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Chapter 17

Evolutionary Personality Psychology

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Introduction

Historically, psychology has been characterized by a dichotomy between branches that focus on human nature and those that focus on individual differences. Initial “grand theories” of personality, such as those advanced by Freud, Maslow, and others, were interested in universal psychological features. For Freud, the emphasis was on sexual and aggressive “instincts” and a universal sequence of psychosexual stages. For Maslow, the focus was on a hierarchy of universal psychological needs, from immediate physiological demands to “self-actualization.” Historically, personality psychology has been the primary branch that has aspired to such broad conceptualizations of human nature.

Over the past few decades, personality psychology has retreated from this grand goal. Most empirical research on personality deals with individual differences, not with human nature, let alone the links between the two (e.g., McCrae & John, 1992). By focusing largely on individual differences (Larsen & Buss, 2018), modern personality psychology has implicitly ceded the study of human nature to other branches such as social psychology. Personality psychology’s restricted focus on individual differences has led some to identify this as a defining feature of the field: “that branch of psychology which is concerned with... the ways in which individuals differ from one another” (Wiggins, 1979, p. 375). Grand theories of human nature that once characterized the field are now regarded primarily as historical relics. The central argument of this chapter is that personality psychology should reclaim its grand goals, and that an evolutionary framework will be central to achieving these goals.

This chapter is organized into three sections. First, we present a conceptual tool – the psychological mechanism – that dissolves the unnecessary (and often false)

dichotomy between “human nature” and “individual differences”. Second, we elucidate the multiple evolutionary processes that have operated on the human mind and the different types of products that these processes yield, which include both species-typical psychological phenomena and individual differences. Finally, we offer a series of suggestions for how these tools can be incorporated into personality research. In offering these recommendations, we hope this chapter contributes to personality psychology by moving toward a more comprehensive framework that uses an understanding of evolved psychological mechanisms to explain and predict the origins of individual differences.

Human Nature: Psychological Mechanisms

“Individual differences” and “human nature” are two major themes that have pervaded most efforts at grand personality theorizing (Buss, 1984). But what *does* human nature refer to? This term is often underspecified and used in ways that are incongruent with modern psychology. For Freud, human nature was defined by “instincts”. For Maslow, it was psychological “needs”. However, a central contribution of the cognitive revolution – which began over 50 years ago – is that the human mind can be best understood in terms of information-processing mechanisms.

In psychology, the term mechanism has been used in different ways, often sowing confusion. We use the term psychological mechanism to refer to an *information processor*. A three-component processor can be used to illustrate this concept. The first component of a psychological mechanism is that it takes cues from the environment as *input*. Second, it processes these inputs through algorithms, decision rules, or other computational procedures. Third, it produces physiological responses, psychological states, and/or manifest behavior as *output*.

This model captures two crucial concepts. First, it highlights that psychological states and manifest behavior are *not* psychological mechanisms themselves. Rather, they are potential *outputs* of psychological mechanisms. Second, the outputs of psychological mechanisms are not fixed, but rather are contingent on the inputs into the mechanisms. This makes psychological mechanisms flexible and highly sensitive to context (see Al-Shawaf, Lewis, Wehbe, & Buss, 2019).

The term “human nature” refers to characteristics of humans that are species-typical. If psychological states and behaviors are the *outputs* of psychological mechanisms, and the production of these outputs is contingent on environmental inputs – which vary both across individuals and within individuals across time and space – then psychological states and manifest behavior are not viable candidates for defining universal human nature. By contrast, the psychological mechanisms – the underlying information processors responsible for producing these outputs – *do* meet the criterion of being a shared characteristic common to all humans. To understand why these psychological mechanisms are species-typical, we turn to evolution by selection.

Evolved Psychological Mechanisms

The process of evolution by selection produces 1) morphological, physiological, and psychological characteristics that 2) interact with the environment in ways that 3) promoted the reproduction of the genes of the individuals who possessed those characteristics (Dawkins, 1982; Hamilton, 1964; Williams, 1966). These characteristics are called *adaptations*. Adaptations that are psychological in nature are called *evolved psychological mechanisms*.

An adaptation exists in the form that it does because it helped to solve a specific problem relevant to survival or reproduction recurrently through evolutionary history (see e.g., Lewis, Al-Shawaf, Conroy-Beam, Asao, & Buss, 2017 for a discussion of adaptive problems and heuristics for identifying them). Stated differently, *each adaptation was shaped by a specific survival- or reproduction-related problem*. Consequently, each adaptation is designed 1) to be activated by input signaling the adaptive problem, and 2) to produce output that typically helped solve that problem in ancestral environments. For example, our callus-producing adaptations are mechanisms that evolved to solve the problem of potential tissue damage caused by repeated friction (input) by producing additional cell layers (output) that protect underlying tissues.

Consider a psychological example. Witnessing one's romantic partner interacting intimately with a potential interloper activates the adaptation of evolved psychological mechanisms for sexual jealousy.

Imagine that you go to a party with your romantic partner. At one point, you see your partner seated very close to someone in a secluded corner of the room. The two are laughing and smiling, the other person's hand is on your partner's thigh, and your partner is touching the other person.

There are several cues to potential infidelity in this situation (Shackelford & Buss, 1997). Such infidelity would have been costly for both ancestral men and women. Consequently, selection has favored anti-infidelity adaptations in both sexes, including psychological adaptations that respond to infidelity cues (input) by motivating behaviors to solve this adaptive problem (output). Psychological *mechanisms* for producing sexual jealousy are a part of universal human nature.

The *outputs* of sexual jealousy mechanisms are a coordinated suite of cognitions, emotions, and behaviors. This can include gathering further information about the potential threat (Schützwohl, 2006); experiencing negative emotions in response to one's mate's interactions with potential interlopers (Buss, 1989, 2000); or aggressive responses to fend off these mating rivals (Buss, 1993, 2000; Buss, Larsen, Westen, & Semmelroth, 1992; Daly et al., 1982; Symons, 1979).

These defenses, however, “are hypothesized to lie dormant until they are activated by cues signaling that [the] adaptive problem is being confronted” (Buss & Shackelford, 1997, p. 348). That is, we should not expect the outputs of sexual jealousy mechanisms (e.g., behavior) unless the mechanisms are activated by input signaling the adaptive problem. This central property of psychological mechanisms – that their output is dependent on environmental input – has the potential to unify propositions of human nature with individual differences.

Universal human nature can produce individual differences.

Between-sex differences. Because both sexes faced the adaptive problem of mate retention, both sexes should be equipped with sexual jealousy mechanisms. Consistent with this, empirical evidence suggests that the sexes do not differ in the frequency or intensity of their jealousy (Buunk & Hupka, 1987). However, because fertilization occurs internally within women, only ancestral men faced the adaptive problem of “paternity uncertainty.” Since a man’s paternity certainty would have been threatened by his mate’s sexual infidelity, jealousy mechanisms in men are hypothesized to be particularly attuned to cues of their partner’s *sexual* infidelity. This threat did not exist for ancestral women, but they did face the risk of losing their mate’s commitment and support – a concern

predicted by their partner's emotional involvement with another woman. As a consequence, women's jealousy mechanisms are hypothesized to be particularly sensitive to cues of their partner's *emotional infidelity*.

A substantial body of evidence provides empirical support for these hypothesized sex differences (Buss & Haselton, 2005; Edlund & Sagarin, 2017). In forced-choice dilemmas, men report that they would experience greater distress in response to a partner's sexual infidelity than to a partner's emotional infidelity, whereas women report the opposite (Buss et al., 1992). These results have been replicated by independent researchers (Wiederman & Allgeier, 1993), using different methods (Buss et al., 1992), and across a large variety of western and non-western cultures (Buunk, Angleitner, Oubaid, & Buss, 1996). These sex differences have also been found using memory tests; physiological measures; and fMRI, which has documented different patterns of brain activation in response to sexual versus emotional infidelity (see Buss & Haselton, 2005; and Edlund & Sagarin, 2017 for summaries of this evidence).

Within-sex differences: individual differences among men. As discussed above, selection would have favored anti-infidelity adaptations in men. Considering the features of evolved mating strategies reveals why we might expect these universal psychological mechanisms to be differentially activated among men—and thereby produce individual differences.

Women's evolved mating strategies and infidelity threat. Ancestral women could have increased their reproductive success by both 1) producing high-quality offspring and 2) securing long-term investment from their mates. To produce offspring of high genetic quality, a woman had to copulate with a man of high genetic quality. However, desirable,

high-genetic-quality men could have increased their own reproductive success by short-term mating with multiple women. Consequently, some women would not have been able to reliably secure both “good genes” (Gangestad & Simpson, 2000) *and* long-term investment from the same man. On this basis, researchers have hypothesized that selection favored a female dual mating strategy of 1) long-term mating with men willing to commit and 2) seeking high genetic quality men for short-term sexual liaisons, or extra-pair copulations (EPCs; Gangestad & Simpson, 2000). Abundant empirical evidence is consistent with this idea of a dual mating strategy in women (e.g., Gangestad, Thornhill, & Garver-Apgar, 2005; but see Buss, Goetz, Duntley, Asao, & Conroy-Beam, 2017 for an alternative view).

An ancestral woman could have reaped genetic and other benefits from an EPC (see Greiling & Buss, 2000), but she would have faced substantial potential costs in doing so. These include potentially losing her long-term partner, as well as reputational damage and a decrease in her desirability as a long-term mate (Forstmeier, Martin, Bolund, Schielzeith, & Kempenaers, 2011). Selection therefore would have favored extra-pair mating mechanisms in women that were only activated under conditions in which the potential costs were outweighed by the potential benefits.

This cost-benefit calculus depends on the mate value of a woman’s long-term mate. A woman with a high-value mate would have gained little genetic benefit from an EPC; the “good genes” (Gangestad & Simpson, 2000) she could have obtained for her offspring from an affair would have been, at best, minimally higher in quality than those from her long-term mate. On the other hand, a woman mated to a low-value man could

have reaped substantial benefits by short-term mating with someone of higher genetic quality.

We should therefore expect extra-pair mating mechanisms to be activated more frequently among women with lower-value mates. In other words, throughout human evolution, the mates of low-value men would have been more likely to be unfaithful (see Cerdá-Flores et al., 1999). These differences between men in the likelihood of their partner's infidelity should result in differential activation of jealousy mechanisms, thereby producing individual differences in manifest sexual jealousy despite the universality of the mechanism itself.

Individual differences in the activation of men's sexual jealousy mechanisms. Infidelity itself is rarely directly observable, but it may be accompanied by numerous observable cues (Shackelford & Buss, 1997). If the mates of low-value men are more likely to have an affair, lower-value men should be exposed to a greater number of these cues. Being exposed to more of these cues should result in greater activation of mechanisms for jealousy – and consequently higher levels of jealous thoughts, emotional responses, and behavior. For these reasons, we should expect universal psychological mechanisms to produce individual differences in sexual jealousy among men. Specifically, we should expect to observe greater activation of jealousy among lower-value men.

The examples presented in this section show how human nature – universal jealousy-producing mechanisms – can produce individual differences in jealousy.

What about “Non-Evolved” Psychological Mechanisms?

So far, we have presented a model of psychological mechanisms (input→processing→output) and provided an illustration of how universal evolved mechanisms can produce individual differences. But what about *non-evolved* psychological mechanisms?

The concept of a non-evolved psychological mechanism is deeply problematic for the following reason. Selection is the only known process capable of producing the complex functional design observed in organisms (Williams, 1966). In other words, there is no known causal process – besides selection – capable of fashioning complex functional mechanisms in the body and mind.

For this reason alone, any psychological theory, including any theory of personality, must fit within a broader evolutionary framework. Stated differently, all psychological theories are implicitly or explicitly evolutionary (Symons, 1987). Although many psychologists do not specify their assumptions about the evolution of the mind, not one has ever proposed a psychological theory that has presumed some other causal process to be responsible for creating human nature.

And yet most personality psychologists have ignored evolution in their domains of study. Approaches to personality based on motives, which have obvious evolutionary relevance, historically have ignored evolution. Researchers studying the ‘self’ have created mini-theories such as self-verification theory, self-enhancement theory, and social identity theory in a theoretical vacuum, uninformed by the evolutionary processes that created the psychological mechanisms in question. Trait psychologists typically have the goal of identifying the statistical structure of individual differences, without an interest in how or why evolution might have shaped that particular structure of personality.

Description is often an important first step in science, but we suggest that the time is ripe for the scientific maturation of personality psychology. The remainder of this chapter will present a set of explanatory conceptual tools that an evolutionary framework can offer to personality psychology.

Evolutionary Personality Psychology: Selective and Non-Selective Models

Selection is only one of several evolutionary processes, but it is often regarded with special privilege, and for good reason: it is the only known causal process capable of producing complex functional design in organisms. Selection is therefore an indispensable tool for understanding the design of the human mind.

Nonetheless, we do not want the reader to conflate “selection” with “evolution”, which includes both selective and non-selective processes (see Al-Shawaf, Zreik, & Buss, 2018, for a discussion of this misunderstanding). These *non-selective evolutionary processes* are also important in understanding human personality. We therefore outline both selective and non-selective evolutionary models for individual differences in personality.

Selective Models: Directional and Balancing Selection

Evolutionary Model 1: Directional selection and universal psychological mechanisms.

Directional selection is the most familiar form of selection. It refers to a process in which one genetic variant that leads to greater reproduction (relative to extant competing variants) is passed down to succeeding generations in greater numbers than competing variants. Over many generations, the variant associated with greater reproduction increases in relative frequency in the population, displacing less successful variants. This process results in a shared genetic architecture: a universal human nature.

Psychological mechanisms are activated by cues ancestrally linked to the particular problem they were designed to solve. Because of this, they will only be activated in particular contexts. Crucially, this suggests that human nature will express itself not as invariant impulses, but rather in variable and context-dependent ways (see Al-Shawaf et al., 2019). Here, we outline several ways in which evolved psychological mechanisms can be activated differentially across individuals as a function of differing environmental inputs, thereby resulting in individual differences in personality.

I. Different inputs into universal mechanisms: early developmental calibration.

Humans with the same psychological mechanisms can experience different events in their development. These different events can serve as inputs into those shared mechanisms, channeling those individuals into alternative, developmentally stable strategies with different outputs.

For example, Belsky, Draper, and Steinberg (1991) propose that resource scarcity, parental unpredictability, or father absence during early development serve as key inputs into evolved psychological mechanisms that produce, as output, developmentally stable differences in mating strategy. According to Belsky and colleagues, the presence of a father in the home during the first five to seven years of life is a reliable cue that adult pair-bonds are enduring and levels of paternal investment are high. In such an environment, pursuing a committed, long-term mating strategy is more beneficial than a strategy of short-term mating. Accordingly, selection would have shaped psychological mechanisms to take the environmental cue of father presence as input, and to calibrate individuals' mating strategy accordingly. Research has borne out certain aspects of this hypothesis: individuals reared in father-present homes exhibit delayed sexual maturation,

later onset of sexual activity, a focus on long-term adult relationships, perceptions of others as trustworthy, expectations that relationships will endure, and heavy investment in a small number of children. Conversely, individuals reared in father-absent homes exhibit earlier sexual maturation, earlier sexual initiation, and frequent partner-switching; perceive others as untrustworthy and relationships as transitory; and pursue uncommitted sexual liaisons.

Belsky and colleagues did not explicitly use the concept of evolved psychological mechanisms, but all theories of environmental influence ultimately rest on a foundation of evolved psychological mechanisms, whether this is made explicit or remains implicit (Tooby & Cosmides, 1990). In Belsky and colleagues' case, the implicit psychological mechanisms are designed to take as input information about the reliability of paternal investment, and process that input to produce distinct mating strategies as output.

Some variants of this hypothesis have received only mixed empirical support, whereas others have been more clearly substantiated (see Del Giudice, 2009; Ellis, Schloemer, Tilley, & Butler, 2012; Mendle et al., 2009). Whatever the eventual empirical outcomes, this illustrative example highlights how selection can favor species-typical mechanisms that shunt individuals toward different adult strategies in response to critical inputs during development. In other words, shared mechanisms combined with differential developmental inputs can lead to individual differences in personality.

II. Different inputs into universal mechanisms: stable situational evocation. If individuals stably occupy different environments or different niches, evolved psychological mechanisms can produce what seem to be stable individual differences (Buss & Greiling, 1999). Imagine a man, Matthew, whose mate frequently flirts with

other men. Such frequent flirting may elicit frequent “mate poaching” attempts from rivals. Such events serve as inputs into jealousy mechanisms that produce suspicions, distress, and mate guarding as outputs. By contrast, Matthew’s brother, Michael, possesses the same psychological mechanism of jealousy, but is not exposed to any of these cues in his romantic relationship. Consequently, Michael does not exhibit these cognitive, affective, or behavioral facets of jealousy. Observers might be misled into concluding that Matthew has the “stable trait” of jealousy, whereas Michael does not. In fact, however, Matthew’s recurrent displays of jealousy – and the apparent trait difference between Matthew and Michael – are in fact attributable to Matthew’s recurrent exposure to jealousy-activating inputs (Buss & Greiling, 1999).

In short, stable occupancy of different environments or niches can produce stable individual differences that appear trait-like, even though their causal origin lies in a universal mechanism that is sensitive to environmental inputs.

III. Different inputs into universal mechanisms: the individual’s own phenotype. Any fitness-relevant feature of the environment can serve as an input into an evolved psychological mechanism (Tooby & Cosmides, 1990, p. 59). This can even include features of an individual’s own body. Indeed, selection should have favored the evolution of psychological mechanisms that 1) take as input aspects of the individual’s own phenotype and 2) produce output calibrated to those features. Evolved psychological mechanisms that regulate their output according to cues from the individual’s own phenotype are called *condition-dependent* psychological mechanisms.

Evolutionarily informed research on anger and aggression illustrates this idea. Because a mesomorphic man can more successfully pursue an aggressive strategy than

can an ectomorphic man (Sell, Tooby, & Cosmides, 2009), selection should have shaped aggression-producing mechanisms to be sensitive to (i.e., take as input) the individual's own body type (modified from Tooby & Cosmides, 1990, p. 58). Research on anger empirically substantiates this idea (Sell et al., 2009).

The heritability of personality differences. Many aspects of an individual's phenotype, including physical attractiveness and strength, are highly heritable (Rowe, Clapp, & Wallis, 1987; Silventoinen, Magnusson, Tynelius, Kaprio, & Rasmussen, 2008). This is important because on the surface, the notion of species-typical personality mechanisms seems to be inconsistent with the heritability of personality traits (Penke, Denissen, & Miller, 2007).

A number of scholars have interpreted the heritability of *manifest personality* as evidence for variation in the genes coding for the *mechanisms* responsible for producing personality (Nettle, 2006; Penke et al., 2007). However, personality models based on genetic polymorphisms leave the lion's share of individual differences in personality unexplained (e.g., see Westberg et al., 2009). Furthermore, it is unclear whether these genetic polymorphisms are associated with 1) differences in the psychological *mechanisms* that produce personality, or 2) differences in *inputs* into personality mechanisms. For example, the number of nucleotide repeats at the AR locus is associated with individual differences in attractiveness and strength, which predict individual differences in extraversion above and beyond genetic polymorphism (Lukaszewski & Roney, 2011). This relationship between attractiveness, physical formidability, and extraversion shows how species-typical psychological mechanisms can produce heritable personality outcomes. If the costs and benefits of extraversion vary as a function of

individuals' heritable attributes such as physical attractiveness and strength, and extraversion-producing mechanisms regulate their outputs based on these attributes, then we should expect extraversion to show up as heritable in behavior genetics studies – but only because it is dependent on physical attractiveness and strength, which are themselves heritable (see Tooby & Cosmides, 1990, for their seminal discussion of this concept, which they coined “reactive heritability”). In this case, heritable individual differences in physical formidability and attractiveness provide input into evolved psychological mechanisms that then produce, as output, different levels of extraversion levels in different individuals.

More generally, if the psychological mechanisms that produce personality take, as input, cues ancestrally linked to the costs and benefits of alternative personality strategies, and those costs and benefits vary as a function of individuals' heritable attributes (such as strength and physical attractiveness), then personality would show heritability in behavioral genetics studies *despite being the output of species-typical psychological mechanisms*. This example illustrates how universal mechanisms, combined with different inputs from individuals' own bodies, can produce 1) individual differences in personality that are 2) stable and 3) appear heritable.

Species-typical psychological mechanisms can produce individual differences that are consistent with the heritability of personality, but so can other evolutionary models. These include both selective and non-selective evolutionary models. We touch on both.

Balancing Selection

Balancing selection is a process in which selection maintains genetic variation because different environmental conditions favor different levels of a trait. There are

several forms of balancing selection, but the two most relevant forms for personality appear to be *environmental heterogeneity in fitness optima* and *frequency-dependent selection* (Penke et al., 2007).

Evolutionary Model 2: Balancing selection – fluctuating selection pressures over time and space. If environments vary, then selection can favor different optima in different environments. Consider variations in the abundance of food. Where (or when) food is scarce, selection might favor boldness and risk-taking that impel an individual to venture out into unknown territory to find food. Under such circumstances, risk-aversion and timidity may lead to starvation. By contrast, when food is abundant, exploratory behavior could needlessly put an individual at risk. If some environments favor boldness and others favor cautiousness, then this variation in selection pressures across environments can maintain both boldness and cautiousness. In short, environmental heterogeneity can maintain heritable individual differences in personality. This is a form of balancing selection.

Both empirical and simulation-based research support this idea. Camperio Ciani, Veronese, Capiluppi, & Sartori (2007) assessed the personality of people living on the mainland and a number of small islands in Italy. Families that were long-time inhabitants (at least 20 generations) of the islands scored lower on extraversion and openness to experience than those from the mainland. Such families also scored lower on extraversion and openness than recent immigrants to the islands. These findings are circumstantial, but they are consistent with the notion that different environments can select for different personality trait levels.

Molecular genetic studies provide further evidence for the idea that balancing selection can maintain heritability in human personality. Chen and colleagues (1999) hypothesized that the 7R allele of the DRD4 gene, which is associated with novelty-seeking (Munafo, Yalcin, Willis-Owen, & Flint, 2008), is favored by selection when people migrate to new environments or inhabit resource-rich environments. Chen et al. provided empirical support for this hypothesis by studying the migration patterns of 2,320 individuals from 39 groups. They showed that migratory populations had a far higher proportion of long-allele DRD4 genes than did sedentary populations. Moreover, independent research has shown that the 7R allele of the DRD4 gene is more advantageous among nomadic than settled populations (Eisenberg, Campbell, Gray, & Sorenson, 2008). This suggests that environmental heterogeneity can select for different optimum personality trait levels in different environments, leading to the evolutionary maintenance of heritable variation on that trait.

Evolutionary Model 3: Balancing selection – frequency-dependent selection.

Strictly speaking, *frequency-dependent selection* is not a second “type” of balancing selection, but rather is a particular case of balancing selection due to environmental heterogeneity. However, for conceptual clarity, and continuing the precedent in the literature, we treat it separately.

Frequency-dependent selection occurs when multiple strategies exist in a population, and the fitness of each strategy depends on its relative frequency in the population. The outcome of frequency-dependent selection is that multiple strategies are maintained in a population at particular frequencies relative to each other.

Biological sex is the most obvious example of frequency-dependent selection. As the ratio of males-to-females in a population increases, the average fitness of males decreases, and vice versa. That is, the approximately equal ratio of males to females in many species *is a result of frequency-dependent selection.*

Some researchers have suggested that frequency-dependent selection may explain psychopathy (see Mealey, 1995). The hallmarks of psychopathy include egocentrism, impulsivity, an inability to form lasting relationships, superficial social charm, and deficits in emotions such as love, shame, guilt, and empathy (Cleckley, 1982). Because over 95% of both men and women do *not* exhibit psychopathy, the “cheating” strategy of psychopathy has a large pool of resources to exploit: the typical human strategy of cooperation. As long as the frequency of psychopaths remains relatively low, psychopaths tend to experience relatively high fitness. In other words, frequency-dependent selection can maintain psychopathy in a population composed primarily of cooperators (Mealey, 1995).

There is some indirect evidence consistent with this hypothesis. First, psychopathy is moderately heritable (see Willerman, Loehlin, & Horn, 1992). Second, some psychopaths appear to pursue an exploitative short-term sexual strategy, which could be the primary route through which genes for psychopathy are maintained in the population (Rowe, 1995). Third, psychopathic men tend to be more sexually precocious, have sex with a larger number of women, have more children out of wedlock, and are more likely to separate from their wives (Rowe, 1995). Finally, psychopaths tend not to target their genetic relatives, suggesting that psychopathy may be an evolved strategy rather than a dysfunction or pathology (Krupp, Sewall, Lalumière, Sheriff, & Harris,

2012).

There are challenges to this hypothesis, including the questions of whether psychopathy represents a distinct category or a continuum (Baldwin, 1995; Eysenck, 1995), whether its frequency is sufficiently high to be maintained by frequency-dependent selection, and whether it represents a recently developed cluster in modern populations or an ancestral evolved strategy (Wilson, 1995). Despite these complications, Mealey's hypothesis nicely illustrates how frequency-dependent selection can maintain different heritable personality strategies in a population.

Non-Selective Models: Selective Neutrality and Mutation-Selection Balance

A widespread misconception is that “evolution” refers to one specific evolutionary process: directional selection. In reality, evolution consists of both selective and non-selective processes. Here, we discuss several non-selective evolutionary models for personality variation.

Typically, selection reduces genetic variation by purging less successful genetic variants from a population. However, selection is constantly accompanied by an influx of new mutations that continuously introduce variation into the population. Mutations can occur on any of the approximately 20,000 genes of the human genome or on any of the regulatory parts of the genome. Recent molecular genetic evidence suggests that approximately 70 new mutations are introduced per individual per generation (Keightley, 2012). This is how new genetic variation is constantly introduced into a population – through mutation.

Generally speaking, selection “uses up” heritable variation. That is, heritable variants that have greater replicative success tend to increase in frequency in the

population, displacing less successful genetic variants. However, there are constraints on selection's tendency to decrease genetic variation, including by winnowing out these less successful variants. These constraints include *selective neutrality* and *mutation-selection balance* (see Al-Shawaf & Zreik, 2018 for a discussion of additional constraints on selection).

Evolutionary Model 4: Selective neutrality. Some mutations neither disrupt nor improve an organism's overall functioning. Because these mutations have no impact on reproductive success, selection will neither systematically increase nor decrease their relative frequency in the population – they are *selectively neutral*.

Early evolutionary thinking identified selective neutrality as one candidate explanation for the heritability of personality differences (Tooby & Cosmides, 1990). However, selective neutrality with respect to personality traits carries the implausible assumption that different trait levels are unlinked to reproductive fitness. This is at odds with what is known about the relationships between personality and life outcomes (Nettle, 2006; Ozer & Benet-Martinez, 2006; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007). Many personality traits are systematically linked with fitness (Buss & Greiling, 1999; Nettle, 2006; Ozer & Benet-Martinez, 2006; Roberts et al., 2007), ranging from the link between conscientiousness and longevity (Deary, Weiss, & Batty, 2010) to the link between extraversion and number of sex partners (Nettle, 2005; Schmitt, 2004). The key point is that many personality traits have clear links to survival and reproductive success (e.g., Alvergne et al., 2010; Jokela, Hintsala, Hintsanen, & Keltikangas-Järvinen, 2010). Selective neutrality is therefore unlikely to be an important explanation for most heritable individual differences in personality.

Evolutionary Model 5: Mutation-selection balance. The models we have presented thus far are based on two different classes of mutations. The first class consists of mutations that are favored by selection. The second class consists of mutations that do not have an impact on reproductive success. There is a third and final class of mutations: those that are deleterious and therefore selected against. Despite their detrimental effects, selection is sometimes unable to work fast enough to eliminate these mutations from the population.

Recent evidence suggests that each human is born with approximately two new deleterious mutations (Keightley, 2012). Selection eventually weeds out harmful mutations (see Fu et al., 2012), but those that are only mildly harmful can take many generations to purge. These heritable mutations can therefore accumulate across generations despite their deleterious effects. Conservative estimates suggest that the average human carries at least 500 brain-disruptive mutations (Fay, Wyckoff, & Wu, 2001; Keller & Miller, 2006).

Nonetheless, people vary tremendously in the number of harmful mutations they carry, called their “mutation load” (Penke et al., 2007). Recent work suggests that individual differences in mutation load might explain the heritability of some individual differences. These include general intelligence (Penke et al., 2007; Deary, Penke, & Johnson, 2010) as well as schizophrenia and autism (Keller & Miller, 2006), although these hypotheses require further empirical study.

Molecular genetic evidence consistent with mutation-selection balance. The last few years have witnessed an explosion of molecular genetic findings relevant to evolutionary models of personality. The most significant change was from analyzing

individual genes or small sets of genomic markers to genome-wide approaches, where researchers investigate hundreds of thousands of genetic markers that are representative of common variation in the genome. More recently, there has been another shift to whole-genome sequencing of all the nucleotide letters in the DNA of individuals under study. While the existing evidence is not yet conclusive and a detailed review is beyond the scope of this chapter, we provide a brief summary of the current state of the evidence here.

The last decade has greatly altered our view of the molecular genetics associated with personality. Meta-analyses of individual genes have yielded null or weak results (Munafo & Flint, 2011). At the same time, sufficiently powered genome-wide association studies (GWAS) have shown that there are no common genetic variants that explain more than 1% of the genetic variance associated with broad traits like those of the Five Factor Model (e.g., Verweij et al., 2012). This means that either 1) there are thousands of genetic variants that each have very small effects on personality trait levels, or 2) there are many different, rare mutations that account for genetic variation in personality (Penke, 2011).

Recent research has attempted to estimate how much of the additive heritability of traits can be explained by all the common genetic variants used in a GWAS – regardless of how much individual variants explain. Interestingly, while this approach is able to explain almost all of the genetic variance in traits such as height (Yang et al., 2010), only a small percentage of the genetic variance in Cloninger's (Verweij et al., 2010) and Eysenck's (Vinkhuyzen et al., 2012) personality traits can be explained this way. Some

researchers (e.g., Verweij et al., 2012) take this as evidence for personality being under mutation-selection balance, an interpretation that we discuss in the following section.

A Comprehensive Framework: Integrating Selective and Non-Selective Models

We have presented five evolutionary models for the origins of variation in human personality: 1) directional selection, 2) balancing selection, 3) frequency-dependent selection, 4) selective neutrality, and 5) mutation-selection balance. A central impetus for presenting these models together in a single resource is that evolutionarily informed work to date has generally emphasized just one or a few of these models (e.g., Lewis, 2015). This narrow focus has enabled researchers to expand on individual models, but also appears to have translated into implicit and unnecessary competition between models.

This is problematic because these models are not necessarily mutually exclusive. Rather, they can offer complementary explanations, with each model accounting for a unique proportion of the variance on a given personality dimension. A central objective for personality researchers should be to integrate these distinct evolutionary models to maximize their combined ability to explain variation in human personality.

For researchers interested in pitting evolutionary models against one another, it is essential to use evidentiary criteria that can discriminate between these models. This is paramount because many criteria are consistent with *multiple* evolutionary models and therefore *not* capable of discriminating between alternative models. For example, Camperio Ciani and colleagues' finding that Italian islanders differ on major personality dimensions relative to Italian mainlanders is consistent with universal psychological mechanisms responding to different environmental inputs (Model 1) *and* with balancing selection favoring different personality levels in different environments (Model 2).

Similarly, mutation-selection balance (Model 5) and condition-dependent psychological adaptations (Model 1) lead to *identical* expected patterns of genetic variation. Consequently, molecular genetic and behavioral genetic data may be incapable of discriminating between these models.

To illustrate the issue of adjudicating between competing models, consider genetic polymorphism at the AR locus. Different alleles at the AR locus are associated with individual differences in both attractiveness and extraversion. If the AR gene is directly involved in the building of psychological mechanisms that calibrate extraversion levels, then we would not necessarily expect downstream products of the gene, such as attractiveness, to exhibit *independent* links to extraversion. Alternatively, if condition-dependent mechanisms calibrate extraversion levels according to attractiveness (Model 1), then we *would* expect links between attractiveness and extraversion over and above genetic polymorphism at the AR locus. Strongly consistent with this model, individual differences in attractiveness and strength predict extraversion levels independent of genetic polymorphism at the AR locus (Lukaszewski & Roney, 2011). This relationship between genetics, physical attractiveness, and extraversion emphasizes the point that a sophisticated evolutionary approach to personality requires an integrated understanding of selective and non-selective evolutionary processes.

Future Directions for Personality Psychology

The above example illustrates that, however appropriate a particular type of data (e.g., molecular genetic) might seem for understanding the evolutionary origins of variation in personality, such evidence is sometimes consistent with multiple distinct evolutionary models. In order to discriminate between these alternatives – a key future

direction for personality research - researchers need to employ evidentiary criteria capable of adjudicating between alternative models. Here, we make a few suggestions toward this goal.

Experimental Studies

The correlational nature of studies on condition-dependent models of personality does not enable researchers to draw conclusions about causation. But in order to adjudicate between condition-dependent models (Model 1) and models of mutation-selection balance (Model 5), it is necessary to design studies that can answer the question of whether the causal arrow runs from condition-linked input to personality output. A combination of experimental and longitudinal designs can help accomplish this.

Here, we outline a general experimental framework by which condition-dependent models can be tested. The overarching hypothesis of condition-dependent mechanisms is that they should output different personality trait levels as a function of differences in exposure to the adaptive problems the mechanism was designed to solve. Condition-linked differences in the frequency at which the relevant adaptive problem is faced should result in the hypothesized personality mechanisms producing differences in trait levels across individuals. Correlational studies (e.g., Lukaszewski, 2013) have shown precisely this pattern. However, in contexts that unambiguously indicate that the relevant adaptive problem is *not* being faced, the mechanisms should not produce that output – regardless of the individual’s condition. Similarly, in contexts that unambiguously indicate that the relevant adaptive problem *is* being faced, the personality mechanism should produce its output in all or most individuals – again regardless of the individual’s condition. Finally, it is primarily under conditions of uncertainty – which

characterize most natural settings – that personality outputs should track individuals' condition (see Lukaszewski & Roney, 2011).

Lewis (2013) tested these hypotheses. His research investigated the hypothesis that evolved psychological mechanisms calibrate individuals' neuroticism levels in response to cues to social exclusion (Denissen & Penke, 2008; Nettle, 2005, 2006). Precisely as expected if humans possess universal evolved neuroticism-calibrating adaptations, individuals exhibited lower levels of neuroticism when their inclusion in social relationships was certain, regardless of their condition. Individuals exhibited higher levels of neuroticism when their *exclusion* in social relationships was certain, irrespective of their condition. Finally, precisely as expected under a condition-dependent model, it was only in contexts that left an individual's social status unclear that participants' neuroticism varied as a function of their condition.

The “Power of the Situation” and the “Importance of the Individual” both lie in the Evolved Algorithm

This finding that the situation may mediate the links between an individual's condition and personality (Lewis, 2013) may also help to shed light on the computational architecture of evolved psychological mechanisms. For an exemplary illustration of the computational architecture of an evolved psychological mechanism, we examine Lieberman, Tooby, and Cosmides' “kinship estimator” (2003, 2007).

Lieberman and colleagues postulate that psychological adaptations to identify and direct altruism toward kin are designed to take, as input, cues recurrently linked to genetic relatedness in ancestral environments (Lieberman, Tooby, & Cosmides, 2003, 2007). This kinship-estimating mechanism 1) takes multiple cues as input (e.g., observing

a newborn nursing from one's own mother, Lieberman et al., 2003, 2007; facial resemblance, Lewis, 2011); 2) hierarchically treats these cues according to their ancestral predictive validity (i.e., their correlations with actual genetic relatedness); and 3) calibrates the outputs of kin-directed altruism and anti-incestuous sentiment according to the interaction between these cues (Lewis, 2011; Lieberman et al., 2003, 2007).

Generalizing this idea, selection would have favored psychological mechanisms that were designed to 1) take multiple cues as input, 2) hierarchically treat those cues, prioritizing those most strongly predictive of the relevant adaptive problem, and then 3) produce cognitive, affective, and behavioral solutions to that problem.

Lewis (2013) provides further empirical support for this model of evolved psychological mechanisms' computational architecture. Unequivocal indicators of an adaptive problem necessarily were the most valid cues that that adaptive problem was being faced. An individual's condition would have been a less predictive cue (e.g., see Kurzban & Leary, 2001). Personality-calibrating mechanisms should therefore be expected to adjust their output according to unequivocal cues when they are available – and only use condition-based cues when unequivocal cues are unavailable. Consonant with this, Lewis (2013) found that when unambiguous indicators of the relevant adaptive problem were present, individuals' personality trait levels were calibrated according to these cues, with condition-based cues having no effect. However, when unequivocal cues were *absent*, individuals' personality trait levels were calibrated according to condition-based cues. These findings highlight the information-processing structure of these psychological mechanisms, which has been a relatively neglected area of research. This gap is not trivial; the psychological and behavioral output of these mechanisms depends

not on the cues *per se*, but rather on the algorithms that the evolved mechanisms employ in the processing of these cues.

To offer a more complete investigation into human personality, future research would do well to include the following. First, research should identify the specific cues that would have been recurrently linked to specific adaptive problems, as these cues are good candidates for inputs into personality-calibrating mechanisms (Buss, 1991; Tooby & Cosmides, 1990). Second, future research should articulate the hypothesized computational architecture of the proposed mechanisms. Toward this goal, researchers should consider the predictive validities of the hypothesized input cues in indicating the adaptive problem. This may provide valuable insight into the mechanism's computational architecture, which ultimately will be indispensable for explaining and predicting the mechanisms' output – in this case, human personality.

Longitudinal Studies

Experimental studies can test for causal relationships between input cues and manifest personality output. However, single-session experimental studies can only test for ‘snapshot’ shifts in personality levels. Such data are inherently unable to speak to whether personality mechanisms calibrate individuals’ “trait” levels across the lifespan in response to changes in condition, social circumstances, or other environmental conditions (see Buss & Penke, 2014). Given the temporal stability of personality, longitudinal research assessing changes in personality over time will be necessary for assessing the heuristic value of different evolutionary models and for discriminating between them.

A key focus of future research should be longitudinal studies that track within-individual changes in the phenotypic characteristics or social environments hypothesized

to serve as input into personality-calibrating mechanisms. Doing this will enable researchers to assess whether these changes predict subsequent changes in individuals' personalities, permitting stronger tests of the hypothesis that personality mechanisms calibrate traits according to shifts in the cost-benefit tradeoffs of different personality strategies across the lifespan. This represents an important step toward the development of a more comprehensive and explanatory framework for variation in personality.

Conclusions

The field of personality psychology is currently characterized by a wealth of empirical research and a successful descriptive taxonomy. However, the time is ripe for the explanatory maturation of personality psychology. To this end, we suggest that the field of personality psychology cannot afford to ignore evolutionary psychology: It provides the only cogent meta-theory for the broader field of psychology and provides a set of conceptual tools and models for transforming personality psychology into a more powerful explanatory science.

Comprehensive theories of personality should aspire to include both a specification of human nature and an account of the major ways in which individuals differ. An evolutionary approach to personality psychology provides both 1) a framework for explaining human nature and individual differences and 2) a theoretically anchored bridge between them. Given this early stage in the development of evolutionary personality psychology, we make no pretense that we have arrived at, or even approximated, an ultimate theory of personality. However, since the evolutionary process is the only known process capable of producing complex organic mechanisms, all theories of human nature must ultimately be anchored in the principles of evolution.

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