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The Behavioural Genetics of Personality Development in Adulthood—Classic, Contemporary, and Future Trends

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Abstract: Behavioural genetic research has led to important advances in the field of personality psychology. When carried out on longitudinal data, behavioural genetic studies also offer promising ways to examine the genetic and environmental origins of personality stability and change. Here, we review the findings of longitudinal twin studies, discuss their implications for our understanding of adult personality development, and point out open questions that need to be addressed by future research. Three general conclusions stand out. First, there is a strong and relatively stable genetic foundation of individual differences in personality throughout the adult life span; second, environmental influences become more important and contribute to an increasing rank-order stability of personality traits from early to middle adulthood; and third, both genetic and nonshared environmental influences contribute to both stability and change in personality traits. Equipped with this knowledge, the most urgent tasks for the next generation of behavioural genetic studies on personality development will be to (i) identify measurable environmental factors that matter and (ii) to capture the interplay between genetic and environmental influences on personality stability and change throughout adulthood. Copyright © 2014 European Association of Personality Psychology

Key words: behavioural genetics; personality development; gene–environment interplay; adulthood

Behavioural genetic research has led to important advances in the field of personality psychology (Krueger & Johnson, 2008). Since the early days of behavioural genetics, numerous twin and adoption studies have examined the genetic and environmental origins of individual differences in personality. Hence, it is now considered a well-established fact that about 50% of the variance in personality characteristics is genetic in origin, whereas the remaining variance can be traced back to nonshared environmental influences—that is, those environmental influences that make individuals within the same family more different from each other. In contrast, shared environmental influences that make individuals within the same family more similar to each other seem to play only a negligible role (for reviews, see Bouchard & Loehlin, 2001; Johnson, Vernon, & Feiler, 2008).

From a developmental perspective, however, the relative proportion of genetic and environmental influences on individual differences might change with age and time and so might the degree to which genetic and environmental forces influence stability and change in personality during different stages across the life span (Krueger, Johnson, & Kling, 2006). Thus, the typical cross-sectional quantitative genetic design is not ideally suited to address questions about the genetic and environmental origins of personality development. When carried out on longitudinal data, behavioural genetic designs offer promising ways to examine the genetic and environmental origins of personality stability and change across the life span (Johnson, 2008).

In the present article, we first outline the advantages and specifics of the quantitative genetic design—especially longitudinal twin studies—for the study of individual differences in personality development over the adult life span. In doing so, we aim to show that quantitative genetics can go beyond the rudimentary 'how much' question about nature versus nurture (Haworth & Plomin, 2010). In the following, we review the findings from the growing number of longitudinal behavioural genetic studies on adult personality trait development in view of three major research questions. Thereby, we aim to carve out well-replicated findings, to discuss their implications for two contemporary theoretical accounts of adult personality development, and to point out challenges and opportunities for future research.

QUANTITATIVE GENETIC STUDIES OF PERSONALITY DEVELOPMENT IN THE ERA OF MOLECULAR GENETICS

Although recent advances in molecular genetics provide exciting additions to the behavioural geneticist's toolkit (Plomin, 2013), traditional quantitative genetic designs—especially twin studies –remain a favourite means to study

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the nature and nurture of personality development. At least four assets of the quantitative genetic method in general and the longitudinal twin design in particular qualify it for the study of genetic and environmental influences on adult personality development.

Net influences of genetic and environmental factors

First, quantitative genetic studies investigate the net influences of genetic and environmental factors simultaneously—regardless of the number of genes and environmental factors involved and irrespective of the complexity of their effects. If all the genetic factors responsible for the heritability (i.e. the net degree to which individual differences are due to genetic differences) of a trait were identified, there would be no more need for quantitative genetic studies because we could measure the genetic contributions directly from each individual's DNA. However, although genome-wide association studies (GWAS) have led to notable successes in other disciplines, it seems unlikely that a substantial number of single nucleotide polymorphisms (SNPs) responsible for the heritability of personality traits will be detected in the near future (Haworth & Plomin, 2010). The revealed associations between SNPs and personality traits from previous GWAS were extremely small, and hardly any of them could be replicated (Vinkhuyzen et al., 2012). These findings suggest a polygenic model in which a large number of genetic variants individually explain very small portions of the phenotypic variance in personality traits. In addition, genetic variants that occur rarely in a population (e.g. mutations) may be involved, and genetic variants may also affect each other (i.e. epistatic interactions), which would result in nonadditive genetic influences on personality differences (Penke, Denissen, & Miller, 2007).

Irrespective of which specific polymorphisms account for personality differences, quantitative genetic designs can control for the net influences of genetic variants and environmental factors. Especially family studies including data from twins provide reliable estimations of broad-sense heritability including both additive and nonadditive genetic influences (Hahn et al., 2012; Keller et al., 2009). Furthermore, depending on the researcher's focus, a quantitative genetic study on personality development can be a study of environmental influences controlling for genetic influences or a study of genetic influences controlling for environmental influences (Haworth & Plomin, 2010; Rutter, 2007). For example, Riese et al. (2014) have shown that twins who differ in their exposure to stressful life events also differed in their levels of neuroticism. That is, controlling for their shared genetic background, there was a significant link between stressful environmental experiences and the twins' personality traits.

Although it may appear counterintuitive to use behavioural genetic designs to control for and rule out genetic influences while highlighting environmental influences, this is actually one of their strongest applications (McGue, Osler, & Christensen, 2010; Moffitt, 2005). We therefore believe that quantitative genetic studies will remain an indispensable instrument to study the genetic and environmental underpinnings of personality development.

The interplay between genetic and environmental influences

Another plus of the quantitative genetic design is its potential to investigate the interplay between nature and nurture, especially when measures of the environment are included (Purcell, 2002). Two different concepts at the genotype–environment interface can be investigated by means of quantitative genetic designs: G × E interaction and GE correlation (Keller et al., 2009; Moffitt, 2005; for a detailed discussion of all different forms of GE interplay, see Rutter, Moffitt, & Caspi, 2006).

G × E interaction refers to situations in which genetic influences are activated or inactivated in response to specific environments, or in which individual differences in the sensitivity to specific environmental influences are genetically influenced (Rutter, 2007). For example, genetic influences on individual differences in positive and negative emotionality have been shown to be lower for individuals who experienced lower levels of parental regard (Krueger, South, Johnson, & Iacono, 2008).

GE correlation refers to situations when individuals are exposed to, evoke, or select environments on the basis of their genetically influenced characteristics, which in turn affect the development of these characteristics (Plomin, DeFries, & Loehlin, 1977). For example, individual differences in sociability are partly genetically influenced, and sociable individuals may be more often invited to parties and social events, which in turn may have a reinforcing effect on their sociable nature.

GE correlation and G × E interaction can act in isolation or together, and both likely play a role in adult personality development (Johnson, 2007). In isolation, both would have different implications for the nature and nurture of personality trait development in adulthood. In particular, GE correlation would have the effect of exposing *genetically related individuals* to environmental influences that match their genetically influenced personality characteristics and make them more similar with regard to these characteristics. On the other hand, GE correlation would have the effect of exposing *genetically different individuals* to environments that make them more different from each other. GE correlation can be positive or negative, and, if not explicitly modelled in quantitative genetic designs, the variance due to GE correlation is confounded with the variance due to genetic influences (Plomin et al., 1977; Scarr & McCartney, 1983).

From a developmental perspective, the active form of GE correlation is often described in terms of ‘niche picking’ (Scarr & McCartney, 1983). This concept describes people's tendency to choose, change, or create environments that complement their genetically predisposed characteristics (e.g. their personality). If the environmental factors in turn influence the characteristics that have initially led to them, GE correlation could be considered a propulsive mechanism of personality development, which would result in an increase of heritability estimates over time.

As mentioned earlier, the concept of GE correlation describes only one way in which nature and nurture might act together to influence an individual's personality. In

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addition, mechanisms of G × E interaction likely play a role in personality development. Independent of GE correlation, G × E interaction involving nonshared environmental influences on personality differences would have the effect of making *genetically related individuals* less similar to each other (Purcell, 2002). Thus, if not explicitly modelled in quantitative genetic designs, variance due to G × E interaction is primarily confounded with the variance due to nonshared environmental influences.

From a developmental perspective, individual-specific (i.e. nonshared) environmental experiences and G × E interaction likely become more important from early adulthood on, when individuals leave their rearing home environment and start to engage in new social contexts, relationships, and roles. If processes of G × E interaction were to accumulate with age, they would lead to age-related increases in the relative contributions of nonshared environmental variance or, in other words, to increased environmentality estimates (i.e. the net degree to which individual differences are due to environmental differences).

In summary, genetic and environmental influences are not independent but often interrelated in highly complex ways. Quantitative genetic studies are suited to examine both the isolated and joint contributions of GE correlation and G × E interaction on personality development, especially when measures of the environment are included (Johnson, 2007). However, if not explicitly modelled in quantitative genetic studies on personality traits, GE correlation is primarily confounded with heritability estimates and G × E interaction with environmentality estimates.

The longitudinal twin design

In addition to the aforementioned more general features of quantitative genetic research designs, there are two more specific aspects of the longitudinal twin design that make it particularly suited for the study of personality development in adulthood. First, the longitudinal twin design allows researchers to examine the genetic and environmental underpinnings of personality stability and change in pairs of genetically related adults of exactly the same age. That is, in contrast to adoption or family designs, age is held constant within pairs of twins (for an overview of quantitative genetic methods, see Plomin, DeFries, McClearn, & McGuffin, 2008).

Second, several advanced analytic techniques have been developed to handle longitudinal data from twins (e.g. Boomsma & Molenaar, 1987; Hewitt, Eaves, Neale, & Meyer, 1988; Neale & McArdle, 2000). Particularly during the last 10 years, the research designs as well as the statistical techniques to analyse longitudinal twin data have been more and more refined. This overall trend towards more methodological rigour parallels the field's increasing awareness of the complexities involved in the nature–nurture interface (see Johnson, 2007, for a review). Furthermore, this development can also be seen as a response to the general call for a more comprehensive and time-sensitive measurement of stability of and change in personality characteristics over the life span (e.g. Biesanz, West, & Kwok, 2003; Luhmann et al., 2014).

NATURE AND NURTURE OF PERSONALITY TRAIT DEVELOPMENT IN ADULTHOOD—A REVIEW OF LONGITUDINAL TWIN STUDIES

Table 1 provides an overview of 20 years of longitudinal twin research on personality trait development in adulthood. The relatively young history of this line of research has generated a diverse collection of studies that have focused on different age groups, time periods, and personality measures. Although each of these studies has made a unique contribution to our understanding of the genetic and environmental underpinnings of adult personality development, they all focused on (at least) one of three broad questions:

(I) Do the relative contributions of genetic and environmental influences on individual differences in personality change across the adult life span?
(II) How stable versus variable are the genetic and environmental differences in personality over time?
(III) To what extent do genetic and environmental factors influence stability and change in individual differences in personality?

These three questions are not only interesting from a behavioural genetic perspective. They also lie at the heart of contemporary theories of adult personality development (see Specht et al., 2014), which seem to come to radically different predictions regarding these issues. Specifically, *ontogenetic approaches* to personality development, such as the five-factor theory (FFT; McCrae & Costa, 2008), state that stability and change in personality development are mainly influenced by genetic factors, whereas environmental influences should play no or only a marginal role in adult personality development. In contrast, *sociogenic approaches* to personality development, such as social-investment theory (SIT; Roberts, Wood, & Smith, 2005), acknowledge the influence of genetic factors but highlight the importance of environmental influences. Specifically, SIT proposes that major life transitions in the domains of love and work—such as marriage, the first job, or parenthood—are driving forces of personality change during early adulthood. Individual differences in the investment in these adult roles (e.g. spouse, employee, or parent) should explain individual differences in personality trait change in young adults.

In the following, we review the findings of previous longitudinal behavioural genetic studies on adult personality development in view of the three aforementioned research questions, discuss their implications for the conflicting propositions of FFT and SIT, and point out challenges and opportunities for future research.

(I): Heritability and environmentality of personality across the adult life span

Are there age differences in the levels of heritability and environmentality across the adult life span? The question of whether the relative contributions of genetic and environmental influences on personality traits remain stable, increase, or decrease across adulthood has been addressed

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Table 1. Longitudinal twin studies on personality trait development in adulthood

Study	Age range (years)	Intervals in years	No. of cohorts	Personality measure	Core questions: I (h^2 change)	II (r_G and r_E)	III.a (GE ➔ S)	III.b (GE ➔ C)	Correction for random error
McGue et al. (1993)	17–37	1 × 10	1	MPQ	*	*	*		ARR
Viken, Rose, Kaprio, and Koskenvuo (1994)	18–59	1 × 6	6	EPI	*	*			
Pedersen and Reynolds (1998)	26–97	3 × 3	2	EPI/NEO-PI	*	*	*		
Loehlin and Martin (2001)	17–92	1 × 8 (+4)	3	EPI (short)	*				
Johnson, McGue, and Krueger (2005)	27–99	1 × 5	1	MPQ	*	*	*		ARR
Read, Vogler, Pedersen, and Johansson (2006)	>80	2 × 2	1	EPI	*	*			
Bratko and Butkovic (2007)	15–23	1 × 4	1	EPQ	*	*	*		
Blonigen, Carlson, Hicks, Krueger, and Iacono (2008)[b]	17–24	1 × 7	1	MPQ	*	*	*	*	
Bleidorn, Kandler, Riemann, Angleitner, and Spinath (2009)[a]	18–59	2 × 5	1	NEO-PI-R			*	*	LGM
Kandler et al. (2010)[a]	16–75	2 × 6.5	2	NEO-FFI	*	*	*	*	LMR
Hopwood et al. (2011)[b]	17–29	7 and 5	1	MPQ	*	*	*	*	LGM
Bleidorn, Kandler, Riemann, Angleitner, and Spinath (2012)[a]	16–70	2 × 5	1	NEO-PI-R			*	*	LMR
Kandler, Riemann, and Angleitner (2013)[a]	16–75	1 × 13	2	FCB-TI	*	*	*	*	LMR

Note: Core questions addressed (* marked studies have tested and reported findings that inform the following listed questions, see text for further details): I (h^2 change) = Do the levels of heritability and environmentality change across the adult life span? II (r_G and r_E) = How stable are the genetic and environmental influences on personality over time? III.a (GE ➔ S) = To what extent do genetic and environmental factors influence stability of personality? III.b (GE ➔ C) = To what extent do genetic and environmental factors influence change in personality?

MPQ = Multidimensional Personality Questionnaire; EPI = Eysenck Personality Inventory; NEO-PI (-R) = NEO Personality Inventory (-Revised); NEO-FFI = NEO—Five Factor Inventory; FCB-TI = Formal Characteristics of Behavior—Temperament Inventory.

Random error was corrected by means of different approaches: ARR = environmental correlation adjusted for retest reliability; LGM = latent growth curve modelling; LMR = longitudinal multiple-rater study.

[a]Studies used data from partly overlapping samples from the Minnesota Twin Family Study (Iacono, Carlson, Taylor, Elkins, & McGue, 1999).

[b]Studies used data from partly overlapping samples drawn from the Bielefeld Longitudinal Study of Adult Twins (Kandler, Riemann, Spinath, et al., 2013).

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by all but two studies listed in Table 1. To this end, twin studies have typically compared the relative influences of genetic and environmental factors on personality traits measured at two or more time points (e.g. McGue, Bacon, & Lykken, 1993) and/or in two or more age groups (e.g. Kandler et al., 2010).

Overall, the findings of these studies clearly suggest significant age trends in the heritability levels of personality traits (for an exception, see Loehlin & Martin, 2001). Specifically, across traits and measurement instruments, several studies suggested slight but significant decreases in heritability throughout the adult life span (e.g. Kandler et al., 2010; Viken et al., 1994; see also McCartney, Harris, & Bernieri, 1990). Recently, Kandler (2012) provided a more formal synthesis of previous findings on age trends in heritability levels of the two broad trait domains of neuroticism and extraversion. Covering studies on age groups from childhood to old age, this meta-analytic review revealed decreases in heritability estimates of neuroticism throughout the entire adult life span (from $h^2 = 0.45$ at age 20 years to $h^2 = 0.20$ at age 80 years). The heritability of extraversion, on the other hand, slightly increased until age 30 years but decreased continuously thereafter (from $h^2 = 0.50$ to $h^2 = 0.35$ at age 80 years).

In summary, previous research suggests age-related changes in the relative contributions of genetic and environmental influences on individual differences in personality traits. Although genetic influences have been shown to be substantial at each age throughout the adult life span, they seem to be most important in early adulthood and tend to decrease during middle and old adulthood. This suggests by implication that the relative contributions of environmental influences on individual differences in personality increase with age.

This general pattern of decreases in heritability and increases in environmentality is notably different from what has been found for cognitive abilities, which are marked by substantial increases in heritability estimates over the adult life span (Briley & Tucker-Drob, 2013; Johnson, 2010). These differences point to distinct ways in which genetic and environmental factors contribute to differences in some personality traits versus cognitive abilities across the adult life span (Kandler, Riemann, & Angleitner, 2013; McCartney et al., 1990).

The observed decreases in heritability and increases in environmentality of personality traits can be explained by different mechanisms. First, decreases in the relative importance of genetic influences may reflect an increase in variance due to new or accumulated nonshared environmental influences on personality. Second, decreasing heritability estimates may also result from a decrease in variance due to diminishing genetic influences. A third possible mechanism involves changes at the gene–environment interface. For example, G × E interaction involving nonshared environmental influences would make the personalities of genetically identical individuals more different from each other and therefore lead to increases in the relative importance of environmental influences and decreased heritability estimates. Direct and interactional influences of genetic factors and the nonshared environment may operate separately or together and may be more or less strongly pronounced at different stages during the adult life span.

Theoretical implications

How can these findings inform the two aforementioned theoretical accounts of adult personality development? Consistent with FFT, the relative influence of genetic factors on personality traits was found to be substantial at all ages throughout the adult life span with the most pronounced influences reported for the period of early adulthood (Kandler, 2012). Conflicting with the predictions of FFT, however, are the findings of decreasing heritability estimates and the increasing importance of environmental variance over the adult life span.

The observed increases in the net contributions of nonshared environmental influences during early adulthood on personality traits are more in line with the predictions of SIT. Individual differences in the timing and mastery of adult-role transitions may partly explain the increases in the relative importance of environmental variance in personality differences during this time. Beyond direct influences of socio-environmental role experiences, also mechanisms of G × E interaction may play a role. For example, the transition to the first job might trigger personality changes, but maybe only in individuals who have a genetic susceptibility to these environmental experiences. As plausible as these explanations may seem, they are still hypothetical and only based on findings of phenotypic longitudinal studies (e.g. Bleidorn, 2012; Neyer & Lehnart, 2007). A behavioural genetic examination of these hypotheses has yet to be conducted.

(II): Stability of genetic and environmental differences in personality across adulthood

As can be seen in Table 1, nearly all studies that have examined age-related changes in heritability have also looked into the stability of genetic and environmental influences on individual differences in personality over time. That is, these studies have not only looked at time-point specific heritability and environmentality estimates but have also examined the degree to which the genetic and environmental differences in personality remained stable or changed over time.

A well-known index to quantify the degree of the rank-order stability of genetic influences is the genetic correlation (r_G). When used for describing the genetic rank-order stability over two measurement occasions, this statistic describes the degree to which genetic differences among individuals remain stable over time. Thus, a genetic correlation of $r_G = 1$ indicates that genetic influences on individual differences persist across measurement occasions; a genetic correlation of $r_G = 0$ indicates no overlap between genetic influences across points of time. Likewise, the degree of environmental rank-order stability can be expressed as the environmental correlation (r_E) across two measurement occasions. Analogously, a perfect environmental correlation of $r_E = 1$ indicates that environmental influences on individual differences persist over time, whereas $r_E = 0$ suggests no overlap between the environmental influences across measurement occasions.

Note that both genetic stability and environmental rank-order stability are independent of the absolute level of heritability or environmentality of a personality trait. For example, individual differences in a trait that are largely due to

DOI: 10.1002/per

environmental influences can be influenced by entirely different environmental factors at two time points, whereas the small amount of genetic influences may be perfectly stable over time (Johnson et al., 2005). In this case, we would expect small heritability estimates at both time points, but the genetic correlation approaching $r_G = 1$. Furthermore, it is important to note that these statistics refer to the stability of individual differences but not to mean-level changes. Hence, a perfect genetic correlation of $r_G = 1$ does not necessarily imply perfect genetic stability of a trait, because mean-level changes may still be genetically influenced.

Viken et al. (1994) were one of the first who examined the degree of genetic and environmental rank-order stability within a longitudinal twin design. Specifically, using self-report data from nearly 15 000 adult Finnish twins, they estimated the genetic and environmental correlations for neuroticism and extraversion over a 6-year period in seven age cohorts ranging from 18 to 53 years at baseline. Across age groups, they found substantial phenotypic rank-order correlations over 6-year periods, ranging around .50–.60 in the youngest cohort to around .70 in the oldest cohort. With the exception of the youngest age cohort, genetic influences on both neuroticism and extraversion were perfectly correlated over the two measurement occasions, suggesting that the same genetic factors contributed to personality variance over time. Although greater than zero, the estimates for the environmental correlations were substantially smaller and ranged between $r_E = .25$ and $r_E = .58$ across age groups.

This pattern of high genetic and relatively lower environmental correlations over time has been replicated by several studies using twin samples from different nations and employing different measures of personality (Bratko & Butkovic, 2007; McGue, Bacon, & Lykken, 1993; Pedersen & Reynolds, 1998; Read et al., 2006). These studies have established strong evidence for a highly stable genetic foundation of individual differences in broad personality traits in adulthood. However, this finding has often been misinterpreted to suggest that genes exclusively account for personality stability whereas change—if there is any—is mainly due to nonshared environmental influences.

Looking closer at the initial results reported by Viken et al. (1994) and considering the findings of other more recent studies (e.g. Johnson et al., 2005), it becomes apparent that the basic interpretation of 'stable genetic vs. changing environmental influences' is too simplistic. One important factor that qualifies this principle concerns the age of participants. Specifically, Viken and colleagues (1994) reported less than perfect genetic correlations for the youngest age cohort. They also observed an increase in the 6-year stability of environmental influences from about $r_E = .30$ at age 18 years to about $r_E = .55$ at age 53 years. This suggests that genetic factors may indeed play a role in personality change—at least during the early years of adulthood—whereas nonshared environmental differences in personality seem to become more stable in middle adulthood.

Another important issue concerns the conceptualization of nonshared environmental influences. Viken et al. (1994) as well as other early behavioural genetic studies on personality development have typically modelled nonshared environmental influences as residual terms. These residuals, however, not only contain variance due to nonshared environmental influences but also variance due to measurement error (as well as variance due to G × E interaction, nonlinearities, or rater-specific effects). In other words, many behavioural genetic studies did not separate nonshared environmental variance from error variance, which is by definition uncorrelated over time. As a consequence, these studies may have underestimated the stability of nonshared environmental differences in personality over time.

Johnson et al. (2005) were one of the first who explicitly discussed this issue with regard to its implications for the interpretation of environmental rank-order stability (see the last column of Table 1 for further studies who have addressed this problem). They examined the genetic and environmental rank-order stability of personality during middle and late adulthood. Their sample, averaging 59.4 years at baseline, completed the Multidimensional Personality Questionnaire (MPQ; Tellegen, 2008) twice over an average retest interval of 5 years. Like prior studies, Johnson et al. reported nearly perfect stability of genetic influences on personality differences. Yet, in contrast to most previous studies, they also emphasized the large and substantial stability of environmental differences. Correcting for test–retest unreliability, this study revealed a median environmental correlation of $r_E = .65$. This led them to conclude that previous studies have likely underestimated the degree of stability of nonshared environmental influences, because both stable genetic and stable nonshared environmental variance seem to play a role in the rank-order stability of personality traits—at least in middle and old adulthood.

Johnson et al. (2005) as well as other earlier studies have used relatively basic procedures to correct for the unreliability of personality measures. More recent studies have used latent variable modelling techniques to disentangle 'true' nonshared environmental variance from error variance. For example, Kandler et al. (2010) used longitudinal multi-rater twin data to analyse the stability of genetic and environmental influences on 'true score variance' in personality traits that were corrected for measurement error and rater-specific variance. Specifically, using self-report and peer report data from a sample of adult German twins, they estimated the genetic and environmental correlations for all Big Five traits over three measurement waves across a 13-year period in two age cohorts. The median age of the younger cohort was 23 years at baseline; the median age of the older cohort was 39 years at baseline. The stability of the genetic variance in all Big Five traits was nearly perfect in both age cohorts and across measurement periods. In contrast, the stability of the environmental variance was relatively low during the first measurement interval in the young cohort with an average environmental correlation of $r_E = .43$ across traits between ages 23 and 29 years. Yet, the environmental correlations increased and nearly reached the level of genetic correlations in the older cohort. Specifically, for the last measurement interval, the averaged environmental stability was $r_E = .86$ between ages 47 and 55 years. That is, whereas genetic influences were highly stable across the adult life span, the stability of environmental influences on individual differences

DOI: 10.1002/per

in all Big Five personality traits strongly increased from early to middle adulthood.

As has been recently pointed out by Turkheimer, Pettersson, and Horn (2014), it is also important to consider the length of the time interval between measurement occasions. To examine the joint effects of age and time interval on the stability of genetic and environmental influences, Turkheimer et al. (2014) integrated the results of 11 studies that reported genetic and environmental correlation coefficients for neuroticism and extraversion across more than one measurement interval and in more than one age group. From the general pattern of results, they concluded that genetic rank-order stability increases to the mid-twenties and remains close to unity throughout the life span with only slight decreases in old age. Furthermore, there was no relationship between genetic rank-order stability and the time interval between measurement occasions. In contrast, the level of environmental rank-order stability increased gradually from early to middle adulthood but seemed to drop off in old age. Furthermore, environmental stability was strongly related to the time interval—the longer the time between measurements, the lower the stability of environmental influences on individual differences in neuroticism and extraversion. Two points should be noted with regard to these findings. First, the results were based on only a small set of studies, and second, only two of them investigated samples including older adults (>75 years; Johnson et al., 2005; Read et al., 2006). More research, particularly on older adults, is required to back up these conclusions.

In summary, there is evidence for a strong and highly stable genetic foundation of individual differences in personality across the adult life span. That is, independent of age and length of time interval between measurement occasions, the stability of genetic influences on personality differences seems to be close to unity. This high genetic rank-order stability is supplemented by increasing rank-order stability of nonshared environmental influences from early to middle adulthood. Yet, environmental stability seems to decrease if measured over longer time intervals and may drop off in late adulthood (Turkheimer et al., 2014; see also Kandler, 2012).

Theoretical implications

Again, different possible mechanisms may underlie these age trends in genetic and environmental stability. First, the high stability of genetic differences in personality across adulthood might suggest that the same genetic influences operate in the same way to influence personality throughout the adult life span (Krueger et al., 2006). The increasing genetic rank-order stability in young adulthood might also reflect the operation of GE correlation, suggesting that individuals increasingly tend to select their niches, consistent with their genetic makeup (Scarr & McCartney, 1983). During middle adulthood, there may be a shift from selection to stabilization. That is, middle- and older-aged adults may become more inclined to protect and sustain the quality of their niches (e.g. their job, place of living, or partner; McAdams & Olson, 2010). The observed increases in environmental rank-order stability, on the other hand, may either imply an accumulating influence of relatively stable nonshared environmental factors or reflect an increasing importance of stabilizing G × E interactions.

In line with FFT, these findings provide further evidence for a strong and highly stable genetic foundation of personality across the adult life span. However, the increasing stability of environmental influences on personality differences is difficult to explain from the perspective of FFT and more in line with the propositions of SIT. According to SIT, the observed increases in environmental stability during the period of early adulthood may be explained in the light of accumulating influences of new and relatively stable environmental experiences such as social-role experiences. These should become more important when young adults leave their parental home environment and encounter novel and unique experiences outside their rearing environment. If individuals show different reactions to these new experiences based on their genetic liability—in other words, if there is G × E interaction—then this would lead to further increases in the relative importance of nonshared environmental influences. Furthermore, if these new environmental experiences are relatively stable over time (e.g. a stable romantic relationship or job environment), they may have enduring influences on individual differences in personality and thus contribute to the observed increases in environmental rank-order stability of personality traits between early and middle adulthood (Kandler et al., 2010).

There already is some evidence from phenotypic research that supports the propositions of SIT (e.g. Bleidorn, 2012; Lodi-Smith & Roberts, 2007; Neyer & Lehnart, 2007). However, it is unclear if and how genetic influences may be involved in these processes. Longitudinal behavioural genetic studies that incorporate measures of potentially relevant environmental influences would be required to investigate the influence of social-role transitions on personality change in the light of G × E interaction (see also later our discussion on future directions).

(III): Genetic and environmental contributions to stability and change in personality

The third broad question addressed by the longitudinal twin studies listed in Table 1 is twofold: To what extent do genetic and environmental influences contribute to (a) stability of and (b) change in individual differences in personality traits? Although related to the two aforementioned questions (I and II), this third broad question goes beyond by asking about the relative degree to which genetic and environmental influences contribute to individual differences in personality stability and change.

Looking at Table 1, it becomes apparent that most studies that have addressed one or both of the two precedent questions have also looked into the genetic and environmental underpinnings of stability in personality traits. These studies have typically used data from two measurement occasions and Cholesky variance–covariance decomposition (or a comparable) methodology to estimate the relative contributions of genetic and environmental contributions to phenotypic rank-order stability in personality traits (e.g. Blonigen et al., 2008).

DOI: 10.1002/per

Independent of the age of the sample or the particular trait domain, virtually all studies reported a substantial contribution of genetic influences to rank-order stability. In contrast, findings were more mixed with regard to the relative contribution of environmental influences. Early studies reported relatively small contributions of environmental influences to stability. However, more recent studies—namely those that were in the position to control for random error—revealed substantial contributions of the nonshared environment to personality stability, particularly in middle adulthood (e.g. Johnson et al., 2005; Kandler et al., 2010). The increasing importance of environmental influences on rank-order stability is also implied in the increasing degree of relative influences of nonshared environmental factors and the increasing environmental stability discussed earlier.

A smaller number of studies have examined the genetic and environmental contributions to personality change (Table 1). Of these studies, more recent approaches have used twin data from more than two measurement occasions and genetically informative latent change or latent growth curve model analyses to examine the genetic and environmental underpinnings of different types of personality change (for an overview of different types of stability and change, see Roberts, Wood, & Caspi, 2008).

For example, Bleidorn et al. (2009) have applied latent growth curve models to multi-wave twin data on Big Five personality traits to examine the genetic and environmental origins of individual differences in absolute-level stability and change. Specifically, they have used self-report data from a mixed-age twin sample collected at three measurement waves over a period of 10 years. The findings of this study showed that individual differences in absolute-level change were best explained by both genetic and nonshared environmental influences. Recently, Hopwood et al. (2011) have used a similar biometric latent growth curve approach to study the genetic and environmental contributions to personality stability and change in a more age-homogenous twin sample of young adults. Although this study has focused on a different age group and used a different personality measure (MPQ), the findings tell a similar story, suggesting that both genetic and environmental factors are important for understanding personality change.

Theoretical implications

In summary, early studies on the genetic and environmental underpinnings of personality stability have mainly stressed genetic influences on rank-order stability. More recently, studies controlling for random error and looking into the genetic and environmental influences on personality change have revealed a more complex picture: Both genetic and nonshared environmental factors act together to guide personality development in adulthood. These findings are partly in line with the predictions of FFT as they stress the importance of an individual's genetic make up for both stability and change in personality. However, most notably, these findings also clearly highlight the relevance of the environment for differences in individuals' trajectories of personality development throughout the adult life span. These results are incompatible with the propositions of FFT but are in line with SIT and other *sociogenic* approaches to personality development (cf. Caspi, Roberts, & Shiner, 2005; Roberts & Caspi, 2003).

Progress report—What have we learned so far?

Three general conclusions can be drawn from the aforementioned reviewed studies. First, there is a strong and relatively stable genetic foundation of individual differences in personality throughout the adult life span. Second, nonshared environmental variance in personality traits becomes more important and increasingly stable from early to middle adulthood. And third, depending on the length of the time interval, the age period, and the particular personality trait of interest, both genetic and environmental influences contribute to stability of and change in personality traits.

These basic principles are generally in line with SIT and other contemporary theories of personality development that stress the relevance of both the person and his or her specific environmental experiences (for an overview, see Specht et al., 2014). Equipped with this knowledge, the time seems ripe to address more specific questions about the kind and operation of gene–environment transactions and interactions involved in adult personality development. To this end, it will be necessary to identify the environmental factors that matter to personality development and to specify the interplay between those environments and people's genetic dispositions over the adult life span.

THE NEXT GENERATION OF BEHAVIOURAL GENETIC STUDIES ON PERSONALITY DEVELOPMENT

Despite the conceptual and methodological progress of the studies reviewed earlier, there still are several unresolved issues that need to be addressed by future research. In our view, the most pressing tasks for future studies would be (i) to identify measurable environments that matter to personality (Turkheimer & Waldron, 2000) and (ii) to capture the interplay between the genetic foundation of personality and the environmental experiences that individuals make (Johnson, 2007). In the following, we will elaborate on these two questions and present strategic steps that may be taken to organize future longitudinal behavioural genetic studies on personality development.

Identifying measurable environments that matter to personality development

The aforementioned reviewed studies consistently suggest that nonshared environmental influences play a major role for individual differences in both stability of and change in personality. But what are the most important environmental factors that contribute to stability of and change in personality?

Like the hunts for specific genetic variants that can explain the large heritability estimates for personality traits (e.g. Vinkhuyzen et al., 2012), the searches for measurable nonshared environmental factors that can account for the

DOI: 10.1002/per

substantial portions of the nonshared environmental variance have been rather discouraging. In a meta-analytic review, Turkheimer and Waldron (2000) found that less than 2% of the nonshared environmental variance in behavioural genetic studies could be accounted for by measurable environmental factors. This finding led them and many other scholars to conclude that nonshared environmental influences were too elusive and idiosyncratic to detect them with the available behavioural genetic designs (e.g. McCrae & Costa, 2008; Turkheimer, 2000).

On the other hand, there is a fast-growing number of theoretical papers and phenotypic studies dedicated to pinpoint the environmental conditions that have the potential to stabilize or change an individual's personality (for an overview, see Specht et al., 2014). For example, the aforementioned SIT (Roberts et al., 2005) stresses the influence of major life transitions and new role experiences on personality development during the period of early adulthood. Evidence from both cross-sectional and longitudinal research seems to support these propositions at the phenotypic level (e.g. Bleidorn, 2012; Lodi-Smith & Roberts, 2007). These studies have also revealed substantial individual differences in the reactions to these life transitions. Specifically, although most people seemed to show positive personality changes (e.g. increases in conscientiousness), a non-negligible minority remains stable or even decreases in desirable personality traits.

Although previous failures to identify measurable nonshared environmental influences should not be dismissed lightly, the recent progress in phenotypic research on personality development may be considered as a promising prospect for future behavioural genetic investigations of measurable environments. For example, the co-twin control design would be a powerful research methodology for putting the propositions of SIT to a behavioural genetic test. Specifically, in a cohort co-twin control study, twins who are discordant for environmental exposure are followed over time to study potential differences in their development (e.g. Riese et al., 2014). Although the co-twin control design can be applied to monozygotic (MZ) or dizygotic (DZ) twins, it is most powerful with data from MZ twins reared together, who share both a common genotype and a similar rearing environment (DZ twins have a common rearing environment but share on average only 50% of their segregating genetic alleles; McGue et al., 2010). That is, the co-twin control design on MZ twins combines the advantages of observational studies and experimental case–control designs, because MZ twin pairs are perfectly matched on a multitude of known and unknown potential confounding factors including their genetic background. A prospective longitudinal co-twin control study would thus allow testing hypotheses about putative environmental influences on personality development while controlling for potential genetic confounds. For example, strong support for the predictions of SIT would be provided by a prospective co-twin control study showing that MZ twins who differ in the timing, investment, or mastery of adult-role transitions also differ in the timing, degree, or direction of personality trait changes.

Specifying the interplay between genetic and environmental influences on personality development

The 'missing-environment' problem may partly arise from the fact that previous behavioural genetic studies were not in the position to address a reality that nearly all modern theories of personality development emphasize, namely the dynamic interplay between the genetic foundation of personality and the socio-environmental experiences that individuals make (Roberts & Caspi, 2003). Therefore, 'capturing all this interplay' (Johnson, 2007, p.423) is what the next generation of behavioural genetic studies on personality development needs to accomplish in the future.

As outlined earlier, the twin design allows addressing two different forms of how genetic and environmental factors interact to shape an individual's behaviour: GE correlation and G × E interaction. Implied by the concept of GE correlation, individuals often evoke, select, or create specific environmental experiences on the basis of their genetically influenced preferences, motives, and traits (Plomin et al., 1977; Scarr & McCartney, 1983). In other words, the occurrence of life events and environmental experiences is not necessarily random, nor is it always independent of an individual's personality. Rather, in line with the idea that genotypes may drive experiences, many studies have shown that putative environmental influences and life events show substantial heritability (e.g. Kandler, Bleidorn, Riemann, Angleitner, & Spinath, 2012; Kandler, Riemann, & Kämpfe, 2009; Kendler, 2001; Kendler & Baker, 2007; Saudino, Pedersen, Lichtenstein, McClearn, & Plomin, 1997).

For example, genetic factors may influence if, when, and how individuals undergo those life transitions proposed by SIT to trigger personality development in early adulthood. For example, becoming a parent has been shown to be related to personality trait changes in young mothers (Hutteman et al., 2014). Yet, fertility decisions and parenthood are not entirely random but are influenced by genetic factors (e.g. Rodgers, Kohler, Kyvik, & Christensen, 2001). Furthermore, there is evidence to suggest that the genetic variance in fertility decisions can be partly accounted for by genetic influences on broad personality traits (e.g. Jokela, Kivimäki, Elovainio, & Keltikangas-Järvinen, 2009; Kandler et al., 2012). Thus, by only looking at phenotypic findings, we cannot rule out the possibility that the same genetic processes influence both parental experiences and personality change. In other words, we cannot rule out third-variable confounds involving genetic influences.

However, longitudinal twin studies can (at least partly) control for the genetic confounds that otherwise cloud the causal interpretation of links between parental experiences and personality change. Again, prospective co-twin control studies designed to follow a cohort of twins during the period of early adulthood would provide a powerful tool to examine the degree to which genetic and environmental factors contribute to the timing, experience, and mastery of normative life transitions such as the transitions to parenthood. Such research would also stimulate the theoretical work on models such as SIT by pinpointing the actual degree to which environmental factors play a role in adult

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personality development when controlling for shared genetic influences.

Another pressing question concerns the degree and ways in which G × E interaction may be involved in shaping developmental trajectories. As noted earlier, processes of G × E interaction likely become more important from early adulthood on when young adults leave their home environment and start to encounter their own unique experiences. According to SIT, life transitions such as entering a romantic relationship, starting a career, or becoming a parent may have unique and lasting influences on a young adult's personality. Mechanisms of G × E interactions offer an intriguing explanation for the substantial individual differences in personality change related to these life transitions. As outlined earlier, although the majority of young adults seem to show personality changes in the direction of greater psychological maturity while undergoing adult-role transitions, a substantial minority remains stable or even decreases in desirable personality traits (e.g. Hutteman et al., 2014). It is reasonable to argue that part of this variation among individuals' reactions to these transitional experiences can be explained by the operation of G × E interaction processes (Moffitt, 2005). Specifically, if young adults react differentially to these experiences on the basis of their genetically shaped characteristics, then this would imply the occurrence of G × E interaction.

The inclusion of G × E interaction in the study of personality development also promises a better chance to detect relevant environmental influences on personality development. Recent cross-sectional demonstrations of G × E interaction have shown that environmental influences can be unexpectedly large for individuals with a specific genetic susceptibility (e.g. South, Krueger, Johnson, & Iacono, 2008). That is, by acknowledging G × E interaction, researchers will move on from asking whether there is any environmental influence on personality development at all to the question of who is most likely affected by a specific environmental condition (Johnson, 2007; Moffitt, 2005)

CONCLUSION

Three general principles can be derived from prior longitudinal behavioural genetic research on adult personality development. First, there is a strong and stable genetic foundation of individual differences in personality throughout the adult life span. Second, nonshared environmental influences on individual differences in personality traits become more important and increasingly stable from early to middle adulthood. And third, both genetic and nonshared environmental influences contribute to stability and change in personality traits. Equipped with this knowledge, we envision a bright future for behavioural genetic research on adult personality development. The core tasks of future studies will be to identify measurable nonshared environmental factors that matter to personality and to capture the interplay between genetic and environmental influences on personality development throughout adulthood. We believe that longitudinal twin studies that follow age-homogenous twin samples over well-defined time periods provide a very strong tool to engage in these tasks.

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