Evolutionary perspectives on the mechanistic underpinnings of personality

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Abstract

Evolutionary theory is the organizing framework for the life sciences because of its unique value in deriving falsifiable predictions about the causal structure of organisms. This paper outlines the relationships of evolutionary principles to the study of phenotypic variation and defines two distinct paradigms for personality science. The first of these, dimensional cost-benefit analysis (DCBA), entails analyzing the reproductive cost-benefit tradeoffs along inductively derived personality dimensions (e.g., the big five) to derive predictions regarding adaptively-patterned variation in manifest trait levels. The second paradigm, ground-up adaptationism (GUA), requires building models of specific psychological mechanisms, from the ground-up, including their variable parameters that result in manifest behavioral variation. After evaluating the strengths and limitations of these paradigms, it is concluded that (1) inductively derived dimensions of person description should not serve as the field's explanatory targets; (2) GUA represents the most powerful available framework for elucidating the psychological mechanisms which comprise human nature and produce its diverse range of behavioral variants; and (3) the goals of adaptationist evolutionary psychology are the same as those guiding personality psychology's next era: to identify the mechanisms that comprise the mind, figure out how they work, and determine how they generate behavioral variation.

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The theory of evolution by natural selection provides a unifying explanation for the origins and functional dynamics of all organisms and the traits that comprise them (Dawkins, 1982; Darwin, 1859; Williams, 1966). Although few modern scientists would deny that humans are evolved beings, it has not been historically common to study our own species' behavior through the lens of evolutionary theory. *Evolutionary psychology* is a collective effort to correct this discontinuity by applying evolutionary and adaptationist principles to elucidate the neurocomputational mechanisms that regulate cognition, behavior, and culture in humans and other animals (Buss, 2012; 2015; Cosmides & Tooby, 2013; Tooby & Cosmides, 1990; 1992; 2015).

Personality psychology seeks to identify the phenotypic dimensions along which individuals differ from one another in persistent ways, as well as the causes and consequences of such trait-like variation (Funder, 2001; John et al., 2008a). Unlike scholars in many other social science fields, personality scientists have a long history of studying the biological and genetic bases of human behavioral traits (Bouchard & Loehlin, 2001; Eysenck, 1967; Gray, 1970). Even so, however, human personality researchers have not typically incorporated modern evolutionary and adaptationist principles into their causal models (Segal, 1993). Nor have they recognized that these principles are relevant to fundamental issues in their field, including the causes of manifest behavioral covariation, the interaction of person and situation variables, the regulation of within-person variation in behavioral states, the meaning and utility of lexical trait constructs, and the ontological status of the internal mechanisms that generate behavioral variation (Buss & Penke, 2015).

This paper explores how evolutionary approaches can facilitate—and have already facilitated—discoveries about the mechanistic underpinnings of manifest personality variation. First, it defines basic evolutionary psychological concepts, and characterizes the relationships between phenotypic variation and evolutionary processes. In the following section, it describes two distinct approaches to studying personality in evolutionary perspective: (1) dimensional cost-benefit analysis of inductively derived personality constructs; and (2) building models of human psychological adaptations from the ground-up, including their variable parameters that generate within- and between-person variation. It is concluded that the second of these approaches is the best way forward for the field, and that the goals of personality psychology are naturally allied with those of an adaptationist framework for elucidating the psychological mechanisms which comprise human nature and produce its diverse range of behavioral variants.

Evolution and phenotypic variation

Although Darwin's (1859) initial version of his theory of evolution by natural selection has undergone multiple rounds of revision and formalization (Dawkins, 1982; Huxley, 1942; Maynard Smith, 1982; Williams, 1966), it was essentially correct in its basic postulates. It is an elegant theory, in that it explains a wide range of phenomena – the origins and functional dynamics of all life forms – with a small set of principles (Tooby & Cosmides, 2015; van Shaik, 2016). At its core, the theory states that evolution by natural selection is the inevitable consequence of four ingredients:

- (1) A population of self-replicators.

- (2) Phenotypic variation among individuals in the population.
- (3) Heredity of phenotypic variation (i.e. transmission of traits from parents to offspring).
- (4) Differential reproduction that is correlated with inheritable phenotypic variation.

Given the co-existence of these four ingredients, populations will undergo evolutionary changes across reproductive generations that occur through a process of *natural selection*—differential rates of reproduction by alternative phenotypic variants. In this process, phenotypic variants that self-replicate at higher rates than alternative variants will come to predominate within populations, which can lead to corresponding changes in universal, species-typical architectures. Phenotypic variants are ‘selected for’ in this way because they cause the organisms in which they reside to interact with their environments in ways that, on average, promote their own representation in future generations more effectively than competing variants (which are ‘selected against’). It is through this process of natural selection that all non-randomly organized components of organisms came to be.

After Darwin’s time, it was recognized that the gene, instantiated as DNA, is the primary mechanism of particulate heredity, and that genetic mutations are the original source of inheritable phenotypic variation (Dawkins, 1982). These discoveries, in turn, were prerequisite for the eventual development of the gene-centered view of evolution: that the primary unit of natural selection is not the species, population, nor individual—but rather, the gene (Dawkins, 1982; Hamilton, 1964; Williams, 1966). Because genotypes at particular genetic loci, and the phenotypes they contingently encode, are usually inherited independently of those at other genetic loci, natural selection operates primarily at the level of the gene. In the gene-centered view of evolution, organisms are squishy robots that genes cooperatively build and operate for the purpose of their own self-replication (Dawkins, 1982). A gene can accomplish this by having effects on a phenotype that increase the reproduction either of the individual in which it resides or that of one’s genetic relatives, such as offspring, grandchildren, and siblings (Hamilton, 1964).

Like the genome, composed of many discrete genes, organisms are highly modular, composed of many individual traits or *adaptations*. An adaptation is a mechanism designed, via natural selection, to solve a specific *adaptive problem*; that is, a logistical challenge that reliably limited reproduction for the ancestors of a given species over long stretches of evolutionary time. For example, if part of an organism’s strategy is to move about, avoid predation, or forage for specific food items, it faces adaptive problems related to representing what objects are in its environment. The existence of such adaptive problems causes natural selection to favor the evolution of visual systems, which are bundles of adaptations designed for converting reflected light, via transduced neural signals, into computational representations of relevant physical objects that exist within an individual’s immediate surroundings (Marr, 1982). Most adaptations do not bear such an intuitively obvious relationship to adaptive problems as visual systems, but it must be true that each adaptation’s design features correspond to the structure of whichever adaptive problems caused their evolution via natural selection.

From an adaptationist standpoint, therefore, the primary goals of the scientist are to (1) define the adaptive problems likely faced by members of a species over their evolutionary history; (2) perform a task analysis of those adaptive problems to formulate hypotheses about which phenotypic mechanisms an organism would need to possess in order to solve those problems; and (3) test these hypotheses to determine whether there is evidence for the existence of design features that exhibit an improbably close functional match with the structure of the adaptive problem(s) in question (Buss, 2012; Lewis et al., 2017; Tooby & Cosmides, 2015; Williams, 1966; Roney, 2016). One can also proceed in the reverse direction: begin with an inspection of a phenotypic mechanism's properties in order to gain insight into the ancestrally recurrent adaptive problems they might be designed to solve (Krasnow & Delton, 2016; Lewis et al., 2017; Tooby & Cosmides, 2015).

By applying these adaptationist principles to derive precise and falsifiable predictions, it is possible in principle to discover and describe all of the mechanisms that together comprise the universal architecture of a given species. This is why evolutionary biological theory is the essential organizing framework for the life sciences, including the study of behavior in all non-human animals. As Theodosius Dobzhansky (1973) pithily put it, "Nothing in biology makes sense except in the light of evolution." By this, he meant that the causal structure of a phenotypic mechanism is likely to remain perpetually inscrutable unless scientists are guided by some idea of what the mechanism is for—*its evolved function*.

Evolutionary psychology

The endeavor of evolutionary psychology was borne of the realization that evolutionary and adaptationist principles should be as essential for the study of human behavior as they are for that of any other animal (Buss, 1989; Daly & Wilson, 1983; Symons, 1979; Tooby & Cosmides, 1990). From this meta-theoretical vantage point, human nature is conceptualized as a bundle of species-typical neurocomputational adaptations: psychological mechanisms designed to solve specific information-processing problems that recurrently limited reproduction for ancestral humans.

Research conducted from this perspective has reverse-engineered many psychological mechanisms whose design features exhibit a close functional match with the structure of specific adaptive problems faced by human ancestors. For example, the adaptive problem of detecting predators selected for mechanisms which constantly scan the visual field for ancestrally valid cues of agency, and direct attention in response to these cues (New et al., 2007); adaptive problems of avoiding exploitation in social exchange relationships selected for mechanisms designed to identify cheaters (in dyadic relationships) and free-riders (in collective actions), and to prevent these individuals from enjoying the benefits of cooperation (Cosmides et al., 2010; Delton et al., 2012; Krasnow et al., 2016); the adaptive problem of incest avoidance selected for mechanisms designed to estimate the genetic relatedness of the self to other individuals, and to inhibit sexual attraction to people estimated to be close relatives (Lieberman et al., 2007); the adaptive problem of pathogen avoidance selected for a suite of mechanisms designed to prevent and mitigate the costs of exposure to pathogens (Murray & Schaller, 2016; Tybur et al., 2009); the adaptive problem of avoiding ingestion of plant toxins selected for mechanisms designed to learn which local plants are edible via social observation (Wertz & Wynn, 2014); adaptive

problems related to the regulation of conflict escalation selected for mechanisms designed to accurately estimate others' physical formidability from visual and auditory cues (Sell et al., 2009a; 2010); adaptive problems related to coalitional conflict and cooperation selected for a suite of mechanisms for tracking alliances based on observable cues of coordination and conflict (Kurzban et al., 2003; Pietraszewski et al., 2014); the adaptive problem of maintaining long-term pair-bonds selected for motivations to implement "mate retention" tactics (Shackelford & Buss, 1997); and adaptive problems related to capturing benefits via social relationships crafted mechanisms that differentially value others on the basis of cues that would have ancestrally predicted their generation of net benefits as mates (Buss, 1989; Buss & Schmitt, 1993; Conroy-Beam & Buss, 2016; Lukaszewski & Roney, 2010), cooperative partners (Eisenbruch et al., 2016), coalition members (Delton & Robertson, 2012), warriors (Patton, 2000), and leaders (Lukaszewski et al., 2016). For detailed catalogues of recently discovered human psychological adaptations, readers are directed to broader reviews (e.g., Buss, 2012; 2015; Cosmides & Tooby, 2013; Tooby & Cosmides, 2015).

Deep vs. manifest structures of adaptations

Psychological adaptations can be described at two broad levels of analysis: *deep structure* and *manifest structure* (Tooby & Cosmides, 1990).

The *deep structure* of an adaptation is defined by its species-typical architecture, including its situational activating conditions and its contingent menu of psychological and behavioral outputs. For example, the emotion of shame has been characterized as an evolved neurocomputational program designed to limit the likelihood and costs of being socially devalued (Sznycer et al., 2012; 2016). Shame activates with the prospect or actuality of others learning negative (i.e. disvalued) information about an actor. Once activated, the shame system mobilizes a suite of possible responses aimed at preventing devaluation (e.g., hiding, destroying incriminating evidence) or, if devaluation occurs, limiting its extent and costs (e.g., signaling appeasement). This theory of shame's deep structure is supported by cross-cultural evidence for the universality of a remarkably strong relationship between the extent to which audiences disvalue various negative acts and traits in others, and the extent to which actors would feel shame if they took those acts or possessed those traits (Sznycer et al., 2016). That is, shame forecasts the magnitude of devaluation an audience would express in response to a given act or trait, and activates in proportion to this forecast. By doing so, the shame system avoids the twin errors of under-activation and over-activation.

The *manifest structure* of an adaptation, on the other hand, is defined by its current internal settings and range of potential phenotypic outputs (Tooby & Cosmides, 1990). The shame program, for example, is not activated at all times, and its activation thresholds, situational triggers, and specific phenotypic outputs vary contingently across individuals, contexts, and social ecologies (Sznycer et al., 2012). Given the costs of activating shame in the absence of threats to one's social value, Sznycer et al. (2012) hypothesized that an individual's shame proneness should be lawfully calibrated: Shame should be sensitive to the expected impact of devaluation on the individual given the circumstances of that individual. One factor that should modulate the cost of being devalued, and therefore the tendency of shame to be mobilized, is "relational mobility"—the ease with which new relationships can be formed in one's

ecology. The easier it is to form new relationships, the easier it is to make up for damaged relationships when one is devalued, and the lower the per-event cost of being devalued by an existing relationship. The shame system is therefore expected to modulate its activation based on cues of relational mobility: The higher the relational mobility, the less frequent or intense the shame response. As predicted, people in societies with low relational mobility (Japan) exhibited higher shame proneness than people in high-mobility societies (Britain; USA) – but this only pertained to shame experienced within existing relationships. Further supporting the theory that shame proneness should be regulated by vulnerability to the costs of social devaluation, within all three countries, individual differences in shame proneness were negatively predicted by socially valued personal characteristics (e.g., physical attractiveness; social connectedness). In sum, shame's manifest structure exhibits adaptively patterned variation across individuals and social ecologies.

The example of shame illustrates the inseparable relationship between the deep and manifest structures of an adaptation. Indeed, it is the deep (universal) structure of shame that specifies the contingencies according to which its (variable) manifest structure emerges within and between both individuals and populations. These considerations belie the common notion that there is any conflict whatsoever between the expectation of a universal psychological architecture and the existence of quantitative phenotypic variation.

Why phenotypic variation? The role of cost-benefit tradeoffs

Implicit in these considerations is the general solution to a problem of central theoretical importance for both evolutionary biology and personality science: Why would natural selection—which is fundamentally a winnowing process that favors the most successful variants—cause the maintenance of quantitative phenotypic variation within and between populations over evolutionary time? This is a question of *ultimate causation*; that is, of which selection pressures caused the evolution or maintenance of an adaptation's deep and manifest structures across reproductive generations.

The answer to this question lies in the ubiquity of tradeoffs between the costs and benefits of specific phenotypic outputs (Ashton & Lee, 2007; Buss, 2009; de Vries et al., 2016; Del Giudice et al., 2015; Lukaszewski & Roney, 2011; Manson & Fairbanks, 2015; Nettle, 2006; Penke et al., 2007; Tooby & Cosmides, 1990; 2015). To elaborate the example from above, activation of the shame program's motivational and behavioral outputs can be beneficial—in that it probabilistically prevents or mitigates the costs of being socially devalued (Sznycer et al., 2016). However, shame's activation also brings costs. The most basic of these is an opportunity cost: any time or energy spent feeling ashamed and formulating remedial actions cannot be allocated toward other functionally important objectives (Sznycer et al., 2012; 2016). Moreover, shame's outputs are counterproductive in relation to most other goals; for instance, shame might motivate actions, such as social withdrawal and signaling of submission, that inhibit the acquisition or maintenance of high social rank or important cooperative alliances. Thus, it is maladaptive to either over- or under-activate shame. This is why, as described above, shame possesses design features which serve to couple its activation with the forecasted threat (or actuality) of social devaluation, and set its activation thresholds in proportion to the perceived likelihood and costs of devaluation (as determined by, e.g., local social mobility and one's

personal characteristics; Sznycer et al., 2012). There is no single most adaptive level of (manifest) shame: the optimal level at a given time, in a given individual, or in a given social ecology, depends on the probabilistic cost-benefit tradeoffs entailed by shame's activation.

Proximate mechanisms to explain variation: Genetic polymorphism, developmental calibration, and immediate situational adjustment

The premise that quantitative variation in shame is adaptively patterned in relation to circumstances that predict its attendant cost-benefit tradeoffs—an explanation at the level of ultimate causation—is compatible with any mechanism of its *proximate causation*; that is, the causes of a given individual's dispositional or current level of manifest shame. At least three broad classes of proximate mechanisms can evolve to orchestrate functionally coordinated variation. Running from least to most ontogenetically fungible, these are: genetic polymorphism, developmental calibration, and immediate situational adjustment (Buss, 2009; Buss & Greiling, 1999; Penke, 2011; Tooby & Cosmides, 1990; 2015).

Genetic polymorphism

Heritable variation in manifest psychological outputs (i.e. personality) can be maintained across generations via a number of evolutionary selection regimes and related processes (see Buss, 2009; Gangestad, 2011; Penke et al., 2007; Penke & Jokela, 2016; Verweij et al., 2012; Zietsch, 2015). For example, if a population were subject to a social ecology characterized by low social mobility over many generations, natural selection could theoretically favor specific genetic variants that tend to promote higher dispositional shame proneness (Buss, 2009; Penke et al., 2007; Tooby & Cosmides, 1990). Under this regime of “fluctuating selection,” variation between populations, or fluctuations within populations over time, in levels of social mobility could maintain specific genetic polymorphisms underpinning heritable individual differences in manifest shame.

Heritable variation can also arise as a side effect of rare (i.e. low frequency) genotypes, which have effects on manifest psychological variation that is not adaptively patterned, but rather fundamentally noisy. Multiple distinct evolutionary processes can maintain rare genetic variants in populations (Tooby & Cosmides, 1990). The primary source of rare variants is “mutation-selection balance,” the process by which mildly deleterious mutations constantly introduce themselves into populations before they can be removed by selection (Penke et al., 2007; Penke & Jokela, 2016; Tooby & Cosmides, 1990). As a result, individuals differ in their overall load of mildly deleterious (i.e. disordering) genetic mutations. Because mutations are random genetic copying errors, their effects on a mechanism's operation, and its resulting psychological outputs, will tend to be noisy and undirected. For example, a given rare genetic variant would be similarly likely to have effects on neural endophenotypes that increase or decrease one's manifest shame proneness.

An important exception to the prediction that rare genetic variants will have directionally random effects on manifest personality levels applies to complex quantitative dimensions that are under positive directional selection—which means that, all else being equal, higher levels of a trait are more adaptive (Penke et al., 2007; Tooby & Cosmides, 1990; Verweij et al., 2014).

Examples of such ‘ability-based’ dimensions that consistently correlate positively with fitness-related outcomes include intelligence(s), social attractiveness, physicality, and immunocompetence. Because higher levels of these dimensions are always more adaptive (all else being equal), random effects of genetic mutations—which are overwhelmingly disordering to complex mechanisms—will typically decrease one’s ability to produce higher levels of the trait in question.

In light of the empirical fact that all manifest psychological traits that have been studied exhibit substantial heritability (Bouchard & Loehlin, 2001), genetic polymorphism will presumably figure in prominently as a proximate causal explanation for the between-person variance in nearly every personality variable that can be operationally defined. As genotype-personality linkages continue to be mapped (e.g., Verweij et al., 2012; 2014), the key question will be whether a given portion of the heritable variance is explained by organizational effects of specific common genotypes on personality endophenotypes (as expected if a selection regime has maintained heritable trait-like variation), directionally random effects of low frequency genotypes (as expected under mutation-selection balance), or other genomic parameters with more indirect effects (e.g., the depressive effects of genome-wide mutation load on fitness-promoting dimensions; see Verweij et al., 2014).

Developmental calibration

Natural selection also crafts mechanisms designed to implement developmental calibration of psychological adaptations in response to cues sampled across ontogeny (Belsky, 2012; Buss, 2009; Del Giudice et al., 2015; Ellis et al., 2009; Penke, 2011; Tooby & Cosmides, 1990). This type of mechanism is expected to evolve when optimal manifest trait levels (i) varied across human ancestors and (ii) reliably tracked specific cues that could be cost-effectively observed and sampled over developmental time (Nettle et al., 2013). For example, if observable cues to local social mobility were reliably present across human evolution, selection could favor design features in the shame program that developmentally calibrate shame proneness in response to cue-based estimates of local social mobility. If so, adults within or between populations would exhibit temporally stable interindividual variation in manifest shame toward existing relationship partners that partly reflects the developmentally canalizing effects of social mobility cues sampled previously in their lifetimes.

Mechanisms of developmental calibration can vary in a number of design parameters that reflect the specific adaptive problems they are designed to solve; for instance, the timing of cue-sampling, the duration of cue-sampling, and the extent to which the mechanism’s settings, once calibrated, are able to be recalibrated later in life via updated cue-based estimates of relevant input variables (Del Giudice et al., 2015; Frankenhuis et al., 2018; Panchanathan & Frankenhuis, 2016). These are theoretical and empirical issues to be addressed whenever advancing a hypothesis regarding a specific mechanism of developmental calibration.

Immediate situational adjustment

Genetic polymorphism and developmental calibration will be most relevant for explaining trait-like (i.e. temporally stable) individual differences in manifest psychological

variation, whether such individual differences are situation-specific or cross-situationally consistent.

It is important to recognize, however, that most of what psychological adaptations are designed to do is regulate psychological and behavioral outputs dynamically within specific situations on a moment-to-moment basis; in other words, they function to implement *immediate situational adjustment* of manifest cognition and behavior. Whether the adaptation in question is an emotional program (e.g., shame, sexual jealousy, gratitude), domain-specific functional motivation (e.g., status acquisition, pathogen avoidance, offspring protection), situation-detection algorithm (e.g., for detection of predators or spousal infidelity), or another type of mechanism (e.g., an internal regulatory variable; see below), it is usually either inactive or not being referenced by whichever mechanisms are currently playing a predominant role in behavioral decision-making. Indeed, individuals regularly encounter a wide array of functionally distinct situations on a daily basis, which may present many combinations of adaptive problems, e.g., food acquisition, pathogen avoidance, coalition formation, mate attraction, potential social devaluation, wayfinding, resource conflict, friendship maintenance, and out-group threat. Thus, most of the variance in an adaptation's manifest structure will not usually occur at the level of trait-like variation between persons (e.g., individual differences in shame proneness), but rather within persons as their behavior is regulated fluidly across the situations they select and encounter on a daily basis (e.g., feeling very ashamed after a significant public failure, but not at all ashamed at most other times).

Extant evidence supports this general expectation. For example, manifest personality states (e.g., behaving in a way that would be described as sociable) vary much less at the average between-person level than they do within persons across moments (Fleeson, 2001; 2007) and types of situations (Fleeson, 2007; Lukaszewski, 2010). These considerations suggest that mapping the causal structure of mechanisms that regulate behavior dynamically will be crucial for understanding both within- and between person variation in manifest personality.

Evolutionary Personality Science

As should be clear by this point, evolutionary psychological meta-theory is not merely compatible with the existence of quantitative personality variation within and between individuals—it leads us to expect the existence of such variation and provides us with the only comprehensive toolkit for understanding its functional significance and mechanistic underpinnings. Indeed, there is now a substantial body of evolutionary psychological research that has generated insights into the causal underpinnings, functional significance, and ontological status of personality constructs (see, e.g., Buss & Hawley, 2011; Buss & Penke, 2015; Tooby & Cosmides, 2015).

There exist two main paradigms for studying personality in evolutionary perspective. The first may be called *dimensional cost-benefit analysis (DCBA)*, wherein inductively derived personality dimensions are analyzed in relation to fitness-linked costs and benefits that might maintain adaptively patterned manifest variation. The second may be called *ground-up adaptationism (GUA)*, which requires mapping the deep and manifest structures of specific

evolved mechanisms for behavioral regulation, using basic principles, without specific intent to explain inductively derived personality dimensions.

In what follows, these two approaches to evolutionary personality science are described and illustrated with reference to selected research programs.

Paradigm #1: Dimensional Cost-Benefit Analysis (DCBA)

Most research in evolutionary psychology that explicitly focuses on “personality” constructs aims to explain the existence and patterning of extant trait dimensions—those which have been inductively derived (or otherwise constructed) by mainstream personality psychologists. Based on the general principle that natural selection maintains adaptively patterned variation as a function of tradeoffs between the costs and benefits at different points along a phenotypic continuum, practitioners of the DCBA approach follow (approximately) the following steps:

- (i) Select one or more focal personality constructs from among the inductively derived dimensions under study in personality psychology, such as the big five or HEXACO traits.
- (ii) Inspect the phenotypic content of the focal dimension to formulate hypotheses about the fitness-linked costs and benefits that may correlate with manifest trait levels—and in relation to which variation on the dimension may therefore be adaptively patterned.
- (iii) Determine empirically whether manifest personality levels actually predict the hypothesized cost-benefit tradeoffs. This can be done by reviewing extant studies, conducting original research, or both.
- (iv) Empirically test whether manifest variation along the focal dimension is non-randomly patterned in relation to ecological or phenotypic factors that predict (or ancestrally predicted) optimal manifest trait levels.
- (v) Formulate and examine hypotheses regarding the proximate mechanisms that generate adaptively patterned manifest variation, such as genetic polymorphism, cue-based developmental calibration, or immediate situational adjustment.

The DCBA approach has been applied to numerous dimensions, including those of the five factor (Nettle, 2006) and HEXACO (Ashton & Lee, 2007) models. For example, it has been hypothesized that individual differences in extraversion have been maintained within and between human populations over evolutionary time as a function of tradeoffs between the costs and benefits of extraverted strategies (Ashton & Lee, 2007; Buss, 2009; Lukaszewski & Roney, 2011; Nettle, 2005; 2006; Schaller & Murray, 2008). Implementing strategies described as extraverted (e.g., sociable, assertive, conspicuous) may promote the capture of various fitness-linked benefits, such as alliance formation, status acquisition, and mating success. However, extraverted strategies can also incur costs, such as exposure to pathogens, accidents, social conflict, devaluation, and various opportunity costs. Indeed, reviews of the empirical literature validate the predicted associations of extraversion levels with specific beneficial and costly

outcomes (Lukaszewski & von Rueden, 2015; Nettle, 2005; 2006). For example, measures of extraversion associate positively with mating success (Nettle, 2005), social rank (Anderson et al., 2001), and number of offspring (reviewed in Gurven et al., 2014; Lukaszewski & von Rueden, 2015; Penke & Jokela, 2016) – but also with having a history of accidents, physical violence, hospitalization, and domestic instability (reviewed in Nettle, 2005). Thus, there is no single optimal level of extraversion that holds across individuals, social ecologies, and time points. Rather, optimal extraversion levels vary in relation to factors that determine the probabilistic cost-benefit ratio of extraverted strategies.

Based on these cost-benefit analyses, researchers have established that extraversion is adaptively patterned in relation to phenotypic and socioecological cues theorized to predict optimal levels. For example, Lukaszewski and Roney (2011) theorized that the cost-benefit ratio of extraverted strategies should be inversely predicted by individual differences in overall *bargaining power*, which is a joint function of one's social value (i.e., the ability to generate benefits for others) and inflict costs on others (i.e., one's formidability) in the social world (Lukaszewski, 2013; Sell et al., 2009b). This is because individuals with greater bargaining power should be more likely to successfully obtain the potential benefits of extraverted strategies (e.g., higher rates of return on status pursuit and relationship initiation), but less likely to incur the potential costs of such strategies (e.g., losing out in social conflicts; opportunity costs of unsuccessful social investments), than individuals with less bargaining power. In support of this general hypothesis, multiple studies have found that extraversion levels are positively associated with interindividual variation in physical attractiveness and (especially men's) physical strength (e.g., Fink et al., 2016; Lukaszewski, 2013; Lukaszewski & Roney, 2011; von Rueden et al., 2015) – which are two (of many) phenotypic features that have reliably influenced humans' relative bargaining power over our evolutionary history (e.g., Lukaszewski et al., 2016; von Rueden et al., 2008).

In addition to phenotypic cues, research suggests that levels of extraversion are adaptively patterned in relation to external socioecological cues. Schaller and Murray (2008), for example, theorized that extraverted strategies would track the local infectious disease risk. This is because, as noted above, exposure to disease-causing pathogens is one of the potential costs of gregarious strategies that entail interacting with many pathogen vectors. In support of this hypothesis, they found that, across the globe, cross-national variation in the prevalence of disease-causing pathogens tracked average levels of extraversion, such that average extraversion levels were lower within nations subjected to greater disease risk. Although this regional correlation could be driven by multiple proximate mechanisms, experimental evidence suggests that the association of disease risk with extraversion is produced in part via mechanisms that implement immediate situational adjustment. Specifically, Mortensen et al. (2010) demonstrated that people immediately down-regulate manifest extraversion levels following experimental exposure to infectious disease cues.

The research arc described above is fairly typical of the DCBA approach to evolutionary personality science, which has been fruitfully applied to many personality dimensions, for example: Big Five and HEXACO dimensions other than extraversion (de Vries et al., 2016; Denissen & Penke, 2008a; Fink et al., 2016; Kerry & Murray, 2018; Lewis et al., 2015; Lukaszewski, 2013; Manson, 2017; Mortensen et al., 2010; Nettle, 2006; Schaller & Murray,

2008; Schmitt, 2004); attachment styles (Del Giudice, 2009; Lukaszewski, 2013; Schmitt, 2003; Simpson & Belsky, 2008); the “Dark Triad” (Jauk et al., 2015; Jonason et al., 2009); pathological personality variants at the extreme tails of normal personality continua (Del Giudice, 2014); and many others.

Limitations of the DCBA approach

The DCBA approach has been generative over the past two decades, resulting in various discoveries about the adaptive patterning of extant personality constructs. However, it is not without its limitations for understanding the mechanistic underpinnings of personality. In particular, it tends to presume the functional significance of inductively derived personality dimensions that may not carve human nature at its joints – which leaves researchers with little choice but to “black box” the psychological mechanisms underlying manifest personality dimensions. In what follows, these related limitations will be briefly explored.

Personality psychologists can’t do research unless they have units of analysis to study, and much research has therefore focused on identifying coherent phenotypic dimensions of variation. This can be done in various ways, but the most frequently studied dimensions were ‘discovered’ via factor-analytic techniques whereby large catalogues of trait descriptors are reduced to a set of more coherent (often orthogonal) dimensions that capture loose correlations among many aspects of person description at the population level, such as the big five and HEXACO dimensions (Lee & Ashton, 2008; McCrae & Costa, 2008; Saucier & Goldberg, 1996). Thereafter, researchers construct psychometric scales to assess these inductively derived dimensions with, for instance, self- and other-report survey items (e.g., John et al., 2008). It is only at this point – once personality constructs and associated operational definitions to measure them exist – that a DCBA-based research program can begin.

The reliance of the DCBA approach upon existing trait constructs thus raises the question: If the research goal is to map the input-output logic of psychological mechanisms and processes that underpin manifest personality variation, does it make theoretical sense for inductively derived dimensions to hold the status of being the field’s explanatory target? Arguably, the answer to this question is either “no” or, at least, “probably not, in most cases.”

There are at least two main problems with devoting the field’s efforts to explaining inductively derived – and hence atheoretical – personality dimensions:

The first problem is that inductively derived personality dimensions are, by virtue of the methods employed in their ‘discovery,’ almost always filtered through our folk grammar of behavioral description (e.g., a behavior or person is “kind,” “dominant,” “diligent”). Such folk trait categories have been characterized as the output of evolved difference-detecting mechanisms – inferential adaptations designed to heuristically describe individuals’ past actions and predict their future behavior (Buss, 2011). Importantly, such mechanisms are evolvable to the extent that they incrementally improved the ability of our ancestors to describe and predict others’ behavioral patterns above chance levels. As such, there is no reason to suppose that difference-detecting adaptations are designed to produce particularly accurate inferences regarding which internal mechanisms regulate behaviors and how (Fiddick et al., 2016). Moreover, to the extent that

behaviors from distinct folk categories (e.g., “hardworking” and “organized”) exhibit any correlation – even weak ones – within individuals, difference-detecting mechanisms are predicted to err on the side of assuming that the inferred presence of a given behavioral disposition implies one’s standing on other behavioral dispositions (Haselton & Nettle, 2006). These sorts of considerations suggest that the folk grammar of behavioral description produced by our difference-detecting adaptations will frequently (i) conflate the behavioral outputs of completely distinct psychological mechanisms and motivations as being members of the same folk trait category (e.g., heterogeneous acts perceived as “agreeable” might reflect either low self-perceived rank or the activation of affiliative motivations), and (ii) assume correlations among behaviors (e.g., between “dominant” and “sociable” acts) when none may exist for a given individual or local population.

For these sorts of reasons, many conceptions of inductively derived personality dimensions hold explicitly that such constructs are purely descriptive folk concepts which do not afford direct inferences into the underlying structure of the mind (Ashton & Lee, 2007; Buss, 2011; Buss & Craik, 1983; Fleeson, 2001; John et al., 2008; Wood et al., 2015). Even knowing this, however, both non-evolutionary and evolutionary subscribers to these trait concepts have tended to employ inductively derived dimensions as their explanatory targets. This is in spite of the fact that (i) there is no a priori reason to assume a universal dimensional personality structure at the population level, (ii) the staggering majority of research on personality structure has been conducted in large, post-industrial societies, and (iii) factor structures such as the big five and HEXACO have failed to replicate when (rarely) tested in smaller-scale societies (Bailey et al., 2013; Gurven et al., 2013) or across a more inclusive set of natural languages (Saucier et al., 2014). Indeed, recent work suggests that the patterning and orthogonality of the covariance structures underpinning these dimensions may be driven by evolutionarily recent increases in the socioecological niche diversity of modern societies (Gurven et al., 2013; Lukaszewski et al., 2017; Smaldino et al., 2018) – which could reflect differences across ecologies in the evoked structure of folk person description categories, actual behavioral covariance, or both.

The claim is not that inductively derived personality dimensions have no relationship with actual manifest behavioral patterns. Indeed, an adaptationist approach leads one to expect that the folk trait constructs produced by our difference-detecting adaptations are usefully predictive of future behaviors and outcomes – which of course they are (Fleeson & Gallagher, 2009; Roberts et al., 2007). Rather, the claim is that these constructs are a sub-optimal starting point for mapping the mechanisms and processes that underpin personality variation. They may essentially function as a red herring for the field by leading researchers to, for instance, posit explanations for non-existent correlations, fail to notice phenotypic correlations that do exist, underestimate the situational specificity of manifest behavior, and remain largely ignorant regarding which or how many distinct psychological mechanisms underpin the behaviors classified similarly within a folk trait category. In short, inductively derived personality dimensions don’t carve human nature at its joints.

The second main problem with the DCBA approach flows from the first: it produces limited insights into the mechanistic underpinnings of manifest behavioral variation. On this point, the proof is in the pudding. Although much has been discovered about the functional patterning of inductively derived dimensions of behavioral description, the heterogeneity of these dimensions has left researchers with little choice but to “black box” the specific psychological processes that

regulate ‘trait-exemplifying behaviors.’ As such, almost nothing is known about them. This is reflected in the call of Fleeson and Jayawickreme (2015) that “what needs to be done next is to identify social-cognitive mechanisms that produce big-five states” (p. 83). As Buss and Penke (2015) accurately noted about this next step, however, it represents “the biggest challenge for evolutionary personality psychology” (p.16).

In light of the ambiguous ontological status of inductively derived personality dimensions, perhaps researchers dedicated to understanding how behavioral variation emerges from domain-specific psychological mechanisms and processes – including evolutionary psychologists, functionalists (e.g., Wood, this volume), network theorists (e.g., Cramer et al., 2012), and social-cognitivists (e.g., Fleeson & Jayawickreme, 2015; Mischel & Shoda, 1995) – should decline to accept this challenge. It is nowhere written that the lexical hypothesis and factor analysis bring unique value to the project of phenotype definition, and it might be past time to break free of their arbitrary constrictures (for similar views from various perspectives, see Baumert et al., 2017; Cramer et al., 2012; Wood, this volume; Wood et al., 2015).

What if there existed an alternative framework that entailed jointly mapping the deep and manifest structures of psychological mechanisms for behavioral regulation, one by one, until they added up to a complete description of human nature and its sundry manifest variants?

Paradigm #2: Ground-Up Adaptationism (GUA)

GUA represents just such a framework. Although it is only now being formally named in this chapter, this paradigm has already been described and exemplified above, in relation to research characterizing shame as an evolved program designed to prevent and mitigate the costs of being socially devalued. Unlike DCBA, the GUA approach does not begin by trying to explain an inductively derived phenotypic dimension of unclear ontological status (e.g., “agreeableness”). Rather, it follows the steps entailed by the well-established adaptationist approach to reverse-engineering the structure of the mechanisms which comprise organisms:

- (i) Define an adaptive problem recurrently faced by members of a species’ ancestors over long stretches of their evolutionary past. (This can be done via empirically informed logical analysis or various forms of quantitative modeling.)
- (ii) Perform a task analysis of this problem’s structure to formulate hypotheses about which design features a phenotypic mechanism(s) would have to be equipped with in order to solve it.
- (iii) Now guided by working hypotheses about a putative mechanism’s evolved function, test these hypotheses (and alternatives) to determine whether there is evidence for the existence of design features (e.g., input-output mappings) that exhibit an improbably close functional match with the structure of the adaptive problem(s) in question.
- (iv) Examine hypotheses regarding the proximate causation of quantitative variation in the mechanism’s manifest settings and outputs (e.g., genetic polymorphism, developmental calibration, immediate situational adjustment).

(v) Determine which, if any, existing (scientific or folk) personality constructs may (partly or wholly) correspond with the putative adaptation's outputs.

The central feature of GUA that distinguishes it from DCBA is its focus on explaining the *species-typical structure of evolved mechanisms* (Al-Shawaf et al., 2017; Buss, 2015; Tooby & Cosmides, 2015; Roney, 2016). This is frequently misinterpreted to imply that evolutionary psychologists neglect adaptively patterned quantitative variation (e.g., Hawley, 2011; Penke et al., 2007; Winegard et al., 2017). This interpretation fails to acknowledge the inseparable relationship between the deep and manifest structures of psychological adaptations (Tooby & Cosmides, 1990). As previously explained, it is the deep (universal) structure of an adaptation that specifies the range of possible outputs that it can produce by design, as well as the contingencies according to which its manifest (variable) structure emerges across individuals, contexts, and cultures. It is also the deep structure of an adaptation that provides targets for manifest variation (e.g., the exact settings of its activation thresholds) in the first place, regardless of the proximate cause(s) of that variation.

The GUA approach has already generated a voluminous body of discoveries about specific aspects of personality variation. Although not typically framed as “personality” research, it is exactly that: research that builds models of psychological adaptations, from the ground-up, including their variable parameters that result in manifest quantitative variation.

In what follows, the GUA approach to personality science will be illustrated with selected examples: research on jealousy, anger, and internal regulatory variables. As we already have for the shame program (see above and Table 1), each of these evolved mechanisms will be characterized in terms of (i) its function and (ii) how the input-output mappings entailed by its deep structure results in adaptively patterned manifest variation (Table 1).

Jealousy

The emotional program labeled “jealousy” has been well characterized as a psychological adaptation designed to prevent and mitigate the costs of infidelity-related threats to valued relationships (Buss, 2000; 2018).

Most research on jealousy has focused on that experienced in response to a partner's (potential or actual) infidelity within socially monogamous mating relationships. Unlike other apes, monogamous pair bonds are a common pillar of human mating systems (Conroy-Beam et al., 2015; Kaplan et al., 2000; Winking et al., 2007). In the currency of evolutionary fitness, committed pair bonds were a highly valuable type of relationship for both ancestral men and women – but only to the degree that one's partner faithfully honored their commitments to remain sexually exclusive and invest cooperatively in shared offspring (Conroy-Beam et al., 2015). Over time, both partners are inevitably exposed to alternative mating opportunities, whether to form a new pair bond with another partner or engage in an extra-pair affair involving sex or resource diversion (Buss et al., 2017; Buss & Schmitt, 1993; Gangestad & Simpson, 2000; Winking et al., 2007). As such, preventing and mitigating the costs of infidelity-related threats to romantic relationships was a key adaptive problem faced by ancestral humans in the mating domain (Buss, 2000; Buss et al., 1992).

Jealousy is an evolved solution to this adaptive problem (Buss, 2000; Buss et al., 1992). The deep structure of jealousy is defined by its contingent mapping of infidelity cues to a menu of possible psychological and behavioral outputs (Table 1). In general, jealousy is activated in proportion to the cue-based belief that one's partner may have engaged in infidelity. Rigorous empirical work has identified an enormous set of valid cues to a partner's infidelity (e.g., Buss, 2000; Shackelford & Buss, 1997), only a sample of which are listed in Table 1. For example, depending on the context, jealousy might be activated in response to observing subtle smiles exchanged between one's partner and a potential interloper, the sudden loss of a partner's sexual interest in oneself, a partner's emission of unexplained signs of guilt, or a variety of other possible inputs. These cues are heterogeneous and frequently relationship-specific, but united by their perceived indication of a partner's potential or certain infidelity.

Once activated, jealousy can orchestrate an array of possible context-specific outputs designed to prevent infidelity or, if it has already occurred, minimize its costs (Table 1 provides an incomplete list). Some of these outputs are likely functional in response to virtually any suspected or confirmed infidelity, such as increased vigilance in monitoring the partner's whereabouts and activities. The likelihood of other outputs being expressed depends on an infidelity victim's perception of their circumstance, such as how much they value the relationship, their estimated probability of being able to salvage the relationship, or the reputational damage suffered by divorcees in the local cultural context. These sorts of factors determine whether the jealous individual will organize their actions toward dissolving the relationship or repairing it (Shackelford et al., 2002). If one's partner is inferred to be merely at risk for engaging in infidelity, the jealous individual might express "mate retention tactics" (Buss & Shackelford, 1997) designed to disincentivize this action by, for instance, increasing investment in the partner, guarding the partner, threatening to abandon the partner, or eliciting retaliatory jealousy. If infidelity is suspected (or confirmed) to have already occurred, possible outputs range from immediate termination of the relationship to various restorative tactics to inflicting physical violence against the partner or interloper (for a comprehensive discussion, see Buss, 2000).

Manifest variation in jealousy proneness – the ease or intensity with which jealousy is triggered – is adaptively patterned in relation to several known phenotypic and socioecological factors. Most notably, research by Buss and colleagues has supported the hypothesis that men and women differ, on average, in their degree of manifest jealousy expressed in response to different types of infidelity (Buss et al., 1992; Buss, 2018). In the event of a partner's infidelity, both partners stand to lose the other's future investment of behavioral and material resources—especially if the extra-pair relationship becomes serious and results in mate switching (Buss et al., 2017). However, men uniquely face the adaptive problem of avoiding paternity uncertainty in the event of a female partner's sexual infidelity. Buss et al. (1992) therefore hypothesized that men and women differ, by design, in whether they experience jealousy more intensely in response to a partner's infidelity that is (i) purely sexual or (ii) involves feelings of love and emotional commitment. Because men uniquely face the problem of paternity uncertainty, men are predicted to express more jealousy in response to sexual than emotional infidelity cues, whereas women are predicted to exhibit the inverse pattern. This average sex difference in context-specific jealousy proneness has now been confirmed in many countries on different continents across the globe (e.g., Bendixen et al., 2015; Buss et al., 1992; 1999; Buunk et al., 1996; Shackelford et al., 2002), suggesting that it may qualify as a human universal (Buss, 2018).

Jealousy proneness also exhibits adaptively patterned manifest variation in relation to circumstances that determine an individual's value in the local mating market – and thus one's vulnerability to the costs of infidelity. For example, jealousy proneness is negatively associated with overall mate value and bargaining power (Lewis, 2013; Sidelinger & Booth-Butterfield, 2007), as well as specific phenotypic features that influence overall mate value, such as physical attractiveness (Lewis, 2013), physical symmetry (Brown & Moore, 2003), and men's height (Brewer & Riley, 2009; Buunk et al., 2008). Moreover, jealousy proneness is also calibrated in response to mate value discrepancies between partners, such that people exhibit elevated jealousy proneness in relationships to the degree that their partner is higher in mate value, or has more alternative options, than oneself (Conroy-Beam et al., 2016; Sidelinger & Booth-Butterfield, 2007). By similar logic, it makes functional sense that jealousy is immediately adjusted in relation to the local sex ratio, such that jealousy proneness is up-regulated when members of one's own sex are available in abundance relative to the other sex (Arnocky et al., 2014).

These (and many other) findings illustrate how jealousy's manifest structure emerges from the contingencies embodied by its deep structure—whether in relation to the specific input-output mappings differentially elicited within a particular sex, culture, or relational context (Table 1), or the functional calibration of overall (or relationship-specific) jealousy proneness in relation to circumstantial factors that modulate the costs and benefits of activating this emotional adaptation (Table 1).

Anger

Members of the same species, by virtue of a shared organic design that leads them to desire the same resources and outcomes, frequently find themselves in conflict. Because resolving conflict through physical combat is costly, natural selection favors design features in organisms that cause them to resolve conflicts through a process of mutual assessment, wherein contests begin with opponents' visual assessments of each other, and escalate only as far as necessary for one individual to estimate that it will eventually lose (Huntingford & Turner, 1987). As predicted by evolutionary game theoretic models of conflict, research on species across the animal kingdom demonstrates that conflict resolution is strongly regulated by combatants' mutual assessments of their opponent's physical formidability (Huntingford & Turner, 1987). Essentially, more formidable individuals are entitled to a greater share of contested resources than less formidable individuals, and the determination of this in advance of costly combat produces net fitness gains for both winners and losers of conflicts.

Humans are an unusually cooperative species, which is to say that we are obligately dependent upon relationships involving various forms of mutual aid and social exchange (Cosmides et al., 2010; Kaplan et al., 2000). A consequence of this is that human entitlement to contested resources is regulated not only by the ability to inflict costs on others, but also the ability to generate benefits as an ally, exchange partner, mate, or leader (Lukaszewski et al., 2016; Sell et al., 2009b; von Rueden et al., 2008). This is reflected in the independent positive effects of formidability and social value on humans' (i) felt entitlement to resources (Lukaszewski, 2013; Peterson et al., 2013; Sell et al., 2009b), and (ii) allocation of contested resources and preferential

treatment to formidable or valuable others (Eisenbruch et al., 2016; Sell et al., 2009b; von Rueden et al., 2008).

What happens when people are undervalued by others, relative to their entitled level of valuation and treatment? This frequently occurs, especially given that others would often prosper by generating fewer benefits for their conspecifics than those individuals might be entitled to. The logic of animal conflict straightforwardly indicates that the long-run disadvantage of being undervalued by others presents an important adaptive problem to be solved.

According to the “recalibrational theory,” anger is an evolved program designed to solve the adaptive problem of being undervalued by others by bargaining for better treatment (Sell, 2011; Sell et al., 2009b; 2017; Tooby & Cosmides, 2015). Anger is activated by cues to another person’s intentional undervaluation of oneself, relative to one’s entitled level of treatment (Table 1). The intensity of anger’s activation is proportional to the degree of undervaluation inferred from the substandard treatment expressed, whether the transgressor has inflicted costs or generated insufficient benefits (Sell et al., 2017). Anger produces various context-specific outputs designed to upwardly recalibrate the transgressor’s valuation of oneself to match the entitled level of treatment (Table 1), including cognitive recalibrations (e.g., down-regulate one’s valuation of the transgressor), non-verbal signals (e.g., the characteristic anger face; Sell et al., 2014), and targeted actions (e.g., threats to inflict costs or withhold benefits; physical aggression). Remarkably detailed cross-cultural research has demonstrated that anger universally motivates bargaining for better treatment via verbal arguments with a common structure (Sell et al., 2017). For example, in anger-based arguments, angry individuals exaggerate the costs imposed on them, whereas transgressors exaggerate the benefits they obtained by imposing the costs or claim that the cost imposition was unintentional. These features make sense if the argument hinges on the extent to which an action relates to the transgressor’s internal valuation of the angry individual. Among available theories of anger and aggression, the recalibrational theory stands alone in its ability to explain the specific array of anger’s input-output mappings and the structure of anger-based bargaining and aggression.

A theory of manifest variation in anger falls naturally out of an understanding of its evolved function and species-typical deep structure (Sell et al., 2009b). Because anger is triggered by an unfavorable discrepancy between one’s entitled level of treatment and treatment received, anger’s activation threshold is effectively set by one’s level of entitlement – which is calibrated, in turn, by an estimate of one’s (relationship-specific or general) bargaining power. This leads to the prediction that determinants of bargaining power – such as formidability, attractiveness, oratorical skill, and social alliances – should play a role in calibrating one’s entitlement, and thereby anger proneness (Sell et al., 2009b). Consistent with this, more physically formidable and attractive people have been found to manifest greater entitlement and anger proneness across multiple societies, from the United States (Sell et al., 2009b) and United Kingdom (Price et al., 2012) to the Aka hunter-gatherers of Central Africa (Hess et al., 2010).

Internal Regulatory Variables (IRVs)

A cursory task analysis indicates that, in order to solve the adaptive problems that caused their evolution, each of the adaptations described above requires access to specific pieces of

information. Shame, jealousy, and anger all calibrate their activation thresholds, in part, to one's relative bargaining power, which is itself a joint function of one's multiply-determined capacities of benefit generation and cost infliction. Because overall bargaining power is, in turn, influenced by many specific phenotypic features (e.g., oratorical skill, physical attractiveness) and circumstances (e.g., the sex ratio; number of local kin), it is impossible for an adaptation to calibrate itself to overall bargaining power unless the mind contains an integrated estimate thereof. These kinds of internal computational magnitudes that hold estimates for multiply determined parameters are referred to as IRVs (Cosmides & Tooby, 2013; Lieberman et al., 2007; Tooby & Cosmides, 2015).

IRVs are potentially critical for explaining a wide range of manifest personality variables (Lukaszewski, 2013). This is because the a given IRV can potentially be accessed by a wide range of specific motivational adaptations that require the information it stores to function adaptively. To carry on the example from above, shame, jealousy, and anger mechanisms are all theorized to calibrate their operation in response to an IRV that has been called the *Power Index* (Balliet et al., 2017; Lukaszewski, 2013; Sell et al., 2009b). The *Power Index* is designed to compute a cue-based estimate of one's bargaining power, whether relative to specific interaction partners (Balliet et al., 2017) or others in the local social world (Lukaszewski, 2013).

The *Power Index* is among a broader class of self-evaluative IRVs (Table 1). For example, the *Inclusion Index* (aka the "sociometer") is designed to estimate one's degree of inclusion in social groups (Leary et al., 1998). As predicted, the *Inclusion Index* tracks both longitudinal (Denissen et al., 2008) and immediate (Leary et al., 1998) experiences of social acceptance and rejection by acquaintances in one's local social world. However, the *Inclusion Index* is not influenced by cues to romantic acceptance and rejection; these are tracked instead by a dedicated *Mate Value Index* (Kavanaugh et al., 2010). Another self-evaluative IRV, the *Status Index*, selectively tracks one's attained hierarchical rank in social groups (Anderson et al., 2008; Mahadevan et al., 2016; Patton, 2000; von Rueden et al., 2008), and functions independently of the *Inclusion Index* (Anderson et al., 2008; Mahadevan et al., 2016).

Although each of these self-evaluative IRVs (and others) are intercorrelated, they store distinct parameters, which can be selectively referenced by various psychological mechanisms for context-specific behavioral regulation. For example, a decrease (or increase) in the value stored in the *Mate Value Index* leads selectively to decreased (or increased) standards for potential mates, but not potential friends (Kavanaugh et al., 2010). An increase in the value stored in the *Status Index* (but not in the *Inclusion Index*) regulates strategies reflected in elevated narcissism and assertiveness (Mahadevan et al., 2016). Meanwhile, a decrease in the value stored in the *Inclusion Index* results selectively in increased vigilance against cues to social rejection (Denissen & Penke, 2008b). As a final example, Lukaszewski (2013) found that a measure of the *Power Index* (i) mediated associations of specific phenotypic features (physical attractiveness and strength) with a wide range of manifest personality strategies (e.g., extraversion, negative emotionality, fear of rejection, attachment styles), and (ii) explained most of the covariation among these distinct personality variables.

In sum, these examples illustrate how IRVs are designed to compute cue-based estimates of critical parameters, which can then be accessed independently by various motivational systems

when the information they store becomes functionally relevant for decision-making (Table 1). For examples of IRVs designed for other functions than self-evaluation, see: the *Kinship Index* (Lieberman et al., 2007); *Welfare Tradeoff Ratios* (Delton & Robertson, 2012; 2016; Tooby & Cosmides, 2015; Sell et al., 2009b); and IRVs for computing distinct parameters of interdependent situations (Balliet et al., 2017).

GUA: The best way forward for personality science

Given the aforementioned limitations of the DCBA approach, the strengths of the GUA approach make it the most promising way to map the mechanistic underpinnings of personality. This is true for at least the following reasons:

- (1) The GUA approach is focused on the design of evolved mechanisms for behavioral regulation from the start; deep and manifest structures of adaptations are discovered in tandem. As such, it avoids reifying inductively derived dimensions of person description that afford little insight into the identity or structure of the mechanisms underpinning observed covariance patterns at the population level. Instead, it carves human nature at its natural joints.
- (2) Predictions regarding the situational specificity and cross-situational consistency of manifest personality variation arise naturally from a GUA-based analysis. As described above, for example, shame proneness towards existing close relationships – but not towards strangers or distant acquaintances – is calibrated to local relational mobility; this results in situation-specific variation in manifest shame proneness between individuals and populations. Meanwhile, shame proneness across multiple relationship contexts is calibrated to one's standing on socially valued traits; this results in (some) cross-situational consistency.
- (3) The GUA approach provides tools for understanding patterns of personality covariance at both the within-person and population levels. As described above, for example, jealousy proneness, shame proneness, and anger proneness are all calibrated in part to the *Power Index*. This predicts that manifest variation in the outputs of these three distinct adaptations will tend to be inter-correlated at the population level. If so, there is no need to posit a mysterious latent psychological construct to explain such covariation, as the causal mechanisms would be known. At the same time, despite the fact that anger and jealousy proneness will be negatively correlated between persons, they will exhibit various situation-specific patterns of covariance within persons. For example, partner-directed anger is one of the outputs of the jealousy program, which predicts positive coactivation of these emotions in some, but not most, situations.
- (4) Eventually, using the GUA approach to build models of many domain-specific psychological mechanisms will help elucidate the nature of existing personality constructs. For example, Lewis (2013) found that manifest variation in jealousy proneness is captured in psychometric scales designed to measure big five neuroticism. Similarly, Lukaszewski & Chua (2018) found that Sell et al.'s (2009b) theoretically derived measure of anger

prone to exhibit a strong negative relationship with HEXACO agreeableness. Although explaining inductively derived dimensions is not a primary goal of the GUA approach, it is potentially important for determining which components of existing broadband constructs capture the outputs of specific mechanisms.

Concluding remarks

After decades in which the primary debates in personality psychology revolved around which and how many trait factors best describe human personality structure, many researchers seem to have coalesced loosely around a set of common goals for the field's next era: identify the mechanisms that comprise the mind, figure out how they work, and determine how they generate manifest behavioral (co-)variation at within-person, between-person, population-level, and cross-cultural levels of analysis.

The objective of this paper has been to illustrate how closely these research goals align with those of adaptationist evolutionary perspectives – in particular the GUA approach to personality science. However, this advocacy is not to dismiss the value of other approaches which emphasize the importance of identifying the social-cognitive processes underlying personality variation. Although adaptationist principles are arguably unique in their ability to generate a priori predictions regarding the causal structure of specific psychological mechanisms, these principles should be supplemented by other perspectives and techniques. For example, GUA-based hypotheses might be examined within the conceptual and analytic frameworks provided by network (Cramer et al., 2012) or functional field (Wood, this volume) models. Such integrative enterprises could produce synergistic advances by leveraging the best theoretical and methodological tools available.

Personality psychology has always been an ambitious discipline; it attempts nothing less than a complete mapping of human nature and all its manifest variants. Evolutionary psychology is likewise ambitious, asserting itself as an organizing meta-theory for all research topics in the behavioral sciences. It is exciting that scientists in both fields have converged on the realization that they must now turn to a crucial, but difficult, task: to discover the mechanistic underpinnings of human behavior, from the ground-up.

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Table 1

Selected aspects of manifest personality variation discovered using ground-up adaptationism (GUA)

<u>Adaptation</u>	<u>Evolved Function(s)</u>	<u>Deep Structure → Manifest Structure</u>		
		<u>Input cues</u>	<u>Context-specific Outputs</u>	<u>Contingent Variation</u>
Shame	Prevent or mitigate costs of being socially devalued	<p>-Potential for others to become aware of one's expression of disvalued act(s), possession of disvalued traits, or experience of disvalued events</p> <p>-Others actually observe (or become aware of) one's expression of disvalued act(s), possession of disvalued traits, or experience of disvalued events</p> <p>-Others express devaluation of oneself, regardless of legitimacy</p>	<p>→ <u>Activation</u>: Intensity of shame proportional to degree of devaluation (or forecasted devaluation)</p> <p><u>Menu of possible outputs</u>:</p> <p>(a) <i>If act/trait/event not yet perceived by others</i>:</p> <p>→ Decide not to take disvalued action</p> <p>→ Destroy incriminating evidence</p> <p>→ Hide from view</p> <p>→ Generate alibi</p> <p>→ Manifest quotidian demeanor</p> <p>→ Generate benefits as precautionary offset to potential loss of value</p> <p>(b) <i>If act/trait/event already perceived by others</i>:</p> <p>→ Signal appeasement</p> <p>→ Signal lack of wrongful intention</p> <p>→ Generate compensatory benefits to restore value</p> <p>→ Hide from view</p>	<p>-Shame proneness calibrated to one's own social value (and thus vulnerability to costs of devaluation)</p> <p>-Shame proneness in close relationships calibrated to estimate of local social mobility (and thus the difficulty of replacing a damaged or lost relationship)</p> <p>-Audience-specific shame (e.g., close friends vs. distant acquaintances) is regulated by circumstances that determine the costs of devaluation by different classes of relationship</p> <p>-Specific behavioral outputs are highly variable and are tailored to the circumstances faced by the individual, but organized by the functional imperative of preventing or mitigating the costs of being devalued</p>

			→ Down-regulate status pursuit → Shift investment towards undamaged relationships → If cooperative overtures not possible, resort to bargaining via intimidation and aggression to restore value	
Jealousy	Prevent or mitigate infidelity-related threats to valued relationships	-Partner's loss of interest in self -Partner's interest in potential interloper -Interloper's interest in partner -Sexual deficiency of self (e.g., erectile dysfunction) -Partner's dishonesty re: their whereabouts -Partner's continued contact with their ex -Unexplained changes in partner's sleeping habits and daily routine -Partner's reluctance to discuss a certain other person -Partner's emotional disengagement	→ <u>Activation</u> : Intensity of jealousy proportional to belief that infidelity is likely <u>Menu of possible outputs</u> : → Vigilant monitoring of partner's whereabouts and social activities → Anger (see below) → Guard partner → Increase investment in partner to repair relationship → Inflict deterrence costs on partner (or threaten to) → Inflict deterrence costs on interloper (or threaten to) → Emotionally manipulate partner → Increase or display one's own mate value → Induce retaliatory jealousy in partner → Appeal to partner's family or friends for intervention → Increase sexual advances toward partner (sperm competition) → Increase investment in partner to repair relationship	-Sex difference in relative jealousy in response to purely sexual infidelity (greater for men) vs emotional/love infidelity (greater for women) -Jealousy proneness calibrated to phenotypic features that influence mate value (e.g., status, wealth, physical attractiveness, etc.) -Jealousy proneness calibrated to mate value discrepancies between (a) self and partner; and (b) partner and alternative potential partners -Jealousy proneness calibrated to perceived local sex ratio (which determines relative difficulty of replacing current partner, depending on one's own sex) -Relationship-specific jealousy proneness calibrated in relation to partner's dispositional mating strategy (e.g., orientation toward casual sex) -Specific behavioral outputs are highly variable and tailored to the circumstances faced by the individual, but organized by the functional imperative of preventing or mitigating the costs of infidelity-related threats to valued relationships

		<p>-Partner exhibiting unexplained signs of guilt</p> <p>-Observation of (or rumor about) partner's romantic or sexual interaction with interloper</p>	→ Dissolve relationship	
Anger	Bargain for better treatment	-Detection of another person's undervaluation of self (relative to entitled level of treatment)	<p>→ <u>Activation</u>: Intensity of anger proportional to degree of computed undervaluation by the transgressor</p> <p><u>Menu of possible outputs</u>:</p> <p>→ Anger face to exaggerate formidability</p> <p>→ Changes in posture to exaggerate formidability</p> <p>→ Threaten to (or actually) inflict costs (to upwardly recalibrate transgressor's future valuation of self)</p> <p>→ Threaten to (or actually) withhold benefits (to upwardly recalibrate transgressor's future valuation of self)</p> <p>→ Bargain for better treatment through verbal argument (by, e.g., exaggerating costs incurred by self)</p> <p>→ Downregulate valuation of the transgressor</p> <p>→ Broadcast anger to others (to signal to them your intolerance of being undervalued)</p>	<p>-Entitlement and anger proneness calibrated to bargaining power (ability to inflict costs + confer benefits)</p> <p>-Anger proneness varies by context as a function of relationship-specific entitlement (e.g., more angered by a low-status than high-status friend's transgression)</p> <p>-Specific behavioral outputs are highly variable and tailored to the circumstances faced by the individual, but organized by the functional imperative of upwardly recalibrating other's valuation of oneself</p>

Self-Evaluative IRVs	Estimate one's standing on critical social dimensions (e.g., inclusion, bargaining power, status, mate value)	-Cues to acceptance in group -Cues to rejection by group	→ <i>Inclusion Index</i>	-Various psychological adaptations calibrate themselves in part to the stored value in the <i>Inclusion Index</i> . For example, motivations for contributing to the group's collective goals; mechanisms promoting investment in existing relationships; shame
		-Self-assessed ability to generate benefits for others -Self-assessed ability to inflict costs on others	→ <i>Power Index</i>	-Various psychological adaptations calibrate themselves in part to the stored value in the <i>Power Index</i> . For example, shame proneness; anger proneness; jealousy proneness; status motivation
		-Cues to others' deference to self in cooperative group -Cues to others' respect for self in cooperative group	→ <i>Status Index</i>	-Various psychological adaptations calibrate themselves in part to the stored value in the <i>Status Index</i> . For example, felt entitlement; motivations to generate benefits through leadership; mating motivations; pride
		-Cues to others' romantic interest in self -Cues to others' romantic rejection of self	→ <i>Mate Value Index</i>	-Various psychological adaptations calibrate themselves in part to the stored value in the <i>Mate Value Index</i> . For example, standards of mate selection; orientations toward committed and uncommitted mating