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An Adaptationist Framework for Personality Science

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Abstract: The field of personality psychology aspires to construct an overarching theory of human nature and individual differences: one that specifies the psychological mechanisms that underpin both universal and variable aspects of thought, emotion, and behaviour. Here, we argue that the adaptationist toolkit of evolutionary psychology provides a powerful meta-theory for characterizing the psychological mechanisms that give rise to within-person, between-person, and cross-cultural variations. We first outline a mechanism-centred adaptationist framework for personality science, which makes a clear ontological distinction between (i) psychological mechanisms designed to generate behavioural decisions and (ii) heuristic trait concepts that function to perceive, describe, and influence others behaviour and reputation in everyday life. We illustrate the utility of the adaptationist framework by reporting three empirical studies. Each study supports the hypothesis that the anger programme—a putative emotional adaptation—is a behaviour-regulating mechanism whose outputs are described in the parlance of the person description factor called 'Agreeableness'. We conclude that the most productive way forward is to build theory-based models of specific psychological mechanisms, including their culturally evolved design features, until they constitute a comprehensive depiction of human nature and its multifaceted variations. © 2020 European Association of Personality Psychology

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The field of personality psychology is animated by the grand ambition of constructing an overarching theory of human nature: one that explains both universal and variable aspects of thought, emotion, and behaviour (Allport, 1937; Buss, 1984; Eysenck, 1967; Jung, 1921; Maslow, 1943; Revelle, Wilt, & Condon, 2011). Since the mid-20th century, personality psychologists have factor-analysed lexical and sentence-length descriptions of behaviour under the assumption that patterns of covariance in these descriptors reveal fundamental traits—the building blocks of personality with which to create a 'periodic table of elements' for the field (Cattell, 1966; Costa & McCrae, 1992; Lee & Ashton, 2008; Saucier & Goldberg, 1996). This approach has produced structural taxonomies of personality—notably the Big Five and HEXACO models—that show impressive ability to predict important life outcomes (Goldberg, 1993; Ozer & Benet-Martinez, 2006; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007; Soto, 2019).

These frameworks have been primarily *descriptive*, as most of their proponents acknowledge; they do not provide an *explanatory* account of the psychological underpinnings of individual differences and within-individual consistency and variability across time and situations (Borsboom, 2013; Borsboom, Mellenbergh, & Van Heerden, 2003; Buss & Craik, 1983; Cervone, 2005; Fleeson & Jayawickreme, 2015; John et al., 2008; Mischel & Shoda, 1995). The field increasingly aspires to a theoretical framework that specifies the psychological mechanisms regulating consistent individual and cultural differences, as well as within-person stability and context dependency (Back et al., 2011; Baumert et al., 2017; Fleeson & Jayawickreme, 2015; Funder, 2006; Revelle & Condon, 2015; Wood, Gardner, & Harms, 2015; Wood, Tov, & Costello, 2015; Wright, Beltz, Gates, Molenaar, & Simms, 2015).

We propose that the adaptationist toolkit of evolutionary psychology provides precisely the meta-theoretical framework that is needed to discover and characterize the psychological mechanisms that generate behavioural regularities and variation within and between people. We begin by explaining why traditional lexical and factor-analytic approaches have limited utility for revealing the mechanistic

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underpinnings of personality. Next, we outline an adaptationist framework for personality science. This framework makes a clear distinction between (i) mechanisms designed to regulate behaviour and (ii) the heuristic trait concepts used to perceive, describe, and influence manifest behaviour in everyday social life. We illustrate the utility of the adaptationist framework by showing that the anger programme—a putative emotional adaptation—is a behaviour-regulation mechanism whose outputs are captured by the descriptive trait factor called 'Agreeableness'. We conclude that the adaptationist toolkit, broadly defined to incorporate the role of cultural evolution, can provide an organizing framework for personality science.

Limitations of traditional personality frameworks for discovering the mechanistic underpinnings of personality

Personality psychology has deeply rooted traditions as a science of behavioural description and prediction. Since the mid-20th century, research focused on identifying the traits that could function as phenotypic units of analysis has relied heavily (though not exclusively) on lexical trait-descriptive adjectives as a source of data, and on factor analysis as a means of data reduction (Cattell, 1945; Goldberg, 1993; Norman, 1963; Tupes & Christal, 1992). The lexical hypothesis holds that, over time, words and phrases are invented and tend to accumulate and spread in natural language because of their utility for communicating about socially or otherwise consequential aspects of human variation; its central tenet, therefore, is that words describing behavioural variation provide a basis for inferring the important dimensions along which human minds vary (Goldberg, 1981, 1993; Saucier & Goldberg, 1996). The lexical hypothesis assumes that important dimensions of personality description will accumulate more synonyms and that the larger synonym clusters will be of universal importance, and so will be present in most or all languages.

Consistent with the lexical approach and its assumptions, the descriptive personality constructs subsequently identified do, in fact, exhibit impressive predictive validity for many important life outcomes, such as risk taking, car accidents, alcoholism, marital conflict, infidelity, marital stability and divorce, occupational success, mating strategies, offspring production, and longevity (Buss, 1991a, 1991b; Goldberg, 1993; Mõttus et al., 2019; Ozer & Benet-Martinez, 2006; Penke & Jokela, 2016; Roberts et al., 2007; Soto, 2019). Because natural languages contain many thousands of items for person description (adjectives, type nouns, and phrases), many of which are at least partly synonymous, researchers have used factor analysis to create broad dimensions of variation based on intercorrelated ratings of descriptors. The resulting factors, which are typically rotated statistically to be orthogonal, serve as 'marker' dimensions for reference within the person description landscape (Cattell, 1966; Costa & McCrae, 1992; Lee & Ashton, 2008; Saucier & Goldberg, 1996). This application produced the Big Five (Goldberg, 1990), Big Six (Saucier et al., 2014), and HEXACO (Lee & Ashton, 2008) factor models that have supplied the phenotypic units of analysis for much of the personality research on individual differences in affect, behaviour, and cognition over the past three decades.

The resultant personality factors, however, provide little insight into the underlying psychological mechanisms that generate the outputs referred to by those factors. To see why, consider an analogy (adapted from Borsboom, 2013; Buss, 1996; Zietsch, 2009): imagine that a scientist attempts to reverse engineer the modern personal computer. To accomplish this, she or he (i) has many people use the computer and rate the machine on a comprehensive list of adjectives, nouns, and phrases previously used to describe computers, then (ii) factor analyses those ratings, and finally (iii) takes the resulting descriptive factors (perhaps labelled, e.g. 'intuitiveness', 'speed', 'aesthetics', and 'affordability') as provisional indications of the underlying structure of computers. Although this would be a good method for identifying the main dimensions of interest from the perspective of computer *users*, it would tell us almost nothing about how computers work or the internal mechanisms that vary somewhat from computer to computer.

This analogy applies equally to human behavioural description. When considering inductively derived person description constructs, it is instructive to apply the distinction between the computational mechanisms operating a machine and the ways human observers perceive the machine's behaviour and describe it with language. Behavioural descriptors appear to be the output of a folk personality psychology—a part of human psychology that functions to interpret, anticipate, and communicate about the behaviour of other people in everyday social life (Buss, 1996, 2011; Buss & Craik, 1983; Dunbar, 1996; Fiddick et al., 2016; Goldberg, 1981; Hogan et al., 1985; Fleeson & Jayawickreme, 2015; Funder, 1995; Saucier et al., 2014; Wood, Gardner, & Harms, 2015). Behavioural description concepts and lexical tags for them (e.g. 'untrustworthy'; 'a real slacker') have heuristic utility in describing and predicting the behaviour of self and others and for manipulating or influencing the reputations of self and others (Buss, 1996). From a scientific standpoint, however, there is no rationale for inferring that these behavioural descriptors accurately capture the underlying psychological mechanisms that produce observable behaviour. As such, lexical trait constructs, heuristically useful and predictive as they may be in human social life, leave a range of fundamental scientific questions completely unanswered: Which psychological mechanisms produce the emotional or behavioural outputs described by each personality construct? How many psychological mechanisms produce outputs that are commonly described by a given lexical item? How many psychological mechanisms with important behaviour-regulating functions lack lexical terms to describe their outputs? What is the relationship between the semantic content of a lexical concept and the phenotypic content of its referents? The descriptive constructs themselves provide no basis for answering these questions (Baumert et al., 2017; Buss & Craik, 1983).

In sum, personality concepts and factors based on between-person covariance of lexical or sentence-based descriptors reveal little about the underlying mechanisms that produce the behaviours being described. It follows that

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lexical and inductively derived trait constructs, although a critical source of evidence regarding the folk psychology of person description and life-outcome prediction, should not serve as the field's primary windows into the mechanistic underpinnings of personality. We contend that a more fruitful approach is to begin by mapping the information-processing structure of the machinery that regulates behaviour. The adaptationist toolkit of evolutionary psychology holds special promise for accomplishing this objective.

The adaptationist toolkit of evolutionary psychology

The theory of evolution by natural selection is the organizing framework for the life sciences because of its unique value for understanding the origins and causal structure of organisms. The meta-theoretical framework known as evolutionary psychology was borne of the realization that the principles of evolutionary theories are as essential to the study of human psychology, behaviour, and culture as they are for understanding the properties of other life forms (Buss, 1984, 1995; Tooby & Cosmides, 1990a, 1992; Tooby & Devore, 1987). In what follows, we explain some key principles of evolutionary theories and illustrate how the adaptationist toolkit of evolutionary psychology can be used to discover and characterize the psychological mechanisms that together comprise the human mind and constitute the mechanistic underpinnings of personality variation.

As formulated by Darwin (1859), the core theory posits that evolution by natural selection is the inevitable consequence of four interacting ingredients:

(1) A population of self-replicators.
(2) Phenotypic variation among individuals in the population.
(3) Heredity of phenotypic variation.
(4) Differential reproduction correlated with inheritable phenotypic variation.

If these ingredients are present, populations of organisms will undergo changes across reproductive generations as they accumulate inheritable attributes that increase rates of reproduction within a given ecology (Fisher, 1930). After Darwin's time, it was established that genes (Mendel, 1865), instantiated as DNA (Hershey & Chase, 1952), are the particulate units of inheritance, and that genetic mutations (copying errors during gene replication) are the original source of genetic variation. Genes are both the primary units of heredity and the units of self-replication on which natural selection acts (Hamilton, 1964; Williams, 1966). These discoveries led to the gene-centred view of evolution, in which organisms and the mechanisms comprising them are essentially 'vehicles' for those genes, which evolved because of their cumulative replicative effects (Dawkins, 1982).

Many remarkable discoveries followed from this view of life. For example, formal models solved the puzzle of why organisms evolve to benefit other organisms by showing that a gene can further its own replication by conferring benefits on those copies of itself that reside in the bodies of genetically related individuals—a prediction with widespread empirical support across diverse taxa of organisms, from plants (Dudley & File, 2007) to invertebrate and vertebrate animals, including humans (Hamilton, 1964; Wilson, 1979). Similar models predicted and explained a host of phenomena that previously seemed inexplicable or counterintuitive, such as the evolution of helping behaviour toward non-kin (Trivers, 1971), parent–offspring conflict (Trivers, 1974), intragenomic conflict (Cosmides & Tooby, 1981), sexual conflict (Parker, 1979), and sexual reproduction itself (Tooby, 1982). These conceptual developments, uniquely derived from evolutionary theories, rendered evolution the overarching framework for all life sciences. It is difficult to overstate the revolutionizing impact of these advances for the study of organisms. It was no hyperbole when Dobzhansky (1984) asserted that 'Nothing in biology makes sense, except in the light of evolution'. Humans and their psychology are no exception.

In recent decades, the meta-theory of evolutionary psychology has been making steady progress in applying principles of evolutionary biology to the study of human psychology and behaviour (Buss, 1995, 2015, 2019; Dunbar, Dunbar, & Barrett, 2007; Henrich, 2015; Sperber, 1996; Tooby & Cosmides, 2015). At its core, this framework holds that humans, like all other species, evolved by natural selection and can therefore be conceptualized as collections of *adaptations*: mechanisms that have been incorporated into human nature by natural selection because they reliably solved adaptive problems—ancestral challenges relevant to survival and reproduction such as finding food, avoiding ingestion of pathogens and toxins, eluding predators, choosing reproductively valuable mates, caring for offspring, maintaining cooperative relationships, and learning about the local physical and social environments.

The adaptationist approach is based on the premise that, if adaptations evolved in past environments because they helped solve specific adaptive problems, it should be possible to reverse engineer existing traits in organisms by considering hypotheses about the selection pressures that caused their evolution (Williams, 1966). Because this process of reverse engineering is susceptible to *post hoc* storytelling, Williams (1966) proposed that candidate adaptations be evaluated according to strict criteria, including whether the phenotype under investigation operates with efficiency and economy and appears organized with otherwise improbable precision to solve a specific adaptive problem—the way a key fits its lock. To conclude that a phenotype is an adaptation designed for a specific evolved function—rather than a by-product of an adaptation or noise (Tooby & Cosmides, 1990a)—it must exhibit evidence of *special design*. Empirically, this can be demonstrated by following a series of steps (Buss, 2019; Lewis, Al-Shawaf, Conroy-Beam, Asao, & Buss, 2017; Schmitt & Pilcher, 2004; Tooby & Cosmides, 1990a, 1992; Williams, 1966):

(1) Identify an adaptive problem recurrently faced by human ancestors (broadly defined) over sufficiently long stretches of their evolutionary past. This can be accomplished through empirically informed logical analysis or computational modelling of selection dynamics.

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(2) Perform a *task analysis* of the adaptive problem; that is, elucidate the precise nature of the problem and the design features an adaptation would need in order to solve the adaptive problem effectively and efficiently.
(3) Now guided by working hypotheses about a hypothesized mechanism's evolved function and information-processing structure, test specific predictions derived from these hypotheses, ideally against competing hypotheses about evolved function or non-adaptive by-product hypotheses.
(4) Examine hypotheses regarding the proximate causation (e.g. genetic variation and developmental calibration) of quantitative variation in the mechanism's parameter settings (e.g. activation threshold) and outputs (e.g. manifest behaviour).
(5) Determine which, if any, existing phenotypic constructs may partly or wholly correspond with the putative adaptation's outputs.

Of course, certain steps are more pertinent to some questions than others. Additionally, the steps need not be done in any particular order; for example, evidence of apparent design in a phenotype can lead to intuitions about which adaptive problem the phenotype might have evolved to solve, which can then inspire formal analyses of the adaptive problem in question (Pietraszewski, 2020; Tooby & Cosmides, 1992). When implemented rigorously, an adaptationist analysis can reveal novel properties of a mechanism that would have remained scientifically invisible without knowledge about the precise function for which the mechanism was designed.

Evolutionary psychologists have now reverse engineered a large array of putative adaptations in humans. For example, the human mind appears to be equipped with psychological mechanisms designed to estimate the genetic relatedness of self to others and, based on these estimates, regulate kin-directed cooperation and incest avoidance (Lieberman, Tooby, & Cosmides, 2007; Sznycer, De Smet, Billingsley, & Lieberman, 2016); facilitate learning in children about which local plants are edible via observations of adults' plant consumption (Wertz & Wynn, 2014); regulate behaviour in order to prevent and mitigate the deleterious effects of pathogen exposure (Murray & Schaller, 2016; Schrock, Snodgrass, & Sugiyama, 2020; Tybur, Lieberman, Kurzban, & DeScioli, 2013); reason about the contingencies of social exchange and exclude cheaters and free-riders from cooperation (Cosmides et al., 2010; Delton, Cosmides, Guemo, Robertson, & Tooby, 2012); represent the features of interdependent social situations (Balliet, Tybur, & Van Lange, 2017); motivate people to engage in third-party punishment in order to deter future acts of exploitation toward oneself (Krasnow et al., 2016); motivate facultative coalitional aggression against other groups (Manson et al., 1991; Wrangham & Glowacki, 2012); track markers of social alliances (Pietraszewski, Cosmides, & Tooby, 2014); generate moral sentiments about domain-specific aspects of social life (Barrett et al., 2016; Boyer, 2007; Curry, Mullins, & Whitehouse, 2019; Petersen et al., 2012; Pinsof & Haselton, 2016); acquire local norms about the contexts of cooperation (Apicella & Silk, 2019; House et al., 2020); and compute the social value of self (Denissen, Penke, Schmitt, & Van Aken, 2008; Leary, Tambor, Terdal, & Downs, 1995) and others (Buss et al., 1990; Delton & Robertson, 2012; Durkee, Lukaszewski, & Buss, 2019; Eisenbruch, Grillot, Maestripieri, & Roney, 2016; Sznycer et al., 2016; von Rueden, Gurven, & Kaplan, 2008) (for recent reviews, see Buss, 2015; Buss, 2019).

An adaptationist framework for mapping variation within and between persons

To the best of our knowledge, the human psychological architecture is qualitatively universal. Just as it has never been discovered that people in some populations have physiological organs such as hearts or lungs that are present in some populations but absent in others, the same applies to psychological adaptations. Modern humans had evolved on Africa by approximately 200kya-150kya, and migrated to other parts of the world more recently, mostly within the past 75k-15k years (van Shaik, 2016). Although simple adaptations such as lactase persistence—the failure to turn off lactase expression after weaning that is prevalent in populations with a history of animal husbandry—can evolve relatively rapidly, it takes selection many generations to build new complex adaptations containing many interacting design features. Consequently, it is to be expected that, when it comes to the fundamental suite of psychological adaptations possessed by humans, we are all Africans with a universal design (Barrett, 2015; Buss, 2001; Tooby & Cosmides, 1990a; 1990b; 1992; van Shaik, 2016).

Mapping the species-typical architecture of a psychological adaptation, perhaps counterintuitively, provides a common framework within which to study psychological and behavioural *variation* occurring at the within-person, between-person, and cross-cultural levels of analysis. Indeed, the primary function of an evolved psychological mechanism is to regulate the behaviour of individuals across moments, life stages, and situational contexts. Accordingly, the mechanistic structure of an adaptation—its activating inputs, computational procedures, and outputs—provides a ready-made causal model to explain within-person variation. Moreover, evolutionary theories provide multiple tools for explaining individual and cross-cultural differences in the operation of species-typical adaptations. For example, mechanisms can be designed to calibrate their exact settings (e.g. activation thresholds) by sampling cues that are diagnostic of the most adaptive modes of operation (e.g. cues to being in a safe vs. a violent social world; cues to one's social value relative to local others) (Buss, 2009; Buss & Penke, 2015; Frankenhuis, Panchanathan, & Barrett, 2013; Hagen & Hammerstein, 2005; Lukaszewski, 2013; Lukaszewski & Roney, 2011; Schaller & Murray, 2008; Sng, Neuberg, Varnum, & Kenrick, 2018; Tooby & Cosmides, 1990b). The components of psychological mechanisms can also vary between individuals due to genetic differences, whether such heritable variation is random (e.g. noisy effects of genetic mutations) or adaptively patterned (e.g. heritable behavioural variation being adjusted to the variable demands of different

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environments) (Buss, 2009; Penke, Denissen, & Miller, 2007; Penke & Jokela, 2016; Tooby & Cosmides, 1990b; Verweij et al., 2012). Finally, psychological variation is also shaped by culturally transmitted information and socioecology (Gangestad et al., 2006; Gurven, 2012; Henrich, 2015; Richerson & Boyd, 2008; Scelza et al., 2019; Smaldino, 2019).

All of these models of quantitative variation in psychology and behaviour share two key assumptions: (i) all variations in the operation of an adaptation arises from situational, developmental, cultural, or genetic influences on universal components of psychological mechanisms, and (ii) it is the very same psychological mechanisms that give rise to behavioural variation within and between people. As such, if scientists are to identify and characterize the universal mechanisms that underpin within-person and between-person variations, it is essential to begin with causal models of these mechanisms (Buss, 1996; Lukaszewski, in press; Tooby & Cosmides, 1990b).

Our primary thesis is that the adaptationist toolkit provides a theory-based framework for characterizing the species-typical psychological mechanisms that, collectively, constitute the human mind. This includes their components that regulate within-person, between-person, and cross-cultural behavioural variations. Once the psychological architecture has been mapped, one can ask whether the descriptive constructs derived by personality psychology (e.g. Agreeableness and Conscientiousness) correspond to the outputs that the architecture generates when it interacts with the relevant developmental and environmental inputs.

A worked example of the adaptationist framework: the anger programme's outputs are described in the parlance of 'agreeableness'

We now present empirical discoveries that illustrate the promise of this mechanism-centred adaptationist framework. We first review adaptationist research that has revealed numerous design features of an evolved emotional programme labelled 'anger'. We then demonstrate that variation in the anger programme's activation and outputs is heuristically described in the parlance of the inductively derived construct labelled 'Agreeableness'—and that this applies to both within-person and between-person variations in anger's activation and expression.

The recalibrational theory of anger

The anger programme appears to be a psychological adaptation designed to recalibrate how much weight the target of the anger attaches to one's welfare when that weight is deemed insufficient (Sell, 2005, 2011; Sell et al., 2017; Sell, Tooby, & Cosmides, 2009). This recalibrational theory of anger resulted from an application of the adaptationist toolkit as outlined earlier.

Define the adaptive problem faced by our human ancestors. The precise degree to which others weight the welfare of the self when making decisions has major fitness consequences for the self. If others attach weight to one's welfare—whether because they value your well-being or fear the prospects of not valuing it—they will take actions that benefit you but cost them, and they will refrain from taking actions that benefit them but inflict costs on you. In contrast, when others place little weight on your welfare, they will be less inclined to render you assistance and more inclined to exploit you.

It has been hypothesized that the human mind is equipped with internal regulatory variables that index the weight attached to another's welfare relative to one's own (e.g. Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). These variables are accessed by behaviour-regulating mechanisms and determine the degree to which the individual will attend to, associate with, assist, defer to, or exploit specific other individuals in one's social world. This internal variable has been termed *welfare trade-off ratio* (WTR) (Tooby et al., 2008). Recent research suggests that WTRs have many of the properties that one would expect to see in an index of human social valuation (Delton & Robertson, 2016; Sell et al., 2017). First, WTRs are target specific (Delton, 2010; Forster, Pedersen, Smith, McCullough, & Lieberman, 2017). Second, resource allocation tasks that pit the welfare of the self against the welfare of specific others (the domain of WTRs) are done with consistency, which supports the hypothesis that a precise internal threshold separates the welfare trade-offs that are worth doing from those that are not (Delton, 2010; Sznycer, Delton, Robertson, Cosmides, & Tooby, 2019). Third, the specific WTR values that an individual has with respect to others are set based on two evolutionarily relevant classes of information: (i) WTR values increase with the ability of other people to inflict costs on the self, whether through physical aggression or other means (Eisenbruch et al., 2016; Gordon & Lea, 2016; von Rueden et al., 2008), and (ii) WTR values increase with the intrinsic social value that other people have (with respect to the self) as mates, kin, trading partners, friends, leaders, and allies (Delton & Robertson, 2012; Eisenbruch et al., 2016; Lieberman et al., 2007; Lukaszewski et al., 2016; Sznycer et al., 2019; von Rueden et al., 2008).

Given WTR's centrality to human cooperation and conflict, a host of adaptive problems would have centred around adaptively recalibrating the values of WTRs in the minds of self and others. One of these is the adaptive problem of being undervalued by others—of being on the receiving end of a WTR that is lower in value than the WTR value one could cost-effectively enforce from another individual. By hypothesis, anger is an emotion programme designed by selection to incentivize insufficient valuers to recalibrate their WTRs upward.

Perform a task analysis of this problem's structure to formulate hypotheses about the adaptation's universal design. In order to recalibrate insufficient valuers, the posited adaptation (i.e. anger) should exhibit all of these features:

i) The anger programme should be activated by cues that the target individual places too little weight on the welfare of the self.
ii) Anger should be sensitive to and seek out information about the target's mental states with respect to the self.

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For example, did the target underestimate the cost that would be imposed on the self? Did the target have an unacceptably low WTR toward the self?

iii) If cues indicate that the target's WTR is unacceptably low, the anger programme should mobilize a sequence of behaviours aiming to incentivize the target to up-regulate her WTR.

iv) Anger should interrupt its operation when there are indications that the target's WTR has been recalibrated, because bargaining beyond this point is counterproductive.

Determine whether there is evidence for the existence of the hypothesized design features. There is now abundant evidence that the anger programme has all these features and that each feature can be more thoroughly mapped with an understanding of its function. Consider the triggers of anger. By definition, a low WTR is indicated when one imposes on another a large cost in order to receive a small benefit and, importantly, when the offender knows the magnitude of the cost, the magnitude of the benefit, and the identity of the victim when they decide to take the cost-imposing action. When angry, people respond to all those three variables in ways predictable from anger's recalibrational function: anger is more intense when the cost imposed on the self is high, when the benefit the offender received for imposing that cost is low, and when the offender knew the identity of the angry person when deciding to impose the cost (Sell et al., 2017). Furthermore, offences are intuitively understood as welfare trade-offs, and victims eagerly seek information about *why* the offender imposed the cost on them so that they can estimate the precise WTR value in the mind of the offender (Sell, 2005; Sell et al., 2017). This will determine whether recalibration is needed, how much recalibration is needed, and what exactly needs to be recalibrated (e.g. did the offender under-value one's welfare or did the offender underestimate how much one values a resource?).

In the early stages of anger, individuals engage the mind of the target with rapid verbal exchanges (i.e. arguments), which are typically non-violent (Averill, 1983) and appear designed to demonstrate to the target of anger that they are employing too low of a WTR (e.g. 'you only care about yourself'). Experiments show that when angry because of a transgression, people make arguments that indicate that the target demonstrated too low of a WTR, that is, 'the cost you imposed on me was very large', 'you did this for a trivial benefit', and 'you knew it was me you were hurting' (Sell et al., 2017).

If the target of anger does not concede in response to verbal arguments, then the angry individual may attempt to change the target's WTR through more forceful bargaining. To do this, anger has evolved to make use of the fact that WTRs are calibrated by cues of the relative bargaining power of the interactants, most importantly formidability (i.e. the ability of the target to impose costs) and cooperative value (i.e. the ability and willingness of the target to confer benefits). Anger can thus recalibrate the target by causing the angry individual to demonstrate their formidability (e.g. threats, aggressive posturing, and actual aggression) or to withhold cooperative value (e.g. the silent treatment and avoidance) (Buss, 1991b; Hagen & Rosenström, 2016; Molho, Tybur, Güler, Balliet, & Hofmann, 2017; Sell, 2011).

Finally, the anger programme is turned off when the target indicates that they have recalibrated their WTR—typically via a plausibly sincere apology composed of statements that acknowledge that their previous WTR was in error (e.g. 'I underestimated you as a friend', 'I shouldn't have done that', and 'you didn't deserve to be treated that way'). Behavioural indicators that upward recalibration of the WTR has occurred are known to deactivate anger in most circumstances even without actual recompense, again indicating that the function of anger is to recalibrate the mind of the target (Sell, 2005, 2011).

Examine hypotheses about the causes of quantitative variation and individual differences. Adaptationist and evolutionary-genetic hypotheses about quantitative behavioural variation are grounded in the premise that the activation of a given psychological mechanism or behavioural output entails cost–benefit trade-offs (Buss, 2009; Del Giudice, 2018; Gurven, von Rueden, Stieglitz, Kaplan, & Rodriguez, 2014; Lewis & Buss, in press; Lukaszewski & Roney, 2011; Nettle, 2006; Penke et al., 2007; Tooby & Cosmides, 1990b; Verweij et al., 2012). The activation and expression of anger can lead to benefits (upwardly recalibrating another person's WTR toward the self) as well as costs (e.g. conflict; damage to the relationship; wasted time and energy). As such, it is functionally imperative that anger—like all behaviour-regulating mechanisms—avoids the dual errors of over-activation and under-activation (Sznycer & Lukaszewski, 2019). Importantly, however, the magnitudes of anger's costs and benefits are not constant across situations (e.g. the identity of the target), cultural contexts (e.g. whether displaying anger is locally considered acceptable), or individuals (e.g. a person with high vs. low status). As such, anger should be designed to calibrate its activation in response to factors that predict optimal levels.

Some hypotheses about individual differences in anger are grounded in the premise that anger evolved from phylogenetically ancient adaptations for aggressive bargaining (Davis & Panksepp, 2011; Montag & Panksepp, 2017). Models of animal conflict suggest that variation in anger should be based partly on bargaining power: just as the animal with more fighting ability demands more resources (Hammerstein & Parker, 1982; Huntingford & Turner, 1987), so the human with more bargaining power demands more deferential treatment and becomes angry over a greater range of offences (Sell et al., 2009). Research confirms that felt entitlement to favourable treatment (i.e. the WTR one expects from others) positively predicts individual differences in anger proneness (Grubbs, Exline, & Campbell, 2013; Sell et al., 2009). Moreover, indicators of physical formidability (e.g. upper-body strength in men) and social value (e.g. attractiveness in both sexes) positively predict felt entitlement and anger proneness (Archer &

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Thanzami, 2009; Hess, Helfrecht, Hagen, Sell, & Hewlett, 2010; Petersen, Sznycer, Sell, Cosmides, & Tooby, 2013; Petersen & Laustsen, 2019; Price, Dunn, Hopkins, & Kang, 2012; Sell, Eisner, & Ribeaud, 2016; Sell et al., 2009; see Fessler, Tiokhin, Holbrook, Gervais, & Snyder, 2014). Similarly, within romantic relationships, partners with more alternative options on the mating market become angered more easily in response to relationship transgressions (Goetz & Maria, 2019).

Anger is also adaptively patterned in relation to socioecological factors that modulate optimal levels. For example, Japanese cultural norms hold that overt displays of anger are more appropriate among people of high than low social class, whereas Western norms hold the opposite (Park et al., 2013). As would be expected, if variation in anger is calibrated to its potential costs and benefits, expressed anger associates positively with social class in Japan but negatively with social class in America (Park et al., 2013).

Determine which, if any, existing psychological constructs may (partly or wholly) correspond with the putative adaptation's outputs. Next, we present the findings of three empirical studies showing that within-person and between-person variations in anger's outputs are described in the lexical parlance of HEXACO 'Agreeableness' [and five-factor model (FFM)/Big 5 'Agreeableness' and 'Neuroticism']. Figure 1 presents the hypothesized model, wherein the anger programme regulates its various outputs, which are then characterized by observers' person perception heuristics and described according to a behavioural lexicon.

The main text provides an overview of these studies; the Supporting Information provides more detailed descriptions of the methods and results, additional findings, and links to raw data. All data and analysis script can be accessed via the Open Science Framework (https://osf.io/evu2k/).

STUDY 1: INDIVIDUAL DIFFERENCES IN ANGER PRONENESS ARE DESCRIBED AS TRAIT 'AGREEABLENESS'

In what follows, we demonstrate that psychometric scales designed specifically to assess individual differences in anger proneness—the anger programme's propensity to activate in response to transgressions—closely tracks the HEXACO dimension of person description labelled 'Agreeableness'.

Methods and results

In order to test predictions derived from the recalibrational theory about individual differences in anger, Sell et al. (2009) developed a 21-item *Anger Proneness* scale, which includes items specifically targeting the anger programme's propensity to activate when undervalued, such as 'I get very angry when someone makes fun of me'; 'If someone insults me, I just let it pass (r)' (Supporting Information S1.2). The Anger Proneness scale (Sell et al., 2009) was later included in another data collection (Study 1a), which also administered the 100-item HEXACO PI-R (Lee & Ashton, 2018) and 50-item International Personality Item Pool (IPIP)-NEO (www.ipip.ori.org). While testing predictions that pertained to both Anger Proneness and personality scales, we discovered that, among 383 young adults (211 women; M_{age} = 19.48; SD_{age} = 1.88), HEXACO Agreeableness (α = .82) was strongly negatively correlated with Anger Proneness (α = .83), $r = -.59$, $p < .001$ (Figure 2A; Table 1). Study 1b directly replicated this finding in a sample of 379 young adults (293 women; M_{age} = 21.12; SD_{age} = 3.76), in which the correlation between HEXACO Agreeableness (α = .82) and Anger Proneness (α = .84) was $r = -.65$, $p < .001$ (Figure 2B; Table 1). Study 1b also included the 14-item Affective Neuroscience Personality Scales (ANPS) Anger scale (Davis & Panksepp, 2011), which includes anger-focused items such as 'When I am frustrated, I usually

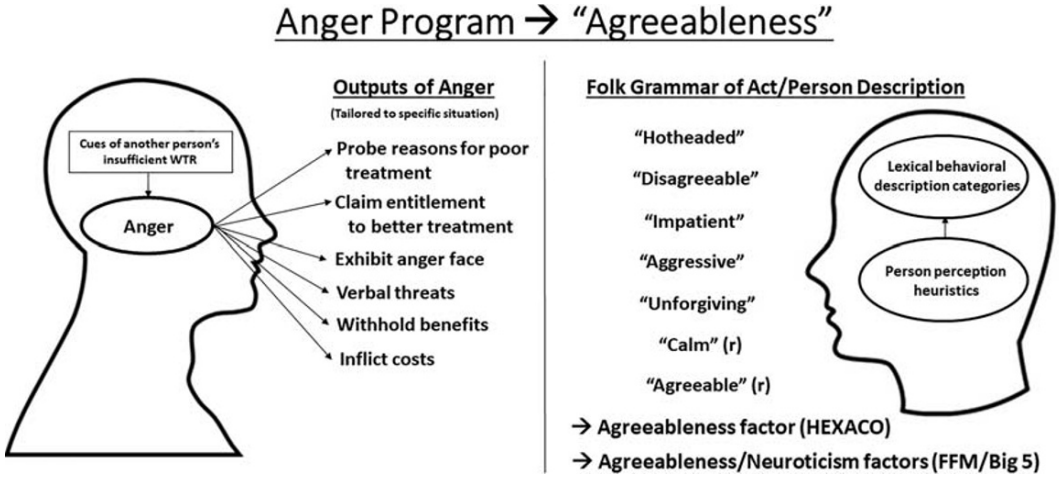

Figure 1. Hypothesized model in which the anger program's activation and outputs are perceived via difference-detecting mechanisms and characterized via heuristic trait concepts, resulting in the observation of (differently oriented) factors in multivariate space.

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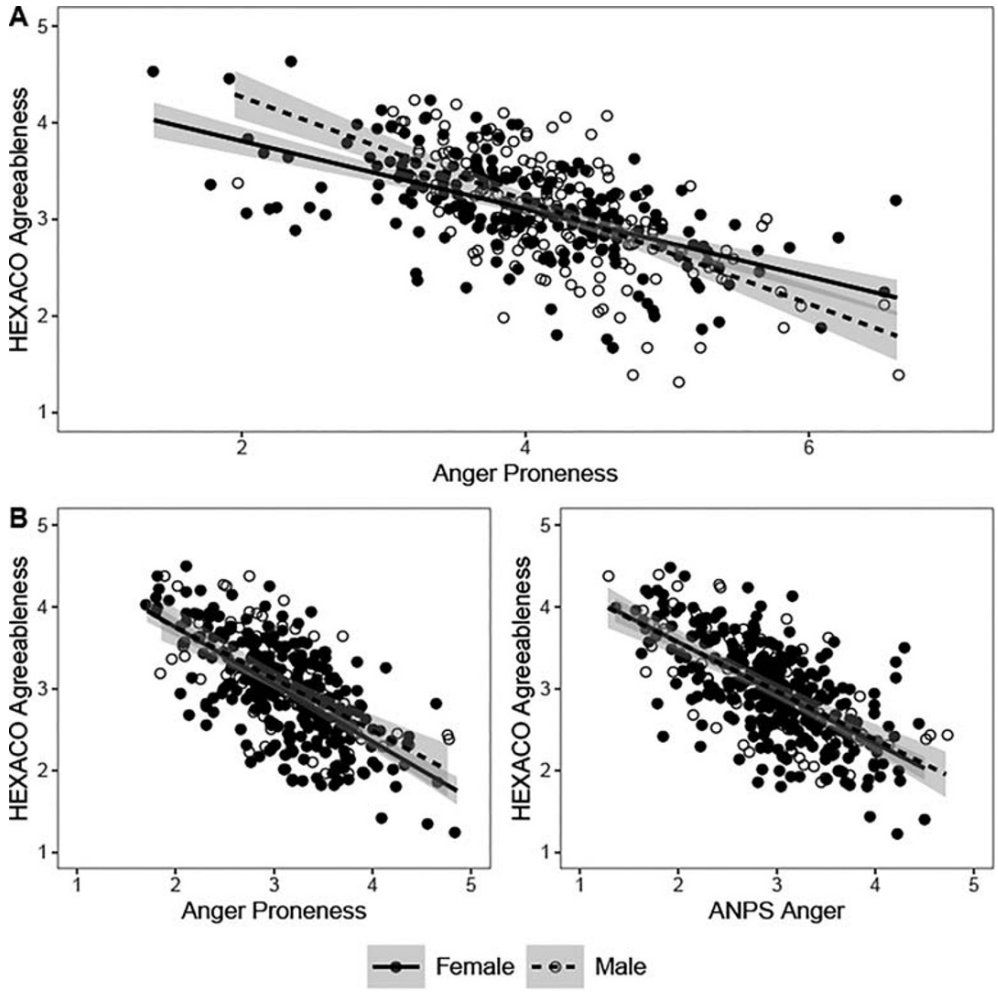

Figure 2. Scatterplots depicting the sex-specific correlations of individual differences in anger proneness scales with individual differences in HEXACO Agreeableness scores in Study 1.

Table 1. Correlations of Anger Scales with HEXACO and Big Five Scales (Studies 1a and 1b)

	Study 1a (N = 383)	Study 1b: (N = 379)	
	Anger proneness	Anger proneness	ANPS anger
HEXACO-100			
Honesty-Humility	− **0.29**	− **0.34**	− **0.37**
Emotionality	− 0.08	0.04	0.19
eXtraversion	0.00	0.07	− 0.02
Agreeableness	− **0.59**	− **0.65**	− **0.65**
Gentleness	− **0.37**	− **0.42**	− **0.40**
Flexibility	− **0.47**	− **0.36**	− **0.37**
Forgiveness	− **0.29**	− **0.44**	− **0.37**
Patience	− **0.58**	− **0.63**	− **0.71**
Conscientiousness	− 0.03	− 0.02	− 0.08
Openness	− 0.11	− 0.06	− 0.11
IPIP-NEO-50			
Agreeableness	− **0.29**	—	—
Conscientiousness	− 0.04	—	—
Openness	− 0.11	—	—
Extraversion	0.08	—	—
Neuroticism	**0.29**	—	—

Note: Bolded values indicate that $p < .01$.
ANPS, Affective Neuroscience Personality Scales; IPIP, International Personality Item Pool.

get angry' and 'I never stay irritated at anyone for very long (r)' (Supporting Information S1.2). ANPS Anger (α = .82) was strongly positively correlated with Anger Proneness (r = .75, $p < .001$) and strongly negatively correlated with HEXACO Agreeableness (r = −.65, $p < .001$) (Figure 2B; Table 1). See Supporting Information S1 for detailed methods for Studies 1a and 1b.

Not only were individual differences in anger correlated with HEXACO Agreeableness, but the former also correlated with each of the Agreeableness facets. Moreover, these correlations were higher than the correlations among the Agreeableness facets themselves. In Studies 1a and 1b, the average correlations of both anger scales (Anger Proneness and ANPS Anger) with the HEXACO Agreeableness facets ranged from .43 to .47 (Table 2). The average correlations among the Agreeableness facets were descriptively somewhat lower, ranging from .36 to .37 (Table 2). This is precisely the kind of signature that one would expect if the anger programme supplied the behavioural outputs that are then intuitively perceived and described as more or less 'agreeable'.

Anger's location in HEXACO versus five-factor model/Big 5 factor space: factor models change, but anger stays the same

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Table 2. Correlations among Anger Scales and the HEXACO Agreeableness factor and facets (Studies 1a and 1b)

Study 1b	Anger Proneness	ANPS anger	Agreeableness	Gentleness	Flexibility	Forgiveness	Patience
Anger proneness	X	n/a	− 0.59	− 0.37	− 0.47	− 0.29	− 0.58
ANPS anger	0.75	X	n/a	n/a	n/a	n/a	n/a
Agreeableness	− 0.65	− 0.65	X	0.72	0.74	0.69	0.77
Gentleness	− 0.42	− 0.40	0.73	X	0.42	0.33	0.40
Flexibility	− 0.36	− 0.37	0.69	0.41	X	0.33	0.42
Forgiveness	− 0.44	− 0.37	0.69	0.36	0.26	X	0.35
Patience	− 0.63	− 0.71	0.78	0.40	0.39	0.39	X

Note: Results for Study 1a are above the diagonal; results for Study 1b are beneath the diagonal. All correlations statistically significant, $p < .001$.
ANPS, Affective Neuroscience Personality Scales.

Additionally, it is important to note that the associations of Anger Proneness with personality differed for the HEXACO and FFM/Big 5 dimensions—in ways that are consistent with rotational differences between these factor models. Several major differences between HEXACO and FFM/Big 5 are that (i) in FFM/Big 5 space, anger-related content loads onto both Agreeableness and Neuroticism, whereas, in HEXACO space, anger-related content loads on onto Agreeableness but not Emotionality; and (ii) certain aspects of FFM/Big Five Agreeableness are moved to the Honesty-Humility factor in HEXACO space (Ashton & Lee, 2007). If the outputs of the anger programme are described in lexical parlance—which has been partitioned differently by the HEXACO and FFM/Big 5 models—then we should expect Anger Proneness to correlate with HEXACO Agreeableness and Honesty-Humility (but not Emotionality), but with Agreeableness and Neuroticism in FFM/Big 5 space. This is precisely what we observe (Table 1). In Study 1a, Anger Proneness correlated with only HEXACO Agreeableness ($r = -.59$) and Honesty-Humility ($r = -.29$). In FFM/Big 5 space, Anger Proneness correlated moderately with both Agreeableness ($r = -.29$) and Neuroticism ($r = .29$).

None of these factor-analytic considerations matter, however, for understanding or assessing individual differences in the anger programme. Factor models may change according to statistical decisions of researchers, but individual differences in anger's activation and outputs do not.

Converging evidence from previous studies

Recent empirical findings provide converging support for our conclusions. For example, in a large Serbian community sample, Sokolovska, Dinić, and Tomašević (2018) found that HEXACO Agreeableness was strongly negatively associated with measures of reactive aggression and aggressive bargaining, and that these aggression measures clustered together with the Agreeableness facets in a network analysis. Cheng, Tracy, and Henrich (2010) found similar patterns in relation to FFM Agreeableness. Montag and Panksepp (2017) found, as we did, that the ANPS Anger scale correlated moderately positively with FFM/Big 5 Neuroticism and moderately negatively with Agreeableness. Additionally, Hilbig, Thielmann, Klein, and Henninger (2016) reported that although HEXACO Agreeableness generally does not predict prosocial decisions in behavioural economic games, it selectively (negatively) predicts retaliatory action in response to unfair offers from other players—exactly the input–output mapping that would be predicted if (i) unfair offers indicate a low WTR, and (ii) Agreeableness describes differences in anger proneness. In a recent longitudinal experience sampling study of daily emotional dynamics, Wendt et al. (2019) found that, across three diverse samples, trait hostility (based on average experiences of anger in daily life) was the only emotional predictor of individual differences in self-assessed FFM/Big 5 Agreeableness. Finally, a recent review of evidence from emic and etic studies suggests that the associations of Agreeableness with anger-based aggression, hostility, and entitlement are cross-culturally universal (Thalmayer & Rossier, 2019).

Conclusions from Study 1

Together, these findings (i) establish that individual differences in the anger programme's propensity to activate are described primarily in the lexical parlance of HEXACO Agreeableness and (ii) underscore the imprecision of factor models in carving up the mind —indeed, the anger programme's inputs and outputs can be predicted and characterized precisely, regardless of their location in any descriptive factor solution.

STUDY 2: FACIAL EXPRESSIONS ARE DESCRIBED AS '(DIS)AGREEABLE' ONLY WHEN THEY ARE PERCEIVED AS ANGRY

In this next study, we tested experimentally whether one of the behavioural outputs of the anger programme—the anger face—selectively influences lexical descriptions of state 'Agreeableness'. The anger face is an early-developing (Stenberg et al., 1983) constellation of muscle contractions, containing both species-typical (Crivelli & Fridlund, 2019; Ekman, 1973) and culturally variable components (Barrett, Adolphs, Marsella, Martinez, & Pollak, 2019; Crivelli & Fridlund, 2019), which is universally recognized as an indication that the person making the expression is angry (Ekman, 1973). The anger face functions to (i) signal the angry person's commitment to recalibrating the WTR(s) of one or more targets (Reed, DeScioli, & Pinker, 2014) and (ii) facilitate bargaining for better treatment by exaggerating the angry person's apparent physical strength (Sell, Cosmides,

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& Tooby, 2014). Although anger can be activated without being expressed in the face, the anger face is a behavioural output of the anger programme that, when deployed, uniquely communicates its activation—and the intent to bargain for better treatment.

Methods

In order to test how the anger face—and other emotional facial expressions—influence lexical descriptions of Agreeableness, we used the FACES stimulus database (Ebner, Riediger, & Lindenberger, 2010; http://faces.mpdl.mpg.de/imeji/), which contains standardized facial photos of people expressing six different facial expressions: anger, disgust, fear, sadness, neutral, and happiness (Figure 3). As described in Supporting Information S2 (which provides a detailed description of the methods), we selected 48 stimulus people, representing men and women across age categories (young adults, middle-aged adults, and older adults). In an online study, 105 subjects recruited from Amazon MTurk (64 female; M_{age} = 31.69; SD_{age} = 9.69) rated the stimulus people on each of the facial emotions contained in the stimulus set (anger, disgust, fear, sadness, and happiness). Another 91 MTurk subjects (47 female; M_{age} = 40.36; SD_{age} = 12.17) rated the same stimulus people on the eight highest-loading indicators of the HEXACO Agreeableness factor from a large international study of personality factor structure (Lee & Ashton, 2008): 'Quick-tempered (−)', 'Hot-tempered (−)', 'Short-tempered (−)', 'Aggressive (−)', 'Agreeable (+)', 'Calm (+)', 'Patient (+)', and 'Peaceful (+)'. In both surveys (emotion ratings; Agreeableness ratings), facial emotion was experimentally manipulated by randomly presenting only one of the six emotion photos for each stimulus person. Thus, each subject rated all stimulus people, but only rated each stimulus person expressing one of the six facial expressions (Supporting Information S2.2). Interrater agreement was high for both the emotion ratings [intraclass correlation coefficient (ICC) = 0.96] and the agreeableness indicator ratings (ICC = 0.98).

Results

Emotion ratings as a function of target expression

We constructed a multilevel model with random intercepts specified for both raters and targets to examine the effect of target expression on emotion ratings (Supporting Information S2.3.1 for model details). Raters discriminatively recognized the emotions signalled by each facial expression; each emotion expression elicited a much higher rating of its corresponding emotion than any other emotion (ps < .001; see Figure S1, Supporting Information S2.3.1).

Agreeableness ratings as a function of target expression

We again constructed a multilevel model with random intercepts specified for both raters and targets to examine the effect of target expression on agreeableness ratings. As predicted if Agreeableness is a lexical description of anger's outputs, the anger face was rated as the lowest on Agreeableness, followed by facial expressions of disgust, fear, sadness, neutrality, and happiness (Table 3; Figure 3). Note that the effect of the anger face was large; for example, the same individuals were rated multiple standard deviations lower on Agreeableness when making the anger face than when manifesting a neutral (d = 1.90) or happy (d = 2.89) expression.

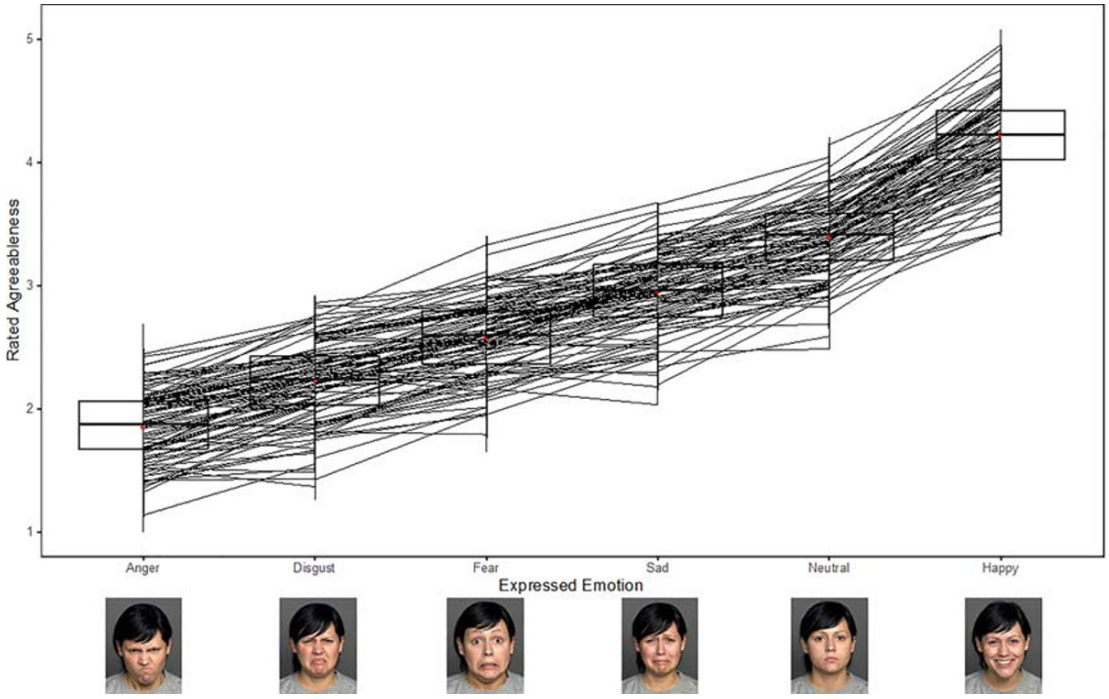

Figure 3. Boxplots showing changes in rated Agreeableness across facial emotion conditions in Study 2. Boxes define medians and quartiles. Each line represents an individual rater's average rating within each facial emotion condition. [Colour figure can be viewed at wileyonlinelibrary.com]

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Table 3. Pairwise comparisons of rated agreeableness between each emotion expression and the anger expression (Study 2)

	Estimate	*SE*	*df*	*t*	*p*
Disgust expression	0.369	0.040	4304.553	9.128	1.05E − 19
Fear expression	0.752	0.041	4298.967	18.141	6.25E − 71
Sad expression	1.112	0.041	4307.076	26.989	2.34E − 148
Neutral expression	1.560	0.040	4303.008	38.740	6.53E − 282
Happy expression	2.398	0.042	4312.212	57.267	0.00E + 00

Note: Estimates are from a cross-classified multilevel model with random intercepts specified for both raters and targets (see Supporting Information S2.3 for details). The anger expression was entered as the intercept, so each estimate represents the difference in rated agreeableness between the anger expression and the rated agreeableness for emotion expression being estimated (positive values indicate lower rated agreeableness for the anger expression). $N_{targets}$ = 48; N_{raters} = 91.

Agreeableness ratings as a function of facial emotion expression

We tested whether the effects of expressed anger on rated agreeableness were mediated by rated anger by constructing two, separate multilevel path models. For the first model, we included only the neutral and anger expression conditions as a dummy-coded variable (neutral expression = 0; anger expression = 1). For the second multilevel path model, we included all emotion expressions as dummy-coded variables. In both models, each of the continuous rated emotions variables (i.e. anger, disgust, fear, sad, and happy) were regressed on the expression variables, and rated agreeableness was simultaneously regressed on the five emotion ratings and expression variables (Supporting Information S2.3.3 for additional details).

These models demonstrated that effects of the anger face on Agreeableness ratings were powerful and specific. When all emotion ratings were competing mediators of the effect of the anger face (vs. a neutral expression) on rated Agreeableness, indirect effects only occurred through ratings of anger ($\beta = -.33$, $p < .001$) and happiness ($\beta = -.09$, $p < .001$); none of the other emotion ratings uniquely predicted rated Agreeableness (Figure 4; Table 4). Overall, direct and indirect effects of the anger face explained 89% of the variance in rated Agreeableness (Figure 4; Table 4).

In second model, which modelled the unique effects of all five emotional facial expressions (each compared to a neutral expression) on rated Agreeableness, each rated emotion was uniquely predicted by its corresponding emotional facial expression (Figure S2). Confirming the results from the first model, the anger face had the largest effect on rated Agreeableness, and indirect effects of all facial expressions only occurred through ratings of anger and happiness (Figure S2; Table S2). Together, these effects explained 88% of the variance in rated Agreeableness. See Supporting Information S2.3.3 for full effects decompositions (Tables S2 and S3).

Conclusions from Study 2

These findings demonstrate that a characteristic output of the anger programme—the anger face—strongly determines lexical descriptions of others' variation in state Agreeableness. They also, however, show that the lexical grammar of the HEXACO Agreeableness factor is applied to other subjectively aversive emotions (disgust, sadness, and fear), albeit

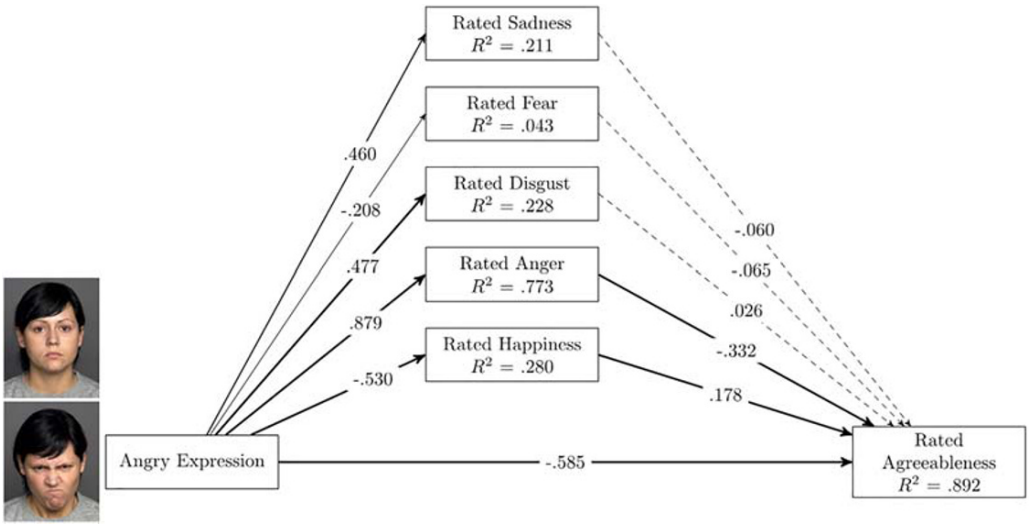

Figure 4. Depiction of multilevel path model testing direct and indirect effects of manipulated facial emotion on rated Agreeableness in Study 2. The paths depict the effect of the anger face (vs. neutral expression) on rated Agreeableness via all rated emotions. All coefficients are standardized estimates. Statistically non-significant associations are represented by dashed paths, and statistically significant associations are represented by thin solid paths ($p < .05$), thicker paths ($p < .01$), and very thick paths ($p < .001$). [Colour figure can be viewed at wileyonlinelibrary.com]

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Table 4. Total, direct, and indirect effects of anger expression on rated agreeableness (Study 2)

Path	Effect	*SE*	*p*
Total	− 0.918	0.014	<.001
Direct	− 0.585	0.067	<.001
Indirect (% mediated)	− 0.333	0.061	<.001
Anger (31.80%)	− 0.292	0.070	<.001
Disgust (1.30%)	0.012	0.027	.654
Fear (1.52%)	0.014	0.012	.275
Sadness (2.94%)	0.027	0.022	.211
Happiness (10.24%)	− 0.094	0.023	<.001

Note: Estimates based on 94 observations across 48 target-clusters (see Supporting Information S2.3.3 for model details). Specific direct effects for each emotion condition and emotion rating are presented in Figure 4 and Table S1.

to a lesser degree. Tellingly, though, indirect effects of facial emotion condition via ratings of facial emotion indicated that facial expressions of aversive emotions only impacted ratings of Agreeableness to the degree that the expressions were interpreted as 'angry'; for example, ratings of disgust *did not* mediate the effect of the disgust facial expression on ratings of Agreeableness. But ratings of anger *did* mediate the effect of the disgust expression (which is incidentally consistent with the adaptationist hypothesis that moral disgust has evolved as anger-like programme that activates in response to observing transgressions against third parties, rather than self-directed transgressions; Molho et al., 2017). Additionally, facial expressions of happiness had direct effects on all emotion ratings (Table S2; Figure S2), consistent with the conclusion that expressed happiness is taken more generally as an indication that no aversive emotions are activated. Interpretations of expressed anger are specific; interpretations of expressed happiness are diffuse.

Overall, the findings support the conclusion that within-person variation in emotional facial expressions is perceived and described as '(dis)agreeable' only to the extent that they are interpreted as angry—which in turn bolsters the more general hypothesis that variation in the anger programme's outputs is at the core of the descriptive construct, HEXACO Agreeableness.

STUDY 3: WITHIN-PERSON AND BETWEEN-PERSON VARIATIONS IN INFIDELITY-INDUCED ANGER ➔ LEXICAL DESCRIPTION OF 'AGREEABLENESS'

Study 3 was conducted to test emotional responses to a situation that is theoretically predicted to activate the anger programme: *a romantic partner's infidelity* (Goetz & Maria, 2019). Because people in monogamous romantic relationships are typically furtive when being unfaithful, cues to a partner's infidelity are probabilistic and often ambiguous, ranging from highly ambiguous (a partner showing decreased sexual interest within the relationship) to unambiguous (observing a partner passionately kissing another person) (Buss, 2000; Lewis, 2013). Given that the function of anger is to motivate bargaining for better treatment when a WTR is revealed to be too low, anger should activate least intensely when infidelity cues are absent or highly ambiguous, and more intensely to the degree that infidelity cues are unambiguous. In short, anger is predicted to activate to the extent that infidelity—and thus the insufficiency of a partner's WTR—is subjectively certain.

As explained below (and in Supporting Information S3), the current study made use of behavioural data from a study conducted by Lewis (2013). As participants in this study, people in romantic couples (i) read vignettes describing five scenarios containing variably ambiguous cues to their partner's infidelity (or fidelity) and (ii) gave written responses describing how they would respond in these five situations. For the current study, we had these passages rated for the author's state anger and state HEXACO Agreeableness.

We made predictions at both the levels of within-person and between-person variations. At the within-person level, we predicted that raters' perceptions of subjects' state Agreeableness across the infidelity scenario conditions would track ratings of state anger. Because the subjects in the study had completed selected scales from the IPIP-NEO-PI-R (Costa & McCrae, 1992)—including Neuroticism, which contains an Anger facet—we were also able to incorporate tests of whether individual differences in anger proneness (and other facets of FFM Neuroticism) predicted raters' perceptions of their written passages. On the basis of the findings from Studies 1 and 2, we expected that the NEO Anger facet (but not the other NEO facets) would uniquely predict between-person variation in rated anger and rated Agreeableness across scenarios, and that the association of NEO Anger with rated Agreeableness would be mediated by ratings of anger.

Methods

As subjects in the original study (Lewis, 2013), 102 heterosexual couples (N = 204) gave detailed written descriptions of how they would respond to five scenario vignettes containing variably ambiguous cues to their partner's infidelity. These scenario vignettes, which are presented in Table 1, describe situations containing variable cues of infidelity risk, from 'certain infidelity (#1)' to 'certain fidelity (#5)'. The intermediate scenarios (#2–4) contain increasingly ambiguous cues of infidelity risk (Table 5). After imagining each of these scenarios involving their actual romantic partner, subjects wrote passages about 'what they would feel, think, say, and do' in a text box. For the current purposes, we had eight blind raters read each of these 1020 passages (204 participants × 5 scenarios) written by subjects and rate them on (i) anger (N = 6) or (ii) a 10-item Agreeableness scale from the HEXACO-60 (N = 2; Ashton & Lee, 2009). Interrater agreement was acceptable for ratings of anger (ICC = 0.86) and agreeableness (ICC = 0.55) (see Supporting Information S3 for a detailed description of the methods).

Results

Rated agreeableness and anger across infidelity scenarios

We compared rated anger and rated agreeableness across infidelity scenarios in two, separate multilevel models. Rated

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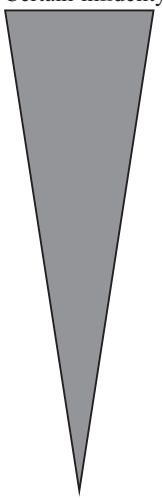
Table 5. Scenario vignettes describing variable cues to a partner's infidelity (i.e. low WTR) in Study 3

Vignette #	Infidelity risk	Scenario
1	Certain infidelity	Imagine you go to your partner's apartment without your partner expecting you. When you walk in to the bedroom, you find your partner in bed with another man (woman).
2		Imagine that your partner starts spending more and more time away from you. She says you she (he) is spending more time with friends, but your friends tell you that they have seen your partner alone with a certain other man (woman) on several occasions. You see your partner that day, and he (she) says she is going to hang out with her (his) friends that night and will not be able to see you.
3		Imagine you and your partner are at a party. At least once during the night you see your partner in a corner of the room talking and laughing with another man (woman).
4		Imagine that your partner starts spending more and more time with his (her) friends and no longer spends as much time with you. He (she) is going out again tonight, and does not invite you.
5	Certain fidelity	Imagine you and your partner have a romantic evening together with dinner and a date and spend the night together. The next morning, you wake up before your partner and are lying in bed.

Note: WTR, welfare trade-off ratio.

anger was specified as the outcome variable in the first model, and rated agreeableness was specified as the outcome in the second model (see Supporting Information S3.4.1 for details). Figure 5 shows changes in mean levels of rated anger and Agreeableness across scenario conditions. As predicted, rated anger was the lowest in the certain fidelity condition and exhibited a stepwise increase along with infidelity risk across the other scenarios, peaking in the certain infidelity condition (Figure 5). Rated Agreeableness exhibited the inverse pattern (Figure 5). See Supporting Information S3.4.1 and Table S4 for a full set of pairwise comparisons across scenario conditions.

Within-person variation and individual differences

We constructed a multilevel path model with anger and agreeableness ratings nested within targets and scenarios, and NEO Anger scores specified as a between-subjects factor (see Supporting Information S3.4.2 for details). Confirming our predictions at the within-person level, within-person changes in rated anger across the scenario conditions tracked within-person changes in rated Agreeableness (Table 6).

In support of our predictions at the between-person level, subjects' NEO Anger scores (but not the other NEO facets) were uniquely positively associated with rated anger and negatively associated with rated Agreeableness across scenarios (Table 6; Figure 6). Moreover, the association of NEO anger with rated Agreeableness was mediated by rated anger (indirect effect: $\beta = -.43$ [95% CI: -0.75, -0.15], $p = .001$) (Figure 6; see Tables S4 and S5 for all specific direct and indirect path coefficients).

Conclusions from Study 3

Taken together, these findings provide evidence that, in the context of romantic partner infidelity, (i) anger activates in proportion to the cue-based certainty that a partner's WTR is too low; (ii) within-person variation across situations in expressed anger is described by observers in the parlance of HEXACO Agreeableness; and (iii) individual differences in anger proneness uniquely predict between-person variation in others' perceptions of verbally expressed (dis)agreeableness through perceptions of expressed anger.

SUMMARY AND INTERPRETATION OF EMPIRICAL FINDINGS

The studies presented earlier support the claim that the anger programme is at least one key mechanism underlying the psychological and behavioural outputs captured in the person description construct, HEXACO 'Agreeableness'. Using a multi-method approach, we showed that self-ratings and other ratings on Agreeableness scales strongly track variation in the anger programme's outputs at both the levels of (i) between-person variation in anger's activation thresholds and (ii) within-person variation in the activation and behavioural expression of anger across situations. That this hypothesis was supported using diverse methods underscores the conceptual replicability of our conclusions.

The recalibrational theory was formulated according to an adaptationist analysis and has since led to multiple discoveries about the architecture of the anger programme. Anger functions to upwardly recalibrate WTRs in the minds of others, but the activation and operation of the programme vary across time, situations, individuals, and relationships. Thus, a detailed understanding of the anger programme leads naturally to a common mechanistic explanation for variation in anger that transcends the typical levels of analysis in personality psychology—for example, within-person versus between-person variation, and cross-situational consistency

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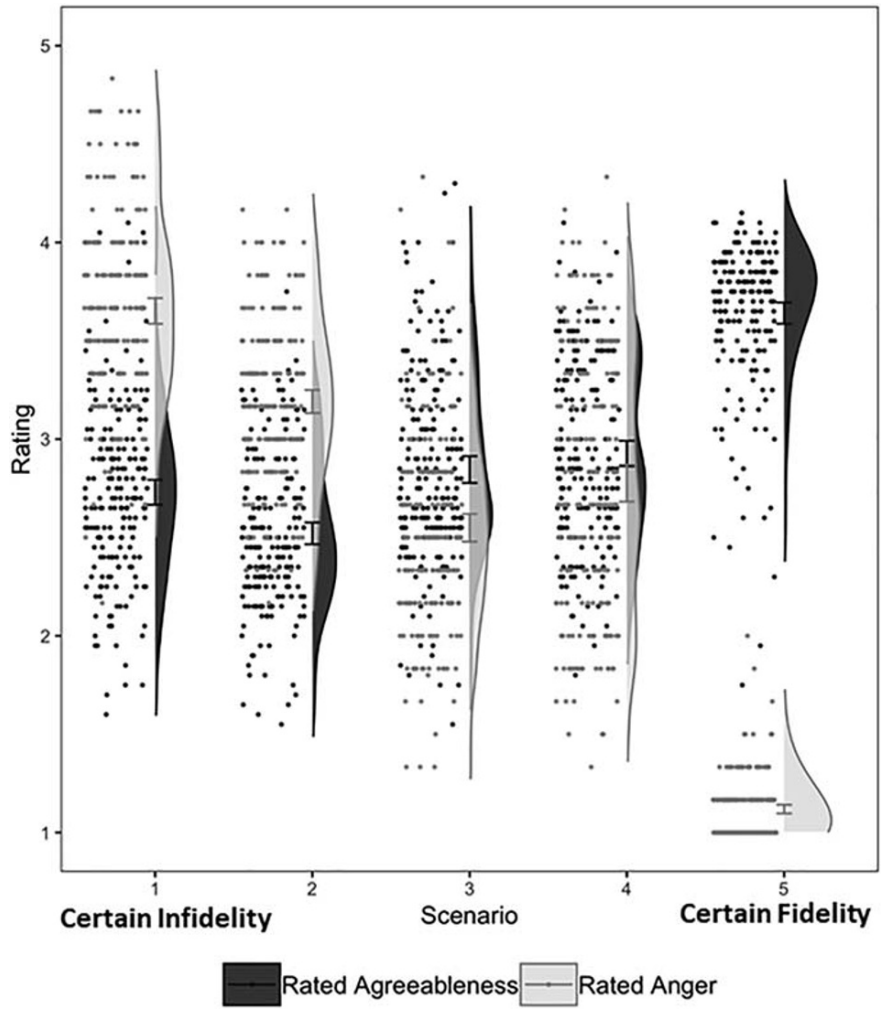

Figure 5. Plot showing distributions of rated Agreeableness and rated anger based on subjects' written passages in response to the infidelity scenario conditions in Study 3 (see Table 5 for scenario vignettes). Error bars are 95% confidence intervals about the mean.

Table 6. Within-subjects and between-subjects direct effects from mediation model of rated Agreeableness and Big 5 NEO Neuroticism facets

	Standardized estimate	*p*	Lower 95% CI	Upper 95% CI
Within subjects				
Rated anger ➔ Rated agreeableness	**− 0.41**	**<.001**	**− 0.465**	**− 0.352**
Between subjects				
Predicting rated agreeableness				
Rated Anger	**− 0.979**	**<.001**	**−1.101**	**− 0.838**
NEO Anger	0.108	.157	− 0.096	0.333
NEO Vulnerability	0.029	.404	− 0.206	0.282
NEO Anxiety	0.069	.304	− 0.197	0.330
NEO Depression	− 0.138	.072	− 0.336	0.049
NEO Self-consciousness	− 0.042	.338	− 0.241	0.150
NEO Immoderation	− 0.086	.147	− 0.248	0.074
Predicting rated anger				
NEO Anger	**0.434**	**.001**	**0.173**	**0.676**
NEO Vulnerability	0.179	.140	− 0.150	0.500
NEO Anxiety	− 0.042	.409	− 0.397	0.319
NEO Depression	0.084	.267	− 0.341	0.180
NEO Self-consciousness	− 0.211	.057	− 0.463	0.051
NEO Immoderation	− 0.004	.486	− 0.223	0.216

Note: Estimates based on 1020 observations across 204 target–clusters (see Supporting Information S3.4.2 for model details). Specific direct effects for each emotion condition and emotion rating are presented in Figure 6 and Tables S4 and S5.

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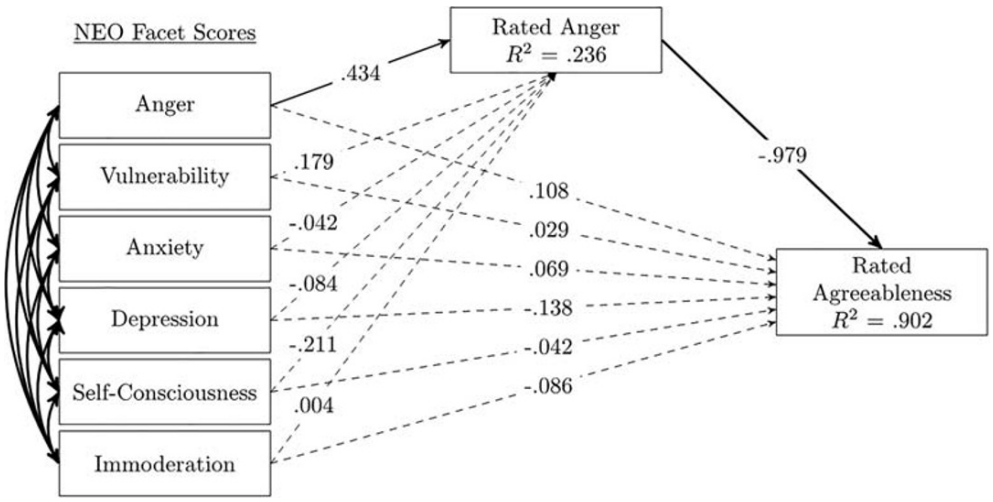

Figure 6. Multilevel path model testing direct and indirect associations of International Personality Item Pool (IPIP)-NEO Neuroticism facets with individual differences in rated anger and rated Agreeableness across scenario conditions in Study 3. All coefficients are standardized estimates. Statistically non-significant associations are represented by dashed paths, and statistically significant associations are represented by thin solid paths ($p < .05$), thicker paths ($p < .01$), and very thick paths ($p < .001$).

versus situationally specific variation. What we established here is that the lexical construct of HEXACO Agreeableness is organized around descriptions of variation in anger's activation and outputs. But the existence of this person description construct was irrelevant for the mapping of the anger programme.

Practitioners of more traditional approaches to personality research might wonder whether the recalibrational theory of anger simply afforded a re-description of a trait construct we already knew about; after all, do not our findings show that variation in anger is nearly isomorphic with variation in HEXACO Agreeableness? We contend that the recalibrational theory does demonstrably add explanatory and predictive value. Indeed, even if one knew that Agreeableness was largely tracking variation in an emotion experienced as and labelled 'anger', this would leave unexplained many of anger's properties that are explained by the recalibrational theory. For example, it would not tell us to expect that within-person variation in anger (and by extension, Agreeableness) in response to a transgression will depend critically on the magnitude of the benefit obtained by the transgressor, holding constant the cost they imposed on the self (Sell et al., 2017). Likewise, it would not afford the prediction that individual differences in anger's activation threshold will be calibrated to relative bargaining power (Goetz & Maria, 2019; Sell et al., 2009). Neither would it lead to the prediction that anger will deactivate on the basis of behavioural evidence that the target has upwardly recalibrated their WTR toward the self, without material recompense (Sell, 2005, 2011). These and many other of anger's design features allow us to predict anger's situation-specific activation and deactivation, toward whom anger will be directed, in whom anger will be more or less likely to activate in response to a given transgression, and which anger-motivated behaviours are more or less likely to be expressed in a given instance (e.g. whether to threaten to inflict costs on the target or probe for the target's reasons for behaving as they did). It seems rather unlikely that the existence of a person description factor would have led to these empirically supported predictions from the recalibrational theory.

Along similar lines, some readers might wonder whether 'anger' is just another lexical folk construct. In this context, it is important to note that the lexical labelling is rather unimportant for the recalibrational theory and the psychological adaptation whose existence it predicts. The recalibrational theory leads to the hypothesis that the human mind will contain an evolved mechanism designed to recalibrate insufficiently high WTRs and suggests various hypotheses about its design features. It was tentatively expected that the activation and expression of this recalibrational mechanism would match up with the phenomenological experience of the state commonly called 'anger'—speculation that, in this case, was supported by the data. As such, the label 'anger' was adopted for convenient and accessible reference. However, it could have been the case that the recalibrational adaptation was found to exist and contain the predicted design features but did not match up with the 'anger' lexical tag; in which case, a different label (and method for quantitative assessment) would have been selected. Even so, we note that as a label, 'anger' has the usual squishiness of lexical trait concepts: there are certain instances in which people describe themselves or others as 'angry' that do not reflect the operation of the evolved mechanism for WTR recalibration (e.g. someone might say they are feeling angry when they are frustrated while struggling with a solitary task). These considerations illustrate the limitations of folk trait categories and lexical tags for them but have no bearing on the utility of adaptationist analyses for discovering psychological mechanisms.

AN ADAPTATIONIST FRAMEWORK FOR PERSONALITY SCIENCE: PROSPECTS AND ADDITIONAL PRINCIPLES

The empirical findings presented earlier illustrate the utility of the adaptationist toolkit for discovering and characterizing

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psychological mechanisms that regulate behavioural variation within and between people. Adopting this mechanism-centred framework may permit scientists to carve the mind at its natural joints without the risk of conflating descriptive (e.g. lexical) trait constructs with underlying causal mechanisms. Conversely, once researchers have developed models of specific mechanisms for behaviour regulation, these mechanisms may constitute the psychological underpinnings of existing descriptive or lexical constructs.

In what follows, we outline some additional principles and prospects of the adaptationist framework that may help guide future research on human variation.

Cultural evolution as an important pathway to psychological design and variation

Thus far, we have presented an adaptationist framework that emphasizes the role of natural selection in causing the evolution of psychological adaptations designed to solve adaptive problems that were recurrently faced by humans across long stretches of our ancestral past. In the case of the anger programme, this would constitute species-typical architecture designed to solve the ancestrally recurrent adaptive problem of being insufficiently valued by others. The adaptationist framework does not imply, however, that a psychological mechanism shaped by natural selection will not exhibit cultural variability in its structure, operations, or outputs. Indeed, humans have evolved to be unusually dependent on socially transmitted information—that is, we are dependent on culture (Henrich, 2015; Kaplan, Hooper, & Gurven, 2009; Richerson & Boyd, 2008; Sperber, 1996; Tooby & Cosmides, 1992; Tooby & Devore, 1987; Van Schaik, 2016). As such, evolutionary psychologists postulate that psychological inheritance occurs via the tandem transmission pathways of genes and culture (Buss, 2001; Richerson & Boyd, 2008; Tooby & Cosmides, 1992). In the process of gene–culture coevolution, the designs of genomically based developmental mechanisms influence the emergence of cultural forms, which in turn constrain and direct the subsequent evolution of psychological designs via natural selection (e.g. Barrett, 2015; Boyer, 2018; Moya & Henrich, 2016). For example, ancestral humans evolved to be obligately dependent on cooked foods—without which we could not likely have evolved our large brains and small guts (Wrangham & Carmody, 2010). But the specific ability to control fire and use it for cooking is not likely encoded in the genome; rather, this ancestral innovation has been culturally transmitted and elaborated across thousands of generations (Wrangham & Carmody, 2010). Thus, cooking can be considered a complex functional behaviour, but it is one whose design and transmission—although enabled by genomically based adaptations such as language, cause-effect inference systems, and specialized learning mechanisms (Pinker, 2010; Tooby & Devore, 1987; Wertz & Moya, 2019)—arose most directly via *cultural evolution*.

Computational models of cultural evolution are used in conjunction with empirical studies to investigate the social transmission dynamics by which cultural designs (e.g. norms, skills, and institutions) arise, spread, and change within and between societies and generations. For example, cultural evolution research has generated empirically supported predictions about how biologically evolved psychological designs shape the cultural evolution of beliefs about bloodletting (Miton, Claidière, & Mercier, 2015), gods (Barlev, Mermelstein, & German, 2017), and food taboos (Placek, Madhivanan, & Hagen, 2017). It has likewise led to discoveries about the influence of socioecology on the cultural evolution of cross-population variation in individualism–collectivism (Dong, Talhelm, & Ren, 2019), tightness–looseness of social norms (Jackson, Gelfand, De, & Fox, 2019), social norms about the contexts of cooperation (Henrich et al., 2005; House et al., 2020), and lexical categories for person description (Kallens et al., 2018; Moya & Henrich, 2016) (for broader treatments, see Barrett, 2015; Boyer, 2018; Henrich, 2015; Morin, 2016; Richerson & Boyd, 2008; Sperber, 1996; Scott-Phillips,; Scott-Phillips et al., 2018; Wertz & Moya, 2019).

The premise that most psychological mechanisms contain design features that are shaped interactively by natural selection and cultural evolution has important consequences for the study of behavioural variation within and between societies. The development and operation of individual psychological mechanisms comprising the mind occurs within a particular cultural context that influences, for instance, which skills are required for subsistence (Kaplan et al., 2009), the situations in which different actions are (in)appropriate (Barrett et al., 2016; Park et al., 2013), and which specific social niches exist (Henrich & Boyd, 2008; House et al., 2020). As such, although we hypothesize that the deep architecture of the mind is substantially universal, we expect the manifest structure and content of human psychology and behaviour to be highly variable at the surface level (Barrett, 2015; Legare, 2017; Lukaszewski, in press; Sng et al., 2018; Tooby & Cosmides, 1990b). For example, a recent computational model predicts that variation in the number and diversity of culturally evolved social niches (e.g. occupational or social roles) across societies will generate cross-cultural variation in the population-level covariance structures of manifest behaviour (Smaldino, Lukaszewski, von Rueden, & Gurven, 2019). The predictions of this model are supported by empirical data showing that personality items vary less, and covary more strongly, in societies with low (relative to high) niche diversity (Gurven, Von Rueden, Massenkoff, Kaplan, & Lero Vie, 2013; Lukaszewski, Gurven, von Rueden, & Schmitt, 2017; Smaldino et al., 2019). This evidence that personality factor structures evolve culturally is perfectly compatible with the adaptationist model of human nature, which holds that the distinct mechanisms comprising the mind can produce many diverse configurations of manifest behavioural variation as they interact with socioecology.

The importance of sample diversity

The premise that the manifest content and structure of psychological adaptations are influenced by cultural and socioecological variation (and vice versa) points to the importance of studying human variation across many diverse kinds of societies. With few exceptions, studies of personality variation and structure have been conducted in modern

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industrialized societies that differ markedly from the smaller-scale societies in which humans evolved and existed for nearly all of our history as a species. Importantly, those few studies that have investigated personality constructs in small-scale ecologies (e.g. forager-horticulturalists) and marginal lexicons have not replicated the personality findings (e.g. the Big 5 and HEXACO factor structures; interrater agreement) observed in modern populations (e.g. Gurven et al., 2013, 2014; Saucier et al., 2014; Smith & Apicella, 2020; Thalmayer, Saucier, Ole-Kotikash, & Payne, 2019; von Rueden, Lukaszewski, & Gurven, 2015). To the extent that evolutionary and personality psychologists wish to understand and assess the full range of human variation in relation to culture and socioecology, it will be crucial to expand sample diversity (Barrett, 2015; Goetz, Pillsworth, Buss, & Conroy-Beam, 2019; Gurven, 2018; Muthukrishna et al., 2020).

We note that low sample diversity is a limitation of the research on anger and Agreeableness we presented earlier. Importantly, although we expect that the findings will generalize to other populations wherein the HEXACO and FFM/Big 5 factor structures replicate, we would not expect all the empirical results to directly replicate everywhere. Even if the abstract input–output mappings of the anger programme exhibit substantial cross-cultural universality (Hess et al., 2010; Sell et al., 2017), the location of anger's outputs in multivariate person description space may vary across populations. Anger can hardly be the mechanistic core of a broadband person description factor that does not 'exist' in a given population; but its behavioural outputs can still be perceived and described according to a similar, culturally evolved, lexicon across cultures.

Psychological adaptations must tailor behavioural decisions to specific situations and cultural contexts

The hypothesis that a psychological adaptation exhibits universal structure that maps activating inputs to behavioural outputs appears to some (e.g. Barrett et al., 2019) as being at odds with the obvious strategic flexibility and cultural sensitivity of human cognition and behaviour—which is indeed a hallmark of our species (Cosmides & Tooby, 2002; Gurven, 2018; Henrich, 2015; Kline et al., 2018; Kaplan et al., 2009; Pinker, 2010; Tooby & Devore, 1987; Van Schaik, 2016). In fact, however, the outputs of a universal psychological architecture are often expected to exhibit manifest variability in relation to situational and culturally evolved variables (Barrett, 2015; Gangestad et al., 2006; Hagen & Hammerstein, 2005). Given the massive set of possible 'on-the-ground' contingencies involved in solving a given adaptive problem in a specific circumstance, an evolved behavioural regulation programme requires access to a decision architecture that can precisely tailor behavioural decisions to the current situational and cultural context (Buss, 1991a; Kyl-Heku & Buss, 1996; Smaldino, 2019; Sznycer & Lukaszewski, 2019; Tooby & Cosmides, 1990a).

Consider the anger programme. Anger, when activated by cues that a target values the self insufficiently, must be able to improvise, or select from among, plausibly functional behavioural outputs—should I try to find out whether the act was done in error, make aggressive threats, or any number of other things? Of course, many situational and cultural factors determine which specific acts are optimal—or even sensical—in a given circumstance. Buss (1991a) proposed a hierarchical structure of behavioural output selection wherein specific behavioural outputs are nested within conceptual act categories. Given that the entire space of specific behavioural outputs that could be deployed in a given situation is nearly infinite—ranging from (rub your tummy) to (make a sexual proposition) to (brandish a weapon)—a decision architecture attempting to select outputs from this space would become paralysed in the face of combinatorial explosion (Tooby & Cosmides, 1992). Rather, anger, when activated, will circumscribe the decision space to the level of broad act categories [(probe reasons for poor treatment) vs. (withhold benefits), etc.] that would have helped solve the adaptive problem ancestrally (Buss, 1991a; Kyl-Heku & Buss, 1996). Next, having selected a broad act category [e.g. (withhold benefits)], anger must be able to tailor plausibly functional behavioural outputs [e.g. (imply I will stop introducing her to influential people) or (tell her I will not be sharing my mongongo nuts with her anymore)] to the details of the current situation, in light of the target's identity, and various situational and cultural variables.

The process by which the specific outputs of behaviour-regulating mechanisms are tailored to a particular situation is understudied (for steps in this direction, see Smaldino, 2019; Wood, Tov, & Costello, 2015) but may provide an example of how species-typical adaptations interplay with culturally evolved features. By hypothesis, anger's broad act categories for WTR recalibration [e.g. (inflict costs) vs. (withhold benefits)] may be substantially universal, whereas the specific anger-motivated behavioural outputs within these categories are improvised, evaluated, and selected in relation to culturally evolved norms (e.g. whether overtly displaying anger is acceptable or disvalued; Park et al., 2013), display rules (e.g. whether certain facial configurations signal anger more than others; Crivelli & Fridlund, 2019), and other features (e.g. the specific methods available in the local ecology for conferring benefits or inflicting costs). As a detailed picture emerges of how anger promotes selection of specific behavioural outputs, we anticipate the existence of massive variability in the surface-level details of anger's activation and expression. However, we also expect that such behavioural diversity will be abstractly unified by anger's recalibrational function: whatever behavioural outputs anger produces in a given instance or culture, they will appear designed to bargain for better treatment when insufficiently valued. A corollary of this analysis is that anger will exhibit more cultural universality at higher levels of abstraction (e.g. broad act categories) than at the more granular level of contextually situated behavioural decisions.

Heuristic trait concepts are useful for navigating social adaptive problems

Although cognitive and lexical trait concepts provide little information about the underlying mechanisms of behaviour

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regulation, they do provide critical windows into how people interpret, communicate about, and influence other people's behaviour. Difference-detecting mechanisms, in short, help people to solve social adaptive problems. Building on early versions of this hypothesis (e.g. Buss & Craik, 1983; Goldberg, 1981), Buss (1991a, 1996, 2011) characterized our behavioural concepts for person perception as components of evolved mechanisms designed to (i) guide interpretation of others' actions in order to predict their future actions with greater-than-chance accuracy (Buss, 1996, 2011; Fiddick et al., 2016; Funder, 1995; Gangestad, Simpson, DiGeronimo, & Biek, 1992; Lukaszewski, in press; Sng, Williams, & Neuberg, 2020; Wood, Gardner, & Harms, 2015) and (ii) communicate strategically useful information about the behaviours of self and others (Buss, 2011; Dunbar, 1996; Gurven et al., 2013; Kallens, Dale, & Smaldino, 2018; Pinker, 2010; Smaldino et al., 2019; Sperber, 1996).

These mechanisms for person perception and description are designed to help navigate adaptive problems posed by interacting with other humans: Who will be a reliable ally or long-term mate (e.g. Conscientiousness)? Who is likely to defect on social contracts (e.g. Psychopathy)? Who will rise in the social hierarchy (e.g. Surgency or Extraversion)? Who can be trusted (e.g. Honesty-Humility)? Who is easily exploitable (e.g. Gullibility)? Who is sexually permissive (e.g. Openness; Sociosexuality)? Where do I stand on these dimensions relative to others? More strategically effective decisions can be made with approximative answers to these sorts of questions than without them. Natural selection, according to this hypothesis, favoured the evolution of difference-detecting mechanisms—including machinery that constructs both behavioural concepts for perceiving and predicting others' actions (e.g. CHEATER; Cosmides, Barrett, & Tooby, 2010) and culturally evolved lexical descriptors for communicating about peoples' reputations or current behavioural states (e.g. 'unreliable'; Buss, 2011; Fiddick et al., 2016: Kallens et al., 2018; Scott-Phillips, 2014). Although research based on hypotheses about difference-detecting adaptations is in its infancy, this theoretical lens provides important links between traditional lexically based personality research and the evolutionary psychological approach advocated in this paper.

CONCLUDING REMARKS

Our guiding premise has been that if we are to discover the mechanistic underpinnings of personality variation, we must begin by asking—and provisionally answering—the fundamental questions of which behaviour-regulating mechanisms comprise the human mind and how they work. We have argued that the adaptationist toolkit of evolutionary psychology—broadly defined to include elements of biological anthropology, cognitive science, cultural evolution, evolutionary genetics, and computational modelling—can help take on this formidable task. To illustrate the explanatory utility and principles of the adaptationist framework, we presented research suggesting that anger is a psychological adaptation whose variable outputs are described in the parlance of the descriptive trait factor, 'Agreeableness'. By mapping the mechanistic design of anger, it is possible to seamlessly account for universality and variation in anger's activation and expression within and between situations, individuals, and cultures.

Looking toward future adaptationist personality research, it seems likely that other psychological adaptations will be discovered to constitute the mechanistic underpinnings of descriptive personality constructs. For example, we report elsewhere that the jealousy programme's outputs are described in the parlance of the HEXACO Emotionality and Big 5 Neuroticism factors (Lewis, 2013; Lewis et al., in prep). The Extraversion factor may descriptively capture the outputs of motivational mechanisms for navigating hierarchies (Anderson, John, & Keltner, 2012; Bernard, 2010; Cheng et al., 2010; Kyl-Heku & Buss, 1996; Neel, Kenrick, White, & Neuberg, 2016; von Rueden et al., 2015; Wood & Harms, 2017), avoiding disease (Schaller & Murray, 2008), and attracting mates (Nettle, 2006). The WTRs individuals hold toward others—and those they expect to receive from others—likely influence many aspects of prosocial and aggressive behaviour (Delton & Robertson, 2016; Sell, 2011; Sznycer et al., 2019; Sznycer & Lukaszewski, 2019; Tooby et al., 2008). Similarly, various psychological mechanisms may calibrate their operation in response to the values stored in internal regulatory variables for indexing one's social value to others (Denissen et al., 2008; Leary et al., 1995), representing the features of interdependent situations (Balliet et al., 2017), and estimating one's own mortality risk (Del Giudice, Gangestad, & Kaplan, 2015). Adaptations motivating the consumption of plant toxins to decrease pathogen burden (Roulette et al., 2014) may help explain variation in reward sensitivity, drug use, and addiction. The approach described and illustrated in this paper provides a general template for how to begin identifying these (and many other) linkages between psychological adaptations and extant personality constructs, including psychological 'disorders' at the extremes of these dimensions (Del Giudice, 2018).

Our hope is that the adaptationist framework we sketched in this paper can guide future attempts to build mechanism-centred models that carve the psychological foundations of personality at their natural joints. This is not, however, to discount the importance of integrating the tools of other frameworks. A productive future would be one in which evolutionary scientists work together with other personality researchers to identify points of connection between their research programmes. We suggest that a marriage of the empirical and quantitative sophistication of modern personality science with the predictive and explanatory power of the adaptationist framework has the potential to achieve the grand ambition that is shared by both of these scientific traditions: to construct a comprehensive model of human nature and its variations.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Figure S1. Boxplots showing emotion ratings as a function of the emotion expressed by the face stimuli. Boxes define medians and quartiles.
Table S1. Direct Paths from emotion expressions to rated emotions.
Figure S2. Multilevel path models testing direct and indirect effects of manipulated facial emotion on rated Agreeableness in Study 2. The paths depict the unique effects of each facial emotion (vs. neutral expression) on rated Agreeableness. All coefficients are standardized estimates. Statistically non-significant associations are represented by dashed paths, and statistically significant associations are represented by thin solid paths ($p < .05$), thicker paths ($p < .01$), and very thick paths ($p < .001$).
Table S2. Total, Direct, Indirect, and Specific Indirect paths to Rated Agreeableness
Table S3. Direct Paths from emotion expressions to rated emotions.
Table S4. Pairwise comparisons of rated agreeableness and rated anger across scenarios.
Table S5. Specific indirect, direct, and total paths from NEO Neuroticism facets to rated agreeableness.
Table S6. Model estimated correlations between NEO Neuroticism facets.

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