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The Importance of Chimpanzee Personality Research to Understanding Processes Associated with Human Mental Health

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Personality research seeks to identify and understand underlying process associated with individual differences in dispositional traits. In humans, individual variation across personality traits have been found to associate with mental health outcomes often times via common neurobiological processes. This shared neurobiological basis demonstrates the value of personality research in elucidating processes associated with mental disorders. More recently, a burgeoning animal personality literature has made efforts to elucidate neurobiological and environmental mechanisms associated with variation in personality—within this literature, chimpanzees (*Pan troglodytes*) represent the most promising model species with respect to optimal translational value to humans. The purpose of the current paper was thus to review the chimpanzee personality literature, with particular emphasis on the organizational, genetic, environmental, and neuroscientific basis of individual variation in personality. We further present a primate-translational operationalization of personality pathology underscoring the notion that personality pathology is rooted within basic dispositions, with evidence of genetic and environmental contributions to such tendencies. Finally, benefits with regard to animal welfare and the National Institute of Mental Health's Research Domain Criteria (RDoC) Initiative, as well as roadblocks associated with curtailment of research involving captive chimpanzees are reviewed. In sum, the current review highlights the importance of translational personality research with chimpanzees as an unparalleled animal model for investigations into the pathophysiology of human mental health.

Personality psychology, sitting at what many argue to be the broadest, most encompassing branch of psychological science, is the study of the dynamic organization of psychological systems that create individual characteristic patterns of behaviors, thoughts, and feelings (Allport, 1961). The field of personality psychology is therefore, concerned with: 1) individual differences, that is, the way in which individuals differ from one another, 2) intrapersonal functioning, that is, the set of emotional and regulative processes taking place within any individual person, and 3) interpersonal functioning, that is, the way in which individuals interact with others in various social settings (Latzman & Shishido, 2013). Importantly, a large and reliable literature demonstrates the importance of variation across personality traits and associations with important outcomes including mental health and well-being. Thus, personality research not only contributes to our understanding of the way in which individuals differ from one another, but it also helps delineate mechanisms/processes underlying mental disorders in humans.

In an attempt to elucidate the evolutionary and biological basis of personality, researchers have begun to examine variation in personality, or various dispositional dimensions, in nonhuman animals; this endeavor has important implications for understanding processes underlying human mental health. As described in more detail below, among the burgeoning animal personality literature, research with nonhuman primates, and chimpanzees (*Pan troglodytes*) specifically, appears to represent a particularly promising area of work from a translational value perspective (Latzman & Hopkins, 2016). Indeed, chimpanzees are not only our closest genetic relatives but humans and chimpanzees live in similarly complex social environments and both possess largely parallel personality traits organized in a similar hierarchical manner (e.g., de Waal, 1996; Freeman et al., 2013; Latzman, Freeman, Schapiro, & Hopkins, 2015a; Phillips et al., 2014). Given this, as shown in Figure 1, the number of publications in the area of chimpanzee personality has been on an exponential rise over the past 20 years.

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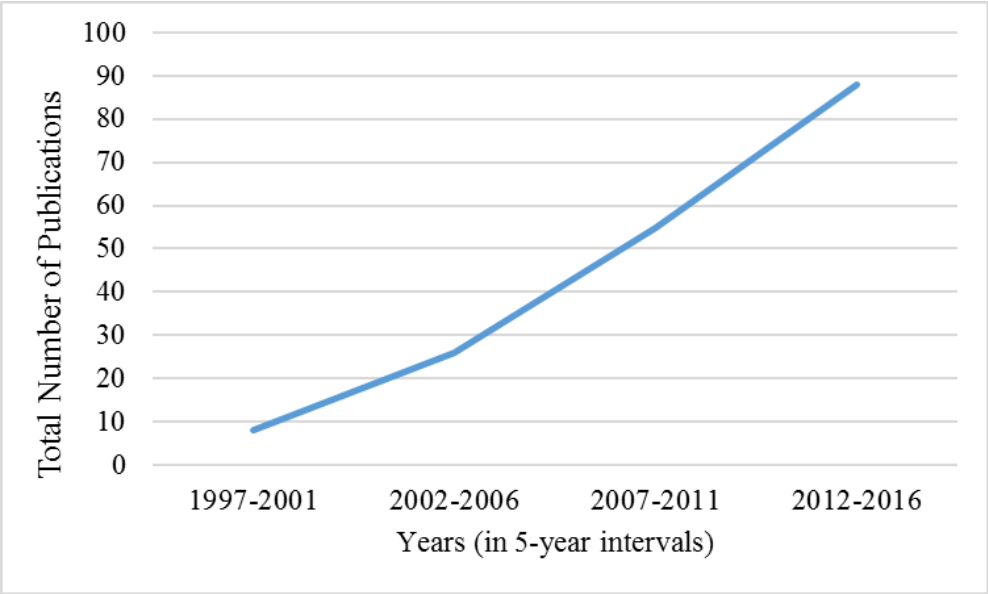

Figure 1. **Total number of publications over the past 20 years in 5-year intervals on "chimpanzee" and "personality"** Using Web of Science, we calculated the total number of publications over the past 20 years on the topic of "chimpanzee" and "personality."

The purpose of the current paper is thus to review the chimpanzee personality literature, focusing specifically on the translational value of this research to humans and the organizational, genetic, environmental, and neural foundations of variation among personality dimensions. Further, we also review ways in which this work has direct relevance to understanding human mental illness. Importantly, as described previously by Latzman, Sauvigné, and Hopkins, (2016a), the goal of this comparative work is not to characterize some chimpanzees as psychologically disordered nor is it to suggest that chimpanzees have the ability to experience mental illness in a way that is similar to humans. Rather, the purpose of this research is to explore the biological and evolutionary foundations of basic dispositional traits, which vary continuously in both human and nonhuman populations and associate with various psychological and behavioral outcomes. Finally, we discuss potential roadblocks to this research moving forward as well as potential next steps. All told, chimpanzee models are uniquely positioned to provide access to highly complex processes associated with basic dispositional traits, largely free from the typical socio-cultural confounds inherent in human studies.

Personality-Psychopathology Relations in Humans

Within both the human and non-human primate literatures, research indicates a relatively consistent five-factor structure of personality (Freeman & Gosling, 2010; McCrae & Costa, 2008; Weiss, King, & Hopkins, 2007). In humans, factor-analytic research consistently reveals five robust, broad personality dimensions (*Big Five*, John, Naumann, & Soto, 2008): Neuroticism, which reflects the general tendency to experience negative emotions and distress; Extraversion, which is thought to reflect sensitivity to reward and is associated with an energetic approach orientation; Openness, reflecting open-mindedness, originality, and intellect; Agreeableness, tendencies towards prosociality; and Conscientiousness, which reflects impulse-control abilities and attention to detail. Another widely used model of personality emerges through the

differentiation of three innate, biobehavioral, temperament dimensions (*Big Three*; Clark, 2005; Clark & Watson, 2008) including two affective dimensions, Negative Emotionality (NEM; reflecting a problematic and upsetting perception of the world) and Positive Emotionality (PEM; reflecting a tendency to engage positively with one's environment), and a third dimension, Disinhibition (DIS), which plays a role in the regulation of perception and interpretation of incoming stimuli (Clark & Watson, 2008; Tellegen, 1985).

Although personality and psychopathology have been historically regarded as distinct constructs, a large body of research has clearly established a strong link between the two. Indeed, regardless of the model through which personality is conceptualized (e.g., Big Five or Big Three), personality traits have been found to strongly associate with various forms of psychopathology (for meta-analytic findings, see Kotov, Gamez, Schmidt, & Watson, 2010; see Figure 2 for examples of meta-analytic associations between personality traits and psychopathology). Indeed, meta-analytic findings confirm the link between low Conscientiousness and impulsivity and a variety of mental health related behaviors, including diet and exercise, substance use behaviors, violence, risky sexual behaviors, among others (Berg, Latzman, Bliwise, & Lilienfeld, 2015; Bogg & Roberts, 2004). Further, Neuroticism has repeatedly been shown to be the core personality trait associated with a wide range of psychopathology, most notably, anxiety and depression (Clark & Watson, 1991; Kotov et al., 2010). Finally, meta-analytic findings provide supporting evidence of low Agreeableness as a strong predictor of aggressive and antisocial behaviors (Miller & Lynam, 2001).

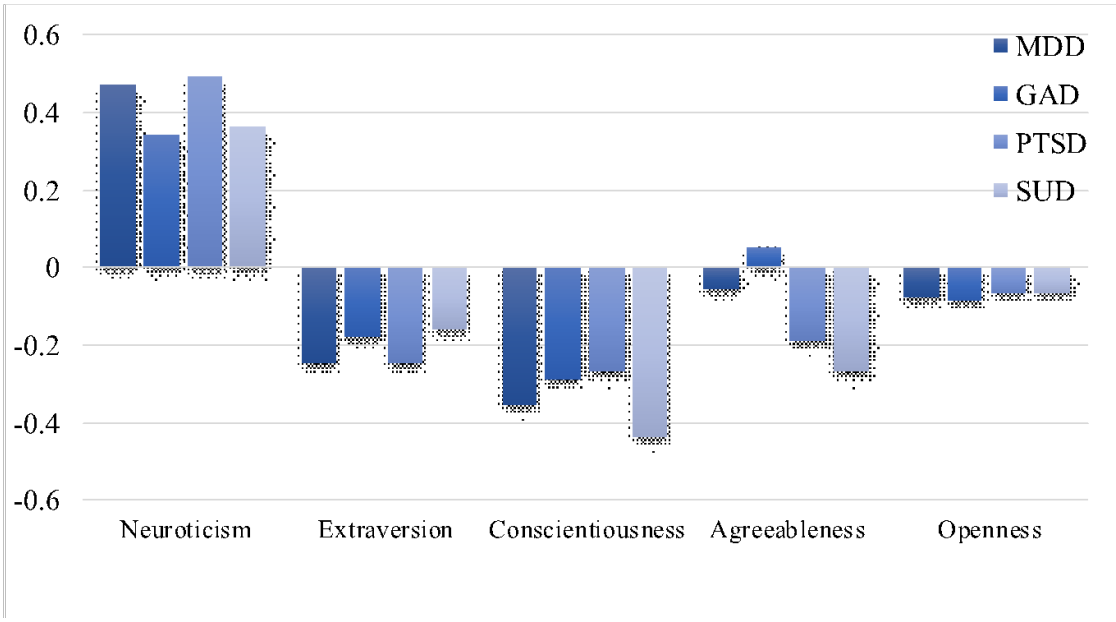

Figure 2. **Meta-analytic effect sizes for associations between personality and psychopathology.** MDD = Major Depressive Disorder. GAD = Generalized Anxiety Disorder. PTSD = Posttraumatic Stress Disorder. SUD = Substance Use Disorder. Adapted from "Linking 'Big' Personality Traits to Anxiety, Depressive, and Substance Use Disorders: A Meta-Analysis," by R. Kotov, W. Gamez, F. Schmidt, and D. Watson, 2010, *Psychological Bulletin, 136*, p. 800, Copyright 2010 by the American Psychological Association. Adapted with permission.

Although the link between personality and psychopathology is clear, there are a number of potential explanations for this relationship which can be summarized by five, not mutually exclusive theoretical models:

predisposition/vulnerability, pathoplasty, complication/scar, spectrum/continuity, and common cause/shared diathesis models (Clark, 2005; Watson, Kotov, & Gamez, 2006; Widiger, 2011).

(1) The predisposition or vulnerability model posits that certain maladaptive personality traits may put an individual at an increased risk of developing a mental disorder. For example, Neuroticism appears to increase the chances of developing later anxiety and mood disorders (Watson, Clark, & Harkness, 1994).

(2) The pathoplasty model asserts that while personality and psychopathology are separable, the manifestation of any specific mental disorder is shaped by personality. For example, as described by Widiger (2011), among individuals suffering from an eating disorder, those diagnosed with anorexia are likely to have reported high levels of conscientiousness prior to the onset of the disorder. Among those diagnosed with binge eating disorder or bulimia, however, research has found these individuals scoring low on conscientiousness before the onset of the disorder (Widiger, 2011).

(3) The complication/scar model argues that personality is affected by psychopathology and, in this respect, the temporal association between the two is reversed from that of the vulnerability model. After a series of major depressive episodes, for instance, an individual's level of neuroticism may increase and not return to premorbid levels even after the depressive symptoms have ceased (Clark, 2005; Tackett, 2006).

(4) The spectrum or continuity model posits that personality traits and psychopathology lie on the same dimension ranging from normal to abnormal. That is, personality and psychopathology differ in degree rather than kind; psychopathology may be an extreme presentation of some specific trait or combination of traits. For example, obsessive compulsive disorder can be considered as an intense or severe form of extremely high levels of conscientiousness (Widiger, 2011).

Finally, (5) similar to the spectrum model, the common cause or shared diathesis model proposes that personality and psychopathology stem from shared underlying predispositions. Clark (2005) argues that three basic temperamental traits (i.e., negative temperament, positive temperament, and disinhibition) underlie both personality and psychopathology. A Big Three temperamental trait such as, for example, disinhibition, is strongly linked to externalizing problems (e.g., conduct disorder; substance use disorders), but also, can be further differentiated into more distinct personality traits (i.e., Big Five Agreeableness and Conscientiousness) with distinct behavioral correlates (e.g., Latzman, Vaidya, Clark, & Watson, 2011).

These final two models (i.e., 4 and 5) strongly support the notion that personality and psychopathology share a common etiology with both determined by innate temperamental traits and further shaped by development and the environment (Caspi et al., 2014; Clark, 2005; Durbin & Hicks, 2014). This conceptualization is not only consistent with the majority of recent research on the relationship between personality and psychopathology, but also simultaneously addresses a leading problem in the categorical system of classifying psychological disorders by explaining the high frequency of co-occurring, or comorbid, disorders.

Consistent with the common cause or shared diathesis model, Clark (2005) points to basic biologically-based temperamental traits as underlying both personality and psychopathology. Specifically, Clark (2005) suggests that where an individual falls on the various dimensions of temperament determines one's vulnerability for experiencing any given mental disorder. This conceptualization is consistent with a hierarchical model of personality, described below, in which more basic dispositional dimensions differentiate into more fine-grained traits. Fundamental temperamental traits not only establish an individual's

predisposition to develop a certain combination of personality traits but also play a key role in the development and course of problematic thinking and behavior. Given the clear importance of personality in the understanding the pathophysiology of psychopathology, recent work has focused on expanding the human personality literature to nonhuman animals. As described above, from a translational perspective, this work has most notably been extended to chimpanzees (*Pan troglodytes*), in hope of elucidating not only the evolutionary basis of personality but also the biological and environmental foundations.

Chimpanzees are a Model Species for the Study of Biological and Environmental Contributors to Personality

The translational value of any animal model lies in the ability of findings for phenomena of interest to generalize between nonhuman animals and humans in ways that reflect common basic processes. From this perspective, chimpanzees represent, by far, the best animal model species for complex behavioral, cognitive, neuroscientific, and neurogenomic research focused on personality. In addition to being the closest living relative to humans on the planet, it is now widely accepted that humans and chimpanzees share many emotional processes, providing the foundation for an unparalleled animal model of human emotion (Phillips et al., 2014). In addition to sharing an extremely high percentage of genes with humans, chimpanzees likewise 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). Moreover, although many primates engage in reconciliation following agonistic encounters, only chimpanzees (and perhaps other great apes) exhibit what de Waal (1996) describes as "consolation." Consolation occurs when a third party member of a social group of chimpanzees hugs, grooms, or otherwise touches the loser in a physical altercation as if to console them. Similarly, chimpanzees share food even with non-kin, suggesting a high degree of prosociality, which de Waal (2008) suggests may similarly be the foundation for altruism and empathy in humans. Other complex socio-emotional and communicative traits that distinguish chimpanzees from other non-human 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 dispositional traits important for understanding variation in personality. Taken together, the value of research with chimpanzees in advancing our understanding of evolutionary and biological processes associated with personality traits is clear.

Potentially most important, a comparative approach using chimpanzees allows for a relatively straightforward analysis of biological and environmental processes contributing to the personality dimensions. Specifically, although biological factors are presumed to account for some variability in personality traits in humans, it is likely that socio-cultural influences also play an important role (e.g., Diener, Oishi, & Lucas, 2003). Almost from birth, social systems and cultural institutions impose expectations on how humans should behave and react in terms of inhibiting impulses, engaging in prosocial behavior (e.g., "share your candy"), and expressing empathy (e.g., "say you're sorry"). Because systematic social and cultural pressures of such types are largely absent in chimpanzees, inter-individual variation in personality traits in apes can be presumed to reflect largely biological mechanisms (Latzman & Hopkins, 2016).

Chimpanzee Personality

Given the importance of research on personality among nonhuman primates in elucidating biological systems underlying personality (Stockard, 1931), nonhuman primates, specifically chimpanzees, have increasingly become the focus of research on the biological and comparative foundation of personality (e.g.,

Freeman et al., 2013; Freeman & Gosling, 2010; Latzman, Freeman, Schapiro, & Hopkins, 2015a). Indeed, as shown in Figure 1, research publications in the area of chimpanzee personality has grown exponentially over the past 20 years. Similar to humans, individual variation in chimpanzee personality has been found to be a predictor of a range of social behaviors (e.g., agonistic, affinitive; Freeman et al., 2013; Massen & Koski, 2014; Pederson, King, & Landau 2005) and caretaker-reported subjective well-being (Weiss, King, & Enns, 2002; Weiss et al., 2009). Additionally, chimpanzee personality has been found to predict interest and willingness to participate in research tasks (Herrelko, Vick, & Buchanan-Smith, 2012), success in problem-solving tasks (Hopper et al., 2014), and even longevity (Altschul, King, Inoue-Murayama, Ross, & Weiss, 2016). Given the clear importance of personality to understanding various behavioral outcomes in both humans and chimpanzees, as well as the clear translational value of chimpanzee personality research to understanding parallel processes in humans, the following sections review what we know to date concerning the factor structure and organization of personality in chimpanzees, and convergence with the human literature, as well as the genetic, environmental, and neural foundations of chimpanzee personality dimensions.

Structure of Chimpanzee Personality

Although the ultimate number of personality factors found in chimpanzees across studies has varied, with some studies reporting six (i.e., Big Five plus Dominance), and others a relatively parallel set of five, the existence of largely parallel dispositional traits among both human and nonhuman primates is clear (e.g., Freeman et al., 2013; Gosling & John, 1999; King & Figueredo, 1997; King, Weiss, & Sisco, 2008; Weiss et al., 2007). In an attempt to ensure comparability with the human personality literature and to determine the factor structure of chimpanzee personality, recent factor analytic research has led to the development of a comprehensive assessment instrument for measuring personality in chimpanzees (Freeman et al., 2013). Importantly, in developing these scales, these authors explicitly considered both the human and chimpanzee personality literatures. Ratings of chimpanzee personality were obtained using caregiver reports using Likert-type scales for individual items. Strong evidence for a five-factor solution largely paralleling the Big Five model reliably found in humans emerged: Extraversion, Agreeableness, Reactivity/Undependability, Dominance, and Openness. Although not typically labeled as such in the Big Five model, Dominance appeared to parallel reverse-keyed Neuroticism reflected in low levels of fearfulness and timidity (Freeman et al., 2013; Latzman et al., 2014). Reactivity/Undependability, however, is a dimension not previously found to emerge in the Big Five model, and consisted of items previously found to load on Big Five Conscientiousness (e.g., *impulsive*, reverse-keyed), Agreeableness (e.g., *deceptive*, reverse-keyed), and Extraversion (e.g., *calm*, reverse-keyed; Digman, 1990). Further, the validity of using human ratings of chimpanzee personality has not only been supported by evidence of high interrater reliability; but also, caregiver judgements of specific personality traits have been found to associate with observed animal behavior (e.g., Pederson et al., 2005; Freeman et al., 2013).

More recently, Latzman et al. (2016a) explicitly tested the transportability of these psychometric personality scales developed in chimpanzees to humans. Until this point, the translational value of the chimpanzee personality literature to humans was largely assumed, rather than empirically demonstrated. Specifically, in a sample of humans, Latzman et al. (2016a) demonstrated that chimpanzee-derived personality scales translate well to humans operating similarly and in expected ways to established human-derived Big Three and Big Five personality scales. These findings provide compelling evidence of the translational value of chimpanzee personality research to studies of humans.

In addition to research supporting the existence of largely parallel, translatable traits in humans and chimpanzees, recent work has demonstrated the existence of a comparable hierarchical structure of personality in chimpanzees (Latzman et al., 2014, 2015a) as compared to humans (for a review, see Markon, 2009). Although distinct conceptualizations of the basic framework of human personality have historically existed (i.e., Big Five, Big Three), a reliable literature has demonstrated that traits are related to one another in an organized hierarchy encompassing these various conceptualizations. Specifically, personality traits can be organized hierarchically such that more fundamental traits (i.e., biobehavioral Big Three temperament dimensions) can be differentiated into more fine-grained traits (i.e., Big Five traits; Digman, 1997; Markon, Krueger, & Watson, 2005; Tackett et al., 2012). Recently, a largely similar, hierarchical structure has been found in chimpanzees (Latzman et al., 2014, 2015a).

In a manner paralleling converging findings in humans, the highest level of chimpanzee personality hierarchy is reflected in two superordinate or metatraits, 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. At the next level of the hierarchy, Alpha differentiated most notably into Disinhibition and NEM, while Beta differentiated into PEM and low NEM. The three dimensions emerging at this level of the chimpanzee personality hierarchy are comparable to the Big Three personality traits found in humans. At the next level, an Impulsivity/low Conscientiousness dimension emerged from a combination of Disinhibition and NEM. In addition to Impulsivity/low Conscientiousness, Agreeableness emerged from PEM and reversed NEM, and Extraversion emerged largely from PEM. Lastly, Dominance, a dimension largely paralleling reversed NEM/Neuroticism in humans, repeatedly found among chimpanzees (e.g., Freeman et al., 2013; Latzman et al., 2014) emerged from a combination of Disinhibition and low NEM. At the final five-factor level of the hierarchy, a structure largely parallel to the Big Five model in humans and consistent with previous factor-analytic findings in chimpanzees (e.g., Freeman et al., 2013) emerged. This level consisted of the four dimensions from the previous level of the hierarchy in addition to an Openness/Intellect dimension, emerging from a combination of Dominance and Extraversion and anchored by items that appear to tap Openness and Intellect-related content.

Taken together, a growing body of chimpanzee personality research confirms the presence of a largely conserved hierarchical structure of personality in both humans and chimpanzees. Indeed, as shown in Figure 3, the comparable nature of the personality hierarchy in both chimpanzees (i.e., Latzman et al., 2015a) and humans (e.g., Markon, Krueger, & Watson, 2005) is clear. 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 of personality (i.e., Big Three, Big Five).

Genetic and Environmental Contributions to Personality

A large research literature supports the notion of personality as heritable in both humans (Bouchard, 2004; Bouchard & McGue, 2003) and chimpanzees (Latzman et al., 2015a; Weiss et al., 2002; Weiss, King, & Figueredo, 2000). Heritability (*h2*) refers to the proportion of variation in a phenotypic trait (i.e., personality) that is due to genetic variation among individuals of a population. Animal models possess a number of strengths when considering the heritability of and environmental contributions to various phenotypes, including personality. In a manner more powerful than traditional analyses done in humans, animal models 1) take into account every relationship in a pedigree, 2) are less sensitive to nonnormality, and 3) are able to quantify different environmental components of variance, such as early social rearing experiences (Charmantier & Garant, 2005; Kruuk, 2004).

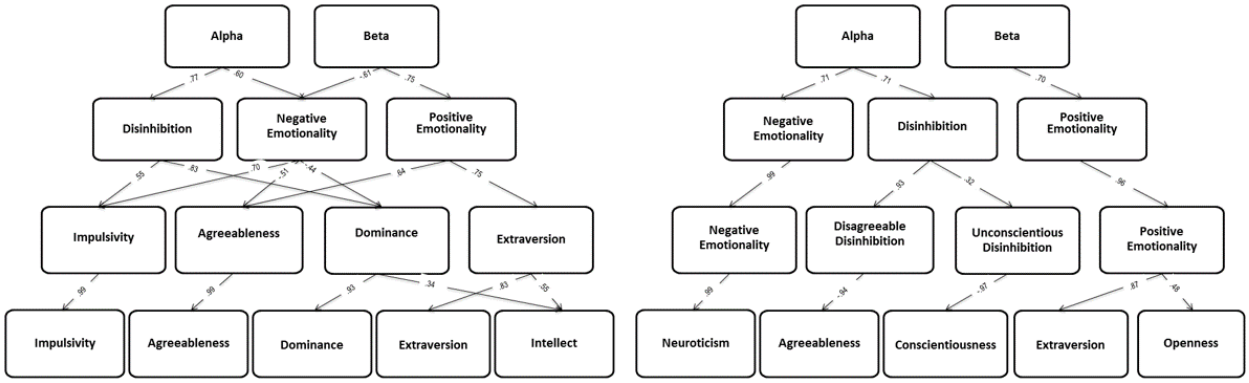

Figure 3. **Hierarchical structures of chimpanzee (left) and human (right) personality**. Adapted from "The Contribution of Genetics and Early Rearing Experiences to Hierarchical Personality Dimensions in Chimpanzees (*Pan troglodytes*)," by R. D. Latzman, H. D. Freeman, S. J. Schapiro, and W. D. Hopkins, 2015, *Journal of Personality and Social Psychology, 109*, p. 894, 2015, Copyright 2015 by the American Psychological Association. Adapted with permission. Adapted from "Delineating the Structure of Normal and Abnormal Personality: An Integrative Hierarchical Approach," by K. E. Markon and R. F. Krueger, 2005, *Journal of Personality and Social Psychology, 88*, p. 148, Copyright 2005 by the American Psychological Association. Adapted with permission.

Quantitative genetic analyses with captive chimpanzees, the focus of the majority of efforts in this area, possess all of these strengths in an unparalleled animal model of human emotion. Indeed, captive chimpanzees' full pedigrees are well-documented allowing for analyses that consider the entire pedigree of each animal. Further, captive chimpanzees experience a variety of early rearing experiences with some being mother-reared and others human nursery-reared. In the studies reviewed below, nursery-reared chimpanzees were separated from their mother within the first 30 days of life, due to 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 three years old (Bard, 1994; Bard, Platzman, Lester, & Suomi,1992). At three years of age, the nursery-reared chimpanzees were integrated into larger social groups of adult and sub-adult 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. The chimpanzees in these studies 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; that is, researchers take advantage of these different rearing experiences in order to determine whether this might have long-term consequences on personality development. Taken together, well-documented pedigrees, along with quasi-experimental manipulation of early social experiences, allows for the unique ability to examine the role of genetic and non-genetic factors (i.e., early rearing), as well as their interaction (gene x environment; GxE), in the explanation of personality.

With regard to the heritability of personality, a large literature has demonstrated a considerable genetic contribution to personality in chimpanzees (Latzman et al., 2014; Weiss et al., 2000, 2002). Recently, within a relatively large sample of chimpanzees (N = 238), Latzman et al. (2015a) noted significant heritabilities of various traits at varying levels of the personality hierarchy. At the most fundamental level of the personality

hierarchy, while the heritability estimate for alpha was not significant, Beta showed significant albeit modest heritability (h^2 = .18). At the next level of the hierarchy, only PEM (the dimension most strongly differentiated from Beta) evidenced a significant heritability estimate (h^2 = .29). At the next level, only Extraversion (most strongly associated with PEM) was found to be significantly heritable (h^2 = .17). Finally, at the five-factor level of the hierarchy, both Extraversion (h^2= .38) and Dominance (h^2 = .20) significant heritability estimates were found. All told, similar to humans (e.g., Jang, Livesley, & Vemon, 1996; Jang, McCrae, Angleitner, Riemann, & Livesley, 1998), genetic factors are clearly important with regard to individual variation in chimpanzee personality. Nonetheless, genetic factors are not the only important source of individual variability.

Indeed, early rearing experiences also contribute to individual differences across a variety of outcomes. For example, Gunnar and Fisher (2006) review literature documenting the effects of neglect and maltreatment during childhood. Although outcomes vary depending on the duration of the trauma, the age of rescue, current life stressors, and other influential variables, results of converging studies suggest that neglect and maltreatment early in life result in vulnerability to a range of maladaptive outcomes (e.g., behavioral problems, substance abuse, personality disorders, etc.). Whereas the importance of early social rearing experiences on emotional and psychological outcomes in non-human animals has been clearly demonstrated (Bennett & Pierre, 2010; Bard & Gardner, 1996; Bard, Bakemen, Leavens, & Boysen, 2014; Latham & Mason, 2008; Suomi, 2006, 2011), results are relatively more mixed in chimpanzees with regard to associations with individual variability in caregiver-rated personality. Early studies suggested significant associations between early social rearing experiences and personality (Murray, 1998); however, more recent studies have failed to find a similar association (Martin, 2002, 2005). The latter findings suggest that rearing experiences have no long-term effect on personality in chimpanzees, though a number of limitations, including relatively small samples and variable approaches to the assessment of personality, exist across studies, making results difficult to interpret.

Nevertheless, more recently, Latzman and colleagues (2015a) found that various dimensions across the hierarchical structure of personality in a sample of 178 chimpanzees varied by early social rearing experiences. Specifically, at the most basic level of the hierarchy, whereas Alpha was not associated with early rearing, a significant but small association emerged between Beta and early rearing ($\eta_p 2$ =.03); mother-reared chimpanzees evidenced higher levels than nursery-reared chimpanzees. At the next level of the hierarchy, only NEM was associated with early rearing ($\eta_p 2$ =.03), with nursery-reared chimpanzees scoring higher than mother-reared chimpanzees. At the final level of the hierarchy, early rearing was significantly associated with both Agreeableness ($\eta_p 2$ =.14) and Openness/Intellect ($\eta 2$ =.09), with mother-reared chimpanzees being higher in Agreeableness and lower in Openness/Intellect. Not only do these findings suggest early social rearing experience result in variability in personality traits across levels of the hierarchy, but also that this effect becomes stronger when going from a small effect at the broader level (*Mdn* $\eta_p 2$ =.03) to a moderate effect at more fine-grained levels of the hierarchy (*Mdn* $\eta_p 2$ =.12). Indeed, early social rearing experiences (i.e., mother- vs. nursery-rearing) seem to have a stronger and more specific effect on more narrow personality traits found at the lower levels of the hierarchy.

Existing research has provided clear support for both genetic and environmental contributors to variability in human personality. These factors, however, appear to not only contribute independently but also interact in influencing personality. Indeed, the interaction between environmental adversity and genetic variation is a key factor in the pathophysiology of a broad range of outcomes in humans (Moffitt, Caspi, & Rutter, 2006). For example, certain environmental variables, such as childhood physical maltreatment or increased levels of stress, are related to maladaptive outcomes (i.e., antisocial behavior, depressive episodes,

respectively). Nonetheless, genetic factors appear to be critically important moderating factors with regard to an individual's sensitivity to environmental stressors and their subsequent vulnerability to maladaptive outcomes (Rutter, 2005). 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).

Further underscoring the importance of considering GxE interactions is the repeated finding in both human and nonhuman primates that heritability can vary depending on the populations and environments that are being studied (e.g., Burt, 2008; Charmantier & Garant, 2005; Hoffman & Parsons, 1991; Krueger, South, Johnson, & Iacono, 2008). In humans, for example, the genetic contribution to individual variation in personality has been found to vary as a result of various familial factors (e.g., parenting, parent-child relationship characteristics; e.g., Krueger et al., 2008; for a review, see Burt, 2008). Examination of GxE interactions in humans, however, is quite challenging, given how difficult it is to precisely quantify environmental experiences. As described above, however, chimpanzee samples, some of whom were removed from their birth mothers as a result of inadequate care, allow for the unique opportunity to explicitly examine the influence of early rearing experiences on the heritability of various dimensions of personality.

Latzman and colleagues (2015a) found a significant GxE interaction in their investigation of chimpanzee personality, whereby heritability of personality dimensions varied by early social rearing experiences. In general, affectively based personality dimensions (i.e., NEM and PEM) emerged as significantly heritable for mother-reared chimpanzees (i.e., a significant proportion of variance in NEM and PEM can be explained by genetic effects), while heritability estimates were largely nonsignificant and small for nursery-reared chimpanzees. Specifically, neither Alpha nor Beta was found to evidence significant heritability estimates for either cohort (mother- or nursery-reared chimpanzees); however, among mother-reared chimpanzees, heritability estimates were considerable and significant for both affective dimensions, NEM (h^2 = .37) and PEM (h^2 = .31). At the lowest level of the personality hierarchy, Dominance (h^2 = .31) and Extraversion (h^2 = .53), the two most affectively based dimensions, evidenced a moderate to high degree of heritability among mother-reared chimpanzees whereas only Extraversion (h^2 = .37) showed similarly high heritability for nursery-reared chimpanzees. All told, such investigations underscore the value of chimpanzee models of personality in which environmental variation can be taken into account with models of quantitative trait evolution. This unique ability to consider varying environmental experiences is useful in quantifying both genetic and environmental contributions, and their interaction, in the explanation of individual differences in personality.

Associations between Genetic Polymorphisms and Chimpanzee Personality

Given strong evidence in support of the heritability of dimensions of personality, researchers have begun to investigate potential genetic polymorphisms that might explain this heritability (e.g., Anestis et al., 2014; Hopkins, Donaldson, & Young, 2012; Hong et al., 2011; Latzman, Hopkins, Keebaugh, & Young, 2014; Staes et al., 2015; Wilson et al., 2017). One particularly promising gene that has received the lion's share of study with regard to socio-emotional dimensions in both nonhuman animals and humans is the vasopressin V1a receptor gene (AVPR1A). Vasopressin is a neuropeptide with multiple physiological functions that has been strongly implicated in the development and evolution of complex social behavior in mammals (Donaldson & Young 2008). Across numerous species, AVPR1A has been found to be expressed in the brain and associated with several social behaviors including aggression, territoriality, and pair bonding behaviors among voles, particularly among males (e.g., Hammock & Young, 2005, 2006; Hammock, Lim, Nair, & Young, 2005; Winslow, Hastings, Carter, Harbaugh, & Insel, 1993; Young & Wang, 2004). The behavioral effects of vasopressin have been found to be mediated predominantly by the V1a subtype of the vasopressin receptor,

although it should be noted that the V1b subtype has received much less attention in the literature. Both, species differences and individual variation in the distribution of AVPR1A in the brain, are thought to underlie inter- and intra-species variation in social behavior (Barrett et al., 2013; Young & Wang, 2004), behaviors known to be particularly relevant to individual variation in trait dispositions. With regard to primates specifically, recent studies with humans suggest associations with a similar repetitive element in the AVPR1A promoter and social behavior, including age at first intercourse (Yirmiya et al., 2006), altruism (Wassink et al., 2004), and pair bond relationships (Walum et al., 2008). Further, AVPR1A promoter polymorphisms have been found to be associated with increased Novelty Seeking, decreased Harm Avoidance (Walum et al., 2008), and increased Reward Dependence (Bachner-Melman et al., 2005). Harm Avoidance is strongly correlated with Big Five Neuroticism and Novelty Seeking and Reward Dependence are strongly correlated with Big Five Extraversion (De Fruyt, Van De Wiele, & Van Herringen, 2000).

Many of the association studies reviewed above have focused on a polymorphic repetitive element known as RS3. In humans, the RS3 repeat region is housed within a larger, ~350 bp tandem duplicated region. The first of these duplicated regions, DupA, spans -3730 to -4074 bp relative to the transcription start site and contains a GT20-26 microsatellite, known as STR1. The second block, DupB, spans -3382 to -3729 bp and contains the complex microsatellite, RS3 [(CT)6-14(GT)8-24]. In chimpanzees, approximately 65% of the AVPR1A alleles have a complete deletion of the DupB region, leading to a 357 bp difference between the DupB+ and Dup- alleles. The deletion of RS3 in some individuals makes chimpanzees a particularly ideal animal model species for assessing the potential role of the AVPR1A gene, and more specifically RS3, on aspects of sociality such as personality.

Although only a few published studies to date have explicitly investigated associations between AVPR1A and personality in chimpanzees, largely converging results suggest an important role for AVPR1A in the explanation of individual variability in personality. Indeed, Hopkins et al. (2012) found that Dominance and Conscientiousness scales were associated with polymorphic variation in AVPR1A, particularly among males. Specifically, for those chimpanzees with one copy of the long allele DupB+/- (versus those homozygous for the short allele, DupB-/-), males had higher Dominance and lower Conscientiousness scores than females. More recently, Latzman, Hopkins, Keebaugh, and Young (2014) extended this work to examine AVPR1A associations with factor-analytically derived personality dimensions across the personality hierarchy, a structure described in detail above. AVPR1A was associated with Alpha at the most basic level of the hierarchy and with Disinhibition and Dominance/low Negative Emotionality at the Big Three level. Similar to findings from Hopkins et al. (2012), these associations were found to vary by sex. Specifically, whereas chimpanzees homozygous for the short allele DupB-/- did not differ by sex, males with one copy of the DupB+ allele evidenced lower levels of Alpha and higher levels of Disinhibition than heterozygous females. Additionally, heterozygous males displayed lower levels of Dominance than heterozygous females. These results are consistent with previous findings with regard to Dominance and Conscientiousness (Hopkins et al., 2012), traits that emerge from Dominance and Disinhibition at a lower level of the hierarchy.

Using behavioral observation methodologies to assess personality rather than caregiver-reports, similar findings have also been reported by Staes et al. (2015) and Anestis et al. (2014). Specifically, within 62 captive chimpanzees, Staes et al. found sex-specific AVPR1A associations with behavioral observations of sociability. Within two separate chimpanzee populations, one captive (N = 64) and one wild (N = 26), Anestis and colleagues (2014) reported significant associations between AVPR1A genotype and a range of social behavioral styles (i.e., personality) and in sex-specific ways. All told, sex-specific associations between AVPR1A genotype and personality appears to be evident.

Male-female differences are not surprising as vasopressin systems in the brain have been found to be sexually dimorphic and thought to regulate social behaviors in sex-specific ways (De Vries, Crenshaw, & Al-Shamma, 1992). One potential explanation for these findings may be the importance of vasopressin in amygdala activation and emotional processing (Meyer-Lindenberg et al., 2009). Specifically, these processes are likely linked to Alpha/Stability and related traits, traits associated with proneness to aggression and territoriality and control over behavior often in the context of social interactions. Indeed, vasopressin appears to play a role in modulating responses to social cues in a sex-specific manner in a variety of species (Donaldson & Young, 2008).

Although the studies reviewed above suggest an important role for AVPR1a in the explanation of individual variability in personality, and in some sex-specific ways, it is important to note that some results using different analytic approaches have diverged in some ways. Specifically, whereas findings of associations between AVPR1A and chimpanzee personality were reported by Wilson and colleagues (2017) who found AVPR1A to be associated with Conscientiousness and Extraversion, these associations were not found to differ by sex. Regardless, all told, AVPR1a appears to be a promising candidate gene for future investigations of the genetic basis of personality. As it is not yet clear whether the differences that are emerging are due directly to gene expression caused by the presence or absence of the DupB region, it will be important for future research to examine whether variations in the DupB region is associated with differences in the expression of the AVPR1A in the brain.

Although the lion's share of this work has considered AVPR1A, another genotype that appears potentially important in the explanation of variability in chimpanzee personality is the serotonin production rate-limiting enzyme - tryptophan hydroxylase 2 (TPH2) gene polymorphism in the ch468R allele (Hong et al., 2011). Specifically, in a sample of 57 chimpanzees, Hong and colleagues (2011) reported that a significant association between the presence of the ch468R allele and caregiver-reported neuroticism. These findings are consistent with, for example, earlier studies in humans, where mutations in this gene are associated with major depression (Zhang et al., 2005). Although the study presents a number of limitations, including a relatively small sample size (N = 57), particularly for candidate gene studies, among others, it does provide further evidence for the genetic basis of personality and for the likelihood that personality is a phenotypic result of the interplay of multiple genes.

Neural Foundations of Personality

Recent neuroimaging research in humans confirms the importance of various brain regions in elucidating the neurobiology of personality (Allen & DeYoung, 2017; DeYoung, 2010). Neuroimaging research in chimpanzees offers unique insight into neurobiological processes shared with humans. For example, as compared to humans, chimpanzees share similar brain organization likely as a result of similarly evolved abilities and physical characteristics including similar life histories (e.g., relatively longer life span); however, chimpanzee environment and social influence can be considered in ways which are difficult to accomplish in human samples. Further, similar to humans, chimpanzee research suggests neuroanatomical contributions to individual variation in personality (Blatchley & Hopkins, 2010; Latzman, Hecht, Freeman, Schapiro, & Hopkins, 2014) providing critical confirmatory evidence for a neurobiological foundation of personality. Blatchley and Hopkins (2010) examined whether individual differences in personality were associated with percent gray matter (PGM) and lateralization of the subgenual cingulate cortex (SGCC) in a sample of captive chimpanzees. In humans, activity in the SGCC is linked to emotional responses (Damasio, Tranel, & Damasio, 1990; Liotti et al., 2000). Further, gray matter (GM) volume in the SGCC in humans has

been found to differentially associate with neuroticism by sex, with a positive association emerging between SGCC GM volume and neuroticism in females and a negative association emerging in males. Blatchley and Hopkins (2010) found PGM in chimpanzees to be associated with Dominance (i.e., low neuroticism) and Conscientiousness in sex-specific ways. Surprisingly, sex-specific associations, however, were inconsistent with findings in humans. Specifically, whereas PGM was positively associated with Dominance and Conscientiousness in males, no associations emerged between personality and PGM in females. Further, personality was not found to associate with asymmetry in either male or female chimpanzees for any trait. Although not entirely consistent with findings in humans, results support models of forebrain involvement in the neurobiological foundation of personality.

The frontal cortex (FC) is likely a particularly promising region as it is an area of the brain subserving functions known to be highly developed in both humans and great apes, and previously found to associate with human personality. For example, Extraversion has been found to associate with grey matter volume of the orbitofrontal cortex (e.g., DeYoung et al., 2010; Rauch et al., 2005) while Neuroticism, Agreeableness, and Conscientiousness associate with volume in the medial frontal gyrus; Conscientiousness also associates with inferior frontal gyrus volume (DeYoung et al., 2010). Extending these previous findings supporting the role of the frontal cortex in the explanation of personality variation in both humans (e.g., DeYoung, 2010; DeYoung et al., 2010; Rauch et al., 2005; Nostro, Muller, Reid, & Eickhoff, 2017) and chimpanzees (e.g., Blatchley & Hopkins, 2010), Latzman and colleagues (2015b) investigated associations between personality traits and GM volume and asymmetry of various FC regions. Frontal cortex GM volume was found to be associated with Big Five personality -- after statistically controlling for age and sex, Dominance, Openness, and Extraversion associated with FC GM volume. Given that Extraversion and Dominance (i.e., low neuroticism) are the two most affectively-based traits, the correlation with average GM volume potentially reflects the control of emotions in the service of goal-oriented behavior. When individual regions were examined, Extraversion and Openness were found to be associated with GM volume of the anterior cingulate cortex and Openness was found to be associated with lower mesial prefrontal cortex volume (at a trend level). These results suggest that in addition to self-regulatory behaviors and emotional control, the anterior cingulate cortex may also be important for the control of appetitive, approach-oriented, dispositional traits consistent with the trait Extraversion. It may be that the anterior cingulate cortex is particularly important for regulating approach-oriented behavior and control of positive emotions. When asymmetries where considered, Dominance and Reactivity/Unpredictability were found to associate with greater rightward asymmetries in the mesial prefrontal cortex and Dominance was also associated with greater leftward asymmetry in the anterior cingulate cortex. With regard to the former, these findings are consistent with previous findings among humans--rightward anterior cingulate cortex asymmetry has been found to be correlated with Harm Avoidance (Pujol et al., 2009), a trait dimension negatively correlated with Neuroticism (De Fruyt et al., 2000).

Taken together, results of the few emerging studies to date on the neural foundations of personality in chimpanzees provide support for the neuroanatomical basis of personality, particularly within the frontal cortex. Results suggest a brain-based explanation for broad personality traits, potentially indicating the evolutionary nature and conservation across species of general dispositions. Such findings are critically important in advancing our understanding of the neural foundation of human personality given the information these results provide for our comprehension of the evolution of the human brain and associated dispositions and behaviors (Rilling, 2014). Indeed, similar to findings in humans (Allen & DeYoung, 2017; DeYoung, 2010), our results confirm the importance of neuroscientific approaches to the study of basic dispositions (i.e., personality) and suggest that many of these associations are comparable in chimpanzees.

Elucidating Foundations of Personality Pathology though Chimpanzee Personality Research: Psychopathic Personality

Personality pathology can be conceptualized as a configuration of (personality) traits that differ from normality in degree rather than kind and result in significant impairment to oneself or others. Thus, understanding the neurobiological and evolutionary basis of personality, the pathophysiology underlying personality pathology can be better elucidated. One example of the utility of chimpanzee models for elucidating the neurobiological foundations of personality pathology is the recent development of a chimpanzee model of psychopathic personality (psychopathy) dimensions.

Psychopathic personality (psychopathy) entails a severe disturbance in behavioral control, social relations, and emotional experience concealed by an outward appearance of normalcy. Psychopathy is a multi-faceted construct (e.g., Lilienfeld, Watts, Smith, Berg, & Latzman, 2015; Patrick, Fowles, & Krueger, 2009) that is not exclusive to criminal populations (e.g., Lykken, 1995; Schneider, 1958; Skeem & Cooke, 2010), although traditionally studied, until relatively recently, predominantly in adult forensic samples. Researchers have recently, though, begun to coalesce around an understanding that psychopathic tendencies are grounded in basic biobehavioral dispositions that vary continuously within the human population and, more recently, in other species (i.e., chimpanzees) as well. Consistent with this conceptualization, recent theoretical and empirical work has sought to more accurately capture the dimensions of the construct (Patrick, 2006), through the elucidation of its component traits (e.g., Lilienfeld & Widows, 2005; Marcus, Fulton, & Edens, 2013; Patrick, Fowles, & Krueger, 2009; Poythress & Hall, 2011). Developed for this purpose, the triarchic model (Patrick et al., 2009) characterizes psychopathy as a configuration of three dimensional trait constructs with distinct biological referents: boldness, meanness, and disinhibition. Disinhibition and meanness (callous-aggression) are anchor dimensions of the externalizing spectrum of psychopathology (Krueger, Markon, Patrick, Benning, & Kramer, 2007), whereas boldness reflects more adaptive aspects of psychopathy (e.g., social efficacy, stress immunity, venturesomeness) that can be viewed in turn as facets of fear/fearlessness (Kramer, Patrick, Krueger, & Gasperi, 2012).

Within this framework, recent investigation of these dispositional dimensions of psychopathy has been extended to our closest living relatives, chimpanzees (Latzman et al., 2016a, 2017a, 2017b), providing a basis for comparative research on their behavioral and neurobiological aspects. Specifically, extending the human literature on the triarchic model, Latzman and colleagues (2016a) developed a chimpanzee operationalization of psychopathic personality organized around the triarchic conceptualization. Specifically, drawing on caretaker-rated items from an existing primate personality instrument, Latzman et al. used a consensus rating approach to formulate scale measures of the three triarchic model constructs for use with chimpanzees. These Chimpanzee Triarchic (CHMP-Tri) scales were then validated both with regard to their translational relevance to humans and their associations with performance on behavioral tasks. Importantly, scales indexing boldness and disinhibition showed expected differential associations with task-performance measures of impulsive and venturesome tendencies, respectively—indicating convergence with findings from the human literature (Patrick & Drislane, 2015). Results from this work indicate that the triarchic model of psychopathy can be operationalized effectively in chimpanzees, an animal species uniquely well-suited for neurobiological investigations of individual variation in broad, transdiagnostic traits (Latzman, Young, & Hopkins, 2016b).

Using the CHMP-Tri model as the basis for further research aimed at uncovering the neurobiological etiology of psychopathy, Latzman and colleagues (2017a) recently investigated the genetic and environmental contributions to the triarchic psychopathy (CHMP-Tri) dimensions. Further, genetic and environmental correlations among individual psychopathy subdimensions were examined, as well as the heritability of a

single extracted psychopathy factor. Also, similar to previous studies on broad personality traits described above, the role of differential early rearing (i.e., mother- versus non-mother, nursery rearing) on the contribution of genetic influences to measured psychopathic tendencies was examined. Consistent with findings in humans (Farrington, 2006; Larsson, Andershed, & Lichtenstein, 2006; Tuvblad, Wang, Bezdjian, Raine, & Baker, 2016), results indicated both genetic and environmental contributions to individual variability in psychopathic tendencies. When examined separately by early rearing background, consistent with previous findings for hierarchical personality dimensions (Latzman et al., 2015a), the heritability of psychopathy dimensions varied by early social learning experiences: Whereas all three triarchic dimensions showed significant heritability among mother-reared participants, heritability was not evident for any dimension in the nursery-reared subsample. Additionally, examination of genetic correlations among the three dimensions for the mother-reared participants revealed a substantial proportion of shared genetic influence in scores for Disinhibition and Meanness, but no significant genetic correlation for Boldness with either of these dimensions. Lastly, scores on the three CHMP-Tri scales were found to load significantly on a general psychopathy factor in the mother-reared apes, which was found to be appreciably heritable.

Although recent findings suggest a strong genetic contribution to individual variation in psychopathic personality dimensions in both chimpanzees and humans, little is known concerning specific genes that might explain this heritability. Latzman, Schapiro, and Hopkins (2017b) thus recently investigated associations between CHMP-Tri scales and AVPR1A, described in more detail earlier, a particularly promising gene known to associate with a range of psychopathy-relevant social behaviors. Among chimpanzees raised by their biological mothers, AVPR1A was found to uniquely explain variability in disinhibition and in sex-specific ways for boldness and a total psychopathy score; however, in contrast, no significant associations were found between AVPR1A and any of the triarchic psychopathy dimensions in chimpanzees raised the first three years of life in a human nursery. Thus, when considered in its entirety, results suggest an important contributory influence of vasopressin genotype variation in the explanation of the development of psychopathy under some but not all early rearing conditions.

All told, initial investigations of neurobiological and evolutionary foundations of personality pathology suggest that basic biobehavioral dispositional dimensions underlying personality pathology can be appropriately assessed in chimpanzees. More specifically, this work further points to contributions of both genetic and environmental influences to psychopathic tendencies, with an important role for a specific environmental factor—early rearing experience—in affecting relative contributions of the two. This line of research provides compelling evidence that psychopathic tendencies, and likely personality pathology more broadly, are rooted in basic, evolutionarily-meaningful dispositions (Fowles & Dindo, 2009; Patrick et al., 2009; Patrick & Drislane, 2015; Skeem et al., 2011), and provide support for a primate-translational operationalization of key neurobehavioral constructs relevant both to psychopathy and to broader forms of psychopathology.

National Institutes of Mental Health's Research Domain Criteria (RDoC) Initiative: Importance of Considering a Primate-Translational Component

A notable feature of the dimensional dispositional constructs investigated in the research reviewed above is that they can be framed explicitly in neurobiological terms. Considering personality dimensions in terms of neurobehavioral dispositions is timely, given the National Institute of Mental Health's RDoC initiative (Insel et al., 2010; Kozak & Cuthbert, 2016), which aims to elucidate the neurobiological bases of mental illness and reframe conceptions of psychopathology around constructs with specific brain referents. The RDoC research

framework specifies biobehavioral constructs, grouped within major domains of functioning, as explanatory referents for understanding clinical problems—and encourages investigation of these constructs using measures from multiple assessment domains ('units of analysis'). Clear counterparts to both the basic structure of personality, as well as the triarchic model dimensions, exist within the RDoC framework. For example, Big Three disinhibition links to the Cognitive Systems domain; negative emotionality and boldness (reversed) links to the Negative Valence Systems domain; and positive emotionality links to Positive Valence Systems domain. Dimensional personality constructs can thus be viewed as trait-dispositional counterparts to these RDoC constructs (Yancey, Venables, & Patrick, 2016). Taken together with a growing body of research (i.e., Latzman et al., 2016b), the value of chimpanzee personality research is clear, highlighting the importance of primate-translational operationalizations of specific domains and constructs within the RDoC framework important to multiple forms of psychopathology (Latzman & Hopkins, 2016).

Benefits to Animal Welfare

Importantly, chimpanzee personality research does not only provide important insights and implications as a result of its translational value to humans but is also critically important for improving the welfare of chimpanzees. Chimpanzees vary in their responses to experiences they may encounter in captive environments, and, as a result of this variability, the degree of well-being experienced by individuals is not uniform (King, Weiss, & Farmer, 2005; Weiss et al., 2002, 2007). The assessment and consideration of individual variation in personality can thus be useful in providing critical information concerning subjective experiences, individual tendencies and dispositions, and can help to guide important management decisions relevant to the welfare of captive animals.

A growing literature has documented the importance of and implications for personality for breeding-, management-, and welfare-related behaviors of captive animals. For example, one of the most potentially important implications that can be drawn from the chimpanzee personality literature relates to social housing and relocation of apes. It is clear that individuals within a social group can affect social compatibility, as well as the stability and success of that group. Such considerations may be particularly important as the National Institutes of Health attempts to "retire" their chimpanzees to locations and accommodations unfamiliar to these apes, most of which have only known their current living accommodations. Individual variation in personality may also influence the effectiveness and quality of care the chimpanzee experiences. Highlighting the importance of considering personality in animal welfare settings, Reamer et al. (2014) found success in training for blood glucose testing, a critical procedure with captive chimpanzees with Type 2 diabetes, to associate with variation in personality. The importance of considering individual variation in apes' responses across an array of animal welfare contexts is clear (Hopkins & Latzman, 2017).

Roadblocks and Limitations

Despite recent decisions by the National Institutes of Health (NIH, 2011) to scale back most research involving captive chimpanzees, all research reviewed above fits clearly within the ethical framework of scientifically justifiable research with chimpanzees as outlined by the Institute of Medicine (IOM; Altevogt, Pankevich, Shelton-Davenport, & Kahn, 2011). Specifically, NIH has not only made the decision to "retire" all NIH-owned chimpanzees (National Institutes of Health, 2015), but also to significantly limit the types of research with captive chimpanzees that NIH will fund and allow. Specifically, NIH has decided to limit even the most minimally invasive procedures (e.g., magnetic resonance imaging [MRI] scans). Unfortunately, these

decisions are inconsistent with the IOM's (Altevogt et al., 2011) report on the value and need of chimpanzees to biomedical and behavioral research as well as NIH's own working group (National Institutes of Health, 2011), both of which highlight the unique value of chimpanzee research to advancing our understanding of human conditions. In fact, some of this work was singled out in the IOM report as being highly translational and of the highest ethical standards. Potentially most notable, for procedures such as MRI imaging, the chimpanzees are trained to voluntarily present for a shot for the anesthesia. The scans are collected at the same time individuals are immobilized for their annual veterinary exam, an approach that was implemented and followed long before the IOM recommended this as a standard procedure. These recent decisions will result in lost opportunities for advancing our understanding of the nature, causes, mechanisms, and treatments of human mental health (Latzman & Hopkins, 2016).

Additionally, NIH owns and currently supports more than 400 chimpanzees currently residing in research and sanctuary settings in the United States. It seems both absurd and wasteful for NIH to continue to financially support these apes, and yet limit their use in the types of non-invasive research projects described above, particularly when the scientific advancements and benefits that might come from these efforts are of significant translational value. Nonetheless, NIH funds have already been spent to establish the chimpanzee genome (Mikkelsen et al., 2005), and the National Chimpanzee Brain Resource (NCBR; http://www.chimpanzeebrain.org), important scientific resources that can be used, in conjunction with multi-modal assessment of chimpanzee dispositional traits, for the type of research reviewed herein. The NCBR offers high-resolution structural Magnetic Resonance Imaging (MRI) as well as Diffusion-Tensor Imaging (DTI) scans of chimpanzees, in addition to fixed specimens and histologically-prepared sections of chimpanzee brains collected postmortem. These resources allow for multi-faceted investigations of the structure and function of the human brain through a comparative approach. In conjunction with multi-modal assessments of chimpanzee dispositional traits, these resources provide invaluable access to the study of neurobiological foundations of behavior. Further, the chimpanzee genome would allow for more feasible sequencing of candidate genes of personality in addition to AVPR1a. In ways consistent with the RDoC Initiative, investigations situated at the intersection of these various resources provide for an unmatched opportunity to identify neurogenomic processes with strong translational value.

Conclusions

A large and consistent empirical literature demonstrates the critical role of personality across a host of important outcomes for both humans and chimpanzees. While the exact nature of the relationship between personality and psychopathology (e.g., predisposition, spectrum, common cause, etc.) is unclear, the two constructs certainly share common biological origins. In sum, the current review highlights the importance of comparative-translational personality research with chimpanzees underscoring the notion of personality dimensions as biologically-based and evolutionarily-derived. The study of the neurobiology of behaviors and traits naturally expressed by humans and other species (i.e., neuroethology) represents an important research platform for accessing aspects of the biology of complex processes (Krystal, 2016). Chimpanzees represent an unparalleled animal model allowing for the novel and sophisticated research on processes underlying human mental health (Latzman & Hopkins, 2016). Indeed, in conjunction with findings from human studies, work of this kind can provide enormously valuable insights into the pathophysiology of mental illness in humans.

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References

Allen, T. A., & DeYoung, C. G. (2017). Personality neuroscience and the Five Factor Model. In T. A. Widiger (Ed.), *Oxford handbook of the Five Factor Model* (pp. 319–352). New York, NY: Oxford University Press.

Allport, G. W. (1961). *Pattern and growth in personality*. Oxford, England: Holt, Reinhart & Winston.

Altschul, D. M., King, J. E., Inoue-Murayama, M., Ross, S. R., & Weiss, A. (2016). Longevity and personality in captive chimpanzees (*Pan troglodytes*) *PeerJPreprints* 4:e1916v2

Altevogt, B. M, Pankevich, D. E, Shelton-Davenport, M. K., & Kahn, J. P. (2011). *Chimpanzees in biomedical and behavioral research: Assessing the necessity.* The National Academies Press: Washington, DC.

Anestis, S. F., Webster, T. H., Kamilar, J. M., Fontenot, M. B., Watts, W. P., & Bradley, B. J. (2014) *AVPR1A* variation in chimpanzees (*Pan troglodytes*): Population differences and association with behavioral style. *International Journal of Primatology, 35*, 305–324.

Bachner-Melman, R., Dina, C., Zohar, A. H., Constantini, N., Lerer, E., Hoch, S., ... Granot, R. (2005). AVPR1a and SLC6A4 gene polymorphisms are associated with creative dance performance. *PLOS Genetics*, *1*, e42.

Bard, K. A. (1994). Evolutionary roots of intuitive parenting: Maternal competence in chimpanzees. *Early Development and Parenting, 3,* 19–28.

Bard, K. A., Bakemen, R., Leavens, S. T., & Boysen, D. A. (2014). Emotional engagements predict and enhance social cognition in young chimpanzees. *Developmental Sciences, 17,* 682–696.

Bard, K. A., & Gardner, K. H. (1996). Influences on development in infant chimpanzees: Enculturation, temperament, and cognition. In A. E. Russon, K. A. Bard, S. T. Parker, A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 235–256). New York, NY: Cambridge University Press.

Bard, K. A., Platzman, K. A., Lester, B. M., & Suomi, S. J. (1992). Orientation to social and nonsocial stimuli in neonatal chimpanzees and humans. *Infant Behavior and Development, 15,* 43–56.

Barrett, C. E., Keebaugh, A. C., Ahern, T. H., Bass, C. E., Terwilliger, E. F., & Young, L. J. (2013). Variation in vasopressin receptor (Avpr1a) expression creates diversity in behaviors related to monogamy in prairie voles. *Hormones and Behavior*, *63*, 518–526.

Bennett, A. J., & Pierre, P. J. (Eds.). (2010). *Nonhuman primate research contributions to understanding genetic and environmental influences on phenotypic outcomes across development.* Oxford: John Wiley & Sons.

Beran, M. J., Savage-Rumbaugh, E. S., Pate, J. L. & Rumbaugh, D. M. (1999). Delay of gratification in chimpanzees (*Pan troglodytes*). *Developmental Psychobiology, 34,* 119–127.

Berg, J. M., Latzman, R. D., Bliwise, N. G., & Lilienfeld, S. O. (2015). Parsing the heterogeneity of impulsivity: A meta-analytic review of the behavioral implications of the UPPS for psychopathology. *Psychological Assessment, 27*, 1129–1146.

Blatchley, B. J., & Hopkins, W. D. (2010). Subgenual cingulate cortex and personality in chimpanzees *(Pan troglodytes*). *Cognitive, Affective, & Behavioral Neuroscience*, *10*, 414–421.

Bogg, T., & Roberts, B. W. (2004). Conscientiousness and health behaviors: A meta-analysis of the leading behavioral contributors to mortality. *Psychological Bulletin, 130,* 887–919.

Bouchard, T. J. (2004). Genetic influence on human psychological traits: A survey. *Current Directions in Psychological Science*, *13*, 148–151.

Bouchard, T. J., & McGue, M. (2003). Genetic and environmental influences on human psychological differences. *Journal of Neurobiology*, *54*, 4–45.

Burt, S. A. (2008). Gene-environment interactions and their impact on the development of personality traits. *Psychiatry, 7*, 507–510.

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*, *12*, 187–192.

Caspi, A., Houts, R. M., Belsky, S. J., Goldman-Mellor, S. J., Harrington, H., Israel, S., … Moffitt, T. E. (2014). The p factor: One general psychopathology factor in the structure of personality disorders?. *Clinical Psychology Science, 2*, 119–137.

Charmantier, A., & Garant, D. (2005). Environmental quality and evolutionary potential: Lessons from wild populations. *Proceedings of the Royal Society B: Biological Sciences, 272,* 1415–1425.

Clark, L. A. (2005). Temperament as a unifying basis for personality and psychopathology. *Journal of Abnormal Psychology, 114,* 505–521.

Clark, L. A., & Watson, D. (2008). Temperament: An organizing paradigm for trait psychology. In O. P. John, R. W. Robins, L. A. Pervin, O. P. John, R. W. Robins, & L. A. Pervin (Eds.), *Handbook of personality: Theory and research,* (3rd ed.) (pp. 265–286). New York, NY: Guilford Press.

Clark, L. A., & Watson, D. (1991). Tripartite model of anxiety and depression: psychometric evidence and taxonomic implications. *Journal of Abnormal Psychology, 3,* 316–336.

Mikkelsen, T. S., Hillier, L. W., Eichler, E. E., Zody, M. C., Jaffe, D. B., Yang, S., & ... Waterston, R. H. (2005). Initial sequence of the chimpanzee genome and comparison with the human genome. *Nature*, *437*, 69–87.

Damasio, A. R., Tranel, D., & Damasio, H. (1990). Individuals with sociopathic behavior caused by frontal damage fail to respond autonomically to social stimuli. *Behavioural Brain Research*, *41*, 81–94.

De Fruyt, F., Van De Wiele, L., & Van Heeringen, C. (2000). Cloninger's psychobiological model of temperament and character and the five-factor model of personality. *Personality and Individual Differences*, *29*, 441–452.

De Vries, G. J., Crenshaw, B. J., & Al - Shamma, H. A. (1992). Gonadal steriod modulation of vasopressin pathways. *Oxytocin in Maternal, Sexual and Social Behaviors, 652,* 387–396.

de Waal, F. B. M. (1996). Good natured: The origins of right and wrong in primates and other animals. Cambridge, MA: Harvard University Press.

de Waal, F. B. (2008). Putting the altruism back into altruism: The evolution of empathy. *Annual Review Psychology*, *59*, 279–300.

DeYoung, C. G. (2010). Personality neuroscience and the biology of traits. *Social and Personality Psychology Compass, 4,* 1165–1180.

DeYoung, C. G., Hirsh, J. B., Shane, M. S., Papademetris, X., Rajeevan, N., & Gray, J. R. (2010). Testing predictions from personality neuroscience: Brain structure and the Big Five. *Psychological Science, 21*, 820–828.

Diener, E., Oishi, S., & Lucas, R. E. (2003). Personality, culture, and subjective well-being: Emotional and cognitive evaluations of life. *Annual Review of Psychology, 54,* 403–425.

Digman, J. M. (1990). Personality structure: Emergence of the five-factor model. *Annual Review of Psychology, 41,* 417–440.

Digman, J. M. (1997). Higher-order factors of the Big Five. *Journal of Personality and Social Psychology*, *73*, 1246.

Donaldson, Z. R., & Young, L. J. (2008). Oxytocin, vasopressin, and the neurogenetics of sociality. *Science*, *322*, 900–904.

Durbin, E. C., & Hicks, B. M. (2014). Personality and psychopathology: A stagnant field in need of development. *European Journal of Personality, 28*, 362–386.

Farrington, D. P. (2006). Family background and psychopathy. In C. J. Patrick (Ed.), *Handbook of psychopathy* (pp. 229–250). New York, NY: Guilford Press.

Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (2013). Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top– down/bottom–up design. *American Journal of Primatology, 75,* 1042–1053.

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology, 72*, 653–671.

Fowles, D. C., & Dindo, L. (2009). Temperament and psychopathy: A dual-pathway model. *Current Directions in Psychological Science*, *18*, 179–183.

Gallup, G. G. (1970). Chimpanzees: self-recognition. *Science*, *167*, 86–87.

Gosling, S. D., & John, O. P. (1999). Personality dimensions in nonhuman animals: a cross-species review. *Current Directions in Psychological Science*, *8*, 69–75.

Gunnar, M. R., & Fisher, P. A. (2006). Bringing basic research on early experience and stress neurobiology to bear on preventive interventions for neglected and maltreated children. *Development and Psychopathology*, *18*, 651–677.

Hammock, E. A. D., Lim, M. M., Nair, H. P., & Young, L. J. (2005). Association of vasopressin 1a receptor levels with a regulatory microsatellite and behavior. *Genes, Brain, and Behavior, 4,* 289–301.

Hammock, E. A. D., & Young, L. J. (2005). Microsatellite instability generates diversity in brain and sociobehavioral traits. *Science, 308,* 1630–1634.

Hammock, E. A. D., & Young, L. J. (2006). Oxytocin, vasopressin and pair bonding: Implications for autism. *Philosophical Transactions of the Royal Society B, 361,* 2187–2198.

Herrelko, E. S., Vick, S. J., & Buchanan-Smith, H. (2012). Cognitive research in zoo-housed chimpanzees: Influence of personality and impact on welfare. *American Journal of Primatology, 74,* 828–840.

Hoffman, A. A., & Parsons, P. A. (1991). *Evolutionary genetics and environmental stress*. Oxford, UK: Oxford University Press.

Hong, K., Weiss, A., Morimura, N., Udono, T., Hayasaka, I., Humle, T., … Muyarama, M. (2011). Polymorphism of the Tryptophan Hydroxylase 2 (TPH2) gene is associated with chimpanzee neuroticism. *PLoS ONE, 6:*: e22144.

Hopkins, W. D., Donaldson, Z. R., & Young, L. J. (2012). A polymorphic indel containing the RS3 microsatellite in the 5' flanking region of the vasopressin V1a receptor gene is associated with chimpanzee (*Pan troglodytes*) personality. *Genes, Brain & Behavior, 11,* 552–558.

Hopkins, W. D., & Latzman, R. D. (2017). Future research with captive chimpanzees in the USA: Integrating scientific programs with behavioral management. In S. J. Schapiro (Ed.), *Handbook of primate behavioral management* (pp.139–156). Boca Raton, FL: CRC Press, Taylor & Francis Group, LLC.

Hopper, L. M., Price, S. A., Freeman, H. D., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success. *Animal Cognition, 17,* 835–847.

Insel, T., Cuthbert, B., Garvey, M., Heinssen, R., Pine, D. S., Quinn, K., . . . Wang, P. (2010). Research domain criteria (RDoC): Toward a new classification framework for research on mental disorders. *American Journal of Psychiatry, 167,* 748–751.

Jang, K. L., Livesley, W. J., & Vemon, P. A. (1996). Heritability of the big five personality dimensions and their facets: A twin study. *Journal of Personality, 64,* 577–592.

Jang, K. L., McCrae, R. R., Angleitner, A., Riemann, R., & Livesley, W. J. (1998). Heritability of facet-level traits in a cross-cultural twin sample: Support for a hierarchical model of personality. *Journal of Personality and Social Psychology, 76*, 1556–1565.

John, O. P., Naumann, L. P., & Soto, C. J. (2008). Paradigm shift to the integrative big five trait taxonomy: history, measurement, and conceptual issues. In O. P. John, R. W. Robins, & L. A. Pervin, (Eds.), *Handbook of personality: Theory and research. 3rd ed.* (pp. 7–38). New York, NY: Guilford Press.

King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality, 31,* 257–271.

King, J. E., Weiss, A., & Farmer, K. H. (2005). A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: zoological parks and an African sanctuary. *Journal of Personality*, *73*, 389–410.

King, J. E., Weiss, A., & Sisco, M. M. (2008). Aping humans: Age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *Journal of Comparative Psychology, 122*, 418–427.

Kotov, R., Gamez, W., Schmidt, F., & Watson, D. (2010). Linking "big" personality traits to anxiety, depressive, and substance use disorders: A meta-analysis. *Psychological Bulletin, 136*, 768–821.

Kozak, M. J., & Cuthbert, B. N. (2016). The NIMH research domain criteria initiative: Background, issues, and pragmatics. *Psychophysiology*, *53*, 286–297.

Kramer, M. D., Patrick, C. J., Krueger, R. F., & Gasperi, M. M. (2012). Delineating physiologic defensive reactivity in the domain of self-report: Phenotypic and etiologic structure of dispositional fear. *Psychological Medicine, 42,* 1305–1320.

Krueger, R. F., Markon, K. E., Patrick, C. J., Benning, S. D., & Kramer, M. D. (2007). Linking antisocial behavior, substance use, and personality: An integrative quantitative model of the adult externalizing spectrum. *Journal of Abnormal Psychology, 116,* 645–666.

Krueger, R.F., South, S., Johnson, W., & Iacono, W. (2008). The heritability of personality is not always 50%: Gene-environment interactions and correlations between personality and parenting. *Journal of Personality, 76*, 1485–1521.

Kruuk, L. E. (2004). Estimating genetic parameters in natural populations using the 'animal model'. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *359*, 873–890.

Krystal, J. H. (2016). Neuroethology as a translational strategy in the era of the NIMH Research Domain Criteria. *Psychophysiology, 53,* 364–366.
Larsson, H., Andershed, H., & Lichtenstein, P. (2006). A genetic factor explains most of the variation in the psychopathic personality. *Journal of Abnormal Psychology*, *115*, 221–230.
Latham, N. R., & Mason, G. J. (2008). Maternal deprivation and the development of stereotypic behaviour. *Applied Animal Behaviour Science*, *110*, 84–108.
Latzman, R. D., Freeman, H. J., Schapiro, S. J., & Hopkins, W. D. (2015a). The contribution of genetics and early rearing experiences to hierarchical personality dimensions in chimpanzees (*Pan troglodytes*). *Journal of Personality and Social Psychology, 109*, 889–900.
Latzman, R. D., Hecht, L. K., Freeman, H., Schapiro, S. J., & Hopkins, W. D. (2015b). Neuroanatomical correlates of personality in chimpanzees (*Pan troglodytes*): Associations between personality and frontal cortex. *NeuroImage, 123*, 63–71.
Latzman, R. D., Hopkins, W. D., Keebaugh, A. C., & Young, L. J. (2014). Personality in chimpanzees (*Pan troglodytes*): Exploring the hierarchical structure and associations with the vasopressin V1A receptor gene. *PLOS ONE*, 9, e95741.
Latzman, R. D., & Hopkins, W. D. (2016). Avoiding a lost opportunity for psychological medicine: Importance of chimpanzee research to the NIH portfolio. *Psychological Medicine, 46*, 2445–2447.
Latzman, R. D., Patrick, C. J., Freeman, H. J., Schapiro, S. J., & Hopkins, W. D. (2017a). Etiology of triarchic psychopathy dimensions in chimpanzees *(Pan troglodytes). Clinical Psychological Science, 5,* 341–354.
Latzman, R.D., Shapiro, S. J., & Hopkins, W. D. (2017b). Triarchic psychopathy dimensions in chimpanzees (Pan troglodytes): Investigating associations with genetic variation in the vasopressin receptor 1A gene. *Frontiers in Neuroscience, 11,* 407.
Latzman, R. D., & Shishido, Y. (2013). Personality psychology. In D. S. Dunn (Ed.), *Oxford bibliographies in psychology*. New York, NY: Oxford University Press.
Latzman, R. D., Sauvigné, K. C., & Hopkins, W. D. (2016a). Translating chimpanzee personality to humans: Investigating the transportability of chimpanzee-derived personality scales to humans. *American Journal of Primatology, 78*, 601–609.
Latzman, R. D., Vaidya, J. G., Clark, L. A., & Watson, D. (2011). Components of Disinhibition (vs. Constraint) differentially predict aggression and alcohol use. *European Journal of Personality, 25*, 477–486.
Latzman, R. D., Young, L. J., & Hopkins, W. D. (2016b). Displacement behaviors in chimpanzees (*Pan troglodytes*): A neurogenomics investigation of the RDoC Negative Valence Systems domain. *Psychophysiology, 53*, 355–363.
Lilienfeld, S. O., Watts, A. L., Smith, S. F., Berg, J. M., & Latzman, R. D. (2015). Psychopathy deconstructed and reconstructed Identifying and assembling the personality building blocks of Clercky's Chimera. *Journal of Personality, 83,* 593–610.
Lilienfeld, S. O., & Widows, M. R. (2005). *Professional manual for the Psychopathic Personality Inventory–Revised (PPI–R).* Lutz, FL: Psychological Assessment Resources.
Liotti, M., Mayberg, H. S., Brannan, S. K., McGinnis, S., Jerabek, P., & Fox, P. T. (2000). Differential limbic–cortical correlates of sadness and anxiety in healthy subjects: implications for affective disorders. *Biological Psychiatry*, *48*, 30–42.
Lykken, D. T. (1995). *The antisocial personalities.* Hillsdale, NJ: Erlbaum Associates, Inc.
Lyn, H. (2012). Apes and the evolution of language: Taking stock of 40 years of research. In J. Vonk & T. K. Shackelford (Eds.), *The Oxford handbook of comparative evolutionary psychology* (pp. 356–378). New York, NY: Oxford University Press.
Massen, J. J., & Koski, S. E. (2014). Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, *35*(1), 1–8.
Marcus, D. K., Fulton, J. J., & Edens, J. F. (2013). The two-factor model of psychopathic personality: Evidence from the Psychopathic Personality Inventory. *Personality Disorders: Theory, Research, and Treatment, 4,* 67–76.
Markon, K. E. (2009). Hierarchies in the structure of personality traits. *Social and Personality Psychology Compass*, *3*, 812–826.
Markon, K. E., Krueger, R. F., & Watson, D. (2005). Delineating the structure of normal and abnormal personality: An integrative hierarchical approach. *Journal of Personality and Social Psychology, 88,* 139–157.

Martin, J. E. (2002). Early life experiences: Activity levels and abnormal behaviors in resocialised chimpanzees. *Animal Welfare, 11*, 419–436.
Martin, J. E. (2005). The influence of rearing on personality ratings of captive chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science, 90*, 167–181.
McCrae, R. R., & Costa, P. T. (2008). A Five-Factor theory of personality. In O. P. John, R. W. Robins, & L. A. Pervin (Eds.), *Handbook of personality: Theory and research,* (3rd ed.) (pp. 159–181). New York, NY: Guilford Press.
Meyer-Lindenberg, A., Kolachana, B., Gold, B., Olsh, A., Nicodemus, K. K., Mattay, V., & ... Weinberger, D. R. (2009). Genetic variants in AVPR1A linked to autism predict amygdala activation and personality traits in healthy humans. *Molecular Psychiatry, 14*, 968–975.
Miller, J. D., & Lynam, D. (2001). Structural models of personality and their relation to antisocial behavior: A meta-analytic review. *Criminology, 39,* 765–798.
Moffitt, T. E., Caspi, A., & Rutter, M. (2006). Measured gene-environment interactions in psychopathology: Concepts, research strategies, and implications for research, intervention, and public understanding of genetics. *Perspectives on Psychological Science, 1,* 5–27.
Murray, L. E. (1998). The effects of group structure and rearing strategy on personality in chimpanzees (*Pan troglodytes*) at Chester, London ZSL and Twycross Zoos. *International Zoo Yearbook, 36,* 97–108.
National Institutes of Health. (2011). NIH research involving chimpanzees. Retrieved from http://grants.nih.gov/grants/guide/notice-files/NOT-OD-12-025.htm
National Institutes of Health. (2015). NIH will no longer support biomedical research on chimpanzees. Retrieved from https://www.nih.gov/about-nih/who-we-are/nih-director/statements/nih-will-no-longer-support-biomedical-research-chimpanzees.
Nostro, A. D., Muller, V. I., Reid, A. T., & Eickhoff, S. B. (2017). Correlations between personality and brain structure: A crucial role of gender. *Cerebral Cortex, 27,* 3698-3712.
Patrick, C. J. (2006). Back to the future: Cleckley as a guide to the next generation of psychopathy research. In C. J. Patrick (Ed.), *Handbook of psychopathy* (pp. 605–617). New York, NY: Guilford.
Patrick, C. J., & Drislane, L. E. (2015). Triarchic model of psychopathy: Origins, operationalizations, and observed linkages with personality and general psychopathology. *Journal of Personality*, *83*, 627–643.
Patrick, C. J., Fowles, D. C., & Krueger, R. F. (2009). Triarchic conceptualization of psychopathy: Developmental origins of disinhibition, boldness, and meanness. *Development and Psychopathology, 21*, 913–938.
Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality, 39,* 534–549.
Phillips, K. A., Bales, K. L., Capitanio, J. P., Conley, A., Czoty, P. W., 't Hart, B. A., ... Voytko, M. L. (2014). Why primate models matter. *American Journal of Primatology*, *76*, 801–827.
Povinelli, D. J., Reaux, J. E., Bierschwale, D. T., Allain, A. D., & Simon, B. B. (1997). Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cognitive Development, 12,* 327–365.
Poythress, N. G., & Hall, J. R. (2011). Psychopathy and impulsivity reconsidered. *Aggression and Violent Behavior, 16,* 120–134.
Pujol, J., Harrison, B. J., Ortiz, H., Deus, J., Soriano-Mas, C., López-Solà, M., ... & Cardoner, N. (2009). Influence of the fusiform gyrus on amygdala response to emotional faces in the non-clinical range of social anxiety. *Psychological Medicine, 39*, 1177–1187.
Rauch, S. L., Milad, M. R., Orr, S. P., Quinn, B. T., Fischl, B., & Pitman, R. K. (2005). Orbitofrontal thickness, retention of fear extinction, and extraversion. *NeuroReport, 16,* 1909–1912.
Reamer, L. A., Haller, R. L., Thiele, E. J., Freeman, H. D., Lambeth, S. P., & Schapiro, S. J. (2014). Factors affecting initial training success of blood glucose testing in captive chimpanzees *(Pan troglodytes*). *Zoo Biology, 33*, 212–220.
Rilling, J. K. (2014). Comparative primate neuroimaging: Insights into human brain evolution. *Trends in Cognitive Sciences*, *18*, 46–55.
Rutter, M. (2005). Environmentally mediated risks for psychopathology: Research strategies and findings. *Journal of the American Academy of Child and Adolescent Psychiatry, 44,* 3–18.
Schneider, K (1958). *Psychopathic personalities (M. W. Hamilton, Trans.).* Springfield, IL: Charles C. Thomas.
Skeem, J. L., & Cooke, D. J. (2010). Is criminal behavior a central component of psychopathy? Conceptual directions for resolving the debate. *Psychological Assessment, 22*, 433–445.

Skeem, J. L., Polaschek, D. L., Patrick, C. J., & Lilienfeld, S. O. (2011). Psychopathic personality: Bridging the gap between scientific evidence and public policy. *Psychological Science In The Public Interest*, *12*, 95–162.
Stockard, R. (1931). *The Physical basis of personality.* New York, NY*:* W. W. Norton.
Suomi, S. J. (2006). Risk, resilience, and gene × environment interactions in rhesus monkeys. *Annals of the New York Academy of Sciences*, *1094*, 52–62.
Suomi, S. J. (2011). Risk, resilience, and gene-environment interplay in primates. *Journal of the Canadian Academy of Child and Adolescent Psychiatry*, *20*, 289–297.
Tackett, J. L. (2006). Evaluating models of the personality – psychopathology relationship in children and adolescents. *Clinical Psychology Review, 26,* 584–599.
Tackett, J. L., Slobodskaya, H. R., Mar, R. A., Deal, J., Halverson, C. F., Baker, S. R., ... Besevegis, E. (2012). The hierarchical structure of childhood personality in five countries: Continuity from early childhood to early adolescence. *Journal of Personality*, *80*, 847–879.
Tellegen, A. (1985). Structures of mood and personality and their relevance to assessing anxiety, with an emphasis on self-report. In A. H. Tuma & J. D. Maser (Eds.), *Anxiety and the anxiety disorders* (pp. 681–706) . Erlbaum Associates, Inc.
Tuvblad, C., Wang, P., Bezdjian, S., Raine, A., & Baker, L. A. (2016). Psychopathic personality development from ages 9 to 18: Genes and environment. *Development and Psychopathology, 28,* 27–44.
Walum, H., Westberg, L., Henningsson, S., Neiderhiser, J. M., Reiss, D., Igl, W., ... Lichtenstein, P. (2008). Genetic variation in the vasopressin receptor 1a gene (AVPR1A) associates with pair-bonding behavior in humans. *Proceedings of the National Academy of Sciences*, *105*, 14153–14156.
Wassink, T. H., Piven, J., Vieland, V. J., Pietila, J., Goedken, R. J., Folstein, S. E., & Sheffield, V. C. (2004). Examination of AVPR1a as an autism susceptibility gene. *Molecular Psychiatry*, *9*, 968–972.
Watson, D., Clark, L. A., & Harkness, A. R. (1994). Structures of personality and their relevance to psychopathology. *Journal of Abnormal Psychology, 103*, 18–31.
Watson, D., Kotov, R., & Gamez, W. (2006). Basic dimensions of temperament in relation to personality and psychopathology. In R. F. Kruger & J. L. Tackett (Eds.), *Personality and psychopathology* (pp. 7–38). New York, NY: The Guildford Press.
Weiss, A., Inoue -Murayama, M., Hong, K. W., Inoue, E., Udono, T., Ochiai, T., ... King, J. E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology*, *71*, 283–292.
Weiss, A., King, J. E., & Enns, R. M. (2002). Subjective well-being is heritable and genetically correlated with dominance in chimpanzees (*Pan troglodytes*). *Journal of Personality and Social Psychology, 83,* 1141–1149.
Weiss, A., King, J. E., & Figueredo, A. J. (2000). The heritability of personality factors in chimpanzees (*Pan troglodytes*). *Behavior Genetics, 30,* 213–221.
Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: Zoological parks and yerkes national primate center. *American Journal of Primatology, 69*, 1–14.
Widiger, T. A. (2011). Personality and psychopathology. *World Psychiatry, 10*, 103–106.
Wilson, V. D., Weiss, A., Humle, T., Morimura, N., Udono, T., Idani, G., ... Inoue-Murayama, M. (2017). Chimpanzee personality and the arginine vasopressin receptor 1A genotype. *Behavior Genetics*, *47*, 215–226.
Winslow, J. T., Hastings, N., Carter, C. S., Harbaugh, C. R., & Insel, T. R. (1993). A role for central vasopressin in pair bonding in monogamous prairie voles. *Nature, 365,* 545–548.
Yancey, J. R., Venables, N. C., & Patrick, C. J. (2016). Psychoneurometric operationalization of threat sensitivity: Relations with clinical symptom and physiological response criteria. *Psychophysiology*, *53*, 393–405.
Yirmiya, N., Rosenberg, C., Levi, S., Salomon, S., Shulman, C., Nemanov, L., ... Ebstein, R. P. (2006). Association between the arginine vasopressin 1a receptor (AVPR1a) gene and autism in a family-based study: Mediation by socialization skills. *Molecular psychiatry*, *11*, 488–494.
Young, L. J., & Wang, Z. (2004). The neurobiology of pair bonding. *Nature Neuroscience, 7*, 1048–1054.
Zhang, X., Gainetdinov, R. R., Beaulieu, J. M., Sotnikova, T. D., Burch, L. H., Schwartz, D. A… Caron, M. G. (2005). Loss-of-function mutation in tryptophan hydroxylase-2 identified in unipolar major depression. *Neuron, 45*, 11–16.

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