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# How Can Animal Studies Contribute to Research on the Biological Bases of Personality?

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In his text entitled *The Physical Basis of Personality*, Charles Stockard (1931) used a frontispiece composed of three pairs of photographs. 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. Stockard suggested that certain morphological features are associated with certain personality traits in both dogs and humans; he argued that the links between morphology and personality common to the two species may be driven by similar underlying biological mechanisms.

Seventy-five years later, there is no question that personality traits have a biological basis. The important questions that remain concern the nature of this basis, in terms of the biological substrates and processes that underlie traits. Many different methods can be used in the service of addressing these questions. Animal studies constitute one such method.

Stockard was not alone in believing that comparative research could illuminate the biological bases of personality. In the 1935 *A Handbook of Social Psychology* (Murchison, 1935), more than a quarter of the 23 chapters focused on nonhuman 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:

None of the chapters in the latest edition of this handbook (Gilbert, Fiske, & Lindzey, 1998) focused on nonhuman animals, and comparative research has virtually disappeared from social psychology.

Yet animal studies have continued to contribute to many other areas of psychology (Domjan & Purdy, 1995). Here we argue that animal studies still have an important contribution to make to personality psychology, especially studies of the biological bases of personality (Gosling & Mollaghan, in press; Vazire & Gosling, 2003). Indeed, with the emergence of new methods in genomics, neuroscience, physiology, and phylogenetics, the potential contributions to be made by animal research are greater than ever. And with recent 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.

In this chapter, we explore the ways in which animal studies can help shed light on the biological underpinnings of personality. In the first part of the chapter, we offer a brief review of recent advances in the field of animal personality. We evaluate the evidence that personality exists and can be measured in nonhuman animals. We also review and summarize the major traits that have been identified. The second part of the chapter uses two related personality traits—dominance and aggression—to illustrate some of the ways in which animal studies can elucidate the connections between biology and personality.

## REVIEW OF RECENT RESEARCH ON ANIMAL PERSONALITY

If comparative research is to help us understand the biological bases of personality, the first steps are (1) to show that personality does indeed exist in animals, (2) to show that it can be measured, and (3) to assess the degree to which personality traits generalize across species.

### Does Personality Exist in Animals?

To anyone who has worked with animals or who even owns a pet, the question of whether personality exists in animals probably seems preposterous. However, the question cannot simply be dismissed. After all, there was a period in the 1970s when a substantial body of psychologists seriously questioned the idea that personality exists in humans, and concerns that personality descriptions are mere anthropomorphic projections continue to be raised.

To address such issues, Gosling, Lilienfeld, and Marino (2003; see also Gosling & Vazire, 2002) recently evaluated the evidence pertaining to the existence of personality in animals. Explicitly drawing on the lessons learned from the debates surrounding the existence of personality in humans (Kenrick

& Funder, 1988), Gosling, Lilienfield, and Marino (2003b) considered three major criteria that must be met to establish the existence of personality traits: (1) Assessments by independent observers must agree with one another; (2) these assessments must predict behaviors and real-world outcomes; and (3) observer ratings must be shown to reflect genuine attributes of the individuals rated, not merely the observers' implicit theories about how personality traits covary. On all three criteria, animal personality research met the standards expected of human personality research, providing strong evidence that personality does exist in animals.

## Can Personality be Measured in Animals?

Having shown that it is meaningful to refer to personality in animals, we must next determine whether it can be measured. One study examined this question directly in a side-by-side comparison of the accuracy of personality ratings of dogs versus humans (Gosling, Kwan, & John, 2003). 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.

## Establishing Cross-Species Equivalence of Personality Traits

For cross-species comparisons to be useful, it is crucial to establish the cross-species generality of traits. For example, we must be confident that fearfulness in rats and fearfulness in humans are essentially the same thing. One response to the challenge of establishing cross-species equivalences in traits is to avoid making cross-species comparisons at the trait level, and instead to focus on the common biological underpinnings of traits that have already been identified in humans. For example, in a phylogenetic analysis conducted across a range of mammals, including tree shrews, rhesus monkeys, chimpanzees, and humans, Lesch and colleagues (1997) focused not on anxiety itself but on a gene sequence associated with anxiety (the serotonin transporter gene-linked polymorphic region, known as *5-HTTLPR*).

Another solution for determining the cross-species equivalence of personality traits is to take some of the principles established in cross-cultural research and apply them in the cross-species context. Consider the issue facing cross-cultural researchers when they go to an entirely new culture and encounter a facial expression that resembles the facial expression ordinarily associated with fear in the researchers' own culture. How can these researchers determine whether the expression that to them resembles fear actually *is* associated with the emotion of fear in this new culture? The solution is to look for similarities across the cultures in terms of the physiological underpinnings, antecedents, and consequences. Thus, if this fear-like expression is associated with physiological responses similar to those associated with known cases of fear, if it follows conditions that logically should induce fear (e.g., discovering a dangerous snake in one's bed), and if it produces reactions that logically should follow fear (e.g., fleeing from the snake), then a strong argument can be made that the fear expression is equivalent in both cultures.

Similarly, if an animal expressing a trait such as fearfulness meets these conditions (similar physiology, antecedents, and consequences), it is reasonable to treat the traits as equivalent across species. Of course, all of these conditions will rarely be formally tested in most cases; instead, it can reasonably be assumed that humans who have become familiar with a species in terms of its ecology and behavioral repertoire can probably recognize the expression of personality traits in that species. Therefore, studies that use personality ratings almost always rely on judges familiar with the target species.

## A Review of Cross-Species Evidence for Personality Traits

A large number of personality traits have been identified in animals, but are there any that show particularly strong cross-species generality? Most empirical studies of animal personality focus on just a single species, so cross-species commonalities must be identified by reviews that combine studies. One review summarized the evidence for cross-species commonalities in personality in 19 factor-analytic studies, representing 12 different species (Gosling & John, 1999). The findings were organized in terms of the human five-factor model plus dominance and activity.

The dimensions of extraversion, neuroticism, and agreeableness showed considerable generality across the 12 species included in the review. Of the 19 studies, 17 identified a factor closely related to extraversion, capturing dimensions ranging from sociability in pigs, dogs, and rhesus monkeys to a dimension contrasting bold approach versus avoidance in octopuses. Factors related to neuroticism appeared almost as frequently, 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 4 of the 12 species; the two major components defining this dimension were curiosity/exploration and playfulness. Chimpanzees were the only species with a separate conscientiousness factor; this factor included the lack of attention and goal-directedness and the erratic, unpredictable, and disorganized behavior typical of the low pole of conscientiousness in humans. Dominance emerged as a clear separate factor in 7 of the 19 studies, and a separate activity dimension was identified in two of the studies.

## DOMINANCE AND AGGRESSION AS PERSONALITY TRAITS

In our selective review of animal studies below, we focus on two traits that have enjoyed considerable cross-species support, and that can be applied without controversy to both humans and nonhumans: dominance and aggression.

Dominance has been considered a trait in several systems of personality developed in the human domain (e.g., Wiggins, 1979). In addition, many socially living animal species show individual differences related to status in the dominance hierarchy, so it is no surprise that dominance was identified in multiple studies reviewed by Gosling and John (1999). Further evidence has recently emerged, most notably in chimpanzees, to suggest that dominance can be considered a separate personality trait (e.g., King, Weiss, & Farmer, 2005).

Another trait expressed in humans and many other species is aggression, appearing several times in the Gosling and John (1999) review and in numerous other studies (see Gosling, 2001). It should be noted that many of the animal studies do not discriminate aggression from dominance; they often use aggressive behavior as a proxy for dominance. The purpose of the present chapter is to show how animal studies might inform human research, not to quibble about the ways traits have been conceptualized or operationalized. Therefore, for the purposes of this chapter we draw on studies from both the dominance and aggression domains, without focusing on the inconsistent distinctions maintained between these traits.

## THE BENEFITS OF ANIMAL RESEARCH

Although animal research should not replace human research, studies in animals have already enriched our understanding of the biological bases of human personality, and it appears that they will continue to do so. In particular, we suggest that animal research affords five essential benefits to the study of personality: (1) greater experimental control, (2) a greater ability to measure physiological parameters, (3) greater opportunities for naturalistic observations, (4) a shorter life span, and (5) greater opportunities to examine personality–health relationships. In this section, we explore these benefits, illustrating each one with animal studies of aggression and dominance. These studies are summarized in Table 20.1.

### Benefit 1: Greater Experimental Control

Animal studies permit experimental manipulations that are not possible in humans. As a result, animal models have yielded new discoveries about the hormones, neurotransmitters, genes, and environments associated with personality traits such as aggression and dominance.

TABLE 20.1. Animal Studies on the Biological Bases of Aggression and Dominance, Categorized According to Benefit

| Study | Animal species and gender | Main findings | Significance for personality psychology | Primary benefit | Secondary benefit(s) |
|---|---|---|---|---|---|
| Berthold (1849/1944) | Male chickens | Castrated chickens developed into nonaggressive capons, but castrated chickens reimplanted with testes in the abdomen developed into normal roosters. | Shows that the testes facilitate aggression. | Hormone manipulation (1a) | Naturalistic observation (3) |
| Briganti et al. (2003). | Male rabbits | Testosterone injections only increased aggression in high-ranking rabbits. | Shows a testosterone × social rank interaction in aggression. | Hormone manipulation (1a) | Naturalistic observation (3) |
| Veiga et al. (2004) | Female starlings | Testosterone-treated females hatched more sons; in addition, these females gained and maintained high social rank. | Shows that testosterone influences social rank in females. | Hormone manipulation (1a) | Naturalistic observation (3) |
| Ferris & Delville (1994) | Adult male hamsters | Hamsters injected with a vasopressin antagonist into the anterior hypothalamus decreased in aggression. | Shows that vasopressin is associated with aggression. | Pharmacological manipulation (1b) | |
| Delville et al. (1996a) | Adult male hamsters | Castrated and testosterone-treated animals administered serotonin and vasopressin agonists in the ventrolateral hypothalamus were less aggressive than animals not administered the serotonin agonist. | Shows interaction between serotonin and vasopressin in aggression. | Pharmacological manipulation (1b) | Hormone manipulation (1a) |
| Nelson et al. (1995) | Adult male mice | Mice lacking gene for neuronal nitric oxide synthase ($nNOS^-$ mice) were more aggressive than wild-type mice. | Identifies a gene associated with aggression. | Genetic manipulation (1c) | |
| Chiavegatto et al. (2001) | Adult male mice | The aggressiveness observed in $nNOS^-$ mice was caused by reduced serotonin turnover and impaired serotonin receptors. | Shows biological mechanism by which a particular gene influences aggression. | Genetic manipulation (1c) | Pharmacological manipulation (1b) |

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|---|---|---|---|---|---|
| Nomura et al. (2002) | Pubertal, young adult, and adult male mice | Male mice lacking the gene for estrogen receptor beta were more aggressive than wild-type mice as adolescents and young adults, but not as adults. | Shows gene × age interaction affecting aggression. | Genetic manipulation (1c) | Hormone manipulation (1a) |
| Ogawa et al. (1997) | Adult male mice | Male mice lacking the gene for estrogen receptor alpha were less aggressive than wild-type mice, despite having average testosterone levels. | Identifies gene associated with aggression, and suggests that the mechanism of action is not testosterone-dependent. | Genetic manipulation (1c) | Hormone measurement (2c) |
| De Jonge et al. (1996) | Female piglets, babies to adults | Piglets raised in a poor environment were more aggressive as adults than piglets raised in an enriched environment. | Shows that early environmental conditions influence adult aggression | Environmental manipulation (1d) | Longitudinal study (4) |
| Newman et al. (2005) | Male rhesus monkeys (3–5 years old) | Monkeys with low activity of the monoamine oxidase (MAO-A) gene that were mother-reared were more aggressive. | Shows a genotype × early rearing environment interaction in aggression. | Environmental manipulation (1d) | Gene promoter sequence variation (2c) |
| Oliveira et al. (2001) | Adult male cichlid fish | Fish watching a fight rose in testosterone, relative to those that did not watch a fight. | Shows an environmental influence on testosterone levels, which in turn may influence dominance and aggression. | Environmental manipulation (1d) | Hormone measurement (2c) |
| Delville et al. (1996b) | Adult male hamsters | Vasopressin receptor binding in the ventrolateral hypothalamus disappeared in castrated animals, but not in testosterone-treated animals; vasopression microinjections did not increase aggression in castrated animals, but did increase aggression in testosterone-treated animals. | Suggests a vasopressin-receptor-dependent mechanism by which testosterone influences aggression. | Hormone receptor binding measurement (2a) | Hormone manipulation (1a) |
| DeLeon et al. (2002) | Adolescent male hamsters | Anabolic–androgenic steroid treatment during adolescence increased vasopressin binding and aggression. | Suggests a vasopressin-receptor-dependent mechanism by which anabolic steroids influence aggression. | Hormone receptor binding measurement (2a) | Hormone manipulation (1a) |

*(continued)*

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| Study | Animal species and gender | Main findings | Significance for personality psychology | Primary benefit | Secondary benefit(s) |
|---|---|---|---|---|---|
| DeLeon et al. (2002) | Adolescent male hamsters | Anabolic–androgenic steroid treatment during adolescence increased vasopressin binding and aggression. | Suggests a vasopressin-receptor-dependent mechanism by which anabolic steroids influence aggression. | Hormone receptor binding measurement (2a) | Hormone manipulation (1a) |
| Filipenko et al. (2002) | Adult male mice | Social defeat resulted in greater expression of serotonin transporter (SERT) and MAO-A messenger RNA (mRNA). | Shows an environmental influence on gene expression, which may in turn influence aggression. | Gene expression measurement (2b) | Environmental manipulation (1d) |
| Pinna et al. (2005) | Female mice | Testosterone therapy increased aggression and decreased mRNA expression for 5-alpha reductase type 1. | Suggests that testosterone influences gene expression and aggression. | Gene expression measurement (2b) | Hormone, pharmacological, and environmental manipulations (1a,1b,1d) |
| Wingfield et al. (1990) | Birds | Testostosterone rose to facilitate intermale competition. | Shows that natural increases in testosterone facilitate aggression only during social instability. | Naturalistic observation (3) | Hormone measurement (2c) |
| Virgin & Sapolsky (1997) | Male baboons | Subordinate individuals that were aggressive after losing a fight had lower cortisol levels than subordinates that were not aggressive after losing a fight. | Shows a relationship between cortisol levels and aggression. | Naturalistic observation (3) | Hormone measurement (2c), personality and health (5) |
| Muller & Wrangham (2004) | Adult male chimpanzees | Testosterone levels and aggression were higher in dominant individuals. | Shows a relationship between testosterone levels and aggression, as well as between testosterone levels and social rank. | Naturalistic observation (3) | Hormone measurement (2c) |
| Muehlenbein et al. (2004) | Adult male chimpanzees | Testosterone levels were correlated with social rank. | Shows a relationship between testosterone levels and social rank. | Naturalistic observation (3) | Hormone measurement (2c) |

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| Holekamp & Smale (1998) | Adult male hyenas | Testosterone levels were higher in immigrant than in native to natal males; Testosterone levels correlated with social rank among immigrant males. | Shows a relationship between testosterone levels and social rank. | Naturalistic observation (3) | Hormone measurement (2c) |
| Adkins-Regan (1999) | Female zebra finches | Neonatal estradiol plus adult testosterone treatment increased aggression. | Shows that neonatal and adult hormone exposure influence adult aggression. | Longitudinal study (4) | Hormone manipulation (1a) |
| Wommack et al. (2003) | Male hamsters | Social subjugation during adolescence accelerated the development of aggression. | Shows an environmental influence during adolescence on the development of aggression. | Longitudinal study (4) | Environmental manipulation (1d) |
| Wommack & Delville (2003) | Male hamsters | Individual differences in coping response during social subjugation in adolescence predicted development of aggression. | Shows an individual difference × social environment interaction in the development of aggression. | Longitudinal study (4) | Environmental manipulation (1d), hormone measurement (2c) |
| Mejia et al. (2002) | Male and female mice | A prenatal pharmacological inhibition of MAO increased aggression in adulthood. | Shows a relationship between prenatal biological environment and adult aggression. | Longitudinal study (4) | Pharmacological manipulation (1b) |
| Granger et al. (2001) | Male mice | High-aggression mice exposed to a postnatal immune stressor were less aggressive as adults. | Shows an early temperament × biological environment influence on adult aggression. | Longitudinal study (4) | Environmental manipulation (1d), personality and health (5) |
| Tuchscherer et al. (1998) | Male and female pigs | Socially dominant pigs had better immune function than socially subordinate pigs. | Shows a relationship between social dominance and immune function. | Personality and health (5) | Naturalistic observation (3) |
| Veenema et al. (2004) | Young adult male mice | Long-attack-latency mice had higher stress responsivity than short-attack-latency mice. | Shows a relationship between aggression and stress reactivity. | Personality and health (5) | Environmental manipulation (1d), gene expression measurement (2b) |

*Note.* The numbers and letters in the “Primary benefit” and “Secondary benefit(s)” columns refer to the numbers and letters of subheads in the text section “The Benefits of Animal Research.”

### *a. Hormone Manipulation*

The ability to manipulate the presence or absence of hormones in animals has existed for a long time. The first formal endocrinology experiment was conducted in roosters by Arnold Berthold (1849/1944). Berthold found that when chickens were castrated during development, they developed into docile capons instead of normal roosters. These capons refrained from fighting with other males and failed to exhibit mating behavior. However, if the castrated capons were implanted with testes from other birds, they developed into normal roosters. Berthold had discovered the effect of the hormone we now know as testosterone on aggression and sexual behavior.

Hormone manipulations continue to be used today. Through techniques such as castration, injection, or capsule implantation, researchers are able to systematically study the relationships among hormones, biological processes, and behavior. In one recent study, rabbits were injected with subcutaneous testosterone propionate or a control substance (Briganti, Seta, Fontani, Lodi, & Lupo, 2003). All testosterone-treated rabbits increased in marking, digging, and defensive behaviors, but only the highest-ranking rabbits in each social group increased in aggressive behavior. This study showed that testosterone has an effect on aggression in rabbits, but that the effect is moderated by social rank.

In another study, female starlings were implanted with testosterone and placed back in their natural setting (Veiga, Vinuela, Cordero, Aparicio, & Polo, 2004). The testosterone-implanted females hatched more sons than the control females for up to 3 years after the treatment. In addition, the testosterone-treated females seemed to gain and maintain high social rank. These results suggest that the testosterone level of the mother has a direct impact on sex differentiation in offspring. In addition, testosterone may influence dominance among female starlings.

### *b. Pharmacological Manipulation*

Advances in pharmacology have allowed scientists to develop synthetic chemicals that can either enhance (agonists) or block (antagonists) the functioning of neurotransmitters (e.g., serotonin) and hormones (e.g., testosterone) in animals. Such drugs have helped researchers examine the specific mechanisms by which neurotransmitters and hormones affect aggression and dominance.

In one study, hamsters injected with a vasopressin antagonist into the anterior hypothalamus decreased in aggression (Ferris & Delville, 1994), suggesting that vasopressin plays a role in the expression of aggressive behavior. In a follow-up study, researchers castrated hamsters and treated half of them with testosterone (Delville, Mansour, & Ferris, 1996a). Next, the researchers injected fluoxetine (a serotonin agonist) or vehicle (a control substance) into the testosterone-treated hamsters. Finally, vasopressin was injected into all testosterone-treated animals. The researchers found that fluoxetine inhibited the effects of vasopressin on aggression, indicating that serotonin may inhibit aggression by blocking vasopressin functioning.

Such studies demonstrate how pharmacological manipulations can be used to understand the biological mechanisms underlying individual differences in aggression and dominance. Moreover, the second study (Delville et al., 1996a) shows how a pharmacological manipulation (the serotonin agonist fluoxetine) can be combined with hormone manipulations (testosterone and vasopressin manipulations) to examine the interplay between neurotransmitters and hormones. Future research in animals is likely to combine multiple methodologies (e.g., genetic, hormone, and pharmacological manipulations) to test complex models of the relationships among genes, neurotransmitters, hormones, and environments. Personality psychologists can profit from such powerful methodologies.

### c. Genetic Manipulation

Technological advances in molecular biology allow animal researchers to remove particular genes from, or insert them into, an animal's DNA. At this time the genetics of laboratory mice are relatively well understood, making them the primary target of genetic manipulation studies. Both knockout mice (those missing a specific gene) and transgenic mice (those in which a gene has been inserted) have been used to investigate the effects of genes on personality traits.

In one study, knockout mice lacking the gene for neuronal nitric oxide synthase ($nNOS^-$ mice) were more aggressive than wild-type (normal) mice (Nelson et al., 1995). This result suggests that nNOS is important for inhibiting aggression. A subsequent knockout study using $nNOS^-$ mice found that the increased aggression in the knockout mice could be attributed to disrupted serotonin functioning (Chiavegatto et al., 2001), suggesting that the effects of nitrous oxide on aggression was mediated by an impairment in serotonin.

In another study, researchers were interested in examining the effects of the estrogen receptor alpha gene on aggression (Ogawa, Lubah, Korach, & Pfaff, 1997). Previous research in mice had discovered that one pathway by which testosterone leads to aggression is through conversion into the hormone estradiol via the enzyme aromatase (e.g., Bowden & Brain, 1978). To find out which specific estrogen genes were involved, the scientists compared knockout mice lacking the gene for estrogen alpha receptors to wild-type mice. The knockout mice had average testosterone levels, but were less aggressive than the wild-type mice (Ogawa et al., 1997). These results suggest that the reduction in aggression was not due to reductions in testosterone, but rather to a disruption in estrogen receptor alpha functioning.

Together, these two studies show how discoveries regarding the relationships between genes and personality traits can be made by using knockout mice models. Such genetic manipulation studies suggest that the genes for nNOS and estrogen receptor alpha, along with several others (e.g., the monoamine oxidase A [MAO-A] gene, Cases et al., 1995; the serotonin 1B [5-HT$_{1B}$] receptor gene, Saudou et al., 1994) play a role in aggression. Because genes cannot be manipulated in humans, animal models afford unique opportunities to illuminate the genetic underpinnings of personality.

### *d. Environmental Manipulation*

Relative to human researchers, animal researchers are able to exercise greater control over the environments of their subjects. Thus animal studies provide excellent opportunities to examine the role of environmental factors, such as rearing practice, in personality development. For example, in a study of female piglets, those individuals raised in poor environments (an indoor farrowing crate) were more aggressive as adults than individuals raised in enriching environments (an outdoor pasture with a half-open farrowing crate; De Jonge, Bokkers, Schouten, & Helmond, 1996). In a study of rhesus macaques, mother-reared individuals had higher social ranks as adults than peer-reared individuals (Bastian, Sponberg, Sponberg, Suomi, & Higley, 2003). Such experimental animal studies may inform our understanding of how early environments affect personality development in humans (whose rearing environments cannot be manipulated experimentally).

## Benefit 2: Greater Ability to Measure Physiological Parameters

Animal studies afford unique opportunities to measure the physiological parameters that may underlie personality. This is because many of the techniques used to examine the biological events that lead to the expression of personality traits require decapitation and examination of brain areas, which are not possible in humans.

### *a. Measuring Hormone Receptor Density*

Autoradiographic technology can be employed in animals to examine the density of hormone receptors in various parts of the brain. High densities in particular brain regions indicate important sites of action for the particular hormone under investigation. Using receptor binding density as an outcome variable, researchers can investigate how various hormones interact to influence personality.

In one study, Delville, Mansour and Ferris (1996b) castrated golden hamsters and implanted half of them with testosterone capsules. Vasopressin and testosterone had been previously linked to aggression, so the researchers decided to examine the effects of testosterone on vasopressin receptor binding. After sacrificing the animals, the researchers performed *in vitro* autoradiography. They found that castrated animals had a very low density of vasopressin receptor binding in the ventrolateral hypothalamus area of the brain. In addition, microinjections of vasopressin failed to increase aggression in castrated males. The authors concluded that testosterone may influence aggression by activating vasopressin receptors within the ventrolateral hypothalamus. Consistent with this result, DeLeon, Grimes, and Melloni (2002) found that anabolic–androgenic steroid treatment in adolescent male hamsters led to increased vasopressin receptor binding in the ventrolateral hypothalamus. In addition, these steroid-treated animals were more aggressive.

Without the ability to measure hormone receptor binding via autoradiography in animals, it would have been much more difficult to examine the testosterone–vasopressin receptor relationship in aggression. Furthermore, this research provides an excellent candidate model for how anabolic steroids may influence aggression in human adolescents through their effects on vasopressin receptors in key areas of the brain.

### *b. Measuring Gene Expression*

The notion that genes and the environment exert independent effects on behavior is now considered simplistic and obsolete. Scientists now know that gene expression itself is influenced by both heredity and the environment (Hamer, 2002; Robinson, 2004). Variation in gene expression affects protein activity, brain processes, and ultimately behavior. Through the development of new genomic techniques using animal models, investigators can measure gene expression by quantifying the amount of messenger RNA (mRNA) produced by a particular gene. The ability to measure gene expression through mRNA allows researchers to consider complex, dynamic models of gene–behavior relationships. Not only can scientists investigate how environmental and hereditary factors interact to influence gene expression, but gene expression variation can also be examined as a predictor of subsequent brain processes and behavior (Gosling & Mollaghan, in press). Thanks to research conducted in animals, psychologists have begun to understand the interplay between hereditary and environmental influences on genetic activity and individual differences.

As an example, consider the animal research examining the effects of social defeat on aggression and the expression of serotonin genes. Social defeat and subordination have been associated with increased serotonin (Blanchard, Sakai, McEwen, Weiss, & Blanchard, 1993) and with decreased aggression (Huhman et al., 2003). Two substances, serotonin transporter (SERT) and MAO-A, are involved in the inactivation of serotonin (Filipenko, Beilana, Alekseyenko, Dolgov, & Kudryavtseva, 2002). Thus the effects of social defeat on SERT and MAO-A gene expression may provide clues about the genetic and biological processes that precede aggression. In one study, repeated exposure of adult male mice to social defeat resulted in greater expression of SERT and MAO-A mRNA than in either mice exposed to social victories or control mice (Filipenko et al., 2002). Thus it seems that social defeat induces the activation of the SERT and MAO-A genes. These findings suggest that the effects of social experiences (social defeats or victories) on aggression may be mediated by differential expression of various genes (SERT and MAO-A) within the serotonin system.

In other animal research, the effects of anabolic androgenic steroids on aggression have been linked to impaired functioning of the neurotransmitter gamma-aminobutyric acid (GABA) and its related genes (e.g., Miczek, Fish, & De Bold, 2003). When female mice underwent long-term testosterone therapy, they increased in aggression but decreased in mRNA expression for 5-alpha reductase type 1, a protein involved in GABA's functioning (Pinna, Costa, & Guidotti, 2005). This result suggests that testosterone treatment causes changes in gene expression, which in turn facilitate a disruption in the GABA neurotransmitter system and lead to increased aggression.

### *c. Other Opportunities for Physiological Measurement*

In addition, animal studies offer several other opportunities for physiological measurement. For example, new imaging techniques allow animal researchers to measure neuronal activity in response to particular stimuli with a greater degree of precision than is possible in human functional magnetic resonance imaging (fMRI) studies (e.g., Whitlow, Freedland, & Porrino, 2002). Consequently, researchers can observe the specific brain areas and neurons involved in a particular biological process or behavior. Another advantage of animal studies is the ease with which neurotransmitter or hormone concentrations can be measured, because these data are normally collected through intrusive access to cerebrospinal fluid, blood, or specific brain areas.

## Benefit 3: Greater Opportunities for Naturalistic Observations

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 greater observational benefits are particularly true of captive animals, which can be closely monitored in some cases from conception until death. However, scientists can also observe wild animals living in natural habitats and collect voluminous behavioral and physiological data. Consequently, questions about how behavior and physiology change over time, across seasons, or in response to environmental triggers can be addressed. Equivalent opportunities for detailed and extensive naturalistic observations are rarer in human research. The relative ease with which naturalistic observations can be performed in animals means that more clues can be collected about the biological correlates and environmental factors that influence personality traits.

Research by Wingfield, Hegner, Dufty, and Ball (1990) in a variety of bird species illustrates the benefits of naturalistic observations of animals. These investigators recorded data on testosterone levels as well as aggressive and paternal behaviors in a wide variety of monogamous and polygynous bird species. Wingfield et al. (1990) proposed the "challenge hypothesis" to account for the relationship between testosterone levels and aggressive behavior in birds. The challenge hypothesis posits that fluctuations in testosterone levels during the breeding season are more closely related to aggressive behavior than to sexual behavior. Specifically, testosterone levels seem to rise as the mating season commences but peak during periods of intermale competition, suggesting that the increases in testosterone levels facilitate aggression. In addition, this theory suggests that testosterone only relates to aggression when there is competition over mates or territory. Thanks to Wingfield and colleagues' research in birds, the challenge hypothesis has been studied and validated in other animal species (e.g., male chimpanzees; Muller & Wrangham, 2004). Unfortunately, this hypothesis has been overwhelmingly overlooked by human researchers of testosterone and dominance (e.g., Mazur & Booth, 1998).

Other researchers have also profited from the naturalistic observational opportunities afforded by animal studies. By studying freely roaming baboons living in the Masai Mara National Reserve in Kenya, Virgin and Sapolsky (1997) uncovered links among testosterone levels, glucocorticoid levels, social status, and aggression. These researchers found that when the status hierarchy was stable, subordinate baboons had elevated glucocorticoid levels and suppressed testosterone levels, relative to dominant baboons. However, they also found individual differences in aggressive behavior and stress responses among subordinate baboons. The subordinate baboons that aggressed against other baboons after losing a fight had higher testosterone levels and lower glucocorticoid levels than did the ones that did not aggress after losing. This finding suggests that individual differences in aggression affect stress responses (Virgin & Sapolsky, 1997). These naturalistic observations shed light on the relationships between endocrinological patterns and individual differences in aggression. Moreover, the finding that displaced aggression is related to lower stress hormone levels suggests that social status and variations in aggression may have health implications for humans.

## Benefit 4: Shorter Life Span of Animals

Longitudinal studies in humans bear heavy financial costs, can have high dropout rates, and may require waiting years or decades to answer the research questions of interest. Due to the shorter life span of many animal species, it is 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. Combined with the other benefits mentioned above, researchers can use animal studies to examine how genes, physiological variables, and the environment influence the development of personality.

For example, one longitudinal study examined how estradiol and testosterone hormone treatments influenced adult aggression in female zebra finches (Adkins-Regan, 1999). Half of the subjects were treated with estradiol for the first 14 days of life. As adults (just 100 days after hatching), the subjects were implanted with testosterone or an empty implant. The females that received neonatal estradiol treatment coupled with adult testosterone treatment were the most aggressive. These results indicate that adult aggression is increased by early-life estradiol treatment and is activated later in life with adult testosterone treatment. Moreover, the researchers were able to conduct this study in a matter of months, whereas an analogous study in humans would have taken years (even in the unlikely event that it had been approved by an institutional review board).

Other research has examined the effects of social subjugation in adolescent hamsters on the development of aggression. To induce social subjugation, male hamsters were exposed to an aggressive adult for several days during adolescence and were tested for aggressive behavior in later stages of development (Wommack, Taravosh-Lahn, David, & Delville, 2003). This form of social subjugation during adolescence was found to accelerate the development of aggressive behaviors. In another study, those hamsters that displayed fewer submissive behaviors during social subjugation in adolescence became aggressive relatively early in life (Wommack & Delville, 2003). These findings reveal that the ontogeny of aggression is influenced by experiences of social subjugation in adolescence.

In yet another study, prenatal pharmacological manipulations were conducted to assess their influence on the expression of aggressive behavior of male and female mice. The researchers found that a prenatal pharmacological inhibition of MAO increased aggressive behavior in adulthood (Mejia, Ervin, Baker, & Palmour, 2002). These results are consistent with other studies linking MAO to aggression and suggest that perinatal MAO exposure may have an impact on the organization of the nervous system, which in turn influences aggression (Mejia et al., 2002).

## Benefit 5: Greater Opportunity to Examine Personality–Health Relationships

One important application of research in personality is to understand the role of personality traits in health. Animal research is particularly well suited for investigating personality–health links, because of the greater experimental control (Benefit 1) and the greater opportunities to measure physiological parameters (Benefit 2) it affords. Not only can animal models reveal relationships between personality traits and health factors, but they can also detail the psychobiological mechanisms and developmental processes that underlie these relationships (e.g., Capitanio, Mendoza, & Baroncelli, 1999). Moreover, animal research can help investigators devise and test preliminary intervention programs that may improve health and well-being for at-risk individuals.

In one study, researchers investigated the relationship between aggression and three biological processes related to stress adaptation. Two lines of mice, a high-aggression line and a low-aggression line, were bred and tested for hypothalamic–pituitary–adrenal (HPA) axis functioning, hippocampal cell proliferation, and serotonin system functioning under typical and stressful conditions (Veenema, Koolhaas, & de Kloet, 2004). HPA axis functioning in response to an acute stressor (forced swimming for 5 minutes) became hyperactive in low-aggression mice, but not in high-aggression mice. In addition, low-aggression mice experienced a 50% reduction in hippocampal cell proliferation after the acute stressor, as well as a reduced increase in serotonin metabolism. Finally, exposure to a chronic stressor led to long-term rises in corticosterone levels in low-aggression individuals, but not in high-aggression individuals. These findings suggest that low-aggression mice have higher stress reactivity than high-aggression mice. In light of these results, the authors concluded that low aggression is predictive of a maladaptive coping style in mice, which may have implications for mood disorders in humans (Veenema et al., 2004).

A second study examined the effects of social status and aggression on immunity in pigs. Groups of pigs were placed together with unfamiliar pigs and tested for aggressive behavior and social dominance (Tuchscherer, Birger, Tuchscherer, & Kanitz, 1998). The results showed that socially dominant pigs had higher lymphocyte proliferation than subordinate pigs, suggesting that social dominance is associated with enhanced immune function.

## Summary of the Benefits of Animal Research

In this section, we have argued that studies in animals afford five major benefits to personality researchers. First, the greater experimental control available in animal methodologies allows scientists to examine the genes, hormones, neurotransmitters, brain processes, and environments that influence traits. Second, the greater ability to measure physiological parameters in animals can yield insights into the biological processes that influence trait expression. Third, naturalistic observational studies of animals may inform us about the physiological correlates as well as the environmental conditions that are related to individual-difference variables. Fourth, the shorter life span of animals enables researchers to conduct relatively efficient longitudinal studies. Fifth, animal research affords greater opportunities to study the relationship between personality and health.

Thanks to these advantages, we believe that animal research can contribute greatly to our knowledge about human personality, particularly about the biological underpinnings of personality traits. We have illustrated this point with animal studies of aggression and dominance, but researchers interested in other traits are equally likely to profit from animal research.

## ANIMAL AND HUMAN PERSONALITY RESEARCH: A TWO-WAY STREET

The focus of this chapter has been on what human researchers can learn from animal studies. However, this should not be taken to suggest that this process is a one-way street with all the useful information going from animal studies to human studies. The greatest progress will be made only if each field continues to draw on the lessons emerging from the other field.

There are many lessons emerging from the literature on human personality that can be usefully translated to the animal domain. For example, the principles of personality measurement are much more fully developed in human research, so animal studies can benefit from the hard-won lessons learned in that field. These include drawing on the effectiveness of rating (vs. coding) methods and the importance of attending to basic psychometric principles, such as construct validity (Cronbach & Meehl, 1955); for example, one review of the literature on dog temperament showed that studies of dogs often attended to convergent validity, but rarely paid attention to discriminant validity (Jones & Gosling, in press).

Another way animal researchers might profitably benefit from human research is in the overall approach taken to individual differences. In many of the studies reviewed here, the animal researchers examined the links between various biological factors and personality traits by changing the traits via environmental or biological manipulations. At the same time, the researchers paid less attention to natural variation in traits, which could also have informed their studies. This emphasis on manipulated differences reflects the standard perspective in the experimental 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 also broaden the range of studies on the biological bases of personality to include the many animal studies that do not use experimental designs.

## LOOKING FORWARD

Seventy-five years ago, Charles Stockard (1931) argued that animal research would help illuminate common biological systems underlying human and animal personality. Today, we know that human and animal personality traits do have common biological underpinnings, as Stockard believed. Furthermore, thanks to modern technological advances, the opportunities to examine these commonalities are greater than ever. With so much knowledge to be gained, it is time to rediscover the long-neglected bridges between personality psychology and animal behavior.

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