesis 2).

A meta-analysis of 20 longitudinal behavior genetic studies found evidence for nonlinear declines in genetic variance relative to increases in environmental variance, with more pronounced declines during childhood and adolescence (Briley & Tucker-Drob, 2014). In contrast, a more recent review (Kandler & Papendick, 2017), which was partly based on a different and newer set of longitudinal and age-group studies, did not find the sharp decline in younger ages, but rather increases of heritability estimates between childhood and young adulthood. There are several methodological explanations for the inconsistent results between these quantitative reviews (see also online Supplemental Materials B for a more in-depth discussion), leading to the conclusion that the discrepancies can only be resolved by assessing personality in different age groups using the same instrument and ensuring measurement invariance across age (i.e., capturing the same personality constructs in different age groups).

Two large-scale twin studies (Kandler, Waaktaar, Mõttus, Riemann, & Torgersen, 2019; Mõttus et al., 2019) using different rater perspectives and invariant personality measures yielded evidence for *increasing* genetic differences relative to environmental differences until adolescence. This finding is in line with the idea that young people are challenged with identity formation and niche picking (McAdams, 2015; Scarr, 1992). They select or avoid and create or manipulate environments to increase person-environment fit. Such dynamic Gene × Environment transactions over time would amplify initial genetic differences in personality traits with increasing age (Scarr & McCartney, 1983). A longitudinal twin family study, however, showed that increasing genetic variance was because of an accumulation of novel genetic factors that come to play during adolescence rather than an amplification of initial genetic differences (Kandler, Waaktaar, et al., 2019). This could be because of the activation and deactivation of genetic variants during development. The authors argued that estimates of novel genetic factors during adolescence may also reflect interactions between genetic and environmental influences shared by twins, which would be captured in the estimate of genetic effects, if not directly estimated (see Purcell, 2002; for mathematical derivations). Shared opportunities to unfold their partly heritable personality in a very similar way are more probable by adolescent twins reared together.

After moving out of the parental home, twin siblings' experiences diverge and more opportunities are likely unshared within twin pairs. As a consequence, interactions between genetic factors and nonshared environmental influences should accumulate across adulthood. If not directly estimated, such interaction effects would be captured in the estimate of nonshared environmental contributions (Purcell, 2002). Taken together, recent studies (Kandler, Waaktaar, et al., 2019; Mõttus et al., 2019) indicated a nonlinear—reversed U-shaped—age trend of the genetic component with a peak in young adulthood beyond a constant increase of environmental contributions across the entire life span (Hypothesis 3).

In summary, the literature provides three plausible explanations for declines in the heritability of personality across age (vs. null hypothesis: no age-related heritability decline; see Figure 1). According to the idea that individual life experiences accumulate with personality maturation across the life span (Hypothesis 1), environmental variance should increase, resulting in increasing trait differences. Increasing environmental pressure against innate differences and epigenetic drift (Hypothesis 2), however, should additionally come along with a continuous decline in genetic variance with age, resulting in more balanced trait differences. A reversed U-shaped genetic variance pattern with a peak in young adulthood could reflect interactions between genetic and environmental influences shared by twins during childhood and adolescence and interactions between genetic and nonshared environmental factors in adulthood (Hypothesis 3), resulting in increasing trait variance in younger ages but balanced trait differences thereafter.

Aims of the Present Study

Most previous behavior genetic studies relied on specific personality trait concepts (see Johnson, Vernon, & Feiler, 2008, for an overview), such as those included in Eysenck's three-dimensional Psychoticism-Extraversion-Neuroticism model (Eysenck & Eysenck, 1985), Tellegen's hierarchical personality trait model (Tellegen & Waller, 2008), or the Big Five/Five-Factor Model (B5/FFM; McCrae & John, 1992). Few behavior genetic studies on personality trait dimensions, so far, were based on the HEXACO framework, which is built upon the very same psycholexical approach that have yielded the B5/FFM, but which has yielded a

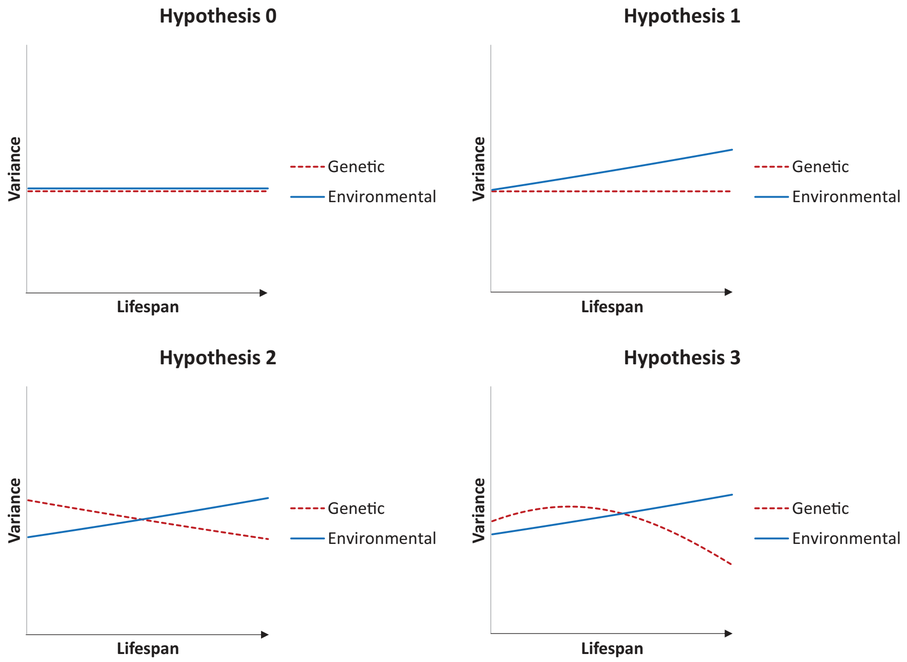

Figure 1. Illustration of four hypotheses on potential age trends of genetic and environmental variance in personality traits across the life span. Hypothesis 0: No age differences; Hypothesis 1: Increasing environmental component; Hypothesis 2: Declining genetic variance and increasing environmental variance; Hypothesis 3: Increasing environmental variance and reversed U-shaped age trend for the genetic variance with a peak in young adulthood. See the online article for the color version of this figure.

maximum set of six cross-culturally replicable personality trait dimensions rather than five (Ashton & Lee, 2007; Ashton, Lee, & de Vries, 2014): Honesty-Humility, Emotionality, Extraversion, Agreeableness, Conscientiousness, and Openness.

Although there is substantial construct-related and structural overlap between the B5/FFM and the HEXACO framework, the inclusion of a sixth personality dimension Honesty-Humility leads to different architectures of HEXACO Agreeableness and Emotionality when compared with their B5/FFM counterparts (i.e., Agreeableness and Emotional Stability vs. Neuroticism; see Ashton & Lee, 2020). In short, HEXACO Agreeableness and Emotionality are rotated versions of their B5/FFM counterparts, such that HEXACO Agreeableness contains lack of irritability content associated with B5/FFM Emotional Stability, and HEXACO Emotionality contains sentimentality content associated with B5/FFM Agreeableness. Furthermore, some content associated with B5/FFM Agreeableness is shifted to Honesty-Humility in the HEXACO framework. Currently, we know relatively little about genetic and environmental contributions to individual differences in HEXACO personality traits, and the few existing studies did not address age trends in genetic and environmental variance (Kandler, Richter, & Zapko-Willmes, 2019; Lewis & Bates, 2014; Veselka et al., 2009).

In addition, most previous studies were restricted in age range and used different methods and measurement instruments to capture personality traits in different ages, leading to inconsistencies of age effects on genetic and environmental components of personality traits (Briley & Tucker-Drob, 2014; Kandler & Papendick, 2017). In summary, the state of the literature calls for a systematic, genetically informative study with a large sample size and age range based on the same well-established measure of personality.

In the current study, we combined data from four twin studies on the HEXACO framework. We examined which of the potential patterns of age trends in genetic and environmental variance in personality traits fit the data best (see Figure 1). The data stem from four European countries (Croatia, Finland, Germany, and United Kingdom), encompassing more than 7,000 twins spanning an age range of 14 to 90 years. These data allowed an examination of linear and nonlinear age trends in genetic and environmental sources in personality differences from adolescence to old age.

Method

Participants and Procedure

For the current investigation, which was not preregistered, we combined data sets from four twin samples collected in four different nations. Table 1 provides an overview of the sample demographics. The combined sample includes 3,008 monozygotic (MZ) and 4,018 dizygotic (DZ) twins. The sample includes more women than men, with the ratio of men to women varying across national subsamples and twin zygosity. Further, the samples vary in their age means, variances, and ranges, with the Croatian sample only encompassing late adolescents and young adults and the U.K. sample mainly containing women in middle and higher age of life. We accounted for these unbalanced distributions (see Initial and Preparatory Analyses for more details).

Ethics statement. All specific study projects were approved by research ethics review boards. Data collection involved no invasive procedures. Participants were informed that participation was voluntary and that they were free to terminate their participation at any time without giving a reason. All participants provided written, informed consent in accordance with the Declaration of Helsinki and EU data protection rules before responding to the surveys.

Croatian sample. The Croatian data stem from a population-based twin sample across six birth cohorts. The sample was formed in several steps. First, the National Centre for External Evaluation of Education (NCEEE) was contacted. Following preliminary agreement, a contract was signed between the principal investigator (Professor Denis Bratko) and the NCEEE to secure the confidentiality of participants' personal contact details. Since NCEEE yearly administers exams based on which national standards of students' academic achievement are evaluated (State Matura Exams), potential twin pairs were identified based on the algorithm administered to six cohorts—school years 2009/2010 to 2014/

Table 1
Sample Demographics

	Study subsamples				
Statistics	Croatian	Finnish	German	U.K.	Total sample
N total	830	2,816	1,142	2,238	7,026
n male	306	879	312	149	1,646
n female	524	1,937	830	2,089	5,380
n male MZ twin pairs	47	135	50	40	272
n female MZ twin pairs	100	414	171	547	1,232
n male DZ twin pairs	45	120	57	31	253
n female DZ twin pairs	101	369	195	494	1,159
n opposite-sex DZ pairs	122	370	98	7	597
Average age	22.15	28.44	38.99	64.73	40.97
Age range	19–28	18–45	14–88	26–90	14–90
Average age (male)	22.03	28.43	35.43	66.74	32.05
Age range (male)	19–25	18–45	14–84	35–90	14–90
Average age (female)	22.22	28.46	40.33	64.59	43.70
Age range (female)	19–28	18–45	14–88	26–90	14–90

Note. MZ = monozygotic; DZ = dizygotic.

2015. This resulted in a dataset of 3,026 potential individual twins. At this time, researchers were only given access to contact information. Potential twin pairs received a postal letter inviting them to participate in the study, describing study goals, procedures, and voluntary participation with no compensation. If potential participants did not want to participate and/or did not allow their NCEEE identification data to be used in the study, they could contact the researchers by postal mail, SMS, or e-mail and request deletion from the database. These persons were not contacted again. A set of questionnaires was sent to 2,649 individual twins together with an additional empty, stamped and return-addressed envelope. A total of 836 individual twins provided written consent to participate in the study and returned the questionnaires. The dataset used in this research is available as anonymized scientific use file after sending a research proposal to the principal investigator. The Ethics Review Board of the Department of Psychology, Faculty of Humanities and Social Sciences, University of Zagreb reviewed and approved the research plan describing the data collection procedure.

Finnish sample. The Finnish data stem from Genetics of Sexuality and Aggression (GSA) Project. Contact information for Finnish twins and their siblings were drawn from the Central Population Registry in Finland with more than 33,000 addresses. Only those who live in Finland were invited by letters in November 2018 to respond to an online survey and provide agreements for data collection, which concluded in the first week of January 2019. All participants were offered entry into a raffle that contained 40 gift vouchers to a Finnish network of companies operating in the retail and service (e.g., restaurants, petrol stations, and hotels) sectors worth €100 each as prizes. In total, 9,564 individuals (6,965 twins and 2,592 siblings, seven unknown) responded, resulting in a total response rate of 29%, with 9,319 (97%) respondents giving consent for the use of their data for scientific purposes. The current analysis includes the 2,816 participants who provided HEXACO data and were members of complete twin pairs. Further details regarding the sample, recruitment, and zygosity estimation are provided in Tybur et al. (in press). The Board for Research Ethics of Åbo Akademi University in Turku, Finland, reviewed and approved the GSA project.

German sample. The German twin sample was collected between January 2016 and January 2018 as genetically informative data of the Study of Personality Architecture and Dynamics (SPeADy). Different strategies were used for the recruitment of twins, such as media calls, attending twin club meetings, and getting contact details from registration offices or former twin studies. The sample cannot be treated as population-based, but it can be seen as heterogeneous with respect to age, gender, family status, and educational level (see Kandler, Penner, Richter, & Zapko-Willmes, 2019, for more details on the recruitment procedure and sample characteristics). All participating twins provided an informed consent and contributed data via an online survey or mailed questionnaires. After both twins of a pair had filled out the forms and questionnaires, they received a personality profile and a €10 voucher for compensation. Contact details and research data were entered into different databases. Research data are available as anonymized scientific use file on request. The Ethics Committee of the Bielefeld University and Medical School Hamburg, Germany, reviewed and approved SPeADy. The twin data were analyzed previously as part of an extended twin family study, but not with respect to age differences (Kandler, Richter, et al., 2019).

U.K. sample. The United Kingdom's largest adult twin registry TwinsUK (http://twinsuk.ac.uk/about-us/what-is-twinsuk/) contributed the fourth subsample of twins with personality data (see Moayyeri, Hammond, Hart, & Spector, 2013, for more details). About 2,200 twins of almost 14,000 twins provided self-reports on their personality. The sample contains considerably more women than men. This is because of the fact that women show greater prevalence rates in the TwinsUK initial phenotypes of interest (e.g., osteoporosis and rheumatic diseases). Thus, the U.K. twin sample cannot be seen as population-based with respect to basic demographics. Access to the twin data is possible as scientific use file after sending a proposal form to the data access manager (see https://twinsuk.ac.uk/resources-for-researchers/access-our-data/ for more details). TwinsUK has ethical approval from the Guys & St Thomas' NHS foundation Trust Ethics Committee. Lewis and Bates (2014) analyzed the twin data against the background of the nature of the hierarchical structure of the HEXACO traits. Age differences, however, were not the focus in this previous study.

Statistical Software

All descriptive statistics and preparatory analyses were done in part with the statistical software packages R 4.0.1 (R Core Team, 2020) and SPSS 26.0 (IBM Corp., 2018). Structural equation model analyses were run using the statistical software package Mx (https://mx.vcu.edu/) and OpenMx (Boker et al., 2011) under R 4.0.1. All statistical analytical scripts are available at the open science framework (https://osf.io/jmz84/). Ethical review does not allow unrestricted open access to the raw data, because the matched twin data structure does not ensure full anonymity, but it does allow the sharing of variance-covariance matrices. Thus, we added matrices for adolescent, young adult, middle adult, and late adult MZ and DZ twins as eight data files to Open Science Framework (OSF). This allows an approximate replication of the patterns described below.

Personality Measures

Participants completed Croatian, Finnish, German, or English versions of the 60-item HEXACO Personality Inventory–Revised (Ashton & Lee, 2009).[1] This questionnaire is a noncommercial personality instrument available in 30 different language versions (see also http://hexaco.org/hexaco-inventory). It captures the six broad HEXACO personality trait dimensions with 10 items per dimension. Descriptive statistics are presented in online Supplemental Materials C. Given the proposed bandwidth of the HEXACO dimensions capturing a broad spectrum of personality differences, internal reliabilities (McDonald's ω_t) for the six 10-item HEXACO composites were acceptable (all $\geq .64$) and comparable across national, gender, and four age-group subsamples (see Table 2).

To estimate congruence of factor loadings between subsamples, we ran principal axis factor analyses with promax rotation allow-

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[1] For Croatian and Finnish twins, the 60-item version was extracted from the longer 100-item HEXACO version, from which data are also available.

Table 2
Internal Reliability (McDonald's ω_t)

Samples	HH	Em	eX	Ag	Co	Op
	HEXACO personality trait scores					
Croatian ($n = 830$)	.75	.81	.81	.74	.76	.81
Finnish ($n = 1{,}142$)	.75	.79	.85	.75	.74	.79
German ($n = 1{,}142$)	.72	.77	.80	.73	.76	.71
U.K. ($n = 2{,}238$)	.64	.73	.76	.74	.70	.75
Female ($n = 5{,}357$)	.71	.73	.81	.74	.72	.77
Male ($n = 1{,}638$)	.76	.70	.83	.72	.76	.76
Age < 20 ($n = 937$)	.74	.78	.83	.72	.77	.73
Age: 20–30 ($n = 2{,}226$)	.74	.80	.84	.75	.75	.79
Age: 30–65 ($n = 2{,}492$)	.71	.74	.82	.74	.70	.77
Age > 65 ($n = 1{,}340$)	.66	.72	.70	.72	.68	.75
Total ($n = 7{,}026$)	.73	.77	.82	.74	.73	.76

Note. HH = Honesty-Humility; Em = Emotionality; eX = Extraversion; Ag = Agreeableness; Co = Conscientiousness; Op = Openness. McDonald's ω_t (the proportion of total common variance of items of a personality dimension) was estimated using the open source functions available in the psych package for R (Revelle, 2019).

ing for six factors for each national, gender, and age group subsample. All factor loadings taken from the structure matrix are shown in Table X1 (https://osf.io/jmz84/). Out of 78 coefficients (comparing six HEXACO factors across 13 group comparisons), only six were less than .85, and each of these surpassed .80 (see Table 3). Guided by recommendations that Tucker congruence coefficients surpass $\phi \geq .85$ (Lorenzo-Seva & ten Berge, 2006), we interpreted factor loadings as invariant across nations and demographic categories.

Initial and Preparatory Analyses

Age distribution. As the current study aimed to investigate age differences in the genetic and environmental components in personality differences across the life span, age was the central predictor (or rather moderator) in our analyses. Although age was not equally distributed (see Figure 2), each age year between 14 and 85 years of age had at least 10 twin pairs. Hence, the age distribution was sufficient to analyze differences in genetic and environmental sources of personality.

Age, gender, and national differences in personality. Because of the unbalanced distributions of demographic variables, we assessed and controlled for potential confounding factors for age trends, such as the gender and nationality of participants. For this purpose, we first computed three dummy variables capturing national differences. The German group served as reference category, because it encompasses the broadest age range (see Table 1). The three dummy variables indicated if a participant is Croatian or not (1 = Croatian; 0 = other), Finnish or not (1 = Finnish; 0 = other), and United Kingdom or not (1 = U.K.; 0 = other). Then, we computed quadratic and cubic age variables as well as an Age × Gender interaction variable based on z-standardized age and a dichotomous gender variable (0 = female; 1 = male).

To test for (confounding) effects of gender, nation, and age on personality, we ran multiple regression analyses with a stepwise procedure for each HEXACO dimension. First, the three dummy-coded nation variables and gender were included as predictors. Second, we added age to test for linear age effects in the presence of potential confounding national and gender differences. Third, nonlinear age and Age × Gender interactions were tested. Results of all six stepwise multiple regression analyses are presented and discussed in detail in online Supplemental Materials D. In short, gender and age differences in personality were in line with previous studies (e.g., Ashton & Lee, 2016). National differences in average levels of personality traits were small and partially attributable to the age differences across the national samples.

Because age and national differences could inflate variance and twin correlations, and gender differences could bias the differences between same-sex and opposite sex twins, we used a regression procedure to correct each HEXACO score for national and gender differences, linear and nonlinear age effects, and the Age × Sex interaction (McGue & Bouchard, 1984). Unstandardized residual scores derived from these regressions were used in the following analyses.

Age, gender, and national differences in trait variance. Variance in some of the HEXACO dimensions varied across gender and nation (see online Supplemental Materials E for Levene tests for variance homogeneity). Thus, we standardized the above-mentioned residuals within each of the eight gender-by-nation groups. This procedure resulted in an average total variance of 1 across nations and sexes, but the trait variance and the genetic and environmental components could vary across age. As a consequence, potential variance inequality across age could not arise from unequal age distributions across the sexes and four nations.

Main Analyses

To examine how genetic and environmental variance components—and, potentially, total trait variance—vary across ages, we first estimated twin correlations for different age groups. If genetic variance increases in proportion to environmental variance (Hypothesis 3 suggests that this can be expected between adolescence and young adulthood), then either twin correlations should in-

Table 3
Factor Congruence (Tucker's ϕ)

Sample comparisons	HH	Em	eX	Ag	Co	Op
	HEXACO personality trait scores					
Female vs. Male	.90	.91	.97	.94	.94	.95
Croatian vs. Finnish	.95	.93	.96	.93	.93	.93
Croatian vs. German	.89	.91	.94	.92	.95	.93
Croatian vs. U.K.	.83	.89	.90	.89	.90	.91
Finnish vs. German	.91	.96	.95	.90	.91	.94
Finnish vs. U.K.	.87	.94	.92	.85	.82	.93
German vs. U.K.	.88	.94	.94	.94	.92	.96
Adolescents vs. young adults	.95	.98	.98	.96	.97	.96
Adolescents vs. middle adults	.93	.93	.95	.94	.94	.88
Adolescents vs. late adults	.80	.90	.88	.92	.86	.88
Young adults vs. middle adults	.96	.96	.97	.96	.97	.94
Young adults vs. late adults	.83	.93	.90	.88	.84	.92
Mid adults vs. late adults	.88	.96	.95	.92	.80	.95

Note. HH = Honesty-Humility; Em = Emotionality; eX = Extraversion; Ag = Agreeableness; Co = Conscientiousness; Op = Openness; adolescents: age < 20; young adults: age 20–30; middle adults: age 30–65; late adults: age > 65; Tucker's ϕ (the cosine of the angle of two vectors of factor loadings of all items on a personality dimension) was estimated on the basis of two different sample vectors of factor loadings of all items on a personality dimension (see Table X1; https://osf.io/jmz84/).

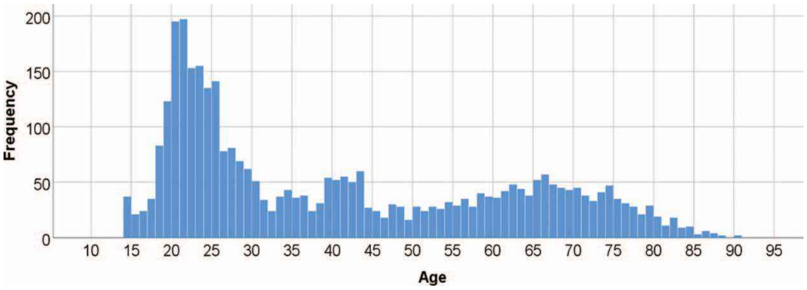

Figure 2. Distribution of the frequency of twin pairs' age in the entire sample. See the online article for the color version of this figure.

crease with age, with a stronger increase for genetically identical MZ twins compared with DZ twins, or the difference between MZ and DZ twin correlations should increase (see Kandler, Waaktaar, et al., 2019). If environmental variance because of factors not shared by twins increases in relation to genetic variance across adulthood (in line with Hypotheses 1, 2, and 3), then both MZ and DZ twin correlations should decline with age.

Next, we ran variance component model analyses allowing for varying components based on varying MZ and DZ twin covariances across age (Purcell, 2002). This twin model (see Figure 3) allows a disentanglement of unstandardized variance components because of additive genetic sources (*A*), environmental influences shared by twins (*C*), and environmental influences not shared by twins plus error of measurement (*E*). These unstandardized variance components are free to vary as linear and nonlinear functions of age (*M*). The *a*, *c*, and *e* parameters represent main effects, the β_A, β_C, and β_E parameters reflect linear age effects, and the β_{A^2}, β_{C^2}, and β_{E^2} parameters constitute quadratic age effects. Model parameters were estimated for each of the six HEXACO personality traits (see https://osf.io/jmz84/ for Mx scripts).

The twin model relied on several assumptions. First, MZ twins share trait-relevant environmental factors to the same degree as DZ twins. This equal-environment assumption has been supported in several studies for a number of traits (e.g., Conley, Rauscher, Dawes, Magnusson, & Siegal, 2013). Thus, differences between MZ and DZ twin similarities are attributable to genetic influences, whereas a lack of differences in their similarities can be attributed to shared environmental influences, and within-pair differences in MZ twins are because of nonshared environmental influences.

Second, nonadditive genetic influences and shared environmental influences cannot be estimated simultaneously. However, to the extent that nonadditive genetic effects are present, but unmodelled, they will inflate estimates of variance components because of additive genetic sources derived from the differences of MZ and DZ twin covariances (Hahn et al., 2012; Hill, Goddard, & Visscher, 2008). Therefore, estimates of additive genetic components are good estimators of full genetic variance, including additive and nonadditive genetic contributions.

Third, the model rests on the assumption that there is no assortative mating of twins' parents regarding the traits investigated,

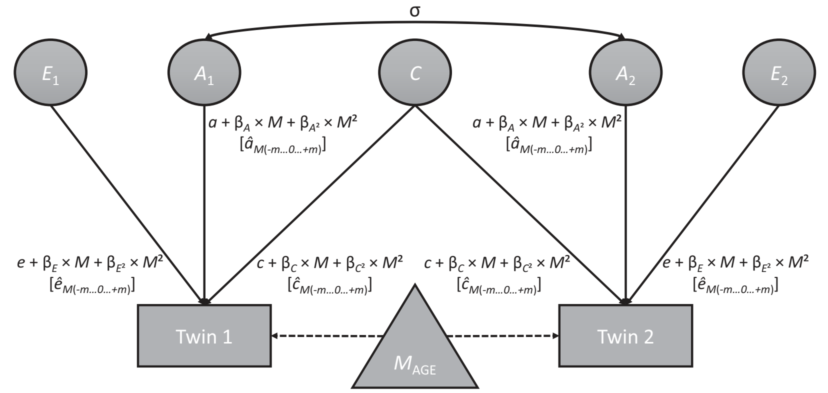

Figure 3. Illustration of the variance components model based on variance and covariance in twin pairs' trait scores. *A*: additive genetic factor; $Var(A) = (a + \beta_A \times M + \beta_{A^2} \times M^2)^2$: additive genetic component as a function of age; *C*: shared environmental factor; $Var(C) = (c + \beta_C \times M + \beta_{C^2} \times M^2)^2$: shared environmental component as a function of age; *E*: nonshared environmental factor; $Var(E) = (e + \beta_E \times M + \beta_{E^2} \times M^2)^2$: nonshared environmental component as a function of age; *M*: age as continuous moderator; latent factors have unit variance and $\sigma = 1$ for MZ twins and $\sigma = .5$ for DZ twins. The Local Structural Equation Modeling estimates for each level of the moderator from $-m$ to m is shown in parentheses. These estimates are based on weighted data rather than data precisely at the level of *M*.

which, if present, could lead to an underestimate of genetic components and an overestimate of shared environmental components. Existing extended twin family analyses suggest nonzero spouse similarity for Honesty-Humility ($r = .25$) and Openness ($r = .27$), but not for the other HEXACO traits (Kandler et al., 2019). Potential contributions of assortative mating, however, do not bias age trends in the genetic component.

Finally, the model assumes the absence of Gene × Environment interactions and transactions. Thus, it allows estimates of the net contributions of genetic and environmental sources to trait variance. Components that vary across age can be interpreted against the background of Gene × Environment interplay across the life span (Briley et al., 2019; Kandler, Zapko-Willmes, Richter, & Riemann, in press).

For the main analyses, age was both condensed to life phases (adolescence: 14–20; young adulthood: 21–30; middle adulthood: 31–65; and late adulthood: >65) and included as continuous moderator variable (*M*). The model fitting procedure works better when moderator values do not exceed 1,000, which would have been the case for age^2 (when age >32 years). Therefore, we recoded age by mean-centering (41 years) and by dividing it by 10. This coding resulted in a mean age value of 0 and a range from -2.7 (original age: 14 years) to 4.9 (original age: 90 years).

In addition to the parametric model fitting tests, we applied a nonparametric approach—Local Structural Equation Modeling (LOSEM; see Briley, Harden, Bates, & Tucker-Drob, 2015, and Mõttus et al., 2019, for more details). This approach produces locally weighted estimates of genetic and environmental components ($\hat{a}^2$, $\hat{c}^2$, and $\hat{e}^2$) for each level of the continuous moderator age (see Figure 3)—here: -2.7 ($-m$) to 4.9 ($+m$). LOSEM is an explorative approach and as such inferior to the confirmatory model fitting tests. However, it is more flexible and can give us a better impression of the exact age-related shift underlying the linear and nonlinear age trends in genetic and environmental variance components—if statistically significant. In particular, LOSEM can identify the exact data-based trend and may allow us to avoid, for instance, interpreting a true nonlinear L-shape as U-shape. Therefore, it is a valuable complement to the model fitting tests (see https://osf.io/jmz84/ for the R code).

Results

Twin Correlations

We first estimated MZ and DZ twin correlations for four age groups (see Table 4; see also online Supplemental Materials F for twin correlations separated by gender and national samples). MZ twin correlations (on average: .46; range = .37–.62) were consistently higher than DZ twin correlations (on average: .19; range = .12–.30) across traits and age groups, indicating substantial genetic influences to trait variance across age. This is in line with findings from a meta-analysis estimating average correlations between different family members, with MZ twins reared either together or apart (*r*s = .47 and .45, respectively) more than twice as similar as DZ twins reared together or apart (*r*s = .20 and .16, respectively; Bratko, Butković, & Vukasović Hlupić, 2017). These findings additionally show that all HEXACO dimensions yielded results comparable with other personality models used in behavior genetic studies.

For all HEXACO traits except Openness, correlations were smaller for adolescent (age <20) compared to young adult twins (age: 20–30): .40 (.36–.48) versus .48 (.41–.57) for MZ twins and .13 (.00–.25) versus .18 (.12–.27) for DZ twins (see Table 4). These patterns were not consistent with Hypotheses 1 and 2, which implied the reverse pattern, as showed for Openness. The general trend could be because of either larger genetic variance (in line with Hypothesis 3), smaller variance because of nonshared environmental contributions in young adulthood (not in line with any

Table 4
Twin Correlations

		All ages		Adolescents		Young adults		Middle adults		Late adults	
Trait	Stats	MZ	DZ	MZ	DZ	MZ	DZ	MZ	DZ	MZ	DZ
	n	1,504	2,009	136	335	416	705	609	642	343	327
HH	*r*	**.37**	**.20**	**.40**	**.20**	**.42**	**.25**	**.37**	**.16**	**.30**	**.15**
	p	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	.007
	95% CI	[.33, .42]	[.15, .24]	[.25, .54]	[.10, .30]	[.34, .50]	[.18, .32]	[.30, .44]	[.08, .23]	[.20, .39]	[.04, .25]
Em	*r*	**.44**	**.15**	**.38**	.08	**.41**	**.15**	**.45**	**.18**	**.50**	**.17**
	p	<.001	<.001	<.001	.165	<.001	<.001	<.001	<.001	<.001	.002
	95% CI	[.40, .48]	[.11, .29]	[.22, .51]	[−.03, .18]	[.33, .49]	[.08, .22]	[.39, .52]	[.10, .25]	[.42, .58]	[.07, .28]
eX	*r*	**.53**	**.22**	**.48**	**.25**	**.57**	**.27**	**.55**	**.20**	**.42**	.12
	p	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	.026
	95% CI	[.49, .56]	[.18, .26]	[.34, .60]	[.15, .35]	[.50, .63]	[.20, .34]	[.49, .60]	[.12, .27]	[.33, .50]	[.02, .23]
Ag	*r*	**.41**	**.12**	**.39**	.00	**.49**	**.12**	**.38**	**.21**	**.36**	.09
	p	<.001	<.001	<.001	.937	<.001	.002	<.001	<.001	<.001	.126
	95% CI	[.36, .45]	[.08, .16]	[.23, .52]	[−.11, .10]	[.41, .56]	[.04, .19]	[.31, .44]	[.14, .29]	[.27, .45]	[−.02, .19]
Co	*r*	**.40**	**.13**	**.36**	.11	**.50**	**.13**	**.36**	**.14**	**.35**	**.19**
	p	<.001	<.001	<.001	.047	<.001	.001	<.001	.001	<.001	.001
	95% CI	[.35, .44]	[.09, .18]	[.20, .50]	[.00, .21]	[.43, .57]	[.05, .20]	[.29, .42]	[.06, .21]	[.25, .44]	[.08, .29]
Op	*r*	**.62**	**.30**	**.66**	**.16**	**.57**	**.29**	**.62**	**.35**	**.76**	**.49**
	p	<.001	<.001	<.001	.003	<.001	<.001	<.001	<.001	<.001	<.001
	95% CI	[.58, .65]	[.26, .33]	[.55, .75]	[.06, .27]	[.50, .63]	[.22, .35]	[.56, .66]	[.71, .80]	[.41, .57]	[.41, .57]

Note. CI = confidence interval; MZ = Monozygotic; DZ = Dizygotic; HH = Honesty-Humility; Em = Emotionality; eX = Extraversion; Ag = Agreeableness; Co = Conscientiousness; Op = Openness. Significant correlations ($p < .01$) are shown in bold; see text for more details.

hypothesis), or both. However, the 95% confidence intervals of twin correlations for adolescents overlapped with those for young adults and none of the six comparisons between adolescent and young adult MZ twins on HEXACO traits were statistically significant (Fisher's zs ≥ -1.78, ps $\geq .07$).

Compared with young adult twins, the correlations again tended to be smaller for middle and late adult twins (age >30) with smaller correlations for the late adults (age >65), except for Emotionality and Openness. This pattern indicated declining heritability estimates. The differences in MZ twins' correlations between young adult twins and twins older than 65 were significant for Honesty-Humility (Fisher's $z = 1.97$, $p = .049$), Extraversion (Fisher's $z = 2.82$, $p = .005$), Agreeableness (Fisher's $z = 2.09$, $p = .037$), and Conscientiousness (Fisher's $z = 2.58$, $p = .010$). For Openness (Fisher's $z = -4.72$, $p < .001$) and Emotionality (Fisher's $z = -1.59$, $p = .112$), however, the trend pointed to the opposite direction and suggested increasing heritability estimates across adulthood (contrasting all expectations). The twin correlations provided a first glimpse of age differences, but they did not allow specific conclusions regarding the genetic and environmental variance underlying the varying twin correlations—that is, whether the trend of heritability was because of varying size of the genetic or the environmental component or both.

Parametric and Nonparametric ACE × Age Variance Component Analyses

To test the three hypotheses, we ran parametric variance component model analyses allowing for varying ACE components across age. We first ran the full ACE × Age interaction model (see Figure 3): $(a + \beta_A \times M + \beta_{A^2} \times M^2)^2 + (c + \beta_C \times M + \beta_{C^2} \times M^2)^2 + (e + \beta_E \times M + \beta_{E^2} \times M^2)^2$ (see online Supplemental Materials G for full model results). Then, we tested whether five reduced and nested models fit the data worse based on χ^2-difference ($p < .05$): (1) a model without C effects, $(c + \beta_C \times M + \beta_{C^2} \times M^2)^2 = 0$; (2) a nonlinear AE × Age (nAE) model removing the nonlinear E × Age interaction following Hypothesis 3, $(\beta_{E^2} \times M^2) = 0$; (3) a linear AE × Age model dropping the nonlinear A × Age interaction following Hypothesis 2, $(\beta_{A^2} \times M^2) = 0$; (4) a linear E × Age model removing the linear A × Age interaction following Hypothesis 1, $(\beta_A \times M) = 0$; and (5) an AE model $(a^2 + e^2)$ allowing for no age moderation according to the null hypothesis. We also used the sample-size adjusted Bayesian Information Criterion (ABIC) as descriptive model fit index. The smallest ABIC indicates the model with a good compromise between model fit and parsimony (Dziak, Coffman, Lanza, Runze, & Jermiin, 2019). A detailed overview of model fit statistics and comparisons is provided in Table 5.

In line with previous research, fit for no-C-effects models was equivalent to full models for all traits, indicating negligible shared environmental influences across the life span. LOSEM also did not provide signal for systematic shared environmental influences across age for any trait ($\hat{c}^2 < .10$).

For Honesty-Humility and Conscientiousness, linear AE × Age moderation models (Model 3) fit as well as more complex models and better than more parsimonious models and showed the smallest ABIC. As can be seen in Figure 4, the respective age trends of the genetic and environmental components are in line with Hypothesis 2. That is, the decline of heritability for these traits across the life span (see h^2 in Figure 5) was attributable to both declining genetic variance and increasing environmental variance across age, but because of a steeper decline in the genetic variance component the total variance tended to decline across the life span (see stacked variance components in Figure 5 and also the online Supplemental Materials Figures G1 and G2 for full ACE × Age variance component model results). LOSEM-based trends also point to decreasing genetic and increasing environmental variance, in particular between age 40 and 60 (see online Supplemental Materials Figure H).

For Extraversion and Agreeableness, nonlinear AE × Age models provided a better fit than models lacking nonlinear genetic parameters, indicating nonlinear age trends for the genetic variance and linear trends for the environmental variance in both traits. Figure 4 illustrates that these trends were in line with Hypothesis 3: The genetic component tended to increase until the 30s and sloped down thereafter, whereas the environmental component linearly increased or remained stable across age. As a consequence, the total variance in Extraversion and Agreeableness followed a reversed U-shaped pattern as a function of the varying genetic component (see Figure 5). These patterns were primarily reflected by LOSEM, with the exception that the nonparametric approach indicated a plateau of the genetic variance until age 40 for both traits and a decline thereafter. The LOSEM-indicated increase of the genetic variance in Agreeableness in old age (>80) must be treated with caution because of the low sample size beyond age 80 and, thus, lower precision of estimates at the tails of the slopes (Briley et al., 2015).

For Emotionality, a linear E × Age moderation model fit as well as more complex models. The significant negative age trend of the environmental component (see Figure 4)—a pattern completely mirrored by LOSEM (see Figure H of the online supplemental materials)—was not in line with any of the hypotheses, because its decline resulted in decreasing total variance and increasing heritability estimates across age (see Figure 5).

While model comparison tests also revealed a reversed U-shaped pattern of the genetic variance in Openness, the $\Delta\chi^2$-tests suggested a No-C-effects model as most suitable to fit the data, indicating nonlinear age effects on both genetic and environmental variance components. The genetic variance increased until the 50s, reached a plateau, and declined after age 60 (see Figure 4). This peak in middle adulthood is not in line with Hypothesis 3. Not in line with any of the hypotheses, the environmental component followed a reversed U-shaped pattern with increases until the 40s and steeper declines thereafter. This pattern produced a left-skewed U-shaped trend of heritability estimates for Openness across age (see h^2 in Figure 5).

Notably, for Openness and Agreeableness, descriptive model comparisons based on the ABIC suggested that model variants favored the null hypothesis of no varying genetic and environmental components. In addition, model comparison tests based on the $\Delta\chi^2$ would not have been significant with a more conservative p value ($p \leq .01$) and LOSEM-based trends rather suggested small shifts in genetic and environmental variance components in Openness and Agreeableness (see Figure H), indicating that these patterns should be interpreted with caution.

To sum up, genetic differences declined at least in the second half of the life span for five traits, whereas no significant age differences were found for Emotionality. That is, for five out of six

Table 5
ACE × Age Variance Component Model Fit Statistics and Model Comparisons

Trait	Model	$-2LogL$	*df*	ABIC	vs. full model:			vs. neighbor model:		
					$\Delta\chi^2$	Δdf	*p*	$\Delta\chi^2$	Δdf	*p*
HH	Full age moderation	19612.27	7,017	−7689.85						
	No C effects	19614.84	7,020	−7696.04	2.57	3	.463			
	nAE × Age moderation	19615.01	7,021	−7698.45	2.74	4	.603	0.17	1	.680
	AE × Age moderation[a]	**19616.06**	**7,022**	**−7700.42**	**3.79**	**5**	**.581**	**1.05**	**1**	**.306**
	E × Age moderation	19628.78	7,023	−7696.55	16.51	6	.011	12.72	1	<.001
	No age moderation	19629.00	7,024	−7698.94	16.73	7	.019	0.22	1	.639
Em	Full age moderation	19555.42	7,017	−7718.27						
	No C effects	19555.42	7,020	−7725.75	0.00	3	>.999			
	nAE × Age moderation	19555.45	7,021	−7728.23	0.02	4	>.999	0.02	1	.888
	AE × Age moderation	19555.47	7,022	−7730.71	0.04	5	>.999	0.02	1	.888
	E × Age moderation[a]	**19556.31**	**7,023**	**−7732.79**	**0.89**	**6**	**.990**	**0.85**	**1**	**.357**
	No age moderation	19563.82	7,024	−7731.53	8.40	7	.299	7.51	1	.006
Ex	Full age moderation	19308.72	7,017	−7841.62						
	No C effects	19309.42	7,020	−7848.75	0.70	3	.874			
	nAE × Age moderation[a]	**19310.73**	**7,021**	**−7850.59**	**2.01**	**4**	**.733**	**1.31**	**1**	**.252**
	AE × Age moderation	19325.33	7,022	−7845.78	16.62	5	.005	14.61	1	<.001
	E × Age moderation	19350.40	7,023	−7835.74	41.68	6	<.001	25.06	1	<.001
	No age moderation	19352.71	7,024	−7837.08	43.99	7	<.001	2.31	1	.129
Ag	Full age moderation	19633.29	7,017	−7679.34						
	No C effects	19633.29	7,020	−7686.94	0.00	3	>.999			
	nAE × Age moderation	**19634.38**	**7,021**	**−7688.49**	**1.09**	**4**	**.896**	**1.09**	**1**	**.296**
	AE × Age moderation	19638.24	7,022	−7689.33	4.95	5	.422	3.86	1	.049
	E × Age moderation	19638.67	7,023	−7691.66	5.38	6	.496	0.43	1	.512
	No age moderation[a]	19640.93	7,024	−7692.97	7.64	7	.365	2.26	1	.133
Co	Full age moderation	19631.94	7,017	−7680.01						
	No C effects	19634.29	7,020	−7686.31	2.36	3	.502			
	nAE × Age moderation	19634.98	7,021	−7688.46	3.05	4	.550	0.69	1	.406
	AE × Age moderation[a]	**19636.78**	**7,022**	**−7690.06**	**4.84**	**5**	**.435**	**1.79**	**1**	**.181**
	E × Age moderation	19643.09	7,023	−7689.40	11.15	6	.084	6.31	1	.012
	No age moderation	19648.19	7,024	−7689.34	16.25	7	.023	5.10	1	.024
Op	Full age moderation	19093.92	7,017	−7949.03						
	No C effects	**19094.01**	**7,020**	**−7956.46**	**0.09**	**3**	**.994**			
	nAE × Age moderation	19098.89	7,021	−7956.51	4.97	4	.291	4.88	1	.027
	AE × Age moderation	19104.85	7,022	−7956.02	10.93	5	.053	5.96	1	.014
	E × Age moderation	19106.46	7,023	−7957.71	12.53	6	.051	1.60	1	.206
	No age moderation[a]	19107.51	7,024	−7959.68	13.59	7	.059	1.06	1	.303

Note. HH = Honesty-Humility; Em = Emotionality; eX = Extraversion; Ag = Agreeableness; Co = Conscientiousness; Op = Openness; best fitting models based on χ^2-difference ($\Delta\chi^2$) tests ($p < .05$) are shown in bold for each trait; see text for more details.
[a] Model variants with the best balance between parsimony and fit indicated by the smallest sample-size adjusted Bayesian Information Criterion (ABIC).

HEXACO dimensions, estimates pointed to smaller genetic variance in old age compared with young and middle adulthood. Variance because of environmental effects shared by twin siblings reared together (c^2) could be treated as negligible, whereas individual differences because of environmental influences not shared by twins (e^2) followed a linear decrease for Emotionality, a decline for Openness in the second half of life, or a linear (or no) increase for all other trait dimensions. In other words, variance components primarily because of individualizing environmental influences tended to increase in relative terms across the entire age range for personality dimensions, except for Openness and Emotionality. That is, the older the identical and fraternal twins were, the larger the differences in Honesty-Humility, Extraversion, Agreeableness, and Conscientiousness.

Discussion

This cross-national twin study provides a systematic investigation into age differences in the genetic and environmental variance components in HEXACO personality traits from mid-adolescence to old age. Results revealed evidence for declining heritability with age for most but not all trait dimensions. We examined three competing hypotheses that might account for declining heritability estimates across the life span (see Figure 1). Strictly speaking, only the age trends of genetic and environmental variance in four traits are directly in line with proposed hypotheses, namely Hypothesis 2 for Honesty-Humility and Conscientiousness and Hypothesis 3 for Extraversion and Agreeableness. For all four traits, environmental differences linearly increased or remained constant across adult ages. Genetic differences for Honesty-Humility and Conscientiousness linearly decrease with age, whereas they were constant and even tended to increase until the 30s and declined thereafter for Extraversion and Agreeableness. The age trends in genetic and environmental differences in Emotionality and Openness are not in line with any of the hypothesized patterns.

The constant and even increasing genetic differences during adolescence and young adulthood for Extraversion and Agreeable-

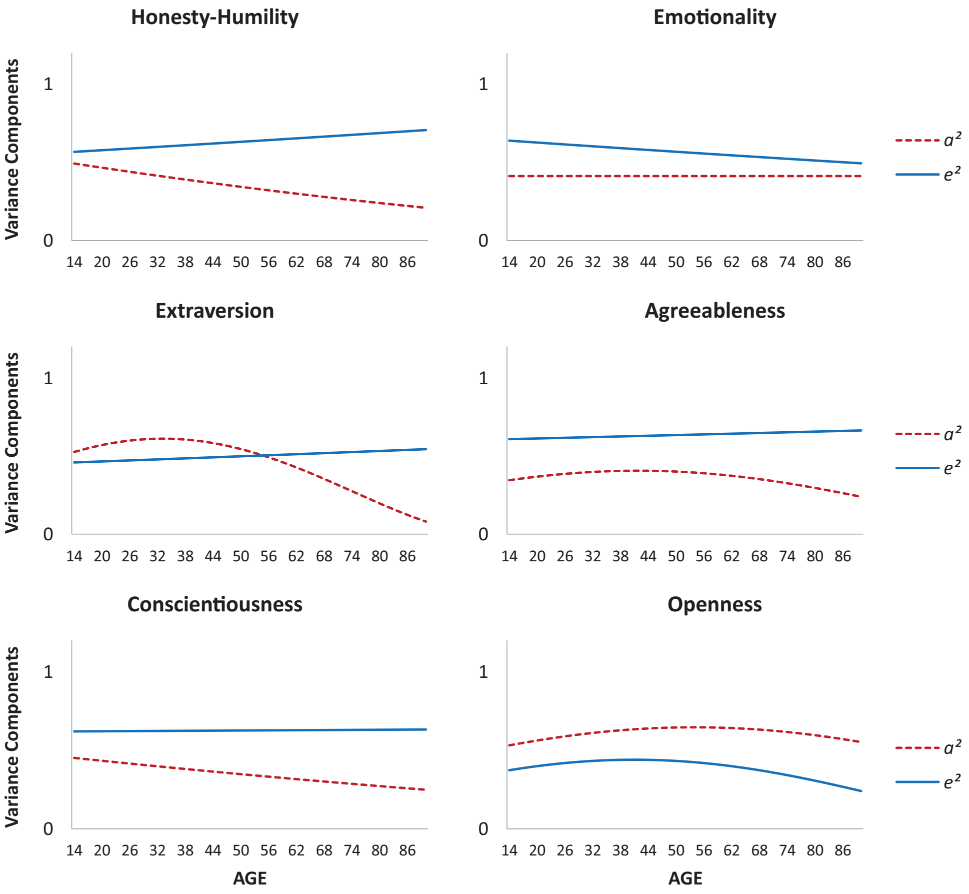

Figure 4. Unstandardized variance components because of additive genetic (a^2) and nonshared environmental (e^2) effects across age based on the best fitting variance component models. See the online article for the color version of this figure.

ness, and also for the first half of life for Openness, are in line with Gene × Environment interplay accounts. With advancing age comes increasing autonomy—particularly during a period of identity formation between adolescence and adulthood—and the opportunity to actively shape and regulate one's own development. People can be attracted to, create or invest in niches and social roles that are consistent with their heritable traits and allow for self-expression, at least in the ecologies sampled from here, which provide opportunities for personality to unfold (Kandler, Waaktaar, et al., 2019; Scarr, 1992; Scarr & McCartney, 1983). Moreover, the individual environment may feed back to influence the development of individual traits. The resulting accentuation of the observable variance in these traits is in line with the *corresponsive principle* of personality development (Caspi, Roberts, & Shiner, 2005, p. 470): "traits that *select* people into specific experiences are the traits that are most *influenced* in response to those experiences."

Although a direct examination of the Gene × Environment interplay underlying the increasing genetic and total variance in these traits is not possible, findings are in line with indirect evidence from longitudinal studies. For example, Denissen and colleagues reported transactional effects between job environment and Extraversion as well as Openness in a 5-year longitudinal study of job beginners, job stayers, and job changers (Denissen, Ulferts, Lüdtke, Muck, & Gerstorf, 2014). More extraverted individuals are more likely to select into jobs that involve social interaction and extraverted behavior, and employment in such jobs further increases Extraversion. In fact, most evidence for corresponsive Person × Environment transactions stems from investigations of young and middle-aged adults (e.g., Denissen, Luhmann, Chung, & Bleidorn, 2019; Lüdtke, Roberts, Trautwein, & Nagy, 2011; Roberts, Caspi, & Moffitt, 2003; Roberts & Robins, 2004; Roberts, Walton, Bogg, & Caspi, 2006; Zimmermann & Neyer, 2013). However, Gene × Environment transactions cannot account for a decline in genetic differences during the adult years. Thus, other mechanisms must also come into play.

Declines in genetic differences for Honesty-Humility and Conscientiousness that are already observable in young ages are in line with the idea that social environments already and increasingly demand trustworthiness and diligence in emerging adults. Resulting investments in social roles may reinforce corresponding or reduce conflicting trait levels (Bleidorn et al., 2013). For example, initiating a career or job for the first time was found to be linked to increases in Conscientiousness. People do not only seek to reach their own inherent goals or express their preexisting tendencies but also follow social values and standards that set the direction of

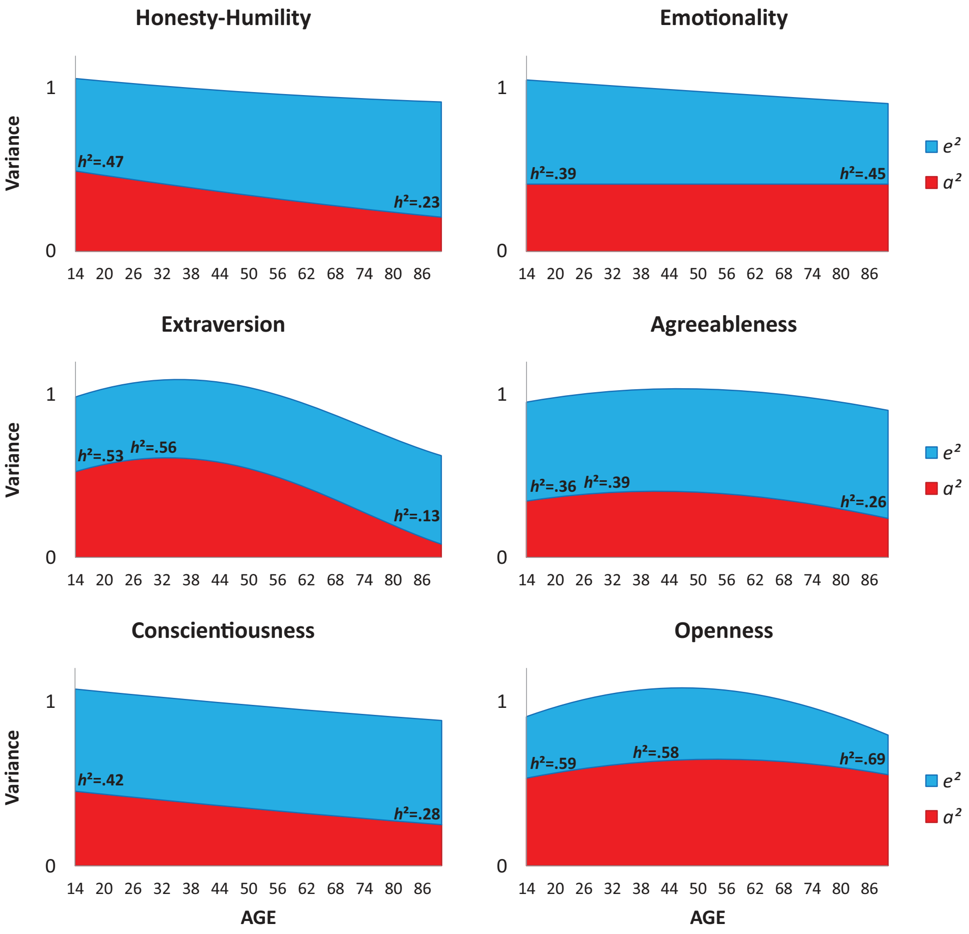

Figure 5. Stacked unstandardized variance components because of additive genetic (a^2), nonshared environmental (e^2) effects and resulting heritability estimates ($h^2 = a^2/[a^2 + e^2]$) across age with highest and lowest values as well as with a third value at the peak or valley for the nonlinear trends based on the best fitting variance component models. See the online article for the color version of this figure.

personality development (Denissen et al., 2019; Denissen, van Aken, Penke, & Wood, 2013). These social norms and values demand uniformity and may limit the unfolding of genetic differences in relevant traits.

Beyond the mere “social limits and pressure” explanation of diminishing genetic variance across the life span, increasing environmental variance in the presence of decreasing genetic variance can reflect epigenetic drift with age. Environmental influences can also act under the skin, affecting hormonal regulation, neurotransmitter release, or even gene expression (e.g., via DNA methylation or histone modification). Epigenetic changes because of environmental influences neither reflect genetic nor environmental influences per se. They can be understood as specific kind of Gene × Environment interaction because they alter the genetic sensitivity to environmental influences, such as the genetic sensitivity to stress (Belsky & Pluess, 2009; Kandler & Zapko-Willmes, 2017). As increasing epigenetic differences between genetically identical MZ twins have been found to be primarily driven by individually unique (nonshared) environmental factors (Tan et al., 2016), the systematic shift from genetic differences to environmental differences may reflect an epigenetic drift across the life span.

Irrespective of whether unique environmental factors reflect the individual social opportunities of personality unfolding or represent epigenetic changes, our findings are largely consistent with the idea that individual life experiences accumulate with personality maturation from adolescence to midadult ages and enrich personality differences. The older people get, the more life experiences mount in a highly idiosyncratic way (Bleidorn et al., 2014). However, this does not seem to be the case for all traits—at least not in our study.

Why did we find a declining trend in environmental differences in Emotionality and a reversed U-shaped age trend for Openness? The age trend of the environmental differences in Openness suggests that the midadult years involve the highest probability of experiencing individualizing influences that act to increase Openness variance. In contrast to the other personality traits, Openness is less about behavioral style and emotion regulation in the context of social behavior and more about cognition and sensitivity to internal and external sensory stimulation (McAdams, 2015). Young adults may be more attracted to and select into environments that allow them to gain new experiences, such as cultural activity, as was reported in a recent study (Schwaba, Luhmann, Denissen, Chung, & Bleidorn, 2018). The observed increase in genetic variance during the first half of life may reflect active Gene × Environment transactions underlying the openness-culture transactions, whereas the parallel increase of individual environmental variance underlying the accentuation of the total variance in Openness may be an accumulation of nonshared chances by twin siblings with increasing age. The attenuation of individual differences in Openness in the second half of life may come along with a general tendency to become less cognitively flexible with age and more conservative, which could increase uniformity.

Why environmental differences in Emotionality decline across age is harder to explain. De Vries and colleagues suggest that Emotionality might partially reflect vigilance against threats to kin (de Vries, Tybur, Pollet, & van Vugt, 2016). If the age and vulnerability of offspring constitute part of the individualizing environment, then we might expect decreased contributions after reproductive years and with offspring's age. However, this account is speculative and should be treated with caution. This finding can also be considered in the light of some important limitations that provides alternative accounts.

Limitations and Future Directions

Range restriction might have contributed to the decline in environmental components in old age. Even though we corrected for national and gender differences, the size-reduced, partly clinical, and primarily female sample of older adults might come along with a range restriction for individual experiences contributing to trait differences. This might be particularly true for Emotionality, which is associated with several clinical symptoms, and could account for the decline of environmental variance in this trait with age.

In a similar vein, the reduced age range of the adolescent sample with the smallest age of 14 years along with a lower sample size could have led to difficulties to detect a reversed U-shaped age trend for the size of the genetic variance (Hypothesis 3). Previous studies on the ages between childhood and emerging adulthood indicated steeper increasing genetic components at least until mid-adolescence (Kandler, Waaktaar, et al., 2019; Mõttus et al., 2019). The MZ twin correlations in our study that tended to be lower for adolescent twins compared to young adult twins for all traits but Openness pointed to this potential pattern, which could have appeared with more statistical power for this life stage.

Although the differences of reliability estimates based on omegas across age groups were small (see Table 2), they tended to be lower for late adulthood (on average .71 for age $>$65 vs. for .76 for age $\leq$65). Despite twin correlations corrected for attenuation because of error of measurement (r/ω) yielded trends across age groups comparable to those of the uncorrected twin correlations (see online Supplemental Materials Table 1), we cannot completely rule out that the decline of the variance in old age might be triggered to some degree by lower internal consistency of the personality trait measures for this age group. The lower internal consistency in older age might be because of stronger differentiations of personality in old age. In other words, personality facets could be less strongly related to each other in old age and, thus, the internal consistency of domain-level scales would be lower. Future projects with more gender-balanced samples in old age could take this consideration into account.

Beyond the aforementioned limitations, the cross-sectional design of our cross-cultural twin study raises the possibility that some of the observed age trends might reflect birth-cohort and national effects. However, the observed age trends of declining heritability for most traits are consistent with meta-analytic findings based on longitudinal designs (Briley & Tucker-Drob, 2014; Kandler & Papendick, 2017) that argues against potential cohort effects. Similarly, the age trends of average levels of personality traits in our study are largely consistent with a Canadian study on about 100,000 individuals (Ashton & Lee, 2016), arguing against potential national effects. Nevertheless, because of partly confounding gender, national, and age differences, the correction procedure to adjust for national and sex differences in variance may have resulted in an overcorrection and could have obscured further age trends in the amount of variance and its genetic and environmental components. Thus, future studies with population-based twin data with respect to age and other important demographics are sorely needed.

Conclusions

Our results suggest that varying heritability estimates for personality traits across the life span are because of different sources that partly differ for different traits and points to unique patterns for each personality trait. For most traits, however, genetic variance tended to decline across age, whereas the reverse was found for the environmental differences. This pattern provides evidence for an increasing relative importance of life experiences contributing to personality differences across the life span. The specific trait patterns of varying genetic and environmental contributions to trait variance suggest different kinds of Gene × Environment interplay that are differently important for different traits and in different ages. Or as McAdams puts it (McAdams, 2015, p. 111): "The relationship between genes and environments, therefore, is not much like a meeting of two independent forces (nature vs. nurture) but instead resembles something more like conspiracy. [. . .] genes and environments conspire to make a person, and to shape the traits that structure how that person moves through life . . ."

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