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The Contribution of Genetics and Early Rearing Experiences to Hierarchical Personality Dimensions in Chimpanzees (*Pan troglodytes*)

Robert D. Latzman
Georgia State University

Hani D. Freeman and Steven J. Schapiro
The University of Texas MD Anderson Cancer Center

William D. Hopkins
Georgia State University and Yerkes National Primate Research Center, Atlanta, Georgia

A reliable literature finds that traits are related to each other in an organized hierarchy encompassing various conceptualizations of personality (e.g., Big Three, five-factor model). Recent work suggests the potential of a similar organization among our closest nonhuman relative, chimpanzees (*Pan troglodytes*), with significant links to neurobiology suggesting an evolutionarily and neurobiologically based hierarchical structure of personality. The current study investigated this hierarchical structure, the heritability of the various personality dimensions across levels of the hierarchy, and associations with early social rearing experience in a large sample ($N = 238$) of socially housed, captive chimpanzees residing in 2 independent colonies of apes. Results provide support for a hierarchical structure of personality in chimpanzees with significant associations with early rearing experiences. Further, heritabilities of the various dimensions varied by early rearing, with affective dimensions found to be significantly heritable among mother-reared apes, whereas personality dimensions were largely independent of relatedness among the nursery-reared apes. Taken together, these findings provide evidence for the influence of *both* genetic and environmental factors on personality profiles across levels of the hierarchy, supporting the importance of considering environmental variation in models of quantitative trait evolution.

Keywords: personality, chimpanzee, heritability, early rearing, gene × environment interactions

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Although distinct conceptualizations of the basic framework of personality have historically existed, a converging literature supports the assertion that traits are related to each other in an organized hierarchy encompassing these various conceptualizations. Indeed, personality traits can be organized hierarchically such that more fundamental traits can be differentiated into more fine-grained traits. Specifically, although the five-factor model (FFM; e.g., Gosling & John, 1999; McCrae & Costa, 2008) is the most widely used taxonomy for organizing personality traits among human and nonhuman primate populations, well-replicated findings have led to an increased understanding of how two-, three-, four-, and five-factor models of personality are hierarchically related among human adults (e.g., Digman, 1997; Markon, Krueger, & Watson, 2005), and youth (e.g., Tackett, Krueger, Iacono, & McGue, 2008; Tackett et al., 2012). More recently, a largely similar, hierarchical structure has emerged among nonhuman primates (i.e., chimpanzees; Latzman, Hopkins, Keebaugh, & Young, 2014), a critical finding for supporting the cross-species nature of trait personality, and further illuminating personality as neurobiologically based and evolutionarily derived (i.e., ancestral) dimensions of primate disposition. Given the phylogenic similarities between human and nonhuman primates, the importance of investigating nonhuman primate models is underscored by the large body of literature confirming the importance of various personality traits to both psychological and physical health in humans (Kotov, Gamez, Schmidt, & Watson, 2010). The current study therefore aimed to replicate and extend the previously found hierarchical structure of personality within a relatively large sample of chimpanzees housed in two separate colonies of apes. Further, given findings of both environmental (e.g., Bennett & Pierre, 2010; Hofer, 1994; Latham & Mason, 2008; Murray, 1998; Oshino, Suzuki, Ishii, & Otani, 2007; Reti et al., 2002; Sánchez, Ladd, & Plotsky, 2001) and genetic correlates (e.g., Bouchard, 1994, 2004; Hopkins, Donaldson, & Young, 2012; Latzman, Hopkins, et al., 2014; Weiss, King, & Enns, 2002; Weiss, King, & Figueredo, 2000) of individual variation in socioemotional traits in both human and nonhuman primates, we further examined the effects of early rearing experiences on, and the heritability of,

Robert D. Latzman, Department of Psychology, Georgia State University; Hani D. Freeman and Steven J. Schapiro, Michale E. Keeling Center for Comparative Medicine and Research, The University of Texas MD Anderson Cancer Center; William D. Hopkins, Neuroscience Institute, Georgia State University, and Division of Developmental and Cognitive Neuroscience, Yerkes National Primate Research Center, Atlanta, Georgia.

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Correspondence concerning this article should be addressed to Robert D. Latzman, Department of Psychology, Georgia State University, P.O. Box 5010, Atlanta, GA 30302-5010. E-mail: rlatzman@gsu.edu

individual variation in personality across various levels of the hierarchical structure.

Chimpanzee Personality

Among nonhuman animals, a converging empirical literature has elucidated largely similar core personality traits as found among humans (e.g., FFM; for a review, see Gosling & John, 1999). In an attempt to ensure comparability with the human personality literature, recent factor analytic research using a combination of top-down and bottom-up approaches has led to the development of a comprehensive new rating scale for measuring personality in chimpanzees, allowing for potentially more valid cross-species comparisons (Freeman et al., 2013). Results of principal components analyses in a sample of 99 chimpanzees, a subset of which are included in the current study, provided strong evidence for a robust five-factor solution largely paralleling the FFM reliably found with human samples. Specifically, the five factors that emerged were labeled Reactivity/Undependability, Dominance, Extraversion, Openness, and Agreeableness. A sixth factor, Methodical, was also suggested but not validated. Although not typically labeled as such in the FFM, Dominance appears to parallel reverse-keyed Neuroticism. Indeed, Dominance is reflected in low levels of fearfulness and timidity (Freeman et al., 2013). Reactivity/Unpredictability, however, is a dimension not previously found to emerge in the FFM, consisting of items that have previously been found to load on FFM Conscientiousness (e.g., impulsive, reverse-keyed), Agreeableness (e.g., deceptive, reverse-keyed), and Extraversion (e.g., calm, reverse-keyed; Digman, 1990). Regardless of the ultimate number of factors that emerge, the existence of largely parallel dispositional traits among both humans and chimpanzees is clear, underscoring the comparable nature of personality dimensions between chimpanzees and humans. In addition to research supporting the existence of largely parallel traits in humans and chimpanzees, recent work has begun to investigate the existence of a largely parallel hierarchical structure of personality (Latzman, Hopkins, et al., 2014).

Hierarchical Nature of Personality

Research indicates that innate individual differences, often referred to as *temperament*, form the basis for personality traits organized into robust, higher order personality dimensions, or "metatraits" (Digman, 1997; Markon et al., 2005). Indeed, adult personality traits emerge through differentiation from three (the Big Three) largely innate biobehavioral temperament dimensions (Clark, 2005). Two of these dimensions are affective, namely, Negative and Positive Emotionality (NEM and PEM), and the third dimension, Disinhibition (vs. Constraint; DIS), is a regulatory system that plays a role in the perception and interpretation of incoming stimuli (Clark & Watson, 2008; Tellegen, 1985). Among humans, converging empirical evidence has revealed robust hierarchical associations between these three temperament traits and dimensions of the FFM (for a review, see Markon, 2009).

Indeed, FFM dimensions can be understood as lower order components of the Big Three (Digman, 1997; Markon et al., 2005). Specifically, Neuroticism, along with some components of low Agreeableness, combine to form NEM at the higher order level; Extraversion and Openness combine to form PEM; and low Agreeableness and low Conscientiousness combine to form DIS. Further, going in the other direction (i.e., above the Big Three), it has been shown that both the FFM and the Big Three have two consistent higher order factors or metatraits. Specifically, low DIS via FFM Agreeableness and Conscientiousness, as well as low NEM or FFM Neuroticism, is captured by Alpha, whereas PEM or FFM Extraversion is captured by Beta (DeYoung, 2006; Markon et al., 2005). Among human youth, recent research has supported the existence of this hierarchical structure cross-nationally, using both informant reports and observer observations (Tackett et al., 2008, 2012). These findings are particularly important, as the elucidation of a trait hierarchy has proven critical for understanding individual differences in personality, psychopathology, and a range of behaviors.

Given the importance of research on personality among nonhuman primates in elucidating biological systems underlying personality (Stockard, 1931), this hierarchical structure of personality has surprisingly only recently begun to be investigated among nonhuman animals. Indeed, although there has been some interest in a general factor of personality among nonhuman primates, with results of single-factor confirmatory factor analyses of first-order factors failing to find evidence for the appropriateness of such a conceptualization (Weiss, Adams, & Johnson, 2011), only one study to date has explicitly examined the hierarchical structure of personality in chimpanzees (Latzman, Hopkins, et al., 2014).

Using a sample of 174 captive chimpanzees from the Yerkes National Primate Research Center (YNPRC), a subset of which are included in the current study, Latzman, Hopkins, and colleagues (2014) found a hierarchical structure of personality largely similar to the reliably found structure in humans. Specifically, using the well-established "Bass Ackwards" approach (Goldberg, 2006) on items from the Chimpanzee Personality Questionnaire (King & Figueredo, 1997), two metatraits emerged as the most fundamental level of chimpanzee personality, similar to those found in humans: One related to whether an animal was generally dominant and undercontrolled, termed "Alpha," and anchored by items including "aggressive," "bullying," and "reckless," and the other related to whether an animal was more playful and sociable, termed "Beta," anchored by items including reversed "depressed," "sociable," and reversed "solitary." These two metatraits then differentiated into a structure similar to the well-known Big Three model, with Alpha differentiating into DIS and NEM/low Dominance and Beta differentiating into largely PEM. Consistent with human findings, traits ultimately differentiated into five factors largely parallel to the FFM.

Heritability of Personality

A large empirical literature supports the hereditary nature of personality in both humans (e.g., Bouchard, 1994, 2004; Bouchard & McGue, 2003; Turkheimer, 2000) and chimpanzees (e.g., Weiss et al., 2000). Further, recent research on the neurobiological basis of these basic traits in chimpanzees (e.g., Hopkins et al., 2012; Latzman, Hopkins, et al., 2014) suggests not only an evolutionary basis to personality (i.e., ancestral) but also a neurobiological one. For example, similar to genetic (e.g., Bouchard, 2004) and neuroanatomical (e.g., DeYoung, 2010) findings in humans, recent research in chimpanzees suggests similar genetic (e.g., Latzman, Hopkins, et al., 2014) and neuroanatomical (e.g., Latzman, Hecht,

Freeman, Schapiro, & Hopkins, 2014) contributions to individual variation in personality. Taken together, there is strong evidence for the heritability of personality, underscoring the importance of considering heritability of various personality dimensions. To date, however, the heritability of dimensions across various levels of the personality hierarchy has yet to be examined. In a manner more powerful than traditional analyses done in humans, animal models have a number of strengths, including (a) their ability to take into account every relationship in a pedigree, (b) they are less sensitive to nonnormality, and (c) they are able to quantify different environmental components of variance, such as early social rearing experiences (Charmantier & Garant, 2005; Kruuk, 2004).

Early Rearing Experiences and Personality

Genetic factors are clearly not the only source of individual variability. Indeed, a large empirical literature supports the importance of early social rearing experiences on emotional and psychological outcomes in both humans (e.g., Hofer, 1994; Kochanska, 2001; Reti et al., 2002; Oshino et al., 2007) and nonhuman primates (e.g., Bennett & Pierre, 2010; Latham & Mason, 2008; Sánchez et al., 2001; Suomi, 2006, 2011). With regard to individual variability in personality specifically, though, results are relatively more mixed in nonhuman primates, including chimpanzees. Indeed, although early studies suggested significant associations between early social rearing experiences and social-emotional outcomes, including personality (Murray, 1998), more recent studies have failed to find such an association (Martin, 2002, 2005), suggesting that rearing experiences have no long-term effect on personality in chimpanzees. A number of limitations exist across studies, making results difficult to synthesize, including relatively small samples and variable approaches to the assessment of personality, among others. Further, recent findings of significant associations between different early social rearing experiences and cortical organization in chimpanzees (Bogart, Bennett, Schapiro, Reamer, & Hopkins, 2014) suggest the importance of continuing to consider early rearing experiences in investigations of individual variability in neurobiologically based processes, such as personality. Nonetheless, similar to the heritability literature, no research to date has investigated the influence of early social rearing experiences on various dimensions of personality across levels of the personality hierarchy in either human or nonhuman primates.

Gene × Environment Interactions

Existing research on both heritability and early social rearing history provide support for the importance of both genetic and early experiential factors in variability in personality. Recent research strongly suggests that these factors likely not only contribute independently but also potentially interact in the shaping of individual trajectories. Indeed, the interaction between environmental adversity and genetic variation is a key factor in the pathophysiology of a broad range of outcomes (Moffitt, Caspi, & Rutter, 2006). The heritability of various traits likely depends on various factors in the environment rendering genes relevant in some subpopulations, but insignificant in others (Rutter, 2005). In other words, underscoring the importance of considering gene by environment (G×E) interactions is the repeated finding that heritability can vary depending on the populations and environments that are being studied (Charmantier & Garant, 2005; Hoffman & Parsons, 1991). Nonetheless, examination of G×E interactions in the development of humans is quite challenging, given how difficult it is to precisely quantify environmental experiences. Our sample of chimpanzees, some of whom were removed from their birth mothers as a result of inadequate care, allows for the unique opportunity to explicitly examine the influence of early rearing experiences (human-reared vs. mother-reared) on the heritability of various dimensions of personality.

Current Study

The aim of the current study was to replicate and extend previous findings of the hierarchical nature of personality in chimpanzees via a set of personality items drawn from a new, empirically and theoretically derived instrument (Freeman et al., 2013) among a large sample of chimpanzees housed in two separate colonies. Further, we examined the role of genetic and nongenetic (i.e., differential early rearing) factors, and their interaction (G×E), on individual variability of personality across levels of the personality hierarchy. As humans and chimpanzees share many emotional processes, chimpanzees represent an unparalleled animal model of human emotion (Phillips et al., 2014). Indeed, in addition to an extremely high percentage of shared genetics, humans share a great deal of evolutionary history with chimpanzees. Further, similar to humans, chimpanzees live in complex social environments that require sophisticated social cognition and behavior to recruit social support, form social alliances, and recognize displays of emotion (de Waal, 1996). Other complex socioemotional and communicative traits that distinguish chimpanzees from other nonhuman primate species include self-awareness, empathy, theory-of-mind and related constructs, extended delay of gratification, long-term planning, and rudimentary linguistic skills (Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999; Call & Tomasello, 2008; Gallup, 1970; Lyn, 2012; Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997). Many of these social and cognitive abilities reflect behavioral traits clearly related to personality. As such, chimpanzee models are uniquely poised to provide access to highly complex processes underlying basic dispositional traits largely free from the typical uncontrollable sociocultural confounds inherent in human studies (Nelson & Winslow, 2009).

Given converging evidence of a hierarchical personality structure in humans (e.g., Markon, 2009) and chimpanzees (Latzman, Hopkins, et al., 2014), as well as clear parallels between chimpanzee and human personality (e.g., Freeman et al., 2013; King & Figueredo, 1997; Weiss, King, & Hopkins, 2007), we expected evidence of a similar hierarchical structure to emerge with regard to chimpanzee personality. Further, given previous findings of genetic correlates of personality in both human (e.g., Bouchard, 1994, 2004; Bouchard & McGue, 2003) and chimpanzee (e.g., Weiss et al., 2000, 2002) samples, we expected personality dimensions to be heritable across levels of the hierarchy. Further, although a large reliable human literature supports the association between rearing experiences and individual variability in personality (e.g., Kochanska, 2001; Reti et al., 2002), these findings have been much more mixed in chimpanzees (i.e., Murray, 1998; cf. Martin, 2002, 2005). Therefore, we did not advance any a priori hypotheses with regard to associations between differential early social rearing experiences and personality dimensions across var-

ious levels of the hierarchy. Nonetheless, lastly, given repeated findings of heritability dependent on environmental experiences (e.g., Moffitt et al., 2006; Rutter, 2005), we expected heritability estimates to vary by early social rearing experiences.

Method

Subjects

Chimpanzees were members of two colonies of apes housed at the YNPRC in Atlanta, Georgia, and the University of Texas MD Anderson Cancer Center (UTMDACC) in Bastrop, Texas. Personality ratings were available for 95 adult and subadult chimpanzees at the YNPRC, including 68 females and 27 males, with apes ranging in age from 9 to 53 years (M_{age} = 24.79, SD = 10.90). Ratings were available for 143 adult and subadult chimpanzees at UTMDACC (of which 99 were part of the original Freeman et al., 2013 study), including 74 females and 69 males, with apes ranging in age from 8 to 51 years (M_{age} = 28.58, SD = 10.60). All apes were combined into a single sample for analyses, resulting in a final sample of 238 chimpanzees.

Animals experienced a variety of early rearing experiences, with 122 being mother-reared, 56 human nursery-reared, and 60 wild-born. For the purposes of the current study, because of the restricted age range (i.e., all quite a bit older) of wild-born animals, they were excluded from early rearing analyses, resulting in a reduced sample of 178 apes for these analyses. Nursery-reared chimpanzees were separated from their mother within the first 30 days of life because of unresponsive care, injury, or illness. These chimpanzees were placed in incubators, fed standard human infant formula, and cared for by humans until they could sufficiently care for themselves, at which time they were placed with other infants of the same age until they were 3 years old (Bard, 1994; Bard, Platzman, Lester, & Suomi, 1992). At 3 years of age, the nursery-reared chimpanzees were integrated into larger social groups of adult and subadult chimpanzees. Mother-reared chimpanzees were not separated from their mother for at least 2.5 years of life and were raised in "nuclear" family groups of chimpanzees, with group sizes ranging from 4 to 20 individuals. It should be noted that all of the chimpanzees in this study were nursery-reared because their biological mothers did not exhibit adequate maternal care at birth, and this required intervention in order to protect the infants' well-being. Thus, the chimpanzees in this study were not nursery-reared with the goal of subsequently determining the effects of early life experiences on development. These data are therefore opportunistic and retrospective; indeed, we took advantage of the fact that some of the chimpanzees received different rearing experiences in order to determine whether this might have long-term consequences on personality development.

All aspects of the research complied with the American Psychological Association's (2012) *Guidelines for Ethical Conduct in the Care and Use of Nonhuman Animals in Research*, followed the Institute of Medicine guidelines for research with chimpanzees, and was done with the approval of the local Institutional Care and Use Committees. All of the chimpanzees were housed in social groups ranging from two to 16 individuals. The chimpanzees were housed in indoor–outdoor compounds and had access to both portions of their enclosures 24 hr a day. During the winter seasons, the indoor facilities were heated, whereas air conditioning or fans and misters were provided in the hotter summer months. Lighting in the outdoor facility followed the typical seasonal cyclic change in sunrise and sunset. Standard tungsten lighting was provided in the indoor facility and the lights were on a 12-hr on–off cycle. The chimpanzees were fed 2 to 5 times per day with a diet that consists of fruits, vegetables, and commercially produced primate chow. In addition, they received a number of foraging opportunities each day. Environmental enrichment, such as simulated tool use tasks or other nonnutritive substrates, were provided to the chimpanzees on a daily basis. At no time were the subjects ever food or water deprived.

Assessment of Personality

Through consideration of both the existing human personality literature as well as those traits that may be specific to chimpanzees, Freeman and colleagues (2013) used a combined top-down and bottom-up approach to develop a 41-item personality questionnaire. Each item consists of a single trait accompanied by a behavioral definition and a Likert-type scale ranging from 1 (*least descriptive of the chimpanzee*) to 7 (*most descriptive of the chimpanzee*). Strong evidence was reported for five factors: Reactivity/Unpredictability, Dominance, Extraversion, Openness, and Agreeableness. These scales have been found to evidence strong convergent and discriminant validity with various in vivo behavior and have demonstrated strong criterion validity with other validated personality scales (Freeman et al., 2013). Further, reliability has been shown to be adequate, both in terms of interrater reliability and internal consistency (Freeman et al., 2013; Hopper et al., 2014; Reamer et al., 2014). Using this instrument, chimpanzees were rated by colony staff members that worked with the animals for an extended period of time and "feel that they have enough experience for an accurate rating." YNPRC chimpanzees were rated by five staff members, and UTMDACC chimpanzees were rated by 17 staff members. The vast majority of apes were rated by at least two raters. Consistent with previously published data on interrater reliabilities for personality ratings in chimpanzees (Freeman et al., 2013; King & Figuerdo, 1997; Weiss et al., 2007), mean interrater reliability using intraclass correlation coefficients (3,k) across all items was .60 and .66 for the YNPRC and UTMDACC colonies, respectively. For each item, the average rating from all raters was computed and used for all analyses.

Data Analysis

Using Goldberg's (2006) "Bass Ackwards" approach, personality items were subjected to a series of principal components analyses for investigating the hierarchical structure of personality. Specifically, a series of orthogonally rotated (varimax) principle components analyses were performed in an iterative manner, extracting first one principal component from all items to represent the first level of the hierarchy, followed by two principle components, and then three, and so on. Next, to examine how lower levels of the hierarchy emerged from higher levels, saved regression-based factor scores were correlated between levels of the personality hierarchy. Based on this approach, a hierarchical structure of personality was constructed by using the correlations as path estimates between each subsequent level of hierarchy and the preceding level. For example, path estimates were examined

between each of the two factors at the two-factor level, the three factors at the subsequent three-factor level, and so on. This approach has been successfully utilized in the past for similar investigations in humans (e.g., Tackett et al., 2008, 2012), as well as in chimpanzees (Latzman, Hopkins, et al., 2014).

Total additive genetic variance (h^2) is the proportion of total phenotypic variance that is attributable to all genetic sources. Total phenotypic variance is constrained to a value of 1; therefore, all nongenetic contributions to the phenotype are equal to $1 - h^2$. Many of the chimpanzees in each colony are related and this allowed for an analysis of heritability using quantitative genetics based on the entire pedigree. To estimate heritability of various personality dimensions across various levels of the hierarchy, we used the software package SOLAR (Almasy & Blangero, 1998). SOLAR uses a variance components approach to estimate the polygenic component of variance when considering the entire pedigree (see Fears et al., 2009, 2011). We next examined the effects of early rearing experiences on personality across various levels of the hierarchy through a series of multivariate analysis of covariance analyses (MANCOVAs). Specifically, personality factor scores across levels of the hierarchy were included as dependent variables, with a dichotomous mother- versus nursery-reared variable as the between-subjects variable. Sex and age were additionally included as a between-subjects factor and a covariate, respectively. Lastly, given the hypothesized importance of early rearing experiences in influencing the heritability of personality, heritability analyses were conducted separately for mother- and nursery-reared chimpanzees.

Results

Preliminary Structural Analyses

To determine the number of factors to extract, we derived eigenvalue Monte Carlo *p* values (e.g., parallel analysis; Horn, 1965), as parallel analysis has been shown to perform well in identifying the number of factors in an exploratory factor analysis model (Hayton, Allen, & Scarpello, 2004; Zwick & Velicer, 1986). As shown in Table 1, these analyses suggested that a five-factor solution best fit the data. We thus extracted up to five factors in our hierarchy.

Hierarchical Structure of Chimpanzee Personality

Results of item-level factor analyses of the 41 items provide support for correspondence of the hierarchical structure of personality established in humans (e.g., Digman, 1997; Markon et al., 2005; Tackett et al., 2008, 2012) and more recently found in chimpanzees (e.g., Latzman, Hopkins, et al., 2014). Specifically, as shown in Figure 1, the two-factor level appears to describe dimensions that resemble Alpha and Beta, with Alpha reflecting the tendency to be more undercontrolled and defiant, and Beta reflecting the tendency to be more sociable. Specifically, the Alpha factor was anchored by items including Mischievous, Aggressive, Impulsive, Bullying, and Defiant; the Beta factor was anchored by items including Affectionate/Friendly, Intelligent, Affiliative, and Inquisitive/Curious.

At the three-factor level, the three dimensions that emerged were similar to the Big Three of DIS, PEM, and NEM, with Alpha most clearly differentiating into DIS (path = .77) and NEM (path = .60), and Beta differentiating most clearly into PEM (path = .75) and low NEM (path = −.61). The DIS factor was anchored by items including Bold, Dominant, Bullying, reversed Timid, and reversed Cautious. The NEM factor was anchored by items including Socially Inept, reversed Relaxed, reversed Calm, Temperamental/Moody, and Excitable; and the PEM factor was anchored by items including Active, Inquisitive/Curious, Inventive, Playful, and Affiliative. At Level 4, DIS differentiated most notably into a Dominance (path = .83) factor, largely parallel to the Dominance factor found in Freeman et al. (2013), and into a factor we labeled Impulsivity (path = .55), anchored by loadings from Temperamental/Moody, Impulsive, and Mischievous. Although this latter factor resembles Freeman et al.'s Reactivity/Unpredictability factor, we chose to label this factor Impulsivity to reflect the nature of the factor as being a combination of NEM (path = .70) and DIS content, while still explicitly linking it to FFM Conscientiousness. In addition to Impulsivity, NEM was negatively associated with Agreeableness (path = −.51), a factor anchored by Affiliative, Affectionate/Friendly, and reversed Solitary; and Dominance (path = −.44), anchored by reversed Fearful, reversed Timid, and Dominant. PEM broke into Extroversion (path = .75), a factor anchored by Playful, Human Oriented, and Active, and Agreeableness (path = .64). Lastly, at the five-factor level, a structure resembling the FFM and consistent with the structure found by Freeman et al. emerged. In addition to the four factors from the previous level, a factor we termed Intellect, similar to Freeman et al.'s Openness factor, anchored by Human Oriented, Persistent, Methodical, and Inventive, emerged with contributions from Extraversion (path = .55) and Dominance (path = .34). Results of all factor analyses are provided in Tables 1 through 4 of the online supplemental materials.

Table 1
Observed Eigenvalues and Monte Carlo P Values

	Eigenvalue number							
	1	2	3	4	5	6	7	8
Observed eigenvalue	9.87	8.12	4.14	2.44	1.76	1.32	1.18	.95
Monte Carlo *p*	.00	.00	.00	.00	.00	1.00	1.00	1.00

Note. The *p*s were calculated by Monte Carlo methods as described in the text.

Associations Between Hierarchical Dimensions of Personality and Age and Sex

Before conducting heritability analyses and investigating the role of early rearing experiences, we performed preliminary analyses examining associations between personality and age and sex across level of the hierarchy. With regard to age, older chimpanzees were found to be lower on both Alpha and Beta at Level 2 (*r*s = −.32 and −.24, *p*s < .001, respectively), lower on NEM and PEM at Level 3 (*r*s = −.22 and −.45, *p*s < .01, respectively), lower on Impulsivity, Agreeableness, and Extraversion at Level 4 (*r*s = −.31, −.21 and −.35, *p*s < .01, respectively), and lower on Impulsivity, Agreeableness, and Extraversion at Level 5 (*r*s = −.30, −.21 and −.35, *p*s < .01, respectively). With regard to sex differences, males were rated higher on Alpha (*r* =

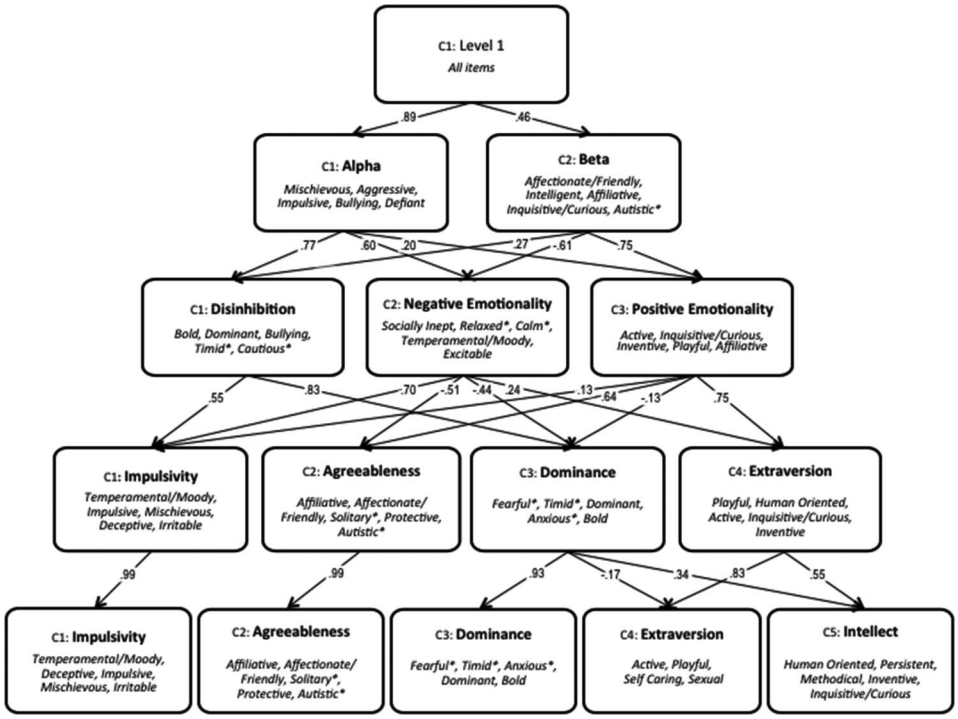

Figure 1. Hierarchical structure of chimpanzee personality.

.17, $p < .05$) at Level 2, NEM ($r = .16$, $p < .05$) at Level 3, Extraversion ($r = .29$, $p < .001$) at Level 4, and Dominance and Extraversion ($rs = .23, .49$, $ps < .001$, respectively) at Level 5. Females were rated higher on Agreeableness ($r = -.19$, $p < .01$) at Level 4, and Agreeableness and Intellect ($rs = -.20, -.19$, $ps < .01$, respectively) at Level 5.

Heritability of Personality Across Levels of the Hierarchy

As described earlier, we next performed estimations of h^2 in personality dimensions across levels of the hierarchy (see Table 2). At the second level, whereas Alpha was not found to be heritable ($h^2 = .13$, $SE = .14$, $p > .15$), Beta was found to be significantly heritable ($h^2 = .18$, $SE = .10$, $p < .05$). At the next level of the hierarchy, only PEM, the dimension Beta most strongly differentiates into, was found to be heritable ($h^2 = .29$, $SE = .11$, $p < .01$). At the next level of the hierarchy, only Extraversion, the lower order dimension most strongly associated with PEM, was heritable ($h^2 = .17$, $SE = .11$, $p < .05$). Lastly, at the final level of the hierarchy, both Extraversion ($h^2 = .38$, $SE = .13$, $p < .001$) and Dominance emerged as significantly heritable ($h^2 = .20$, $SE = .10$, $p < .05$).

Influence of Early Rearing Experiences on Personality Across Levels of the Hierarchy

After determining the extent to which various dimensions were heritable, we next examined associations between differential early experiences (i.e., mother-reared vs. nursery-reared) and the various personality dimensions across levels of the hierarchy accounting for age and sex (see Table 3). At the second level of the hierarchy, although no association emerged between early rearing and Alpha, early rearing was found to be significantly associated with Beta ($F = 5.32$, $p < .05$, $\eta^2 = .03$), with mother-reared apes evidencing higher levels than nursery-reared apes. At level three of the hierarchy, only NEM was associated with early rearing ($F = 5.74$, $p <$

Table 2
Heritability of Personality Dimensions Across Levels of the Hierarchy

Personality factor score	h^2	*SE*	*p* value
Level 2			
Alpha	.131	.143	.159
Beta	**.182**	**.102**	**.018**
Level 3			
Disinhibition	.071	.132	.204
Negative Emotionality	.068	.107	.243
Positive Emotionality	**.292**	**.113**	**.001**
Level 4			
Impulsivity	.041	.143	.381
Agreeableness	.134	.116	.097
Dominance	.061	.099	.250
Extraversion	**.172**	**.108**	**.028**
Level 5			
Impulsivity	.057	.144	.336
Agreeableness	.132	.116	.102
Dominance	**.195**	**.104**	**.018**
Extraversion	**.381**	**.134**	**.000**
Intellect	.000	—	.500

Note. $N = 238$. *SE* = standard error. Heritability estimates significant $p < .05$ shown in boldface.

Table 3
Associations Between Early Rearing Experiences and Personality Dimensions Across Levels of the Hierarchy

Personality factor score	Mother-reared	Nursery-reared	*F*	*p* value	Partial eta^2
Level 2					
Alpha	.12 (.91)	.07 (1.21)	.00	.99	.00
Beta	.15 (.76)	−.30 (1.48)	**5.32**	**.02**	**.03**
Level 3					
Disinhibition	.13 (.97)	−.18 (1.16)	2.89	.48	.00
Negative Emotionality	−.01 (.87)	.37 (1.18)	**5.74**	**.02**	**.03**
Positive Emotionality	.14 (.83)	−.04 (1.36)	.29	.59	.00
Level 4					
Impulsivity	.22 (.85)	−.11 (1.01)	3.18	.08	.02
Agreeableness	.28 (.79)	−.58 (1.40)	**27.12**	**.00**	**.14**
Dominance	−.00 (1.01)	−.10 (1.06)	.34	.56	.00
Extraversion	−.09 (.93)	.44 (1.13)	**17.70**	**.00**	**.09**
Level 5					
Impulsivity	.20 (.85)	−.08 (1.28)	2.29	.13	.01
Agreeableness	.28 (.79)	−.58 (1.40)	**27.45**	**.00**	**.14**
Dominance	.07 (.96)	−.22 (1.19)	3.03	.08	.02
Extraversion	.03 (.93)	.21 (1.16)	3.50	.06	.02
Intellect	−.20 (.96)	.45 (1.06)	**18.67**	**.00**	**.10**

Note. Mother-reared, $n = 122$; nursery-reared, $n = 56$. F-values significant $p < .05$ shown in boldface. All models control for age and sex.

.05, $\eta^2 = .03$), with nursery-reared apes scoring higher than mother-reared apes. At the next level of the hierarchy, both Agreeableness ($F = 27.14$, $p < .001$, $\eta^2 = .14$) and Extraversion ($F = 17.70$, $p < .001$, $\eta^2 = .09$) were significantly influenced by early rearing experiences, with the effect sizes for these associations falling in the medium range. Specifically, compared with mother-reared apes, nursery-reared apes were found to exhibit lower levels of Agreeableness and higher levels of Extraversion. Lastly, at the final level of the personality hierarchy, early rearing significantly influenced both Agreeableness ($F = 27.45$, $p < .001$, $\eta^2 = .14$) and Intellect ($F = 18.67$, $p < .001$, $\eta^2 = .10$), with a medium effect for both. None of the rearing by sex interactions were significant.

Heritability of Personality Dimensions Vary by Early Rearing Across Levels of the Hierarchy

Lastly, to examine the way in which heritability of various personality dimensions may be influenced by early rearing experiences, we ran heritability estimates separately for mother- and nursery-reared apes. As shown in Table 4, the heritability of various personality dimensions clearly varied by early rearing experience, with affectively based personality dimensions emerging as heritable for mother-reared apes and personality largely nonheritable for nursery-reared apes. Specifically, whereas neither Alpha nor Beta were found to be heritable for either mother- or nursery-reared chimpanzees, both affective dimensions, NEM ($h^2 = .37$, $SE = .21$, $p < .05$) and PEM ($h^2 = .31$, $SE = .20$, $p < .05$), were found to be significantly heritable for mother-reared but not nursery-reared apes at Level 3. At Level 4 of the hierarchy, the two most affectively based dimensions, Dominance ($h^2 = .31$, $SE = .19$, $p < .05$) and Extraversion ($h^2 = .53$, $SE = .21$, $p < .01$), were found to be significantly heritable for mother-reared but not nursery-reared chimpanzees. Finally, at Level 5, the dimensions of Dominance ($h^2 = .47$, $SE = .19$, $p < .01$) and Extraversion ($h^2 = .92$, $SE = .10$, $p < .01$) remained heritable for mother-reared apes. Extraversion ($h^2 = .37$, $SE = .17$, $p < .01$) was also found to be heritable for nursery-reared apes at this level.

Discussion

The current study provides strong support for the existence of a hierarchical structure of personality in chimpanzees largely parallel to that found in humans. Further, the current study represents the first investigation to date of the heritability of personality

Table 4
Heritability of Personality Dimensions Across Levels of the Hierarchy by Early Rearing Experiences

	Mother-reared			Nursery-reared		
Personality factor score	h^2	*SE*	*p* value	h^2	*SE*	*p* value
Level 2						
Alpha	.351	.255	.071	.000	—	.500
Beta	.029	.161	.424	.151	.152	.141
Level 3						
Disinhibition	.228	.218	.121	.267	.252	.122
Negative Emotionality	**.368**	**.209**	**.013**	.000	—	.500
Positive Emotionality	**.314**	**.203**	**.034**	.196	.145	.072
Level 4						
Impulsivity	.343	.267	.083	.000	—	.500
Agreeableness	.106	.152	.203	.181	.145	.088
Dominance	**.308**	**.190**	**.024**	.186	.234	.194
Extraversion	**.527**	**.212**	**.004**	.106	.157	.237
Level 5						
Impulsivity	.357	.264	.069	.000	—	.500
Agreeableness	.109	.151	.215	.179	.146	.089
Dominance	**.469**	**.188**	**.001**	.247	.206	.094
Extraversion	**.916**	**.101**	**.001**	**.369**	**.170**	**.008**
Intellect	.158	.160	.133	.086	.253	.362

Note. Mother-reared, $n = 122$; nursery-reared, $n = 56$. h^2 estimates significant $p < .05$ shown in boldface.

dimensions across levels of the hierarchy and the influence, uniquely and interactively, of early social rearing experiences on personality. Consistent with recently published findings in a subset of the participants in the current study using a different chimpanzee personality instrument, we found a hierarchical structure of personality largely parallel to that found in both human adults (e.g., Markon, 2009) and youth (e.g., Tackett et al., 2012). Consistent with previous findings (e.g., King, Weiss, & Farmer, 2005; Weiss et al., 2007), both age and gender differences emerged across levels of the hierarchy. Further, we found significant heritabilities of various traits at different levels of the personality hierarchy, as well as significant effects of early social rearing experiences on individual variability in personality. Lastly, we found strong evidence that the heritability of personality varies by early social rearing experiences revealing an important G×E interaction in the explanation of variation in personality in chimpanzees.

Personality Is Organized Hierarchically in Both Humans and Chimpanzees

Consistent with recently published findings in a smaller sample of chimpanzees using items from a different chimpanzee personality instrument (i.e., Latzman, Hopkins, et al., 2014), results of the current study support the hierarchical nature of chimpanzee personality. Importantly, the reliable structure that emerged largely parallels the hierarchical structure repeatedly found among both human adults (Digman, 1997; Markon, 2009) and youth (Tackett et al., 2012). Alpha, a dimension reflecting a tendency to behave in an undercontrolled, agnostic manner, and Beta, a dimension reflecting a tendency to behave in an approach-oriented, affiliative manner, emerged at the highest level of the hierarchy. At the next level of the hierarchy, Alpha differentiated most notably into DIS and NEM, whereas Beta differentiated into PEM and low NEM. This latter finding is similar to findings in humans, in which Beta is characterized by not only PEM but also nonneglible loadings from NEM and DIS (Markon et al., 2005).

At the next level, a dimension we termed Impulsivity emerged from a combination of DIS and NEM, with a stronger loading from the latter than the former. This dimension may have well been labeled reversed Conscientiousness, given clear parallels to FFM Conscientiousness (Digman, 1990), or Reactivity/Undependendability, given the largely similar factor found by Freeman et al. (2013) in chimpanzees. We chose, however, to label it Impulsivity to both retain the clear link to reversed FFM Conscientiousness, as well as to more clearly reflect the nature of the dimension being anchored by items including Temperamental/Moody, Impulsive, and Mischievous. In addition to Impulsivity, Agreeableness emerged from PEM and reversed NEM, and Extroversion emerged largely from PEM. Lastly, Dominance, a dimension repeatedly found among chimpanzees (e.g., Freeman et al., 2013; Latzman, Hopkins, et al., 2014), anchored by items including reversed Fearful, reversed Timid, Dominant, reversed Anxious, and Bold emerged from a combination of Disinhibition and low NEM. Lastly, at the final five-factor level of the hierarchy, a structure, largely parallel to the FFM in humans and consistent with previous factor analytic findings in chimpanzees (e.g., Freeman et al., 2013), emerged consisting of the four dimensions from the previous level of the hierarchy in addition to a dimension labeled Intellect. Consistent with the previously elucidated hierarchical structure in chimpanzees (Latzman, Hopkins, et al., 2014), Intellect, a dimension that might have also been labeled Openness (e.g., Freeman et al., 2013), emerged from a combination of Dominance and Extroversion and was anchored by items including Human Oriented, Persistent, Methodical, and Inventive. It is important to note that the makeup of this final dimension may be a reflection of the relatively small number of potential loadings. Our decision to term this factor Intellect was based on a number of considerations, including the items that made up this factor in addition to recent research that suggests that a very similar factor, termed Openness by Freeman et al., correlates with performance on a puzzle task (Hopper et al., 2014). Regardless, given the broad nature of the Openness/Intellect dimension in the larger literature (DeYoung, 2015), as well as the relatively few items tapping this dimension in the current study, additional research is needed to more fully elucidate this dimension in chimpanzees. Taken together, results support the presence of a largely conserved hierarchical structure of personality across species. Further, considering the reliable findings in humans and now converging evidence in chimpanzees, these collective results strongly suggest an evolutionary and neurobiological basis for general dispositional traits and the ways in which they associate across various conceptual models.

Heritability of Personality and Influence of Early Social Rearing Experiences

Consistent with previous findings of significant heritabilities in humans (e.g., Bouchard, 1994), and partially consistent with previous chimpanzee findings (e.g., Weiss et al., 2000, 2002), various dimensions of chimpanzee personality were found to be heritable. Specifically, Beta and its more fine-grained traits of PEM at Level 3, and Extraversion at Levels 4 and 5, were found to be significantly heritable with heritability estimates ranging from .17 for Extraversion at Level 4 to .38 for Extraversion at Level 5 (*Mdn* h^2 across Beta-related dimensions = .24). In addition, consistent with previous findings in chimpanzees (e.g., Weiss et al., 2000), Dominance at Level 5 of the hierarchy emerged as significantly heritable (h^2 = .20). Nonetheless, it is important to note that these results are not entirely consistent with previous findings among either humans or chimpanzees. Indeed, whereas a large human literature has reliably found significant heritabilities across various personality traits (Bouchard, 1994, 2004), in addition to Dominance at the final level of the hierarchy, we found only Beta-related traits to be significantly heritable. With regard to divergences with the chimpanzee literature, previous studies have found Dominance, but not other FFM-related traits, to be significantly heritable (e.g., Weiss et al., 2000).

There are a number of potential explanations for these discrepant findings. For example, it is important to note that substantial variability in estimates of heritability may result from measurement effects (Bouchard, 1994), making direct comparisons between studies difficult. Further, the method we employed to estimate heritabilities is different from what is typically used in human studies, potentially accounting for between-species differences (Weiss et al., 2000). Indeed, as described earlier, when compared with typical approaches used in human studies, our approach takes into account every relationship in a pedigree, making it less sensitive to nonnormality. With regard to previous findings in chim-

panzees, discrepancies may be a result of an increased amount of statistical power to detect significance in the current study compared with previous studies. Indeed, although not statistically significant, among the 145 chimpanzees included in their sample, Weiss and colleagues' (2000) heritability estimates for Surgency, a dimension parallel to Extraversion, are largely consistent with our findings. Regardless, these results further underscore the assertion that a genetic basis for personality has a substantial evolutionary history. Results do, however, raise questions regarding nongenetic influence on variation in personality.

To begin to address this question, in addition to the heritability of personality across various levels of the hierarchy, results of the current study also support the importance of early social rearing experiences on individual variability in personality dimensions. Indeed, consistent with findings in humans (e.g., Kochanska, 2001; Oshino et al., 2007; Reti et al., 2002), but only partially consistent with previous findings in chimpanzees (e.g., Murray, 1998; although for contrasting findings, see Martin, 2002, 2005), we found that early social rearing experiences (i.e., mother- vs. human nursery-reared) were significantly associated with individual variability in personality dimensions across levels of the hierarchy. Specifically, compared with nursery-reared animals, mother-reared apes were significantly higher on the broad Beta dimension, as well as on Agreeableness at Levels 4 and 5 of the hierarchy. Compared with mother-reared chimpanzees, nursery-reared chimpanzees, on the other hand, were significantly higher on NEM at Level 3, Extraversion at Level 4, and Intellect at Level 5 of the hierarchy. Importantly, the effect sizes for these associations increased at Levels 4 and 5 of the hierarchy (*Mdn* $\eta^2 = .12$ for differences found at Levels 4 and 5 vs. *Mdn* $\eta^2 = .03$ for differences found at Levels 2 and 3). These findings suggest that early social rearing exerts a stronger influence on more fine-grained personality traits compared with broad basic levels. With regard to the finding of nursery-reared animals scoring higher on Extraversion at Level 4 and Intellect at Level 5, one potential explanation for these findings may be that the item Human Oriented loads on Extraversion at Level 4 and Intellect at Level 5, at least partially driving this finding. Taken together, contrary to previous findings suggesting that early social rearing experiences have no long-term effect on personality (Martin, 2005), our findings suggest an important long-term contribution of early social rearing on variation in personality across levels of the hierarchy, with the effect being moderate at more fine-grained levels of the hierarchy.

Heritability of Chimpanzee Personality Varies by Early Social Rearing Experience

In addition to direct effects of early social rearing experiences in the development of personality, the interaction between early rearing and genetic variation resulted in differences in the heritability of personality across levels of the hierarchy. Indeed, with the exception of Extraversion at Level 5 of the hierarchy, among nursery-reared chimpanzees, none of the personality dimensions across the various levels of the hierarchy were found to be significantly heritable. For the mother-reared apes, however, starting at Level 3 of the personality hierarchy (i.e., three factor level), personality was found to be strongly heritable across levels of the hierarchy. Indeed, the affective dimensions of personality, NEM and PEM, were found to be heritable (*Mdn* $h^2 = .34$). Additionally, the more specific traits of Dominance and Extraversion associated with these broad affective dimensions at lower levels of the hierarchy were also found to be heritable at Levels 4 and 5 of the hierarchy (*Mdn* h^2 at Level 4 = .42, *Mdn* h^2 at Level 5 = .70). Assuming early rearing by biological mothers represents a more favorable condition, these results appear consistent with meta-analytic findings of increased heritability of traits under such conditions (Charmantier & Garant, 2005). Results further suggest that, at least for mother-reared animals, the evolutionary history of personality may be specific to affective dimensions (i.e., NEM and PEM).

Limitations

There are several limitations to this study. Although the Goldberg (2006) method used in the current study has been widely used in previous studies examining the hierarchical nature of personality, it could be argued that principle components analysis with a varimax rotation may not be the optimal approach for explicating a hierarchical structure. Indeed, in addition to concerns regarding the exploratory nature of such an approach (as opposed to a more confirmatory approach), a hierarchical structure inherently implies correlated factors, an implication that is explicitly disregarded using an orthogonal rotation. As such, although our approach is one of the more widely used for such situations, it will be important for future research to replicate the current findings with other methodologies. Further, although widely used in both the human and nonhuman primate literatures, our use of caregiver-reported personality, based on a series of adjectives and descriptions, is only one of a number of potential approaches to assessing various dispositional traits. Similar to recent findings among youth, in which observational coding methodologies have been used (e.g., Tackett et al., 2008), it will be important for future research to replicate these findings using other methodologies, including structured behavior observations through, for example, well-defined ethograms. Further, although comparable with previously published findings, interrater reliabilities across items were moderate. Although we aggregated across raters, whereby increasing reliability, it will be important for results to be independently replicated. Additionally, it is important to note that results of our hierarchical structural analyses were based on 41 items that may not have been varied enough to fully cover the broad range of personality dimensions. As such, additional research is needed with varied approaches to the assessment of personality, including the use of instruments with more, and potentially more varied, item content. Nonetheless, underscoring our confidence in these results, though, is the relatively large and convergent literature in humans (for a review, see Markon, 2009), and our previous chimpanzee findings utilizing a different personality instrument (i.e., Latzman, Hopkins, et al., 2014), which has resulted in parallel findings.

Although results of the current study strongly suggest an important role for early social rearing experiences in the explanation of personality, both independently and in interaction with genetics, chimpanzees experience a variety of early experiences when raised by their biological mothers in age-graded groups of conspecifics or by humans in a nursery setting. As such, our categorization of apes into two groups based on the relatively gross topographical way in which they were raised when very young likely obscures important variability within each group. Nonetheless, such a concern could

result in a more conservative approach to investigating the role of early social rearing experiences, potentially resulting in stronger conclusions based on the current set of findings. Lastly, it might also be argued that early rearing differences could be attributable to genetic differences between offspring born to mothers that were capable of raising them and offspring born to mothers that were unable to provide adequate care. As has been described previously (Bogart et al., 2014), although offspring in each of the two early rearing groups were not entirely heterogeneous, the degree of genetic diversity was comparable between them.

Conclusions

Taken together, results of the current study have a number of important implications. Results support the existence of a hierarchical structure of personality across species, thereby providing an important contribution to the larger literature aimed at merging various traits models of personality into a coherent, integrated framework. Our findings further provide evidence for the influence of *both* genetic and environmental factors on personality profiles across levels of the hierarchy. Lastly, our findings underscore the importance of taking into account environmental variation in models of quantitative trait evolution. Considered within the context of a nascent, yet converging, empirical literature, these findings provide strong support for the notion of personality dimensions as biologically based and evolutionarily derived.

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