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Original Article

Evolution, situational affordances, and the HEXACO model of personality☆

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ABSTRACT

The existence of individual differences in personality can be puzzling from an evolutionary perspective. This paper offers a general framework for addressing this puzzle by combining insights from evolutionary, situational, and personality perspectives. To arrive at this framework, we first discuss three key evolutionary models for explaining personality variation: (1) selective neutrality, (2) mutation–selection balance, and (3) balancing selection. Second, we review four models of personality: (1) the general factor of personality, (2) the big two, (3) the big five, and (4) the six-dimensional HEXACO model. Third, we use situational affordances and trait activation perspectives to offer an integrative model of HEXACO domain-specific situational affordances. Finally, we use these perspectives to provide 18 propositions about situation, trait, and outcome activation (STOA) mechanisms which may help explain the maintenance of individual differences in six dimensions of personality.

Individual differences lie at the heart of many evolutionary psychological theories and research programs. In laboratory settings, experimental evolutionary psychologists frequently find that individual differences interact with experimental manipulations—i.e., that particular ecological factors are associated with specific responses in certain individuals (e.g., Ainsworth & Maner, 2012; Maner, Gailliot, Rouby, & Miller, 2007; Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010; Park, Faulkner, & Schaller, 2003). Outside of the laboratory, individual differences in personality have been found both to affect the selection of environments that afford the expression of certain behaviors (e.g., Camperio Ciani & Capiluppi, 2011; Camperio Ciani, Capiluppi, Veronese, & Sartori, 2007; Chen, Burton, Greenberger, & Dmitrieva, 1999; Matthews & Butler, 2011), and to relate to fitness-relevant outcomes, including mortality, physical health, divorce rates, and occupational success (e.g., Booth-Kewley & Vickers, 1994; Ozer & Benet-Martinez, 2006; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007). Laboratory and field findings thus seem to suggest that individual differences in personality influence the situations people encounter and select, how people react to situations, and what outcomes people obtain. Given the potential implications of these findings for our understanding of the evolution of human behavior, it is unsurprising that scholars have called for integrations between evolutionary and personality perspectives (e.g., Buss, 1991, 2009; Buss & Hawley, 2010; MacDonald, 1995; Michalski & Shackelford, 2010; Nettle, 2006; Nettle & Penke, 2010; Penke, Denissen, & Miller, 2007). Although progress has been made in this respect (e.g., MacDonald, 1995; Nettle, 2006), the last 10 years have seen critical developments in not only personality but also in situational psychology—a topic highly relevant to our understanding of the evolution of personality. Hence, now is an opportune time to reappraise where we stand, what we know, and what questions remain.

Here, we provide an updated evolutionary view on personality by combining and integrating (1) a balancing selection account (Penke et al., 2007), (2) the HEXACO model of personality (Ashton, Lee, & De Vries, 2014), (3) domain-specific situational affordances (DSSA) based on the DIAMONDS situations model (Rauthmann et al., 2014; Reis, 2008), and (4) situation, trait, and outcome activation (STOA) mechanisms (e.g., Buss, 1987; Tett & Burnett, 2003). To accomplish this, we first review different perspectives on the origins of personality variation. We then provide an overview of prominent models of personality, including the general factor of personality model (Musek, 2007), the big two model (DeYoung, 2006), the big five model (Goldberg, 1990), and the six-factor HEXACO model (Ashton et al., 2014). Subsequently, we use a balancing selection account to inform our thinking about trade-offs between high and low levels of the HEXACO personality dimensions. Furthermore, we combine insights from balancing selection and

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the HEXACO model with recent work on situational affordances (Rauthmann et al., 2014; Sherman, Rauthmann, Brown, Serfass, & Jones, 2015) and situation, trait, and outcome activation mechanisms (Buss, 1987; Tett & Burnett, 2003), which allow us to more fully specify in what way different traits (i.e., personality factors) may yield functional benefits. We conclude by detailing a number of propositions implied by this proposed integration between evolutionary, personality, and situational perspectives.

1. The enigma of personality variation[i]

From an evolutionary perspective, the existence of individual differences in human personality can be enigmatic. All else being equal, natural selection tends to weed out variation that deviates from optimal adaptations to the local environment (Tooby & Cosmides, 1990). Variability in personality should thus result from either selective neutrality (i.e., the absence of optimal traits in a given environment) or mutation–selection balance (i.e., a high rate of mutation, offsetting selection pressures). Empirically, however, selective neutrality and mutation–selection balance appear to offer inadequate—or at least incomplete—explanations of personality variation. That is, the presence of fitness consequences (Ozer & Benet-Martinez, 2006; Roberts et al., 2007) and the preponderance of non-additive genetic variance (V_{NA}) relative to additive genetic variance (V_A) in personality traits (Penke et al., 2007; Verweij et al., 2012)[ii] seem to run counter to selective neutrality predictions. Similarly, small and often counterbalancing effects of mutations in coding single nucleotide polymorphisms (SNPs) on personality seem inconsistent with predictions based only on mutation–selection balance (e.g., McCrae, Scally, Terracciano, Abecasis, & Costa, 2010).

Balancing selection, which posits that genetic polymorphisms are maintained because the fitness pay-offs of resulting phenotypes vary across time and place, offers one potential solution to the personality puzzle (Penke et al., 2007). Two special cases of balancing selection include frequency-dependent selection (Buss, 2009; Dall, Houston, & McNamara, 2004; Nettle, 2006) and niche specialization (Bergmüller & Taborsky, 2007; Montiglio, Ferrari, & Réale, 2013). Under frequency-dependent selection, the fitness of alternate genotypes varies as a function of their prevalence in the population (Ayala & Campbell, 1974; Gangestad & Simpson, 1990; Wilson, 1998). In contrast, niche specialization (or: environmental heterogeneity) refers to conditions under which the fitness of alternate genotypes varies as a function of different pay-offs in different environments (Bergmüller & Taborsky, 2007; Montiglio et al., 2013; Penke et al., 2007). Whereas fitness pay-offs vary with the prevalence of alternate genotypes under frequency dependent selection, fitness pay-offs are not dependent on the prevalence of an alternate genotype under niche specialization, but rather result from the 'match' between the genotype and the environment. According to Penke et al. (2007), both niche specialization and frequency-dependent selection result in allele variants, which result in individual differences in neurophysiological mechanisms, which in turn—when exposed to environmental influences—result in characteristic reactions to different situations. In combination, these are referred to as personality traits.

This view of personality is not uncontested. Based on SNP data from a sample of more than 8,000 individuals from Finland and Australia, Verweij et al. (2012) concluded that personality variation reflects mutation–selection balance instead of balancing selection or selective neutrality. However, these findings are limited by the fact that, until now, it has been impossible to explain more than 21% of personality variation using SNP data (Penke & Jokela, 2016; Power & Pluess, 2015). Only a handful of SNPs have been found to relate to personality, and questions remain regarding the robustness and replicability of these findings (Plomin, 2013). That is, although most scholars agree that personality is heritable (e.g., Bouchard & Loehlin, 2001; Jang, McCrae, Angleitner, Riemann, & Livesley, 1998), the genetic loci and mechanisms influencing personality have yet to be identified for most if not all of heritable personality variation (what is known as the 'missing heritability' mystery; James, 2014). Hence, until it is possible to explain a greater amount of heritable personality, findings based on SNP data, including those reported by Verweij et al. (2012), have a limited ability to confirm or falsify selective neutrality, mutation–selection balance, or balancing selection accounts of personality.

With the current state of knowledge, it is reasonable to assume that each process contributes to the maintenance of personality variation. Selective neutrality maintains variability in personality by allowing for relatively high levels of mutation load due to an absence of optimal trait levels, whereas mutation–selection restricts some of this variability but still causes non-optimal trait levels to be maintained in the population (Ozaki et al., 2003). Balancing selection ensures that relatively large individual differences co-exist in populations because of fluctuating, time and place dependent, optimal trait levels (Penke et al., 2007). In line with others (e.g., Nettle, 2006), we believe that balancing selection probably best explains the origin and maintenance of personality. That is, variation in personality is likely to have arisen because situations differed in the extent to which they benefited individuals with different levels of traits. But what are these traits that vary across individuals? Different models categorize personality variation along different dimensions, and differences between models have important implications for how we understand the situations that might have given rise to personality variation. Next, then, we turn to this topic: the content of personality trait variation.

2. Competing models of personality

Around the time that Charles Darwin (1871) speculated about the origins of individual differences, Francis Galton (1884), his half-cousin, pondered their structure. Galton's (1884) "lexical" approach—counting the number and type of words used to express character—laid the foundation for modern personality research. Research using the lexical method is predicated on the lexical hypothesis (Goldberg, 1981), which is based on the following four assumptions: 1) individual differences that are important in human interactions have been encoded in language, 2) the more important an individual difference is, the more languages have one or more words for it, 3) sufficiently encompassing dictionaries of a language provide a repository of words related to individual differences, and 4) cross-cultural factor analytic studies of dictionary words (most often adjectives) that refer to individual differences in behaviors will reveal the most important dimensions of personality.

The lexical method has led to the emergence of the big five (B5; Goldberg, 1990) or five-factor model (FFM; Costa & McCrae, 1992), which comprises the dimensions extraversion, emotional stability/neuroticism (B5/FFM), agreeableness, conscientiousness, and intellect/openness to experience (B5/FFM). After the development of the big five, the field reached a virtual (if brief) consensus about the structure of personality—a consensus that resulted in an explosion of big five research from the 1990s onwards. However, the big five is contested by two streams of research. On the one hand, researchers have claimed that the big five are not at the apex of personality, but that either one higher-order factor, called the 'General Factor of Personality' (GFP; Musek, 2007) or two higher-order factors (DeYoung, 2006; Digman, 1997) underlie the big five personality dimensions. The GFP model has had an especially strong impact on the evolutionary psychology community, with researchers arguing that the GFP reflects variability in life history strategies, with one pole of the GFP corresponding with a slow (*K*-selected) life history strategy, and the other pole corresponding with a fast (*r*-selected) life history strategy (Figueredo & Rushton,

[i] For an exhaustive discussion of all possible mechanisms involved, see Arslan and Penke (2015).

[ii] V_A is directly passed on from parent to child, whereas V_{NA} is not. Consequently, V_A is much more likely to be affected by selection than V_{NA}.