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A Human Model for Primate Personality

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Abstract

In this article I review the literature to determine how successful the latent trait theory model of personality from differential psychology has been for studying personality in nonhuman primates. The evidence for the success of this model is quite good and offers insights and directions for personality research in primates and other animals. This, I conclude, stems from a) the human trait model's simplicity and b) the fact that the human differential model of personality developed in the face of harsh criticism, which led researchers to test and refine their models.

Keywords: behavior, emotion, evolution, personality, primate, trait

Animal Models of Human Behavior and *Vice Versa*

The question of whether studies of human behavior can contribute to the understanding of behavioral evolution is an old one, and the debate that it has engendered is ongoing. In this paper I will show that using a "human model" of personality, developed within differential psychology, to study the evolutionary origins of individual differences in behavior, affect, and cognition, i.e., personality, in nonhuman primates (from now on, primates) has been a successful enterprise. Moreover, in a move that I hope does not distress the editors, I will sidestep answering directly the question posed by this special issue. Instead, I will describe why the human model is useful for studying primate personality and how it came to be that way.

Before discussing human models, I will present an overview of animal models. Animal models have been an important and powerful tool for learning about the evolutionary origins of humans behavior [1]. One would think then that critics of this model would be limited to the likes of creationists [2]. Unfortunately, displeasure and discomfort with the notion that we can learn about our behavior and its evolution by studying animals has not been limited to people outside the purview of evolutionary biology. For example, because he viewed them as excusing human vices, such as sexism, Stephen J. Gould wrote essays for scientific and lay audiences that criticized adaptationist explanations for human behavior that were based on studies of animals [3].

To some, the use of human models to understand animal behavior is also

controversial. Using humans as models to understand the evolutionary bases of behavior has a history that dates back at least as far as the use of animal models. The use of human models is rooted in the notion that evolution is gradual, and so related species will tend to be similar [4]. Prominent examples of the use of human models in the history of comparative psychology include Wolfgang Köhler's investigations into the intelligence of chimpanzees [5], and work by Robert Yerkes [6] and his colleagues, Donald Hebb [7] and Meredith Crawford [8], on chimpanzee personality. These and similar pursuits continue into the present day and have been enjoined by others (see articles in this issue).

The view that human behavior can inform us about animal behavior has been criticized by biologists and psychologists. One criticism is that the use of human models is an exercise in anthropomorphism [9]. In other words, the research is viewed as fatally flawed because researchers are said to project human characteristics onto animals. Another criticism invokes Morgan's Canon by stating that using human models risks incorrectly ascribing behaviors in animals to cognitive processes that are present in humans, instead of explaining these behaviors using simpler processes, such as associative learning [9–11].

If one were to try to discern what motivates these critics, one might conclude that they are attempting to preserve what some believe to be humans' "unique" place in nature. After all, these critics do not appear to apply the parsimony demanded by Morgan's Canon to descriptions of human behavior. Moreover, these critics appear to promote a more cautious approach to the study of animal behavior [11], which is not necessarily a bad thing. However,

in their pursuit of these goals, these critics ignore the question of whether using human models enables us to answer important questions about the evolution of behavior, cognition, or emotions.

So, how successful has the human model been as a foundation for primate personality research? I will beg off reviewing the literature. Instead, I will show that a major model of human behavioral traits has been an excellent starting point for understanding animal, and specifically primate, personality. I will do so by first discussing findings from behavioral ecology. On this point, I will be brief, but only because, despite attempts to bring these fields together [for discussions, see 12–14], the human model that I will describe has not yet been as influential in the behavioral ecology literature. I will then discuss in detail how this human model has been used by comparative psychologists to improve our knowledge about primate personality. Then, before concluding with a note about why this human model is so successful, I will highlight insights that it may lend to research on the personalities of primates, and possibly other animals.

The Two Disciplines of Animal Personality Research

Roughly speaking, two approaches are used to study animal personality. One is rooted in ethology and behavioral ecology, and the other is rooted in comparative psychology.

Behavioral ecologists who study personality base some of their methods

and constructs on studies of temperament in human infants and children [15, 16].[1] Methods for studying temperament were probably adopted by this group because they were based on behavioral experiments, such as novel object tests and behavioral observations, which could be modified to suit the study of personality in animals, and because they appealed to an aversion to so-called "subjective" measures [16].

The adoption of methods and constructs from human temperament research has been a boon for behavioral ecology for it has helped address two central questions about behavioral evolution. The first question concerns the origins of personality per se [17]. Specifically, why do behavioral differences persist in populations, especially when tracking environmental changes with behavioral changes would be a superior strategy. The second question concerns the maintenance of genetic, specifically, additive genetic, variation in populations. In other words, if personality traits are related to survival and/or reproductive success, how is the genetic variation in these traits maintained over generations within populations [18].

Behavioral ecologists identified plausible answers to both questions. Behavioral flexibility may be limited by, for example, covariations among traits, i.e., so-called "behavioral syndromes", that are mediated by common genetic effects, environmental effects, or other mechanisms [19]. Genetic variation may be maintained, for example, by changes, both over time and across environments, in whether a trait is related to higher, lower, or average fitness [e.g., 20]. Another plausible explanation is that the additive genetic variation

[1] And these measures appear to have been adopted from Hebb's work on chimpanzee temperament [7].

underlying personality reflects life-history trade-offs [21]. In other words, the standing of any individual on a personality trait is associated with benefits, such as reproducing more rapidly, which are balanced by costs, such as shorter survival times, so that the fitness for all individuals within a population is approximately equal.

The second approach has been adopted mostly by comparative psychologists. This approach is derived from human differential psychology, which is the study of psychological and behavioral differences within populations and between populations. When studying personality, comparative psychologists usually gather data on many traits, often by obtaining ratings, but also by other methods, including behavioral observations and/or behavioral tests. Comparative psychologists seek to understand, for example, what underlying dimensions these measures identify, how much genetic and environmental influences contribute to these differences, and the behavioral, real-world, and fitness consequences of these differences.

It is not clear why some comparative psychologists were drawn to the methods of human differential psychology. One possibility is that many of the founders of comparative psychology studied primates, including chimpanzees. The similarities between human and primate behavior may thus have led them to believe that personality could be readily measured, even by the use of ratings [e.g., 8]. An equally important factor may have been the influence of Robert Yerkes, for not only was he one of the most famed comparative psychologists of his day, he was also a leading figure in human intelligence research [22]. As such, expertise in psychometrics and measurement theory was close at hand.

So what is this human model that has been adopted by comparative psychologists? Starting with work by Charles Darwin's cousin, Sir Francis Galton, in 1884 [23], and extending into the modern era, research on human personality garnered multiple, replicated findings. These findings point to there being underlying processes that generate the behaviors and other signals that are the bases of our impressions of our own personalities and the personalities of others, including animals. These processes could be stable, functional characteristics of individuals, or processes that generate distributions of behavior with means and standard deviations [24] or reaction norms [25].

Whatever they are, because these processes cannot be directly measured, their existence is inferred from data, such as observations of behavior, reactions to behavioral tests, or answers to questionnaires. This conception of personality, then, resembles Robert Hinde's conception of rank as an "intervening variable" [26] or, as it is now known, a latent variable.

The work by comparative personality psychologists is largely based on a latent trait model of personality, which was developed in differential psychology. It is therefore worth reviewing findings from human data that support this model of personality.

First, personality traits are correlated in such a way as to suggest that they can be summarized by a few broad, weakly-correlated "dimensions" or, as they are sometimes called, "domains", together referred to as the personality structure [27]. There was disagreement at one time concerning how many domains were needed to summarize human personality differences [e.g., whether there are five or three dimensions, 28–31]. However, the field, for the

most part, has since come to agree that five major domains describe human personality variation [32].[2] This personality structure has been identified in many human cultures [34], although indigenous societies may prove to be exceptions [35].

Second, there is consensus between individuals and their friends, family, and others about where individuals stand on a particular trait or dimension [36]. Moreover, as one would expect if these impressions of raters were getting at something "real" about the person, agreement is stronger for people who know the individuals well [36].

Third, personality is mostly stable over time. Specifically, although there is disagreement about how stable personality traits are in adulthood and the degree to which change is attributable to biological versus environmental influences [37, 38], considerable research shows that individuals' relative standings on personality traits are stable [39] and that mean-level changes are not large [40].

Fourth, studies of twins, siblings, and families indicate that personality traits and domains have a genetic component [41]. Finally, studies of twins show that the domains defined by lower-level traits are products of common genetic influences and not because the lower-level traits that make up these domains have similar meanings or because we use folk theories of what traits belong together when we rate our own personality or the personalities of others [42–44].

These findings, then, indicate that personality measures tap into a few

[2]This debate has been rekindled as some now suggest that there is a sixth domain, honesty-humility [33].

basic underlying dimensions that describe how people differ from one another. However, they do not speak to whether these differences are related to something outside of the context in which they were measured. This is an important question that needs to be addressed if one seeks to determine the evolutionary bases of variation along these domains. In the past, the question of whether personality traits were real and valid was the source of heated debate [45]. However, there is now mostly agreement that individual differences in personality are associated with behaviors in other contexts [for impressive recent studies, see 46, 47]. There is also considerable evidence that individual differences in personality are associated with later life outcomes, such as relationship stability, success in school and work, socioeconomic status, happiness, mental and physical health, and length of life [48–51].

The Latent Trait Model and Primate Personality

Turning to our close animal relations, we can ask to what extent the evidence supports the latent trait model of personality in primates. Is there similar evidence for the interrater reliability, stability, heritability, and the external validity of primate personality measures?

Interrater reliability

Throughout the history of primate personality research, consensus of observers or raters has been well-documented. At the level of personality do-

mains, for instance, interrater reliabilities are comparable to and sometimes exceed those obtained when a person is rated by his or her peers [52]. Moreover, in ratings-based studies of primates, the interrater reliabilities of items are often obtained [e.g., 53]. These reliabilities are, as expected, lower than those of the domains [54]; however, they are similar to the interrater reliabilities of items from well-respected measures of human personality [55], such as the NEO Personality Inventory-3 [56], and to the repeatabilities of behavioral measures of animal personality [57].

Stability

Narrative descriptions of changes in the personalities of chimpanzees were reported by Robert Yerkes [6]. However, it was not until later that researchers conducted empirical studies on the rapidity and direction of these changes, and whether they led to changes in the rank-order of individuals on traits or domains. For the time being, I will consider only the latter question as the former question is not informative with respect to whether the latent trait model is applicable to primates.

Because obtaining stability estimates requires collecting personality measures at multiple time points, there have been fewer studies that investigated personality stability. That said, personality stability has been examined in multiple species, including three species of *Macaca* (rhesus monkeys, pigtailed macaques, and crab-eating macaques), brown capuchin monkeys, and the four species of great apes (orangutans, gorillas, chimpanzees, and bonobos).

Overall, there is good evidence for the stability of personality across many traits and domains, often over several years. These findings came from studies in settings as diverse as zoos and sanctuaries, laboratories, and the field, and in studies that used ratings to assess personality [58–65] and studies that used behavioral observations and tests [66–69]. In addition, one of these studies [58] found that among female rhesus monkeys who gave birth for the first time between assessments, there were marked declines in the stabilities of the confident and sociable domains, but not for the excitable domain

Heritability

Quantitative and molecular investigations into the genetic bases of animal personality variation have received considerable attention [70]. Although molecular genetic tools for studying the genetics of primate personality are more readily available than ever before, compared to its human counterpart, this research is in its infancy. Fortunately, statistical methods for estimating the genetic and environmental variation of traits from pedigrees allow researchers to address many of the same questions about primate personality [71].

Studies using these statistical methods have found that a moderate proportion of the variation in ratings-based personality dimensions of chimpanzees [72, 73], orangutans [74], and bonobos [75] to be attributable to additive genetic effects. Results consistent with these findings have been found in studies that use behavioral measures, including one of semi-free-ranging female rhesus macaques [67] and one of zoo-housed bonobos [75].

Validity

Reviews of animal personality in primates and other animals frequently address whether ratings-based measures are associated with behaviors, and invariably conclude that they are [for a review, see 52]. Less has been written about whether personality traits or domains are associated with life outcomes in primates. It is thus more difficult to reach a definitive conclusion on this question. However, studies have revealed associations between primate personality and measures related to social status [76, 77], learning, cognitive performance, and information processing [78–81], and health [82, 83].

A further question is to what extent do the personality structures tell us something about the species. The first thing to note when addressing this question is that researchers who study primate personality lack the kinds of data—twin self-ratings and self-/spouse-ratings—used to show that human personality domains are products of genetic relationships between traits. Fortunately, evidence from primate studies has been used to show that primate personality structures are not artifacts of the semantic similarities among the items that make up a scale, and they do not reflect implicit theories of personality or anthropomorphic projection, either. Some evidence comes from studies of personality ratings. For one, chimpanzees in zoos, a naturalistic sanctuary, and a research center [84, 85] all possess a similar set of six personality domains. The culture from which raters come also appears to have little influence on the personality domains that emerge from ratings of chimpanzees [86]. Note that there are possible exceptions: the differences between the personality domains of bonobos in zoos [65] and those in the wild

is fairly pronounced [87]. Additional indirect evidence comes from studies that show that, although there is some overlap, closely-related species, such as white-faced and brown capuchin monkeys [88], various macaque species [53], and humans, chimpanzees, and bonobos [65, 89], differ with respect to the personality domains that they possess.

There is also direct evidence that the personality dimensions identified by ratings are real. For one, the personality domains that emerge from behavioral observations in Hanuman langurs [90], crested macaques [91], and bonobos [92] resemble what we would expect based from ratings-based studies of these and closely-related species [for a discussion, see 93]. In addition, a study of chimpanzees and orangutans tested whether the personality domains revealed by ratings were products of bias or artifacts, and found that they were not [94]. Finally, the study of macaques cited above [53] found that differences in structure are meaningful: the configuration of traits related to aggression and social competence was related to the degree to which a species was despotic versus tolerant.

Insights from the Human Model

There is, then, reason to be optimistic. The latent trait model of personality that was developed by differential psychologists is a good model for describing primate personality. Thus, insights about personality in primates, and probably other species, can probably be gleaned from studies of human personality.

Who is rating or observing?

As I already mentioned, studies of humans find that the interrater reliabilites of ratings are good. However, studies of humans also find that interrater reliabilities differ as a function of who is doing the rating [36]. In addition, one study found that the type of personality trait that is being rated *and* from whom the rating is coming from jointly influence interrater agreement [95]. This study found, for example, that traits related to neuroticism were more accurately rated by the target and traits related to openness were most accurately rated by others.

These findings are consistent with our intuitions, i.e., that feelings of anxiety are less "visible" and that people like to think of themselves as 'creative' and 'intelligent'. These findings have important implications for studies of primates and other animals. For one, we should not expect uniformly high interrater or interobserver reliabilities or, if behavioral tests are used, repeatabilities; some traits may be harder to judge, see, or capture, respectively. Second, studies will benefit from multiple types of raters or observers with different perspectives. Studies that use behavioral tests may similarly benefit if they adopt multitrait-multimethod studies [96] and record a range of behaviors, including those that may not appear to be important.

Personality and aging

Earlier, I summarized the evidence for personality stability. However, as I noted then, the presence of rank-order stability does not exclude there being personality change. In fact, among humans, a modest to moderate

degree of personality change is ubiquitous: people increase in agreeableness and conscientiousness, and decline in neuroticism, extraversion, and openness [40].

Studies of primates have also found age differences in personality. These studies include those based on ratings [e.g., 77] and behavioral tests and observations [e.g., 68]. However, it appears that only two studies tested whether the rate of personality change in primates matches the rate found in humans. This is because the other studies did not scale the primate species' age to match that of humans. The two studies that did so found that the rate of change, if not always the direction, closely matched that of humans [60, 97].

One implication of these findings from studies that compare age effects on human and primate personality is that, regardless of how personality is measured, studies that test for species differences need to match on or control for developmental effects. Those that do not risk confounding species differences with age differences.

Genes, the environment, and genes for environments

As noted earlier, there is ample evidence from quantitative studies of personality that additive genetic effects explain a respectable portion of the variation in personality that we see in primates, including humans. One finding of these studies that surprises some people is that virtually none of the environmental influences on personality are those that would make siblings resemble one another [41]. Children, in other words, do not resemble

one another or their parents because of common rearing effects, but because they share genes with these family members. This finding leads to two questions [98]. First, how can we explain associations such as those between high maternal rank and protectiveness and greater vigilance on the part of infant rhesus monkeys [99]? Second, are there features of the environment that influence personality development?

The answer to the first question is that correlations, such as those found in rhesus macaques that I described above, could be the product of gene-environment correlations. For example, genes shared by the mother and child could be related to rank and/or protectiveness in the mother and vigilance in the infant, resulting in a passive gene-environment correlation [100]. Other gene-environment correlations may also explain associations between parental, social, or physical environments and personality. Active gene-environment correlations refer to a situation in which genetically-influenced personality traits or domains lead individuals to seek out specific environments or experiences [100]. To take a hypothetical example, correlations between how far mothers allow their offspring to stray and reduced infant anxiety may occur because venturesome infants may stray farther away from their mothers. Finally, evocative gene-environment correlations refer to a situation in which the personality of an individual elicits responses from others [100]. A hypothetical example of this sort of gene-environment correlation would be that infants who have a more difficult personality, e.g., those who are more aggressive or less compliant, may cause mothers to treat those infants differently than those with an easier temperament.

So far as I am aware, there have not been many (if any) direct tests to see,

for example, whether correlations between parental behavior and offspring personality in primates are, in fact, attributable to gene-environment correlations. Direct tests of these alternative hypotheses could include examining the genetic correlation between the purported causes and personality. Thus, the extent to which associations between parental or environmental differences and personality in primates are causal, and not mediated by genetic effects, remains largely unknown.

A possible answer to the second question also emerges from studies of humans that estimate the heritabilities of personality traits and domains [41]. The non-genetic effects that exist appear to be those that cause siblings to differ from one another, including the relative crudeness of personality measures. A one-time popular belief was that birth order might explain personality differences among human siblings; however, there is no scientific evidence for such an effect [101]. On the other hand, the possibility that peers influence personality development is plausible [for a discussion, see 98] and supported by some data [e.g., 102], and by the important role that social learning plays in primate (and human) behavior [103].

In addition to partitioning primate personality variation into that accounted for by genetic and different environmental influences, there is also a desire to find personality genes. In the early human literature, research in this area took the form of candidate gene studies where researchers tested for associations between variants of some gene and personality traits [104]. The genes investigated in these studies often were chosen because they were related to a neurotransmitter, hormone, or receptor, believed to be related to personality or temperament. However, these studies were based on small

samples and their findings did not replicate [105]. Fortunately, the decreasing price of technologies that enable researchers to genotype tens of, or even hundreds of thousands of, genetic polymorphisms, and the pooling of very large data sets, has led to a renewed burst of research and the discoveries of genetic polymorphisms related to human personality that are far less likely to be false positives [106].

At the time this article was written, the search for personality genes in primates largely used the methods of candidate gene studies. There has been cautious optimism about some findings. For example, an association has been found in two independent samples between polymorphisms of the arginine vasopressin receptor 1A gene and conscientiousness in chimpanzees [73, 107]. Even so, a lesson from the human literature is that the effects of single genes on personality will be small [108]. Consequently, molecular genetic research in primates needs to rethink how such studies are conducted. One possibility is for researchers to pool their samples and focus on genes for personality identified in high-powered studies of humans. Another possibility is to test whether polygenic scores [109] for personality traits, psychiatric conditions, or behaviors, derived in studies of humans can be used to predict personality phenotypes in primates or other species.

How the human model informs behavioral ecology research

I have held off discussing ways in which the human model could be a useful starting point for behavioral ecologists. I have largely done so because

researchers in this area tend to focus on non-primate species. Consequently, I do not expect that some of the findings I discussed earlier, such as those pertaining to shared environment effects, to hold in these species. I will thus restrict this section to a discussion about latent variable models of animal personality and some idle speculation about behavioral syndromes.

The mixed effects models used by behavioral ecologists to test for the repeatability of behavioral traits [110] imply that the traits measured in these studies are also products of underlying processes. This fact has only recently been openly acknowledged, but this insight has already led to the development of structural models of multiple traits in, for example, birds [111].

Regarding behavioral syndromes, as noted earlier the human literature suggests that correlations among lower-level traits are attributable to common genetic influences [43], which appear to be largely the same, even across different populations (cultures) [44]. In addition to these findings, as I previously noted, there appears to be some conservation of this structure across species [65, 89]. Studies of behavioral syndromes are finding that the phenotypic and genotypic structures of personality traits match in animals, too [112]. Thus, personality structures and behavioral syndromes may be homologous.

If behavioral syndromes and personality structures do indeed describe the same phenomenon, then research on behavioral syndromes could be informed by the human literature. This could lead to a better understanding of why these correlations, whether they are in humans, primates, or other animals, are preserved. It may be, for example, that the costs of any trait or traits

within a syndrome/domain are offset by the benefits associated with other traits in that domain. Another scenario to consider is that one trait, or single traits, by themselves, are either neutral with respect to fitness, strongly related to fitness, or harmful, but, taken together, are strongly related to fitness [for a detailed discussion, see 19]. Moreover, as I noted elsewhere [14], research on human personality profiles related to maladaptative behavior may provide insights into the origins of behavioral syndromes. Specifically, this literature may highlight combinations of traits that lead to poorer functioning and reduced fitness. Personality profiles of high achievers, such as Presidents of the United States, may also lead to a better understanding of the mechanisms that maintain and disrupt correlations among personality traits [113].

The Triumph of the Human Model

Although it is tempting to conclude on a triumphant, self-vindicating note, doing so would waste an opportunity to consider why the human model has been successful when applied to the study primates and, perhaps, to other species. Two reasons, both based on observations of the characteristics of successful fields of scientific research [114], come to mind.

The first reason is that trait theories of human personality are simple, straightforward, and linear descriptions of the major features of personality. This is despite the fact that human personality is bound to be multiply determined by many thousands of genes, the effects of which may vary across situations, samples, and cultures. Models of human personality that attempt

to account for all of these influences (or even a handful of them) are bound to be useless for understanding primate personality.

The second reason is that trait theories were challenged in the late 1960s and early 1970s [45]. Trait theorists responded to these challenges by conducting research that tested these claims. In other words, the reactions to these criticisms led to models that better described human personality and, apparently, did a fairly good job in describing primate personality, too.

Researchers who seek to use the human model to understand behavior or cognition, then, need to attend to whether the model of the phenomenon derived from human data has the right level of description. If not, it may be worth devising and testing simpler models for animals. More importantly, it is vital to not be overly sanguine; initial research should, as rigorously as possible, try to rule out the human model as an acceptable description of the phenomenon. John Capitanio's initial foray into personality research is an excellent example of this practice [115].

Thus, there is no reason why young researchers should not look to humans to try to better understand some behavioral or cognitive phenomenon in animals. However, doing so requires more than researchers who are bold and imaginative enough to devise tests of these models. These researchers also have to be willing to be their own worst enemy, and humble enough to reject human models if they fail critical tests. It is only thus that we will find better models to understand these phenomena in animals and humans alike.

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