Available online at www.sciencedirect.com
ScienceDirect
Brain, Behavior, and Immunity 22 (2008) 651–661
BRAIN, BEHAVIOR, and IMMUNITY
www.elsevier.com/locate/ybrbi

Full-length Review

Bridging human and animal research: A comparative approach to studies of personality and health

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Received 19 October 2007; received in revised form 21 January 2008; accepted 22 January 2008
Available online 14 March 2008

Abstract

This article evaluates a comparative approach to personality and health research. We (1) review evidence showing that personality exists and can be measured in animals, (2) illustrate the benefits of animal studies for human personality research, (3) illustrate the benefits of human studies for animal personality research, and (4) provide guidelines for making cross-species comparisons. We conclude that a comparative approach can provide unique insights into personality psychology, especially into research on personality, immunity, and health.
Published by Elsevier Inc.

Keywords: Personality; Comparative research; Immunity; Health; Animals; Humans; Psychoneuroimmunology

1. Introduction

Comparative research has played and continues to play a central role in many areas of psychology, including learning, sensation and perception, memory, and psychopathology (Domjan and Purdy, 1995). Here we argue that comparative research also has an important contribution to make to personality psychology, especially to studies of personality and health. Indeed, with advances in genomics, neuroscience, and phylogenetics, the potential contributions to be made by cross-species research are greater than ever. And with continued progress in the measurement of personality in animals and in identifying cross-species generalities in personality traits, the assessment of personality in animals also stands on increasingly solid ground.

The idea that animals can be used to study connections between personality and biological processes is not new. In his 1931 text *The Physical Basis of Personality*, Charles Stockard used a frontispiece composed of three pairs of photographs (see Fig. 1). Each pair included two faces side-by-side, one depicting a dog and the other a human, to illustrate some striking similarities in physical features between the dogs and humans. He suggested that similar underlying biological mechanisms were responsible for the similarities in both the morphological features and the personality traits associated with each pair.

Stockard was not alone in his assertion that comparative research can contribute to personality psychology. In the 1935 handbook of social psychology (Murchison, 1935), more than a quarter of the 23 chapters focused on non-human subjects. In the 1954 handbook, the number of chapters on animals had diminished but the usefulness of comparative research was still being championed; in one chapter, Hebb and Thomson argued that social psychology will "be dangerously myopic if it restricts itself to the human literature" (p. 532). Unfortunately, this warning was not heeded, and personality research in animals fell out of favor. Yet over the past decade, investigators across a broad array of fields have again begun to examine animal personality. As a result, new discoveries about personality processes are emerging that could not have emerged with human research alone.

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0889-1591/$ - see front matter Published by Elsevier Inc.
doi:10.1016/j.bbi.2008.01.008

Fig. 1. Frontispiece from Stockard's (1931) *Physical Basis of Personality*.

In this article, we explore the ways in which this new wave of cross-species research can provide unique insights into personality and immunity research. Our goal is two-fold: (1) to demonstrate to animal researchers that animal personality exists, can be measured, and has important implications for immunity and health; and (2) to demonstrate the value of animal personality research to researchers of human immunity and health. We start by asking some basic questions: What is personality? And why is it important to research on health and immunity? Second, we review the latest developments in the resurgent field of animal personality. We evaluate the evidence that personality exists and can be measured in non-human animals. We also review and summarize the major traits that have been identified. Third, we explore the ways in which animal studies can contribute to personality and immunity research in humans. Fourth, we illustrate how insights from human personality studies can help advance animal

personality research. Finally, we provide some guidelines for a comparative approach to personality psychology.

2. What is personality?

Most theoretical and empirical work on personality has been conducted in humans. Human-personality psychologists come in a variety of orientations and often differ in the personality constructs they emphasize. There is no one specific definition of personality that would satisfy all researchers who study personality. Only a broad definition would satisfy most. One such broad definition of personality is the characteristics of individuals that describe and account for consistent patterns of affect, cognition, and behavior (Pervin and John, 1997).

It is worth noting a few additional constructs relevant to personality so that the literatures on them can be incorporated into this review. Temperament is a construct closely related to personality. In human research, temperament has been defined by some researchers as the inherited, early appearing tendencies that continue throughout life and serve as the foundation for personality (Goldsmith et al., 1987). Although this definition is not adopted uniformly by human researchers, animal researchers agree even less about how to define temperament. In some cases the word "temperament" appears to be used purely to avoid using the word "personality," which some animal researchers associate with anthropomorphism. Other animal researchers prefer terms such as "behavioral syndromes" or "behavioral types" to describe personality (Sih et al., 2004). For the purposes of this article, we do not distinguish between these terms; we refer to all of them collectively as "personality."

3. Why is personality important to health and immunity research?

Research in humans has demonstrated important relationships between personality, immunity, and health (Segerstrom, 2000). One robust finding is that lower conscientiousness predicts negative health outcomes, including an increased risk of all-cause mortality (Christensen et al., 2002; Martin et al., 2007; Weiss and Costa, 2005; Wilson et al., 2004) and more rapid disease progression (O'Cleirigh et al., 2007). For example, O'Cleirigh et al. (2007) tracked patients living with HIV and measured markers of disease progression over the course of 1 year; higher conscientiousness predicted increases in CD4 cells and decreases in viral load, indicating slower disease progression in high-conscientiousness individuals.

Other research has examined the relationship between neuroticism and health, although the results have been mixed. Some studies found that neuroticism increased the risk of physical health problems (Goodwin et al., 2006) and mortality (Christensen et al., 2002; Shipley et al., 2007; Wilson et al., 2004), others found that neuroticism was a protective factor (Weiss and Costa, 2005), and yet others found null relationships (Martin et al., 2007). These contradictory findings suggest that the effect of neuroticism on health may be moderated by additional factors, such as characteristics of the study samples, the environment, or other individual difference variables.

Personality traits such as sociability and hostility have also been linked to health outcomes. For example, one study of 334 human adults found that higher levels of sociability were associated with lower susceptibility to the common cold (Cohen et al., 2003). High sociability also predicted behavioral markers of social support, including more daily social interactions, and more pleasant social interactions. Another 20-year longitudinal study of 2105 men in the Air Force Health Study showed that depression, hostility, and anxiety were all independently associated with an increased risk of developing coronary heart disease (Boyle et al., 2006). Importantly, the combination of depression, hostility, and anxiety was a stronger predictor of coronary heart disease than any of these personality traits alone. Taken together, these studies demonstrate some important personality–health links, but how exactly do personality traits such as conscientiousness, sociability, and hostility influence an individual's susceptibility to disease, illness, and mortality?

One possible mechanism is that personality may influence how an individual responds to his or her environment (Capitanio, in press). Specifically, personality can affect (1) which environments an individual appraises as challenging, and (2) how an individual copes with the challenging environment (Capitanio, in press; Sapolsky, 1998; Segerstrom and Miller, 2004). The individual's appraisal and coping style can influence the physiological stress response, such as activation of the hypothalamic–pituitary–adrenal axis and sympathetic nervous system (Capitanio, in press; Sapolsky, 1998; Segerstrom and Miller, 2004). These stress response systems can affect immune function, making the individual more or less vulnerable to illness and disease or influence the course of disease (Segerstrom and Miller, 2004). In short, personality traits are thought to affect how an individual reacts to the environment, leading to changes in immunity that may be mediated by physiological stress response systems (Capitanio, in press; Sapolsky, 1998; Segerstrom and Miller, 2004).

4. Review of animal personality literature

If comparative research is to help understand personality, immunity, and health, the first steps are to show that personality does indeed exist in animals and that it can be measured (Gosling and Harley, in press; Mehta and Gosling, 2006).

4.1. Does personality exist in animals?

To pet owners and many people who work closely with animals it seems self-evident that animals possess consistent individual differences in behavior; that is, they appear

to exhibit patterns of behavior that in humans would be referred to as "personality traits." However, many people, even some working in the sciences, have been reluctant to concede that personality exists in non-human animals. Their concerns range from philosophical arguments regarding the uniqueness of humans to methodological concerns about the perils of anthropomorphism (Gosling, 2001).

To address concerns about the existence of personality in animals, Gosling et al. (2003b; see also Gosling and Vazire, 2002) recently proposed three criteria from the debate concerning the existence of personality in humans: (1) assessments by independent observers must agree with one another; (2) those assessments must predict behaviors or other real-world outcomes; and (3) observer ratings must be shown to reflect genuine attributes of the individuals rated, not just the observers' implicit theories about how personality traits covary.

4.1.1. Criterion 1: Independent assessments must agree

If individual differences in personality exist and can be detected, then independent observers should agree about the relative standing of individuals on personality traits (Gosling et al., 2003b). Studies of humans rating other humans typically elicit interobserver agreement correlations in the region of .50 (e.g., Funder et al., 1995), supporting the idea that humans agree with their ratings of one another and providing a standard by which judgments of animals can be evaluated.

There is now a substantial corpus of research showing that observers agree strongly in their ratings of animals. Gosling (2001) summarized the findings from 21 rating studies of animal personality; the mean interobserver agreement correlation was .52, matching the magnitude of consensus correlations typically obtained in human research.

4.1.2. Criterion 2: Assessments must predict behaviors and real-world outcomes

For personality traits to be of any use, ultimately they must predict behaviors and real-world outcomes. Though few animal studies exist in which personality measures have been tested (Gosling, 2001), the evidence for concurrent and predictive validity is strong. Personality traits have been shown to predict specific behaviors (Pederson et al., 2005), occupational success (Maejima et al., 2006), and health outcomes. For example, Capitanio et al. (1999) found that, four to six weeks after experimental inoculation with the simian immunodeficiency virus, high sociable animals had lower viral load than did less sociable individuals.

4.1.3. Criterion 3: Ratings must reflect attributes of targets, not observers' implicit personality theories

Several studies of personality structure in animals have identified a number of broad dimensions, which often resemble dimensions found in studies of humans (Gosling and John, 1999). These findings could be taken as evidence that animals have personality. However, it is possible that observers are not detecting the true structure of personality traits in animals, but are instead simply "filling in the blanks" using their knowledge of human personality structure. Although most animal studies of personality structure are based on personality ratings (e.g., "curiosity"), a small number of studies are based on behavioral tests (e.g., response to novel object) and carefully recorded ethological observations (e.g., time spent exploring environment). Unlike the ratings-based factors, such behavior-based factors cannot be explained solely in terms of observers "filling in the blanks" on the basis of the semantic similarity of the traits. Moreover, in cases where cross-study comparisons can be made, the factors obtained from behavioral codings resemble factors obtained from observer ratings, suggesting that both methods assess the same underlying constructs (Gosling and John, 1999). Overall, the findings suggest that the structure of personality ratings is based, at least in part, on real attributes of the individuals being rated.

4.2. Can personality be measured in animals?

Having shown it is meaningful to refer to personality in animals, the next step is to determine whether it can be measured. This question was examined directly in a study comparing side-by-side the accuracy of personality ratings of dogs to the accuracy of personality ratings of humans (Gosling et al., 2003b). Parallel procedures and instruments were used to compare personality judgments of 78 dogs and their owners in terms of three accuracy criteria: internal consistency, consensus, and correspondence. On all three criteria, judgments of dogs were as accurate as judgments of humans, again suggesting that personality differences do exist and demonstrating that personality traits can be measured in animals.

4.2.1. Rating versus coding

Broadly speaking, the two main methods for measuring personality in individual animals are coding of an animal's overt behaviors, and subjective ratings of broad traits by knowledgeable observers (e.g., human caretakers). These two methods reflect different resolutions to the supposed trade-off between quantifying personality in terms of objective behaviors and using humans to record and collate information more subjectively. Behavioral coding methods are used to gather data from test situations designed to elicit personality-relevant responses (e.g., exposure to a novel stimulus) or from observations of naturalistic behavior (Freeman et al., in press). Ratings are used to gather data from either of the above contexts (test situations and naturalistic behavior) as well as drawing on the accumulated experience of humans who know the animals well. To quantify personality traits with the rating method, humans are generally asked to rate each of the animals on a number of personality traits. There are typically multiple observers who complete ratings, and occasionally the ratings are

made at several points in time (Gosling, 2001; Weiss et al., 2006).

Behavior codings have been used more widely than ratings in animal-personality studies; a review by Gosling (2001) found that 74% of animal-personality studies had used behavior codings to assess personality, and only 34% had used trait ratings. However, direct comparisons of the two methods suggest that rating methods may be better than behavior coding methods for capturing personality traits because rating methods are generally more reliable, are not as subjective as is sometimes assumed, and are much more practical (Vazire et al., 2007). In one study, the mean intraclass correlation (a measure of reliability) was .42 for behavior codings, but was .61 was trait ratings, suggesting that trait ratings are well-suited for detecting consistencies in animals' behaviors, the very foundation of personality (Vazire et al., 2007). Behavior codings in contrast are often difficult to measure reliably, particularly when observations are made across different times of day or under varying conditions. But even when behaviors can be coded reliably, they may reflect other characteristics of the environment (e.g., situational influences) and not personality. Thus, the extant data suggest that behavior codings are not poor measures of *behavior,* but that they may be poor measures of *personality*. Behavior coding methods may be better suited for experimental manipulations, where researchers are concerned with detecting the effects of situational variables on behavior (Vazire et al., 2007).

4.3. Personality dimensions across species

Empirical research on animal personality is essentially comprised of studies of traits—behavioral regularities that are relatively consistent across time and contexts. Commonly studied personality traits include: exploration, boldness, fearfulness, aggression, general activity, emotionality, confidence, and timidity.

To get a better idea of which traits emerge in structural analyses of personality, Gosling and John (1999) reviewed 19 factor analytic studies across 12 non-human species. They used the most widely accepted structure of human personality—the Five Factor Model (Wiggins, 1996)—along with the additional factors of Dominance and Activity to organize their findings. The Five Factor Model is a hierarchical model with five broad factors, representing personality traits at the broadest level of abstraction. These five bipolar factors are commonly labeled Extraversion, Neuroticism, Agreeableness, Conscientiousness, and Openness. The dimensions of Extraversion, Neuroticism, and Agreeableness showed considerable generality across the 12 species included in their review. Of the 19 studies reviewed, 17 identified a factor closely related to Extraversion, capturing dimensions ranging from Surgency in chimpanzees, Sociability in pigs, dogs, and rhesus monkeys, Energy in cats and dogs, Vivacity in donkeys, to a dimension contrasting Bold approach versus Avoidance in octopuses. Of course, the way these personality dimensions are manifested depends on the species; whereas the human scoring low on Extraversion stays at home on Saturday night, or tries to blend into a corner at a large party, the octopus scoring low on Boldness stays in its protective den during feedings and attempts to hide itself.

Factors related to Neuroticism appeared in 15 out of the 19 studies, capturing dimensions such as Fearfulness, Emotional Reactivity, Excitability, and low Nerve Stability. Factors related to Agreeableness appeared in 14 studies, with Affability, Affection, and Social Closeness representing the high pole, and Aggression, Hostility, and Fighting representing the low pole. Factors related to Openness were identified in all but four of the 12 species; the two major components defining this dimension were Curiosity-Exploration and Playfulness. Dominance emerged as a clear separate factor in seven of the 19 studies, and a separate Activity dimension was identified in two of the studies.

Chimpanzees were the only non-human species with a separate Conscientiousness factor, which was defined more narrowly than in humans but included the lack of attention and goal-directedness and erratic, unpredictable, and disorganized behavior typical of the low pole. The existence of a separate Conscientiousness factor in only humans and their closest relative suggests that the trait evolved relatively recently in the evolution of *Homininae*. The finding is consistent with the fact that both humans and chimpanzees have relatively developed frontal cortices, the area of the brain associated with higher executive function like making plans and controlling impulses (Beer et al., 2004).

5. The benefits of animal studies for personality, immunity, and health research

The above review demonstrated that animal personality exists, that it can be measured, and that there is considerable cross-species similarity in the dimensions of personality. These insights provide the foundation for a comparative approach to personality psychology. In this section, we discuss the obstacles that face human studies and illustrate how animal studies can help overcome some of these obstacles in research on personality, immunity, and health.

Research on personality and health in humans faces several challenges. Most notably, human researchers rely heavily on longitudinal data for drawing conclusions about personality, immunity, and health. But longitudinal studies in humans can take decades to complete, and are costly and logistically challenging because of the long lifespan and slow time course of disease progression. If health and immunity scientists were to rely on human studies alone, it could take several decades or more to identify personality–health relationships, to understand the factors that influence these relationships, and to delineate the mechanisms by which these relationships come about. Another challenge for human research is that it is difficult or

impossible to experimentally manipulate biological and environmental variables that are relevant to personality–health relationships (e.g., rearing experience, hormone levels) because of ethical and practical considerations (Gosling, 2001; Mehta and Gosling, 2006; Vazire and Gosling, 2003). As a result, even the most comprehensive human studies are subject to important limitations. Equivalent animal studies can be conducted with more efficiency and in more detail, and thus have the potential to inform research on human immunity and health.

Although animal research should not replace human research, studies in animals have already enriched our understanding of personality–health links and it appears that they will continue to do so. Animal models of sociability–health and neuroticism–health relationships may be particularly informative for human research because the findings in animals generally parallel those in humans (sociability as a protective factor; neuroticism as a risk factor in some studies, but unrelated to health outcomes in others; Capitanio, in press). Findings from animal research on coping–health and infant temperament–health links also show striking similarities to the human data, so a comparative approach can inform these areas of research as well (Cavigelli et al., 2006; Sapolsky, 1998; Schwartz et al., 2003; Vegas et al., 2006). Models in animals do not yet exist for the study of conscientiousness and health, but it may be possible to develop them in some species (e.g., chimpanzees, Gosling and John, 1999). Overall, parallel findings on personality, immunity, and health suggest that human researchers can look to animal models to address questions that are difficult or impossible to address with human data alone.

Animal studies are particularly well-suited for identifying two classes of variables that are relevant to personality–health relationships: mediators and moderators. Mediators are factors that stand between personality traits and health outcomes. These can include behavioral factors that may be influenced by personality, such as aggression and exploration, as well as biological factors, such as endocrine function, gene expression, brain activity, and immune parameters. Moderators are factors that affect the direction and magnitude of personality–health relationships. For example, certain environmental variables (e.g., rearing environment, stress exposure) could moderate relationships between personality traits and health outcomes; that is, a specific trait could have a beneficial impact on health under certain environmental conditions, but the same trait could negatively influence or have no influence on health under other conditions. In particular, we suggest that there are four major benefits of animal studies for understanding personality, immunity, and health:

5.1. Benefit 1: Greater experimental control

Animal studies permit experimental manipulations that are not possible in humans. These include the manipulation of biological (e.g., hormones, neurotransmitters, genes) and environmental factors (e.g., rearing conditions) that may influence personality and immunity. For example, research in non-human primates has shown that experimental manipulation of an animal's early life experience can affect both personality and immunity (cf. Capitanio, in press). These studies show that prenatal stress and maternal separation lead to the development of a behaviorally inhibited/low sociability personality, lower cellular immune function, and increased natural killer (NK) cell function. In contrast, nursery rearing leads to the development of a high-emotionality personality, enhanced cellular immune function and decreased NK function (Capitanio, in press). These findings suggest that early life experiences might also influence the sociability–immunity or neuroticism–immunity relationships in humans. Animal research also permits selective breeding that can result in production of large numbers of animals with desired temperament characteristics, as illustrated in the Mouse Phenome Database (www.jax.org/phenome). These large populations can be used to study how personality traits such as neuroticism or sociability affect immunity, disease, and mortality.

5.2. Benefit 2: Greater ability to measure physiological parameters

Animal studies afford greater opportunities to measure physiological parameters—such as markers of immune function, gene expression, and neuroendocrine function—that may be related to personality traits and health outcomes. For example, a recent study by Vegas et al. (2006) exposed tumor bearing and non-tumor bearing mice to social stress. The researchers measured corticosterone responses to a social stressor and behavioral coping strategies during the stressor. Immune function was measured 1 h and 3 days after the stress, and tumor development was measured 15 days after the stressor. The researchers found that social stress led to increased corticosterone levels and tumor development. However, mice characterized by a defensive and avoidant coping strategy during the social stressor showed the most severe tumor development. These findings suggest that social stress exacerbates tumor development, but that this effect depends on an individual's coping strategy in response to the social stressor. Such animal models can greatly inform human research because avoidant and defensive coping styles also predict negative health outcomes in humans (Sapolsky, 1998; Segerstrom and Miller, 2004).

5.3. Benefit 3: Greater opportunities for naturalistic observation

The observational opportunities afforded by animal research are far greater than those available in human research; relative to humans, animals can be observed for greater periods of time, in more detail, and in more contexts. These observational data allow researchers to study relationships among personality, the environment, and health in far greater depth than is possible in humans. To

illustrate, consider a research program by Capitanio, which for over a decade has been accruing personality data on over 175 rhesus monkeys (see Weinstein et al., in press, for a description of this research program). Members of Capitanio's group assessed their personalities at 5–10 years of age, identifying a four-factor structure, which was later confirmed with confirmatory factor analysis in a separate subsample. Animals were tested in a variety of social and nonsocial situations and behavioral and physiological measures were obtained in these situations for up to several years following the initial personality assessments; personality was found to predict various measures of social behavior and emotionality, plasma cortisol concentrations, tetanus- and herpesvirus-specific antibody responses, heart rate, and central nervous system functioning. Most recently (see contribution in this issue), this group has demonstrated that Sociability scores moderate the response to a social stressor, and influence the expression of genes associated with innate immune responses. This latter finding shows that the effect of sociability on immunity depends on the social environment, which could inform the study of sociability and health in humans (as another example of the benefits of naturalistic observations, see Robert Sapolsky's (1998) research program of naturalistic studies of personality, stress, and health in male olive baboons).

5.4. Benefit 4: Reduced time and cost of longitudinal studies

Fourth, the shorter lifespan of many animal species make it possible to conduct longitudinal studies that yield important insights in a timely manner and at a fraction of the cost of equally comprehensive human studies. Thus, animal research is well-suited for understanding the causes of personality development as well as the onset and progression of disease over the lifespan. For example, Cavigelli et al. (2006) used a longitudinal design to track female rats prone to spontaneous mammary and pituitary tumors. They assessed variation in exploratory temperament during infancy and hormonal function at various periods during the lifespan. They found that individuals with low-exploratory infant temperament died earlier than individuals with high-exploratory infant temperament. Moreover, there was evidence for differences in prolactin, estrogen, and progesterone functioning among low-exploratory and high-exploratory individuals. Taken together, the results demonstrate that infant non-exploratory temperament may be linked to tumor development and lifespan via neuroendocrine mechanisms. This animal model can inform human research because studies in humans have also identified an inhibited versus exploratory infant temperament style and have shown that it predicts outcomes relevant to stress and health (e.g., emotional reactivity; Schwartz et al., 2003).

5.5. Future directions

This section illustrated the benefits of animal research for personality, immunity, and health research, and we highlighted some recent studies that capitalized on these benefits. However, health researchers have only begun to tap the potential of animal studies, and there are many issues in the human literature that animal models may help resolve in the future. As reviewed earlier for example, research linking neuroticism to mortality has produced inconsistent findings, suggesting that the effect of neuroticism on mortality may be moderated by additional factors, such as the social environment, behaviors, or characteristics of the samples (Martin et al., 2007). Given the longevity of humans, it may take several decades to resolve this controversy with human data alone. Studies in shorter-lived animal species, however, may help explain the mixed findings on neuroticism and mortality, or at least point to potential answers that can guide further research in humans. As another example, human researchers have uncovered a robust positive relationship between conscientiousness and longevity (Christensen et al., 2002; Martin et al., 2007; Weiss and Costa, 2005; Wilson et al., 2004), but have struggled to identify mediators of this relationship (e.g., Martin et al., 2007). The challenges of human research make this issue difficult to resolve with studies in humans alone. But if an equivalent animal model could be devised (e.g., in chimpanzees, Gosling and John, 1999), this model could be a more efficient and cost effective means to identify the pathways through which higher conscientiousness leads to longevity.

As illustrated by the examples in this section, animal research can contribute greatly to our understanding of human personality and health. And the contribution of animal studies will only continue to grow as more animal models are developed that parallel personality–health relationships established in humans. We focused on the benefits of animal studies for personality, immunity, and health research, but researchers interested in other areas of personality (e.g., personality perception, personality development, the biological bases of personality) are equally likely to profit from animal research.

6. Applying lessons from human personality research to animal studies

The focus of this article thus far has been on what human researchers can learn from animal studies. However, the greatest progress will be made only if information flows both ways. In this section, we outline some of the major lessons emerging from the human personality literature that can be usefully translated to the animal domain.

6.1. Lesson 1: Applying principles of personality measurement

The principles of personality measurement are more developed in human research so animal studies can benefit from the lessons learned in that field. As mentioned earlier, behavior coding is the most widely used method for assessing personality in animals, followed by subjective ratings

(Gosling, 2001). But human personality research suggests that ratings are the superior method for assessing personality because ratings are generally more reliable and more practical. Even in a laboratory setting, human social behavior is very difficult to code reliably, and the coding process is labor intensive (Gosling et al., 1998, 2003a). Vazire et al.'s (2007) analysis in chimpanzees also indicates that ratings may be better than behavior coding for assessing personality, which suggests that the rating method should be used more widely in animal personality research.

Freeman et al. (in press) recently provided guidelines for the development of personality rating scales for use in non-human animals. They proposed a three-step model designed to maximize comparability across various species and to ensure comprehensiveness in generating trait-items specific to the species of interest (Gosling, 1998). The steps of this model are:

Step 1: Generate a comprehensive list of behavioral traits from three sources: previous research on animal personality, previous research on human personality, and expert nominations (Gosling, 1998).
Step 2: Eliminate redundancy from the list of behavioral traits suggested in step 1, preferably with the help of experts.
Step 3: Define each of the adjectives in terms of species-specific behavior.

Freeman et al. (in press) also offered additional recommendations for developing animal personality rating scales based largely on lessons from human personality psychology, including the use of multiple observers who know the animals well, and the computation and reporting of interrater reliability among the observers.

It should be noted, however, that the rating and behavioral coding methods both have strengths and weaknesses (Freeman et al., in press; Vazire et al., 2007). For example, it may not always be possible to implement the rating method if raters who know the animals well are not available. And although it is difficult and time-consuming to code behaviors, coding provides a very detailed and objective analysis of behavior in a specific context, which may be useful in some studies. Thus, when the time and resources are available, the best approach is to use a combination of behavioral-coding and trait-rating methods. One benefit to using both methods is that a researcher obtains information about both a context-relevant behavior (from behavioral-coding) as well as a broader view of the animal's personality (from trait-rating). In addition, multi-method designs allow better assessment of reliability and validity than their single-method counterparts (Pederson et al., 2005).

Another measurement issue emphasized in the human personality literature relevant to animal personality research is the importance of construct validity (Cronbach and Meehl, 1955). Construct validity includes ensuring that a particular personality assessment tool, such as a rating scale, measures the personality trait it should be measuring (convergent validity) but does not measure traits it should not be measuring (discriminant validity). Although human personality researchers generally pay attention to both kinds of validity, one review of the dog-temperament literature showed that studies often attended to convergent validity but rarely paid attention to discriminant validity (Jones and Gosling, 2005).

6.2. Lesson 2: Developing a framework for personality

Human personality psychology has gained some consensus on a basic, unifying framework for understanding the structure and organization of personality: The Five Factor Model (Wiggins, 1996). This model is not universally accepted, but it does provide a common language for human-personality researchers to compare findings. In contrast, animal personality researchers have not yet developed a common framework for characterizing personality within a specific species, let alone across species. In fact, most personality research in animals tends to focus on single dimensions of personality (e.g., emotionality) rather than multiple personality dimensions relevant to the species (Capitanio, in press).

Researchers can move toward a unifying framework by using a standardized set of personality characteristics that is supplemented with species-specific characteristics. This strategy would maximize comparability across species but also ensure comprehensiveness in the range of personality traits represented within the species of interest (Gosling, 2001).

6.3. Lesson 3: Theoretical richness of personality psychology

The human personality literature has more theoretical richness than the animal personality literature. For example, many theories of human personality distinguish between personality traits and motives (Capitanio, in press), and human researchers have laid out how these different levels of personality interact with each other (Winter et al., 1998). In contrast, animal personality research has yet to make a distinction between traits and motives. And although animal researchers distinguish between other aspects of personality, such as traits and coping styles, studies in animals have not yet clarified how these two aspects of personality are related. Perhaps animal researchers can draw on the theoretical developments in human personality psychology to help advance research on animal personality, immunity, and health.

6.4. Lesson 4: Overall approach to personality research

Another way animal researchers might benefit from human research comes in the overall approach taken to personality and individual differences (Mehta and Gosling, 2006). In many animal studies, researchers examine the links between various biological factors, personality traits, and health outcomes by changing the traits via

environmental or biological manipulations. At the same time, the researchers tend to pay less attention to the natural variation in traits that could also have informed their studies. This emphasis on manipulated differences reflects the strong focus on experimental control that pervades the animal literature, but there is no reason why these very same researchers could not shift their focus slightly to also draw on the naturally existing differences among animals. Such a shift in perspective would broaden the range of personality traits and health outcomes that are studied, which in turn, may yield new discoveries that would not emerge as readily with experimental designs. For example, comprehensive naturalistic studies that measure a variety of naturally occurring personality traits, biological factors, behaviors, and health outcomes may point to a previously unknown mediator or moderator of a personality–health relationship. Naturalistic research may also demonstrate new links between personality traits, immunity, and health. These discoveries could then be used to guide more controlled studies that manipulate key variables. Such an approach would increase the power to detect effects in controlled experiments, and as a result, would likely reduce the time, costs, and number of animals studied in these experiments.

7. Principles for cross-species comparisons in personality psychology

The sections above illustrated the benefits of animal and human research for understanding personality–immunity links. Ultimately though, the advantages of a comparative approach will emerge only when researchers can draw on studies conducted across species. In this section, we discuss some basic principles for making such cross-species comparisons (Gosling and Harley, in press; Mehta and Gosling, 2006).

One challenge facing any comparative researcher is determining the degree to which apparently similar traits really are tapping the same underlying trait. How can it be determined that what appears to be boldness in squid or trout or chimpanzees is in any way similar to boldness in humans? After all, there are very few literal similarities in how the same trait could be expressed across species. There are numerous cases of easy errors of interpretation; for example, the chimpanzee facial display in which the lips are retracted so that clenched teeth are exposed reflects fear, not happiness as might be assumed by the expression's apparent similarity to a human smile.

To solve this challenge, cross-species researchers can draw from the lessons learned by cross-cultural researchers. In a sense, a comparative researcher asking whether the apparently sociable behavior of a rhesus monkey reflects the sociability that we know in humans is analogous to the cross-cultural emotions researcher asking whether the apparently angry expression of a hitherto isolated group of humans reflects the anger that we know in our own culture. The solution to determining cross-cultural equivalence of anger expressions is examining what comes before and after the expressions, and where possible, looking for commonalities in underlying physiology. Thus, if this expression that resembles anger comes after an event that might reasonably elicit anger and results in actions that might reasonably follow anger and displays the physiological signature of anger, then the researcher can be reasonably confident that the facial expression does indeed reflect anger as we know it. Likewise, an animal researcher can examine the apparently sociable behavior in the context of what comes before and after the behavior and, where possible, if it shares physiological, biological, and genetic commonalities with human sociability. In essence, this procedure is what many animal researchers already do implicitly and explains why researchers with experience of a species do not make mistakes about behavior (e.g., mistaking a chimpanzee's fear grin for a smile). Nonetheless, this procedure offers a set of steps that researchers can take when they encounter unfamiliar species or when they want to establish cross-species equivalences empirically. As an example of an empirical approach to establishing cross-species equivalence, Flint (2004) reviewed evidence that the set of genes that influences emotionality in rodents also influences neuroticism in humans. These similarities were offered as evidence for cross-species equivalence in human neuroticism and rodent emotionality.

8. Conclusion

In 1931, Charles Stockard argued that by studying humans and animals side-by-side researchers could illuminate cross-species commonalities underlying biology and personality. Despite several decades in which the study of non-human animals was largely ignored by personality psychology, comparative research in personality is now on the comeback. The past 5 years in particular has shown incredible growth in comparative personality research, as researchers capitalize on its advantages for addressing questions that are difficult or impossible to address with humans or animals alone (Mehta and Gosling, 2006). And with rapid advances in neuroscience, genomics, and personality measurement, the potential translational contributions of cross-species research will only continue to grow. This article illustrated the benefits of a comparative approach for personality and immunity research, but we anticipate that in the coming years cross-species research in personality will continue to influence many other diverse fields, ranging from genetics, neuroscience, and psychology to behavioral ecology, primatology, and veterinary medicine.

Acknowledgments

Preparation of this article was supported by National Science Foundation Grant No. 0731216 awarded to

SDG. We thank Zezelia Olson and the three anonymous reviewers for their helpful comments on previous versions of this manuscript.

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