Animal personality and health

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(Accepted: 11 February 2005)

Summary
Animal models are used to study the physiological mechanisms underlying disease progression. In this paper, I examine the benefits of using animal models to study how personality or stable individual differences (in behavior and physiology) influence disease susceptibility and resilience. Such an expansion of animal model use, to study the relationships among personality, physiology, and health, provides a unique complement to human studies. Human studies are necessarily correlational and involve minimally-invasive physiological measures, whereas animal studies can involve experimental manipulations of potentially causal variables. For example, with animal models, genetic and environmental precursors of personality can be manipulated to test how behavioral response biases affect health, and physiological parameters can be manipulated to observe resulting changes in behavioral traits and health. In addition to these experimental benefits, lifespan longitudinal studies can be conducted with short-lived animal models to address cumulative, potentially subtle effects of personality on health. In general, animal models allow for greater in-depth analyses of physiological processes underlying relationships between personality and health, and a means for determining causal mechanisms.

Keywords: temperament, neophobia, behavioral inhibition, shyness, disease, endocrinology, immunology.

Introduction
Long before the Greek humoral theory of health and individual differences, humans have tried to understand why some individuals are resilient whereas
others are more susceptible to certain diseases. Individual and population differences have received renewed interest. In the United States, for example, this rekindling is reflected in the National Institutes of Health promotion of research on ‘Health Disparities’ among social and ethnic groups. At present, there are multiple perspectives on the roots of these individual differences, including environmental predictors (e.g., toxin exposure) and internal predictors (e.g., genetics, personality) of health. In this paper, I will explore the viability of using animal models to understand individual differences in personality and disease resilience/susceptibility and progression.

Animals provide a powerful lens for investigating physiological mechanisms underlying the development of disease, ranging from arthritis (Van de Langerijt et al., 1993), diabetes (Atkinson & Leiter, 1999; Makino et al., 1980) and hypertension (Schmid-Schönbein et al., 1991) to Alzheimer’s disease (German & Eisch, 2004), anxiety disorders (Kalin, 2004) and depression (Solberg et al., 2001). These models have proven useful in testing treatments for human disease. However, animal models rarely take into consideration individual differences in disease progression and the physiological processes that make some individuals more resistant than others. Here I explore the idea that the use of animal models can be expanded to include how personality and physiology are related and what impact this relation may have on health and disease progression. In particular, I focus on expanding this line of work with small, short-lived animals for which stable behavioral and physiological differences have been identified among individuals. Many studies have shown that individual differences exist in a variety of animal species, including those often used as models for studying disease processes (see Table 1 for a list of individual differences identified in rats alone). Furthermore, these individual differences have been compared to human personality traits (e.g., shyness/boldness, Wilson et al., 1994; novelty-seeking, Della et al., 1996; extraversion/introversion, Gosling & John, 1999; coping styles, Koolhaas et al., 1999).

In this goal to elucidate how animal models can be used to better understand the relationship between personality, physiology and health in humans, I will examine three specific areas. First, I will identify specific personality traits associated with certain physiological processes to establish the basis that behavioral traits can predict health and disease susceptibility/resilience. Second, I will identify specific areas in which animal models can complement human research and review some of the advantages of animal studies.
Table 1. Studies with rats that show significant individual differences in behavioral and/or physiological responses to environmental stimuli. *Specifically bred for this trait.

<table>
<thead>
<tr>
<th>Rat strain/line</th>
<th>Trait</th>
<th>Citation</th>
</tr>
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<tbody>
<tr>
<td>Wistar*</td>
<td>active avoidance, HPA axis reactivity</td>
<td>Driscoll &amp; Battig, 1982, Gentsch et al., 1982, Aubry et al., 1995</td>
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<tr>
<td>(Roman high &amp; low avoidance)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long-Evans hooded</td>
<td>fearfulness, HPA axis reactivity</td>
<td>Meaney et al., 1991, Caldi et al., 1998</td>
</tr>
<tr>
<td>Wistar</td>
<td>novelty-seeking and harm-avoidance</td>
<td>Ray &amp; Hansen, 2004</td>
</tr>
<tr>
<td>Wistar</td>
<td>active vs. passive (proactive vs. reactive) coping, cardiovascular &amp; glucocorticoid responses</td>
<td>Korte et al., 1992</td>
</tr>
<tr>
<td>Wistar* (high &amp; low anxiety-related behavior)</td>
<td>anxiety-related behavior, HPA axis reactivity</td>
<td>Landgraf et al., 1999, Ho et al., 2002</td>
</tr>
<tr>
<td>Sprague-Dawley</td>
<td>HPA axis recovery &amp; glucose responses</td>
<td>Garcia &amp; Armario, 2001, Marquez et al., 2004</td>
</tr>
<tr>
<td>Wistar</td>
<td>sociability, serotonin levels</td>
<td>Tõnissaar et al., 2004</td>
</tr>
<tr>
<td>Wistar</td>
<td>slow vs. fast learning, glucocorticoid response</td>
<td>Sandi et al., 2004</td>
</tr>
<tr>
<td>Sprague-Dawley</td>
<td>slow vs. fast learning, locomotor response to amphetamine</td>
<td>Dellu-Hagedorn, 2005</td>
</tr>
<tr>
<td>Long-Evans hooded</td>
<td>maternal behavior (licking/grooming), dopamine</td>
<td>Champagne et al., 2004</td>
</tr>
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</table>

And third, I will examine a specific behavioral response bias — ‘neophobia’ or fear of novelty — to explore: (a) how a simple and stable behavioral trait can be identified in animals, (b) how this trait is comparable to human traits, and (c) the physiological correlates of these behavioral traits and how, ultimately, these processes may influence health.
First, I will review the general definition of personality accepted by human personality researchers. That is, personality is defined as a set of inter-related traits that are stable within an individual across time and across situations (Fiske, 1949; Funder & Colvin, 1991). In humans, test-retest of the same trait across time has shown correlation coefficients in the range of 0.4 to 0.6 for traits considered stable. Similar correlation coefficients have been calculated in animals (Dingemanse et al., 2002). A significant amount of research has converged in the last decade to support the idea that, like humans, animals display stable behavioral traits both across time and across situations, and that these traits can be selected for over time. (Stevenson-Hinde et al., 1980; Capitanio, 1999; Gosling & John, 1999; Drent et al., 2003).

Personality, physiology and health

In humans, we often assume that personality affects health through differential health maintenance behaviors (e.g., diet, drug use, medical visits, exercise, etc.). Certain animal model studies test these assumptions by identifying individual differences in susceptibility to drug use (e.g., Piazza et al., 1989, 1990; Kabbaj et al., 2001, 2004; Homberg et al., 2004) based on a priori traits. However, personality or behavioral traits may affect health because they reflect differential physiological profiles that make individuals more or less susceptible to certain specific diseases. Animal research provides a unique level of analysis for understanding the relationship between personality and health in that they provide a means for studying how physiological traits are related to behavior and how they may affect disease progression and health.

It should be noted that behavioral/physiological traits should be considered according to both their positive and negative influences on health. Specific behavioral/physiological traits present in a population reflect traits that have been selected over evolutionary time. Thus, specific traits cannot be thought of as simply detrimental or beneficial to overall health. In particular, specific traits may be associated with resilience to certain diseases and susceptibility to other specific illnesses (Korte et al., 2005). It must also be mentioned that certain traits associated with specific benefits during the reproductive phase of the lifespan may be associated with only negative health
consequences during the aging/non-reproductive phase of life (e.g., agonistic pleiotropy). Because disease resilience has been the focus of less research than disease susceptibility, I will concentrate on disease susceptibility, with the understanding that both susceptibility and resilience should be the focus of future research (e.g., Korte et al., 2005).

In humans, specific personality traits have been linked to specific physiological mechanisms and health consequences (e.g., Friedman & Rosenman, 1971; Williams et al., 1980; Kagan et al., 1987; Kagan & Snidman, 1991; Spangler, 1997; Segerstrom et al., 1998; Habra et al., 2003; Dawe & Loxton, 2004). Similarly, animal behavioral traits have also been shown to be associated with specific physiological biases (Gentsch et al., 1982; Kavelaars et al., 1999; Koolhaas et al., 1999; Ruis et al., 2000; Carere & van Oers, 2004; Tönissaar et al., 2004). Given the following conditions: 1) that stable behavioral differences exist among individuals, 2) that these behavioral differences are associated with stable physiological differences, and 3) that these traits may develop relatively early in life (e.g., infancy: Kagan & Snidman, 1991; juvenility: Verbeek et al., 1994), it is a reasonable hypothesis that biological manifestation of personality will affect life-long physiological processes and therefore will affect the progression of disease. Select research has explored the relationship between behavioral characteristics, associated physiological response biases, and consequential health outcomes in animals (Gentsch et al., 1982; Walker et al., 1989; Sandi et al., 1991; Capitanio et al., 1999; Kavelaars et al., 1999; Laudenslager et al., 1999; Maninger et al., 2003; Cavigelli & McClintock, 2003; Capitanio et al., 2004). Several of these studies are of particular interest because they link behavioral traits to differential stress and immune reactivity and thus provide a clear mechanism by which personality traits can influence health and disease processes. Differential immune responses among individuals could explain why certain individuals are more resilient to specific diseases than others. For example, ‘low-sociable’ monkeys that have reduced antibody titers after social separation and relocation will be more prone to disease processes during times of stress (Maninger et al., 2003). These studies are promising in the potential application to understanding differential susceptibility — based on behavioral/personality traits — to disease in humans.

Complements of animal research

Currently, there are several controversies in the field of human personality research (Pervin, 2002), some of which may be theoretically informed by
animal studies. One such controversy is the identification of a universal set of personality traits. At present there are many hypotheses as to the structure of personality traits (Cervone, 2005). Researchers use many different units to measure human personality: traits, motives, and cognitions (Pervin, 2002). Depending on the unit of analysis, very different personality structures or categories can be hypothesized, each subsuming different aspects of one another. By determining which animal traits are commonly found across a variety of species, we can identify universal elements of personality that may have been selected over evolutionary time. Gosling & John's (1999) examination of the ‘Five Factors’ in animals has shown that humans can reliably identify certain traits across a variety of species. This suggests that there are some traits genetically selected for across a variety of species, and that some traits are more universal than others. These latter traits potentially provide the basis for more complex traits identified in humans. For example, the ‘Openness to New Experiences’ trait from the Five Factor Model (Costa & McCrae, 1992) may be a combination of some more basic traits such as boldness and anxiety, novelty-seeking and harm avoidance (Ray & Hansen, 2004). Further work on individual differences across animal species may reveal universal elements of personality, also present in humans (e.g., shyness-boldness as identified by Wilson et al., 1994), and thus provide solid ground for understanding human personality traits that have a long evolutionary history and potentially strong associations with physiological processes. By exploring common traits from comparative studies, we may gain insight into the basic personality traits in humans that are most strongly associated with physiology and health. For example, Williams and colleagues' found that the ‘hostility’ trait (one component of the ‘Type A’ personality trait) was the trait most closely associated with severe coronary artery blockage. Were it possible to identify a homologue to ‘hostility’ across a variety of animal species and to map that trait onto human hostility, we might gain a more sophisticated understanding of the behavioral/physiological pathway leading to coronary heart disease.

A second issue in the study of human personality concerns measurement. Traits or temperament are usually measured using questionnaires (Funder, 2001, cf Garcia-Coll et al., 1984). To minimize the subjectivity of these measures, researchers often collect data on one individual from multiple questionnaires to arrive at a more objective measure. Another method to collect
objective trait measures is to observe and record individual behavioral responses in a variety of situations. This latter method is more objective than questionnaires and can prove highly productive (e.g., Kagan et al., 1987; Fox et al., 1994). However it is necessarily more time consuming and the logistics of collecting unbiased observations of human behavior can be rather tricky. A promising variation is the ‘experience sampling method’, developed to collect data on activity and thoughts at random times across the day (Csikszentmihalyi & Larson, 1987). This method could provide a productive alternative to quantify individual differences in responses to real world situations. But of course, the method is susceptible to individual report biases, depending on the relative desirability of certain motives and traits. Herein lies another advantage of studying personality in animals. To identify animal personality, researchers must rely on observations of behavioral responses to various environmental conditions. In particular, researchers can use either direct behavioral observation (e.g., Archer, 1973) or they can rely on interviews with human caregivers that have observed animals in various situations (e.g., Stevenson-Hinde & Zunz, 1978; Gosling & John, 1999). The latter method mimics questionnaire methods used with humans. The first method of direct observation provides an objective advantage over human studies, for identifying reliable/stable individual differences among individuals. In addition, beyond objectivity, direct behavioral observations can be reasonably conducted over long periods of time with animals, and ever increasing advances in technology allow for longer and more detailed behavioral sampling.

A third limitation in human personality research is the relatively short interval between test and retest when assessing the stability of a trait over time. That is, test-retest intervals are relatively short when considered as a proportion of the entire human life span (e.g., an interval of several months or even years is relatively short given the normal human lifespan). These necessarily short intervals limit our ability to understand the stability of a trait over the life span, although some studies are successfully stretching this time interval to a significant portion of the early developmental period (e.g., Schwartz et al., 1999, 2003). The length of the human lifespan makes it difficult to determine if a personality trait was present before a health problems began or if the trait developed concurrently with a health problem and is simply indicative or a response to the health problem and not predictive (e.g., Bell et al., 1993, cf. Schnurr et al., 1990). Again, animal studies can be useful here since animals (particularly many small animals) have much shorter lifespans.
than humans. Beyond collecting more objective measures of personality, we can conduct test-retest sessions relatively far apart, in terms of the average lifespan of a study species, to determine trait stability over a significant portion of the life span (e.g., young adulthood to late adulthood: Dellu et al., 1996; infancy to late adulthood: Cavigelli & McClintock, 2003). In addition, personality traits can be measured early in the lifespan of short-lived animals, followed by measures of health resilience at the middle and end of the lifespan. If behavioral-physiological traits are relatively stable over time, but the health effects of such profiles are relatively weak in early life, it is still possible that the health consequences of a stable trait may only be manifest during the latter half of the lifespan. Given this long-term cumulative effect, animal models provide the benefit of tracking behavior, physiology and health from infancy to the late life to determine life-long impacts on health. Life-long studies also provide ample opportunity to identify periods of minimal and maximal flexibility in personality, the development of these traits from childhood to old age, and the environmental conditions that may destabilize a trait within an individual. Thus, there are several advantages to studying animal personality traits, associated physiological biases, and resulting health consequences. As opposed to studies with long-lived humans, studies with short-lived animals can provide information on the stability of a personality trait over the entire lifespan. By studying traits over the lifespan we can measure the relative stability of different traits, and in addition, we can study conditions (environmental, developmental, etc.) that lead to instability or change (e.g., Fernández-Teruel et al., 1997; Steimer et al., 1998; Greco & Morris, 2002; Bolhuis et al., 2004). Such work will provide important information on genetic-environment interactions in the development of behavioral traits.

Finally, a clear benefit of studying personality traits and health in animals is that different traits can be selected for through specific breeding programs (e.g., Driscoll & Battig, 1982; Gariépy et al., 2001; Drent et al., 2003; Landgraf, 2003; Sluyter et al., 2003). Breeding experiments allow us to determine the relative impact of traits on accompanying physiological processes and health. But even more intriguingly, breeding programs combined with ever increasing genetic screening possibilities enable us to study the links between behavioral and physiological response biases. And furthermore, these programs can be combined with environmental manipulations to understand
how genetic and environmental influences combine to make certain individuals more susceptible to disease in specific environmental conditions. Genetic inheritance plays an important role in determining whether an individual will show a specific personality trait (Plomin & Rowe, 1979; Robinson et al., 1992; Berton et al., 1997). However, it is important to emphasize that this inheritance is not the only factor affecting this behavioral trait (Plomin & Rowe, 1979; Goldsmith & Lemery, 2000). More and more we are able to study the synergy between environment, development and genetics.

Animal neophobia as a model of human behavioral inhibition

In this final section, I will provide a specific example of how animals may be studied to further understand the relation between personality and health in humans. The specific example is that of behavioral inhibition, often termed shyness, in children. Behavioral inhibition is described as withdraw and extreme motor & vocal inhibition when initially exposed to unfamiliar places / people / events (Garcia-Coll et al., 1984). Wilson et al. (1994) presented the idea that behavioral inhibition in children may be analogous to shyness in animals. In this case, Wilson and colleagues described shyness as the tendency to shrink from risk and novelty. In young children behavioral inhibition is relatively common, although for some children this trait is a stable behavioral response style (Kagan et al., 1987). The analogous behavioral trait in animals is neophobia — a stilted or avoidant behavioral response to novel physical objects.

Behavioral inhibition in children

In the United States, it is estimated that approximately 15% of children exhibit stable signs of behavioral inhibition — a behavioral predisposition that indicates a fear of the unfamiliar under several testing conditions and a general avoidance of such situations (Garcia-Coll et al., 1984; Kagan & Snidman, 1999). Other terms that have been used to describe this kind of trait have included ‘shyness’ or ‘fearfulness’ (Fox et al., 1994; Gunnar et al., 1996). At present, we know these children are more prone to certain health problems, including increased risk for later anxiety disorders (Hirshfeld et al., 1992; Turner et al., 1996; Kagan & Snidman, 1999), and increased allergies (Kagan & Snidman, 1991). In addition, when personality traits are assessed in older adults (from 60-86 years of age), individuals that self-identify
as curious survive longer than less curious individuals, assessed 5 years later (Swan & Carmelli, 1996). The full suite of potential health problems may be more complicated, including potential health benefits that have not yet been identified.

Physiological correlates of behavioral inhibition include elevated basal (i.e. unstimulated) levels of circulating glucocorticoids (i.e. cortisol) and greater activation of the HPA axis in response to challenging situations (Tennes et al., 1977; Kagan et al., 1987; Nachmias et al., 1996; Schmidt et al., 1997; Dettling et al., 1999; Blair et al., 2004). In addition, behaviorally-inhibited children experience increased variability in cardiac output (Kagan et al., 1987) and increased activation of amygdala responses to novel stimuli (Schwartz et al., 2003). Some of the health problems identified above may be a consequence of chronic or repeated hypothalamic-pituitary-adrenal (HPA) axis activation (Sapolsky, 1985; Brindley & Rolland, 1989; McEwen, 1991; Shively et al., 1997; Dhabhar, 1999). Alternatively, benefits of this trait may stem from this same increased HPA activity, particularly if that increased activity results in acute elevations of glucocorticoids (e.g., enhanced memory consolidation — Roozendaal, 2002, heightened cell-mediated immunity — Dhabhar & McEwen, 1996). These advantages may be most evident during the prime of life whereas the disadvantages may be more prevalent at the end of life. The most pronounced health consequences of this trait may only be present at the end of life, given the cumulative effects of allostatic load associated with altered stress physiology (e.g., hypertension & thyroid disease, Bell et al., 1993).

It has become increasingly clear that although acute elevations in glucocorticoids can be beneficial (McEwen & Sapolsky, 1995; Dhabhar & McEwen, 1996), chronic or repeated elevations can cause a host of health problems (Sapolsky, 1985; Shively et al., 1997; Dhabhar, 1999). Given this dichotomy, it is possible that this physiological trait in shy individuals could be either beneficial or harmful to their health, depending on how long they experience elevations in glucocorticoids. It is thus very important to determine if fearful individuals experience longer glucocorticoid exposure than non-fearful individuals, or if they just experience greater concentrations in the blood after a challenge. If shy individuals experience long-term changes in their basal set point of glucocorticoid secretion (e.g., allostasis), or lengthened exposure, they may be prone to the suite of negative health consequences associated with chronic glucocorticoid elevations (McEwen, 1991).
Given that this behavioral response style emerges prior to adulthood (e.g., infancy: Kagan & Snidman, 1991; juvenility: Verbeek et al., 1994), represents a stable behavioral trait in many individuals (Reznick et al., 1986; Fox et al., 1994) and is associated with elevated HPA activity (which can be either beneficial or detrimental to health) it is important to determine how this relatively common trait develops over the lifespan and the conditions that may ameliorate or accentuate it (Chung & Evans, 2000). Such long-term experimental studies are possible with animal models.

**Neophobia in animals**

Neophobia has been described in a variety of animal species. The rat, in particular, provides an interesting animal model for experimental and life span studies. The rat is a social and short-lived species for which extensive background information is available on neural and endocrine mechanisms underlying behavior. In addition, the relatively short lifespan of the rat allows for experimental studies to investigate the causes and consequences of behavioral inhibition on physiology and health. (Mouse models may prove more productive for genetic analyses.) Preliminary studies with neophobic rats have shown that their glucocorticoid response levels are elevated and that they die much earlier than more exploratory rats (Cavigelli & McClintock, 2003).

Many different terms have been used to describe traits related to neophobia. Some of these include ‘emotional reactivity’, ‘high avoidance’, ‘behavioral inhibition/shyness’, ‘slow to explore’ and ‘reactive coping’ in response to novel situations (Denenberg, 1969; Driscoll & Battig, 1982; Schmidt et al., 1997; Garcia-Coll et al., 1984; Wilson et al., 1994; Verbeek et al., 1994; Koolhaas et al., 1999). Neophobia, a fear of novelty, is probably at the root of many different traits identified across a variety of species (see Table 2). This assumption is supported by physiological mechanisms underlying many of these traits: hyperactivity of the hypothalamic-pituitary-adrenal axis. Low exploration animals show elevated glucocorticoid responses to novel situations (e.g., Gentsch et al., 1982; Dellu et al., 1996; Kabbaj et al., 2000; Cavigelli & McClintock, 2003; Levine et al., 1967). Shy or behaviorally-inhibited children have elevated glucocorticoid responses to novelty (Kagan et al., 1987; Nachmias et al., 1996). This heightened adrenal response results from release of corticotropin-releasing hormone in the brain (Plotsky &
Table 2. Terminology to describe behavioral responses to novelty: many different terms to describe two universal responses.

<table>
<thead>
<tr>
<th>Animal (Species)</th>
<th>Trait</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Many</td>
<td>Shy-bold</td>
<td>Wilson et al., 1994</td>
</tr>
<tr>
<td>Many</td>
<td>Proactive-Reactive Coping</td>
<td>Koolhaas et al., 1999</td>
</tr>
<tr>
<td>Amoebae &amp; Insects</td>
<td>Approach-Withdrawal</td>
<td>Schneirla, 1959</td>
</tr>
<tr>
<td>Rat</td>
<td>Behavioral Inhibition</td>
<td>Takahashi &amp; Kim, 1994</td>
</tr>
<tr>
<td>Marmot</td>
<td>Approach-Avoidance</td>
<td>Armitage, 1986</td>
</tr>
<tr>
<td>Pig</td>
<td>Proactive-Reactive</td>
<td>Ruis et al., 2000</td>
</tr>
<tr>
<td>Pig</td>
<td>Exploration/Curiosity</td>
<td>Forkman et al., 1995</td>
</tr>
<tr>
<td>Hyena</td>
<td>Curiosity</td>
<td>Gosling, 1998</td>
</tr>
<tr>
<td>Vervet monkey</td>
<td>Curious/playful</td>
<td>McGuire et al., 1994</td>
</tr>
<tr>
<td>Rhesus monkey</td>
<td>Curious/playful</td>
<td>Bolig et al., 1992</td>
</tr>
<tr>
<td>Chimpanzee</td>
<td>Openness</td>
<td>King &amp; Figuerdo, 1997</td>
</tr>
<tr>
<td>Human infants</td>
<td>Approach-Withdrawal</td>
<td>Schneirla, 1959</td>
</tr>
<tr>
<td>Human toddlers</td>
<td>Uninhibited-Inhibited</td>
<td>Garcia-Coll et al., 1984</td>
</tr>
</tbody>
</table>

Vale, 1984) which is associated with the fear response and has been shown to be elevated in monkeys with a fearful temperament (Kalin et al., 2000). Thus physiological mechanisms underlying fear also underlie ‘emotional reactivity’, ‘high avoidance’, ‘shyness’, ‘slow exploration’ and ‘reactive coping’ in novel situations. For this reason, I will use ‘neophobia’ to describe a basic trait that most likely underlies all of these behavioral traits. Given the simplicity of the neophobia concept (a bias to initially withdraw from novel situations) it may prove more predictive of behavior than more complex personality complexes. In addition, neophobia (or shyness/behavioral inhibition) is one of the few traits identified from behavioral observations, as opposed to questionnaires, in humans (e.g., Garcia-Coll et al., 1984).

Neophobia as a personality trait

The term neophobia has been most frequently used to describe a transient state in animals after experiencing a new environmental condition or drug (e.g., Collier et al., 2004). However, I will use this term to describe a behavioral trait that can be stable within an individual over time and across contexts, akin to a personality trait. Support for this trait as a potentially stable trait within an individual is based on breeding experiments that show that slow exploration and high avoidance behavior can be selected for over generations (Driscoll & Battig, 1982; Drent et al., 2003), and from ecological
studies identifying consistent behavioral differences among individuals in the natural habitat (see Wilson et al., 1994). From an evolutionary perspective, a neophobic trait could be maintained within a social species through density- and frequency-dependent selection (Wilson et al., 1994), and such a trait could be maintained due to advantages attendant on living in variable environments (Sih et al., 2004; Dingemanse et al., 2004). Individuals that are wary in novel situations will be at an advantage in environments with heavy predation, and easily located resources. Being fearful in a novel environment has obvious adaptive advantages, and the associated heightened glucocorticoid activity in neophobic individuals provides a benefit of increased memory consolidation (Roozendaal, 2002) during novel experiences. Clearly, this is advantageous in terms of making sense of novelty and providing a background of information for future encounters with similar stimuli. It seems logical that this behavioral and physiological response to novelty may have evolved very early in species. Given the adaptive importance of predator avoidance and the rapid and comparable physiological mechanisms underlying the fear and stress response, neophobia may be one of the most elemental behavioral responses to have evolved. In the same way that hostility is a more elemental trait of the complex ‘Type A’ trait, neophobia may underlie other complex behavioral traits. By understanding this neophobic tendency in animals, we may best understand other more complicated traits in individuals (e.g., coping styles, learning styles, etc.). In particular, a trait like neophobia may be more stable within individuals over time than other more complex, multi-faceted traits. And a more elemental trait may be more closely associated with physiological traits (e.g., Williams et al., 1980).

In studying stable behavioral traits and potential implications for health, it is important to identify the physiological underpinnings of the behavioral trait of interest (Koolhaas et al., 1999). Only by understanding the physiological correlates of a trait can we understand any potential implications on health and disease susceptibility/resilience. As an example, at present, there are two documented physiological correlates of exploratory behavior in rats. Some studies show elevated glucocorticoid responses in low exploratory individuals (Levine et al., 1967; Gentsch et al., 1982; Cavigelli & McClintock, 2003), others show elevated response in highly exploratory animals (Dellu et al., 1996; Kabbaj et al., 2000). In these latter studies, high exploration rats have been termed ‘novelty-seekers’ and are more susceptible to drug use and have decreased expression of glucocorticoid receptors in the
hippocampus. These conflicting results may be due to differences in testing procedures/apparatus. In the former studies, where low exploration is associated with elevated glucocorticoid responses, the apparatus for testing exploratory behavior (e.g., shuttle box or exploration arena) is not particularly anxiety-provoking because it is presented repeatedly or because it is relatively complex, thus offering intrinsic rewards to a curious and non-fearful individual. In the latter studies, in which elevated glucocorticoid responses are associated with high exploration, the one-time testing apparatus (e.g., light/dark box and elevated plus maze) is more sparse and potentially more anxiety-provoking for a species prone to predation. In addition, the lack of complexity (fewer objects to inspect) provides little intrinsic reward, and locomotion or activity in such an arena may reflect escape behavior. Thus, the former tests may access willingness to explore a novel space whereas the latter tests access motivation to escape an open space. By measuring physiological correlates of such behavioral responses (both in animals and humans), we gain access to motivational factors underlying these behavioral responses. Elevated glucocorticoid reactivity in low exploration animals (in the former tests) may indicate fear of novelty, whereas elevated glucocorticoid reactivity in high exploration animals (in the latter test) may reflect fear of an open space and motivation to escape the noxious arena. Understanding the physiological underpinning to behavioral traits in animals is key to understanding motivational factors underlying behavioral responses and in understanding how personality/behavioral traits influence health.

Given that neophobic individuals have stronger or longer stress responses to novel stimuli, and that novelty is a frequent experience, it is possible that these individuals experience greater exposure to HPA hormones over the life span. Such increased exposure is comparable to ‘allostatic load’ discussed by McEwen and colleagues (Sterling & Eyer, 1989; McEwen, 1991), and suggests that this increased exposure can lead to negative health implications. In particular, these individuals may be more susceptible to chronic disease processes such as diabetes and hypertension (Brindley & Rolland, 1989).

Future directions

If animal models are to be used with any success to further understand human personality and health, there are several areas of research that must be addressed. The first, and most important, is to explore in more detail how
human personalities compare to animal personalities. We know that certain traits in animals are as stable over time as those found in humans. Now, we must make sense of how different measures of individual differences compare across species. One method for making these comparisons is to use similar behavioral tests across a wide variety of species, including humans. Thus, for human traits identified with behavioral measures, similar, species appropriate, tests should be used with animals (e.g., Cavigelli & McClintock, 2003). Or, behavioral measures should be combined with structured questionnaires completed by experienced animal caregivers (Gosling & John, 1999). On the same note, research on human personality benefits from a combination of questionnaire and behavioral observation data.

A second method for comparing personality traits across a variety of species is to combine behavioral data with physiological measures (Koolhaas et al., 1999). Which behaviors are associated with specific physiological biases (endocrine, nervous, immune, genetic)? Physiological measures provide insight into the motivational state underlying behavioral traits. If a behavioral trait has evolved in synchrony with a physiological trait, this connection is probably of functional significance, and may be important across a variety of species. Such links may help us identify universal personality traits repeated selected for over evolutionary time (i.e. across many species).

Finally, one of the greatest contributions that animal models can make to human studies of personality and health is to identify species in which to study gene-environment interactions. With increasingly powerful genetic measurement techniques and the ability to produce refined genetic knockouts, including those that have genes ‘turned on’ and ‘turned off’ at specific developmental time points, we can now study how specific environmental factors at specific developmental time points can interact with genotype to produce variable phenotypes.

**Summary**

These brief considerations serve to point out how animal models linking behavioral and physiological traits may shed light on individual differences in susceptibility and resilience to disease among humans. In the previous section, I discussed homologues between research on human and animal personalities and sought to identify some common links with stress and immune reactivity. Secondly, I examined the benefits of animal models in the
field of personality and health research. A major benefit in this regard is the possibility of experimental manipulations with animals — all but impossible with humans. Finally, I offered a specific example of how animal research may complement human personality research — i.e. how neophobia in animals compares to shyness or behavioral inhibition in children. In particular, I identified commonalities of these traits at the behavioral level and commonalities of HPA axis function at the physiological level. Future research in this area will need to concentrate on identifying behavioral traits comparable among species, and to identify comparable physiological correlates if we are to understand potential health implications of personality.

References


