

In R. Burgess and K. MacDonald (Eds.), *Evolutionary Perspectives on Human Development*, 2nd edition, pp. 207–242. Thousand Oaks, CA: Sage, 2005.

**This document is an exact copy of the content of the paper, with “in press” references updated. It closely resembles the original in terms of pagination, but it is not exact.

8

PERSONALITY, EVOLUTION, AND DEVELOPMENT

Kevin MacDonald

Research in personality has revealed that five personality dimensions appear regularly in cross-cultural research and among children and adults. The traits of the *five factor model* (FFM) have been isolated in American English (Goldberg, 1990), Dutch (De Raad, 1992), German (Ostendorf, 1990), Russian (Digman & Shmelyov, 1996) and Chinese (Trull & Geary, 1997), among other languages. In addition to the very large personality literature in adults, the FFM has been supported in children (Graziano & Ward, 1992; John, Caspi, Robins, Moffitt, & Sthouthamer-Loeber, 1994; Kohnstamm, Halverson, Mervielde, & Havill, 1998; Lamb, Chuang, Wessels, Broberg, & Hwang, 2002; McCrae et al., 2002).

An evolutionary approach based on the idea of an evolved system provides a powerful paradigm for personality, a paradigm that would move personality to the very center of thinking about children’s development. The basic interest in personality research should be on establishing the set of evolved systems underlying personality differences. Typically, personality research and theory are viewed as fundamentally about individual differences (e.g., Caspi, 1998). Individual differences are certainly an important part of the story, but within a systems perspective, individual differences within the normal range represent variation in evolved systems. Research in neuroscience has revealed that the mammalian brain contains highly specific emotional and motivational systems (e.g., Panksepp, 1998). In the same way, all humans have a respiratory system and a circulatory system that are designed to carry out fundamental biological functions. However, there is important variation among people in these systems,

ranging, for example, from relatively high to relatively low lung capacity. These differences have important real-world implications for athletic ability and longevity. Genetic variation is ubiquitous, even for adaptations (e.g., West-Eberhard, 2003). And as discussed below, people are intensely interested in the phenotypic, and by implication, the genetic diversity underlying personality.

The systems perspective focuses on the following questions, none of which would be deemed relevant if individual differences were the only concern (see Figure 8.1):

1. What is the function of the system? Each personality system was designed by natural selection to solve problems of survival and reproduction in ancestral environments. In evolutionary argot, personality systems are therefore adaptations (see Ch. 2).
2. How does the system change with age, and do age differences conform to evolutionary expectations?
3. Are there sex differences in the system that are understandable in terms of evolutionary theory?
4. Which environmental cues trigger the system? For example, decreased oxygen results in more rapid breathing, and the presence of perceived threat triggers the behavioral inhibition personality system. An important question for personality psychology is whether the cues that trigger particular systems are the result of evolved, domain-specific connections between cues and system responses (e.g., fear of snakes or spiders) or whether they result from general-purpose information processing mechanisms (e.g., fear resulting from understanding the details of a conspiracy) (see Ch. 2 for a discussion).
5. How does the system interact with other systems? The respiratory system interacts with the circulatory system so that, for example, lowered lung capacity puts pressure on the heart. In the area of personality, there are a great many interactions among systems designed to perform different, often opposing, functions, as between systems designed to obtain rewards, systems designed to inhibit approach to immediate sources of reward in pursuit of long-term goals, and systems designed to avoid sources of threat. A systems theory of personality expects to find conflicts between systems, resulting at times in psychological ambivalence.
6. How do individual differences in the system affect interaction among systems? People who vary in the efficiency of their respiratory systems respond differently to the same environmental stressors, and this affects interactions with other systems. In the same way, fearful people respond differently to a situation with possible rewards than do people who are less prone to fear. The systems perspective thus sheds light on one of the central problems of personality psychology: how to conceptualize the interactions among situations and personal

traits. Because these systems are so intimately interconnected, the genetics underlying personality is extraordinarily complex (see Ch. 2 for a discussion).

7. Along what dimensions does the system vary? Lungs, for example, vary in size, susceptibility to disease, efficiency, and so on. This is perhaps the most difficult and unresearched area of personality psychology, but there is evidence that several types of psychopathology are associated with being extreme on personality systems.

8. What are the systematic group differences in personality systems? Examples include sex differences, age differences, birth order differences, and ethnic differences.

-
- I. Personality Systems as Universal Psychological Mechanisms:
 - A. Personality Systems as Universal Design Features of Humans Homologous with Similarly-Functioning Systems in Other Vertebrates
 - B. System X Context Interactions and Compartmentalization
 - C. System X System Interactions
 - D. System X Context X Trait Interactions
 - E. System-Specific Environmental Influences
 - II. Approaches to Group Differences in Universal Mechanisms Based on Evolutionary Theory
 - A. The Evolutionary Theory of Gender Differences in Personality
 - B. Evolutionary Approaches to Age Differences in Personality Systems
 - C. Evolution and Birth Order Differences in Personality
 - D. Life History Theory and Personality
 - III. Evolutionary Perspectives on Individual Differences
 - A. Individual Differences within the Normal Range as Variation in Viable Strategies
 - B. Individual Differences at the Extreme Ends of the Normal Range as Maladaptive or High-Risk Strategies
 - C. Social Evaluation: Individual Differences in Others' Personalities as a Resource Environment
 - D. Self-Evaluation and Self-Presentation of Personality Traits as Mechanisms for Maximizing One's Resource Value in the Social Environment
-

Figure 8.1. Levels of an Evolutionary Perspective on Personality

Personality Systems as Universal Psychological Mechanisms

A basic idea, then, is that there are two worlds of personality psychology, the world of universal psychological mechanisms and the world of individual differences. The mind is conceptualized as a set of mechanisms designed by natural selection to solve adaptive problems. Although the social evaluation of individual differences is indeed an important aspect of an evolutionary approach (see below), at a fundamental level, these mechanisms are conceptualized as adaptive systems that served a variety of social and nonsocial functions in the environment of evolutionary adaptedness (EEA) (see Ch. 2 for a discussion). This perspective expects to find homologous (i.e., inherited from a common ancestor) systems in animals that serve similar adaptive functions, and it expects that these systems will be organized within the brain as discrete neurophysiological systems. It expects that each system will be responsive to particular environmental contexts (resulting in System X Context Interactions) and that different personality systems will be in competition with each other within individuals, leading at times to psychological ambivalence.

An evolved systems perspective does not expect a 1:1 mapping of the factors emerging from factor analysis with evolved mechanisms. There are several reasons for this. Factor rotations are arbitrary in the absence of strong theory. For example, I have argued that an evolutionary perspective is much more compatible with a factor rotation yielding factors of Dominance/Sensation Seeking and Nurturance/Love rather than Extraversion and Agreeableness (MacDonald, 1995, 1999b). (For a contrary view, see Depue & Collins, 1999, who advocate Gregarious/Aloof and Arrogant/Unassuming as fundamental causal dimensions of personality covering the same factor space.) As Trapnell and Wiggins (1990) pointed out, the difference amounts to a rotational difference between two different ways of conceptualizing the same interpersonal space. Nevertheless, an evolutionary perspective is better conceptualized with Dominance/Sensation Seeking and Nurturance/Love as the primary axes of interpersonal space, since this conceptualization maximizes theoretically important sex differences and is thus likely to have been the focus of natural selection. Evolutionary theory predicts that in species with sex-differentiated patterns of parental investment, the sex with the lower level of parental investment (typically the males) is expected to pursue a more high-risk strategy compared with females, including being prone to risk taking and reward seeking, and less sensitive to cues of punishment. This follows because the

high-investment sex (typically females) is expected to be able to mate relatively easily and is highly limited in the number of offspring (Trivers, 1972). However, mating is expected to be problematic for the low-investment sex, with the result that males must often compete with other males for access to females, while mating for females is much less problematic. Depue and Collins (1999) have claimed that the traits associated with behavioral approach (i.e., sensation seeking, neophilia, exploratory behavior, risk-taking, boldness, sensitivity to reward, and impulsivity) are heterogeneous. But within the evolutionary theory of sex, they form a natural unit: They all involve risky behavior that would benefit males more than females. They are thus much more likely to be the focus of natural selection than are Extraversion and Agreeableness.

While there are robust sex differences favoring males in Dominance and Sensation Seeking (Trapnell & Wiggins, 1990; Zuckerman, 1991), sex differences in Extraversion are relatively modest and actually favor females (McCrae et al., 2002; Srivastava, John, Gosling, & Potter, 2003). This is because Extraversion scales include items related to dominance and venturesomeness, which are higher among males, as well as items related to warmth and affiliation, which are higher among females (see discussion in Lucas, Deiner, Grob, Suh, & Shao, 2000). From the evolved systems perspective developed here, the concept of a trait consisting of warmth and affiliation does not fit well with a trait consisting of dominance, sensation seeking, and exploratory behavior. And in fact, as discussed below, at the level of brain functioning, these systems are quite separate: There are unique neurochemical and neuroanatomical substrates for love and for behavioral approach, respectively (Bartels & Zeki, 2000; Depue & Morrone-Strupinski, 2005; Panksepp, 1998). Focusing on the highly sex-differentiated traits of Dominance and Sensation Seeking, on one hand, and Nurturance/Love, on the other, is not only much more compatible with a theoretical understanding of how evolution must have worked but is also compatible with what we know of the systems actually found in the brain.

A related reason for focusing on these highly sex-differentiated traits is that they exhibit theoretically expected age changes, while there is little evidence for mean age changes in Extraversion (McCrae & Costa, 1990; McCrae et al., 2002). The “young male syndrome” describes the pattern in which sensation seeking, impulsivity, and aggression—all associated with the behavioral approach systems—peak in young adulthood exactly at the time when young males must compete for mates and establish themselves in the dominance hierarchy.

Furthermore, personality psychology is based on ratings of people by themselves and others, so that the most socially salient features of people are

emphasized and these bear only indirectly on the underlying systems. The factor of Neuroticism refers to a tendency toward negative emotionality, but at the system level, research reveals separate systems of affect intensity (involving a general tendency toward both positive and negative emotionality) and inhibitory systems dominated by the emotions of fear and anxiety. The psychological salience of Neuroticism in everyday evaluations of self and others provides a poor clue to the underlying systems. Similarly, the emergence of Extraversion in factor analysis may well reflect the social salience of these dimensions in everyday life: People who combine positive emotionality, affiliation (close personal bonds, being warm and affectionate), and attention seeking (dominance) are highly valued, while people who are sociopathic, emotionally distant, and withdrawn do not meet other people's interests as friends or companions. But at the systems level, these people differ on two quite separate evolved systems designed for two quite different purposes with two quite different, evolutionarily expected patterns of sex and age differences.

The evolved systems perspective is compatible with a hierarchical analysis in which the superfactors emerging from factor analysis share genetic and phenotypic variance with lower-level mechanisms. For example, Panksepp (1998) has argued that the mammalian brain contains a "foraging / exploration / investigation / curiosity / interest/ expectancy / SEEKING" system (p. 145), what I term "behavioral approach." This system is aimed at obtaining resources, including food and sexual partners, from the environment and overlaps anatomically and neurophysiologically with aggression—not surprising, since aggression is a prepotent way of dealing with the frustration of positive expectancies (Panksepp, 1998, p. 191). To say that this is a system implies some common neurophysiological structure among these different components, but it also is compatible with differences among them, as between aggression and other aspects of behavioral approach or between exploration and interest. There are also species differences in behavioral approach; for example, predatory aggression is a component of behavioral approach in cats, but not in rats (Panksepp, 1998, p. 194). Furthermore, an evolutionist would expect a sex difference in seeking sexual gratification and social dominance but not in seeking food or companionship (sociability). An evolutionary interpretation suggests that these differences accrued over evolutionary time as primitive foraging and mate attraction systems became elaborated and that they effectively resulted in "facets" of personality: mechanisms that share anatomical and neurological structures as well as genetic and phenotypic variance with each other and are therefore nested under one or more of the superfactors of the FFM. However, it is an open question whether each factor of the FFM would

have exactly six facets as evolutionarily meaningful mechanisms nested beneath each personality factor, as in the NEO-PI-R (Costa & McCrae, 1992).

These ideas are related to the following thought experiment about how the systems underlying the FFM may have evolved. A functionalist perspective proposes that the systems underlying personality serve very basic needs of the animal. Among even the most primitive mammals, there must be approach systems to obtain resources, prototypically foraging and mate attraction systems. There must also be withdrawal systems to avoid threats, prototypically a fear system (Gray 1987; LeDoux, 1996). There must also be a system of arousal regulation (affect intensity) designed to energize the animal to meet environmental challenges or opportunities; in the absence of such a system, the animal would either be permanently aroused, a highly wasteful posture, or it would be permanently underaroused and less able to meet environmental challenges. For species that develop pair bonds and other types of close relationships involving nurturance and empathy, one expects the evolution of a system designed to make such relationships psychologically rewarding. And for species that must carry out projects requiring attention to detail and inhibiting present pleasures for long-term gains, one expects the evolution of a conscientiousness system.

Ideally, one would be able to trace the evolution of these systems over time and chart the differentiation of these systems in different lineages, for example, as approach systems become linked with social dominance and aggression and with systems assessing risk (impulsivity, sensation seeking, etc.), self-confidence, and sociability. One would also chart the inhibitory and excitatory connections among these systems. And one would attempt to determine whether natural selection is favoring one extreme of individual differences or the other and what types of psychopathology are linked with being extreme on these dimensions.

Unfortunately, this program of research is still in its infancy. Nevertheless, existing data support several aspects of this model. The functionalist account of the systems underlying the factor space of the FFM is strengthened by findings that individual differences in personality are associated with individual differences in physiological systems common to all humans. There is considerable evidence linking personality systems with specific brain regions and neurochemicals (Eysenck 1967, 1982; Gray 1982, 1987; MacDonald 1988, 1995a). Moreover, functionally and neurophysiologically similar systems localized in particular parts of the brain and characterized by particular neurochemical profiles are apparent in animal research; excitatory and inhibitory connections between these systems are well established (e.g., Gray 1982, 1987; Panksepp, 1998; see below).

There is also evidence for personality traits in wolves (shyness/boldness, social dominance) (MacDonald, 1983) and sunfish (shyness/boldness) (Wilson, 1994) conceptually linked to FFM dimensions, and there is evidence that individual differences in personality among chimpanzees can be understood within the FFM framework (Figueredo & King, 1996; King & Figueredo, 1994). Reviewing the data for 12 quite different species, Gosling and John (1999) found evidence for Extraversion (E), Neuroticism (N), and Agreeableness (A) in most species: E was found in 10 species (but not rats and hyenas); N was found in 9 species (but not in vervet monkeys, donkeys, and pigs); A was found in 10 species (but not in guppies and octopi). Conscientiousness (C) was found only in humans and chimpanzees. These results surely do not mean that rats and hyenas do not have behavioral approach systems designed to obtain resources or that vervet monkeys do not have fear systems or systems of affect intensity. These findings may indicate that although these animals have these systems, individual differences are not observable. For example, Figueredo and King (1996, 2001) have hypothesized that social species are more likely to show individual differences than nonsocial species. On the other hand, it would not be surprising that guppies and octopi do not have mechanisms of pair bonding and close relationships, since such relationships are not part of these animals' ecology. Nor would it be surprising that humans and other relatively advanced animals were uniquely involved in long-term projects requiring delay of gratification and close attention to detail (i.e., conscientiousness); less cognitively advanced species, species that respond to environmental challenges mainly via preprogrammed responses, may fail to exhibit differences in focused effort. The point is that the systems perspective expects animal personality psychology to mirror the ecology of the animal.

Personality as a Set of Evolved Systems

I begin with a thumbnail sketch of the systems underlying personality (see MacDonald, 1995).

1. The Behavioral Approach System. The behavioral approach system is related to Surgency/Extraversion in the FFM and Dominance in the circumplex model of interpersonal descriptors (Wiggins & Trapnell, 1996; Wiggins, 1991). At the heart of behavioral approach is Dominance/Sensation Seeking, which consists of individual differences in social dominance as well as several other highly sex-differentiated behaviors, including sensation seeking, impulsivity, and sensitivity to reward. Among adults, behavioral approach is also associated with aggressiveness and higher levels of sexual

experiences (Zuckerman, 1991), while impulsivity, "High-Intensity Pleasure," and aggressiveness are components of behavioral approach in young children (Rothbart, Ahadi, Hershey, & Fisher, 2001). The behavioral approach personality systems are designed to motivate approach toward sources of reward (e.g., sexual gratification, social status) that occurred as enduring and recurrent features of the environments in which humans evolved. Approach systems are a human universal but, because of genetic and environmental variation, some of us are more predisposed toward social dominance, reward seeking, sensation seeking, and impulsivity than others.

A theoretically attractive line of research indicates that an important aspect of behavioral approach is dopaminergic reward-seeking mechanisms (Cloninger, 1987; Gray, 1982, 1987; Panksepp, 1982, 1998; Zuckerman, 1991). In rats, the dopaminergic reward-seeking mechanism involves energetic searching, investigating, and sniffing objects in the environment as possible sources of reward, but this seeking behavior is motivationally generalized: It can be directed at any of a variety of specific rewards depending on the context (Panksepp, 1998). The emphasis on reward-seeking mechanisms underlying behavioral approach reflects the typical manner in which evolution shapes the motivation to engage in behavior (Wilson, 1975). Evolution has resulted in affective motivational systems that are triggered by specific types of stimulation (e.g., the taste of sweet foods, the pleasure of sexual intercourse, the joy of the infant in close, intimate contact with its mother), and it is difficult to conceptualize how it could have done otherwise. The evolutionary basis of motivation is the evolution of affective systems underlying particular adaptive behaviors in the environment of evolutionary adaptedness.

Differences in attraction to reward are thus central to behavioral approach. Newman (1987; see also Avila, 2001; Derryberry, 1987) found that compared with introverts, reward has a relatively greater effect on responding among extraverts and especially among disinhibited subjects (psychopaths). The responding of some subjects was actually facilitated by punishment. Gray (1987) proposed close linkages between behavioral approach mechanisms and positive emotions, and Heller (1990) noted that the left hemisphere contains high levels of dopamine reward mechanisms and there are massive projections from the dopamine receptors to the left frontal areas associated with positive affect.

The most sexually differentiated aspects of behavioral approach are maximized during late childhood and early adulthood, while non-sexually differentiated aspects of behavioral approach appear early in infancy and are strongly associated with positive emotionality. Sensitivity to reward emerges very early in life as a dimension of temperament and is independent of

measures of behavioral inhibition, the latter system developing in the second half of the first year (Bates, 1989; Rothbart, 1989a; Rothbart & Bates, 1998). In early infancy, there are individual differences in the extent to which infants approach rewarding stimulation, as indicated by attraction to sweet food, grasping objects, or attending to novel visual patterns. This trait is sometimes labeled “exuberance,” defined as an “approach-oriented fact of positive emotionality” (Pfeifer, Goldsmith, Davidson, & Rickman, 2002; see also Fox, Henderson, Rubin, Calkins, & Schmidt, 2001). Children who are high on behavioral approach are prone to positive emotional response, including smiling, joy, and laughter available in rewarding situations and the pleasant social interaction sought by sociable children.

Sensation seeking, including the promiscuous sexual activity loading on the Disinhibition subscale (Zuckerman, 1979), and aggression (Wilson & Daly, 1985) peak in late adolescence and young adulthood, followed by a gradual decline during adulthood. As noted above, this “young male syndrome” is highly compatible with evolutionary thinking: Sex-differentiated systems are expected to be strongest at the time of sexual maturation and maximum divergence of reproductive strategies. Because mating is theorized to involve competition with other males, the male tendencies toward sensation seeking, risk taking, and aggression are expected to be at their peak during young adulthood when males are attempting to establish themselves in the wider group and accumulate resources necessary for mating. However, boys are higher on behavioral approach even during infancy in cross-cultural samples (see Rothbart, 1989a for a review); and sex differences in aggression (Eagly & Steffan, 1986), externalizing psychiatric disorders (conduct disorder, oppositional/defiant disorder), risk taking (Klein, 1995), and rough-and-tumble play (which is often associated with aggression) can be seen beginning in early childhood (DiPietro, 1981; Humphreys & Smith, 1987; MacDonald & Parke, 1986; O’Brien & Huston, 1985). Beginning in infancy, boys engage in more large-motor, physically intense activity (Eaton & Enns, 1986; Eaton & Yu, 1989). Increases in activity level are the clearest effect of prenatal exposure of genetic females to androgens (Ehrhardt, 1985; Ehrhardt & Baker, 1974). In factor analytic work, activity level appears to line up in the same area as dominance and sensation seeking (see Larsen & Diener, 1993). The social interactions of boys are also more characterized by dominance interactions and forceful, demanding interpersonal styles (Charlesworth & Dzur, 1987; Cowan & Avants, 1988; LaFrenière & Charlesworth, 1983; Savin-Williams, 1987). On the other hand, females are more prone to depression, which is associated with low levels of behavioral approach (Davidson, 1993; Fox, 1994). Indeed, anhedonia and negative mood are primary symptoms of

depression within the *Diagnostic and Statistical Manual of Mental Disorders (DSM-IV*; American Psychiatric Association, 1994) classification.

Taken together, the data on behavioral approach indicate that over development, there is differentiation of behavioral approach from a relatively simple dimension involving differences in activity level and approach to novel objects, visual displays, and sensory stimulation; to sociability and positive emotionality during early infancy; and to aggression, dominance, and rough-and-tumble play during early childhood. This undergoes further differentiation and intensification as children approach reproductive competence and behavioral approach begins to include attraction to sexual gratification.

2. Nurturance/Love. Nurturance/Love, the second factor emerging from the circumplex model, underlies relationships of intimacy and other long-term relationships, especially family relationships involving reciprocity and transfer of resources to others (e.g., investment in children) (Kiesler, 1983; Trapnell & Wiggins, 1990; Wiggins, Trapnell, & Phillips, 1988). This trait is not considered to be a temperament dimension of childhood, but individual differences in warmth and affection observable in early parent-child relationships, including secure attachments, are conceptually linked with this dimension later in life (MacDonald, 1992, 1997, 1999a). Secure attachments and warm, affectionate parent-child relationships have been found to be associated with a high-investment style of parenting characterized by later sexual maturation, stable pair bonding, and warm, reciprocally rewarding, nonexploitative interpersonal relationships (Belsky, Steinberg, & Draper 1991).

The physiological basis of female pair bonds appears to involve specific brain regions (Bartels & Zeki, 2000) and the hormone oxytocin in humans but not in other mammals (Insel, Winslow, Wang, & Young, 1998; Panksepp, 1998; Turner, Altemus, Enos, Cooper, & McGuinness, 1999). In prairie voles, a monogamous species, oxytocin receptors are found in brain regions associated with reward (Insel et al., 1998), supporting the proposal that pair bonding is a reward-based system that functions to facilitate intimate family relationships and parental investment (Depue & Morrone-Strupinski, 2005; MacDonald, 1992). The stimuli that activate this system act as natural clues (in the sense of Bowlby, 1969) for pleasurable affective response. Intimate relationships and the nurturance of the objects of affection are pleasurable, and such relationships are sought out by those high on this system.

If indeed the main evolutionary impetus for the development of the human affectional system is the need for high-investment parenting, females are

expected to have a greater elaboration of mechanisms related to parental investment than males. Females, because of their very high investment in pregnancy and lactation, are expected to be highly discriminating maters compared with males and more committed to long-term relationships of nurturance and affection (e.g., Buss & Schmitt, 1993). Females score higher on the IAS-R-B5 LOV scale by a very robust 0.88 standard deviations (Trapnell & Wiggins, 1990). This dimension involves the tendency to provide aid for those needing help, including children and people who are ill (Wiggins & Broughton, 1985), and would therefore be expected to be associated with ideal child-nurturing behaviors. This dimension is strongly associated with measures of femininity and is associated with warm, empathic personal relationships and dependence (Wiggins & Broughton, 1985).

The tendency for females to be more strongly attracted to intimate relationships and pair bonding has empirical support. Girls are more prone to engage in intimate, confiding relationships than are boys throughout development (Berndt, 1986; Buhrmester & Furman, 1987; Douvan & Adelson, 1966). Females also tend generally to place greater emphasis on love and personal intimacy in sexual relationships (e.g., Buss & Schmitt, 1993; Douvan & Adelson, 1966). Females are more empathic and desire higher intimacy in relationships (Lang-Takoc & Osterweil, 1992), and both sexes perceive friendships with women as closer, richer, more intimate, more empathic, and more therapeutic (e.g., Wright & Scanlon, 1991). Developmentally, sex differences related to intimacy peak during the reproductive years (Turner, 1981), a finding that is compatible with the present perspective that sex differences in intimacy are related to reproductive behavior.

Being extreme on Nurturance/Love is linked with psychopathology. Dependency disorder is characterized by being unusually prone to needing love and social approval (Widiger, Trull, Clarkin, Sanderson, & Costa, 2002). Several studies have linked dependency disorder to being high on FFM dimensions: Cloninger's (1987) Reward Dependence; Wiggins and Pincus's (1989) IAS-R-B5 LOV; Widiger et al.'s (2002) Agreeableness. Dependency disorder is overwhelmingly a female disorder (e.g., Kernberg, 1986). Males, on the other hand, are more likely to be at the opposite extreme of sociopathy, characterized by a proneness to cruelty and lack of remorse for harming others (Draper & Harpending, 1988). Being low on agreeableness is also linked with paranoid personality disorder and antisocial personality disorder (Widiger et al., 2002). Within the IAS scheme, the cold-quarrelsome scale, which is opposite to the warm-agreeable scale reflects autonomy in interpersonal relationships and "the disposition

not to be warm, cooperative, and nurturant when such behaviors would be appropriate” (Wiggins & Broughton, 1985, p. 42).

Finally, Nurturance/Love is separate from security of attachment (MacDonald, 1992, 1999a), with functions, different emotions, a different distribution among the primates, a different pattern of theoretically expected sex differences, different mechanisms (a neurological reward system versus the internal working model), and different patterns of heritability. Regarding the latter, recently Bokhorst et al. (2003; see also O’Connor & Croft, 2001) found negligible heritability for attachment security; many studies have shown the heritability of personality dimensions related to Nurturance/Love (e.g., Bouchard, 1996). Nurturance/Love and security of attachment underlie different aspects of close relationships. Reflecting its function as a system designed to protect the infant in times of uncertainty, the attachment system assesses the extent to which others can be trusted to help. The Experiences in Close Relationships Inventory (ECR) (Brennan, Clark, & Shaver, 1998), a measure of adult attachment, contains two factors, labeled Avoidance and Anxiety. The Anxiety factor is a measure of security conceptualized paradigmatically as fear of abandonment, while the Avoidance factor measures the extent to which people are attracted to close relationships for their own sake.

3. The Behavioral Inhibition System and Conscientiousness. The behavioral inhibition system (BIS) functions to monitor the environment for dangers and impending punishments (Gray, 1982, 1987; LeDoux, 1996). The BIS responds with the emotions of fear and anxiety to signals of uncertainty or anticipated punishment. Individual differences in behavioral inhibition are observable beginning in the second half of the first year of life with the development of the emotion of fear and expressions of distress and hesitation in the presence of novelty (Rothbart, 1989a; Rothbart & Bates, 1998). Children who are high on behavioral inhibition respond negatively to new people and other types of novel stimulation (Fox et al., 2001; Kagan et al., 1987). Physiological research on behaviorally inhibited children indicates that these children generally have a more responsive sympathetic nervous system. This sympathetic dominance can be seen by the finding that behaviorally inhibited children tend to have a high and stable heart rate in unfamiliar situations, indicating that these children are highly aroused by unfamiliarity. Inhibited children also appear to have a highly sensitive amygdala, a limbic structure implicated in fear reactions (Fox et al., 2001; Kagan & Snidman, 1991). Many behaviorally inhibited children respond intensely to novel situations, and in particular, they tend to be highly prone to tension, anxiety, and fear in these situations.

The conscientiousness system underlies perseverance in tasks that are not intrinsically rewarding but are important to fulfill long-range goals. The trait of Conscientiousness involves variation in the ability to defer gratification, persevere in unpleasant tasks, pay close attention to detail, and behave in a responsible, dependable manner; not surprisingly, conscientiousness increases with age in children (Lamb et al., 2002). Beginning at about 10 to 12 months of age, temperament research has revealed a trait of effortful control involving focused attention on tasks and the ability to inhibit inappropriate approach tendencies (Rothbart, Ahadi, & Evans, 2000). Rothbart et al. (2001) have shown that this trait is related in adults to Conscientiousness in the FFM.

The psychiatric disorders most associated with conscientiousness are obsessive-compulsive personality disorder (OCD) and antisocial personality disorder (e.g., irresponsible and delinquent acts, failure to honor obligations or plan ahead) (Widiger et al., 2002; Widiger & Trull, 1992). OCD tends to co-occur with a variety of phobic states and other anxiety disorders (e.g., Marks, 1987; Öhman, 1993). An important aspect of Gray's (1982, 1987) theory is that anxiety is a critical emotion of obsessive-compulsive disorder. Gray views phobias and obsessive-compulsive behavior as linked to the same systems because of the central role for anxiety in these disorders. From this perspective, the adaptive function of the Conscientiousness system is to check for possible threats emanating from the environment, including physical contamination, non-attainment of goals related to self-preservation, and other possible sources of danger and punishment.

The frontal cortex has been implicated in many of the behaviors associated with Conscientiousness. Mesulam (1986; see also Luria, 1980; Tucker & Derryberry, 1992) notes that humans and monkeys with prefrontal cortex damage have difficulty focusing attention, planning orderly sequences of behavior, inhibiting immediate but inappropriate response tendencies, delaying gratification, persevering in tasks that take a great deal of effort, and planning for the future. Furthermore, Tucker and Derryberry (1992) reviewed data indicating that lesions of the frontal cortex were effective for patients with chronic anxiety and sometimes even produced a pathological lack of anxiety, a primary negative emotion of the Conscientiousness system.

There is also evidence for mutual inhibitory influences between the mechanisms underlying Conscientiousness and behavioral approach systems. Mesulam (1986) described reciprocal inhibition between frontal and the parietal lobes, the latter viewed as an approach system characterized by diffuse attention and impulsive responding. There are also reciprocal inhibitory influences between the BIS and the reward-based approach system (Avila, 2002; Fox, 1994; Gray, 1987). In the rat at least, the inhibitory

influences from the BIS are more powerful than the reverse. Both systems may be aroused in particular situations, as when a previously rewarded behavior has been punished.

These results have implications for thinking about conflicts between evolved systems as well as for situation specificity. The systems underlying behavioral approach and behavioral inhibition are psychometrically and neurophysiologically independent, implying that individuals can be more or less sensitive to rewards and more or less sensitive to punishment (Avila, 2001; Pickering, Diaz, & Gray, 1995). Nevertheless, each system has inhibitory effects on the other system, so that in a situation with both potential rewards and potential punishments, both systems are activated. Individuals high on behavioral approach evaluate the risks involved and engage in behavioral approach, while introverts, being less attracted to the potential rewards, are more likely to have approach tendencies inhibited. Impending punishments trigger the BIS even for individuals moderately high on behavioral approach; however, a situation characterized overwhelmingly by potential reward with little risk activates the reward/approach systems even for individuals with powerful inhibitory tendencies. The result is what one might term “System X Trait X Situational” variation, where the “System” is understood as a universal mechanism responsive to particular perceived environmental contingencies and the “Trait” represents individual differences in proneness to activating particular systems.

Attentional mechanisms are implicated in Conscientiousness. Indeed, within the FFM, attention deficit hyperactivity disorder (ADHD) is most strongly linked to low Conscientiousness (Nigg et al., 2002). Tucker and Derryberry (1992; see also Tucker & Williamson, 1984) have proposed that left frontal systems mediate attention that is tightly focused on possible environmental threats as well as planning to meet these environmental contingencies. Amphetamine is typically prescribed for individuals with ADHD and helps them engage in effortful, planned behavior and to focus attention on important environmental cues. Large doses of amphetamine result in repetitive, stereotyped (i.e., novelty avoidant), overfocused, hypervigilant, and eventually paranoid behavior. Tucker and Derryberry noted that the compulsions of obsessive-compulsive disorder patients are stereotyped and often tightly focused on imagined threats emanating from the environment (germs, dirt). Unlike the extraverted attention characterized by an habituation bias, the attentional style associated with the attributes of Conscientiousness is narrow, focused, and has a redundancy bias.

The evolutionary theory of sex outlined above suggests that females would tend to adopt a more conservative strategy and thus be higher on measures of conscientiousness and more prone to anxiety disorders. Nevertheless, males

must also be acutely concerned with threats emanating from the environment, particularly the social environment, and be able to defer gratification in the pursuit of long-term benefits. Because the mechanisms underlying behavioral approach are distinct from those underlying Conscientiousness and there are mutually inhibitory relationships between them, the most that could be predicted is that males, because of their high levels of behavioral approach, would have a somewhat greater tendency to be biased toward lower levels of Conscientiousness.

Evolutionary theory predicts that females will be more sensitive than men to physical dangers. Females are more prone to most anxiety disorders, including agoraphobia and panic disorder (e.g., Weissman, 1985; *DSM-IV*; *DSM-IV* is correct). Girls report being more fearful and timid in uncertain situations than boys and are more cautious and take fewer risks than boys (Christopherson, 1989; Ginsburg & Miller, 1982). Girls are also more compliant than boys beginning in the toddler period and throughout childhood (Kochanska & Aksan, 1995).

The widespread occurrence of social phobias (Gray, 1987; Marks, 1987) is compatible with evolution of mechanisms finely tuned to evaluation by the group. It is interesting in this regard that the general tendency for females to be higher on phobias and other indicators of fearfulness and caution is not found for social phobia (Marks, 1987; *DSM-IV*). Social phobias involve fears of negative evaluations by a group, and one might speculate that there were evolutionary pressures on group-living males for concern for status within the group. Öhman (1993) found that angry faces are among the potentially phobic stimuli (including also snakes and spiders) able to condition autonomic responses that are more resistant to extinction than those conditioned to neutral stimuli—findings that suggest innate feature detectors related to social fears. Feelings of guilt and excessive social responsibility are also common symptoms of obsessive-compulsive disorder, another anxiety disorder that also fails to consistently show a sex difference (*DSM-IV*; Weissman, 1985).

4. *Affect Intensity*. Affect intensity functions to mobilize behavioral resources by moderating arousal in acutely demanding situations in the service of both approach and avoidance behaviors. Affect intensity may be viewed as a general behavioral “engine” that is used both in the service of behavioral approach and behavioral avoidance. It is a behavioral scaling system that allows the organism to scale its responses to current environmental opportunities and threats. This system is well studied at the neurophysiological level, where research implicates catecholamine systems that energize both positive and negative emotion systems (Panksepp, 1998,

pp. 109–110, 117). Among temperament researchers, there is general consensus that there are two independent dimensions of reactivity and regulation (see, e.g., Ramsey & Lewis, 2003; Rothbart, 1989a, 1989b; Rothbart & Bates, 1998). Children who are highly reactive respond intensely to stimulation, reach peak arousal at lower stimulus intensity, and have a relatively low threshold for arousal. These children are often viewed as having a weak nervous system in the sense that they are easily aroused and overstimulated. In the presence of high levels of stimulation, these high-reactive individuals inhibit their responding and tend to withdraw from the source of stimulation. On the other hand, they respond very intensely to even low levels of stimulation. Low-reactive children may be said to have relatively strong nervous systems in the sense that they have a relatively high threshold of stimulation and do not become aroused by stimulation which would overwhelm a high-reactive individual. Low-reactive individuals are thus more likely to be found in highly stimulating environments, although at extremely high levels of stimulation, even these individuals begin to inhibit their responding and withdraw from stimulation.

Emotionally intense individuals respond relatively strongly to emotional stimulation independent of the emotion involved, including both positive and negative emotions (Larsen & Diener 1987). People high on affect intensity are prone to fast and frequent mood changes and lead varied and variable emotional lives. Clinically, affect intensity is related to cyclothymia, bipolar affective disorder, neurotic symptoms, and somatic complaints (nervousness, feeling uneasy, shortness of breath). Several developmental studies have found that proneness to both positive and negative emotions under moderate levels of stimulus intensity is associated with reactivity as indicated by measures of vagal tone and event-related potentials (Fox, 1989; Gunnar & Nelson, 1994; Porges, 1991). Recently, Garey et al. (2003) identified a generalized arousal component in the behavior of mice across experiments, investigators, and mouse populations. This factor accounts for about one third of the variance in arousal-related measures.

Affect intensity may be viewed as a generalized motivation-enhancement system that can be directed toward behavioral approach (Dominance/Sensation Seeking) as well as behavioral avoidance and checking for possible threats in the environment (Conscientiousness and Behavioral Inhibition). The catecholamine systems underlying arousal are nonspecific; they induce arousal in a wide variety of systems (Panksepp, 1998). Individuals high on affect intensity are thus highly motivated to intensive interaction with the environment. For example, Fox et al. (2001) found that reactive children who showed continuity of behavioral inhibition were prone to negative emotional responding and had a pattern of right

frontal asymmetry in their EEG patterns. On the other hand, highly reactive exuberant children had a pattern of left frontal asymmetry. Reactive children are thus prone to intense emotional response, but they may be biased toward positive or negative emotions. Of the children classified as unreactive on the basis of EEG data, some were consistently inhibited while others were consistently uninhibited; most were not classifiable as consistently either. Again, these data illustrate the independence of reactivity from behavioral inhibition and behavioral approach systems.

Affect intensity is most closely associated with Neuroticism in the FFM (Larsen & Diener, 1993). Watson and Clark (1992) show that Neuroticism is associated with all four of their dimensions of negative affect: guilt, hostility, fear, and sadness. However, these negative emotions also tend to be associated with the other systems underlying the FFM: hostility (negatively) with Nurturance/Love, sadness with introversion, fear with conscientiousness, and guilt with Nurturance/Love and Conscientiousness. Neuroticism also appears to be related to a wide range of personality disorders that also load on other systems (Costa & McCrae, 1986; Widiger & Trull, 1992). High affect intensity thus energizes negative emotional responding in general. However, affect intensity also provides a powerful engine for positive emotional responses that are central to other physiologically and psychometrically independent systems (Aron & Aron, 1997; Panksepp, 1998, p. 117).

5. *Openness to Experience*. The Openness to Experience factor taps variation in intelligence and what one might term “optimal Piagetian learning”: intrinsically motivated curiosity and interest in intellectual and aesthetic experience combined with imagination and creativity in these areas. Openness increases during adolescence, a time when, with increasing cognitive sophistication, adolescents exhibit greater interest in a wide range of experiences (McCrae et al., 2002). Openness is also related to scores on standardized measures of cognitive ability, including verbal and mathematical achievement tests (John et al., 1994; Lamb et al., 2002). Openness is thus related to domain-general cognitive abilities tapped by such measures and discussed in Chapter 2 as an adaptation to uncertain, rapidly changing environments.

An Evolutionary Perspective on Environmental Influences

The results of behavior genetic research indicate that environmental variation has considerable influence on phenotypic variation in personality,

but with the exception of Agreeableness, there is no evidence that environmental variation is shared within families (e.g., Bouchard, 1996). Within an evolutionary systems perspective, environmental influences are conceptualized as involving specific types of stimulation directed at particular evolved systems. Thus, environmental influences affecting the Conscientiousness system would be expected to be events related to inhibiting inappropriate approach behaviors in children (perhaps by parental discipline), while environmental influences related to Nurturance/Love would be expected to involve warmth and affection that typically occur in close family relationships.

For example, Fox et al. (2001) found that inhibited children placed in day care within the first 2 years were more likely to change to a noninhibited pattern, and suggested that this may be due to greater experience with nonfamily members. Elsewhere, I have argued that given the status of the human affectional system in promoting close relationships, the primary source of environmental influences would be adult caretakers, typically family members (MacDonald, 1992, 1997). If the relevant environmental stimulation is that which we label warm and affectionate, this type of stimulation is unlikely to come from other sources, at least during infancy and early childhood. It is thus not surprising that Agreeableness shows evidence of shared environmental influence (Bouchard, 1996; Tellegen et al., 1988). Similarly, shared environmental influence has been implicated in security of attachment (Bokhorst et al., 2003). In general, behavior genetic studies have shown more evidence of shared environmental influence in infancy and early childhood (e.g., Plomin, 1994).

Developing emotional ties to children may also be considered an aspect of parental investment. The idea that there was natural selection for high-investment parenting among humans is widely held among evolutionists (e.g., Fisher, 1992; Flinn & Low, 1986; Geary, 1998; Lancaster & Lancaster, 1987; Lovejoy, 1981; MacDonald, 1988, 1992). High-investment parents provide high-quality environments for their children, and these environments contribute to the child's development. Parental investment involves the provision of certain environments, and parents incur a considerable cost in providing these environments: Parental investment includes developing a strong emotional relationship with the child, providing relatively high levels of verbal stimulation and parent-child play, and active parental involvement in monitoring virtually every aspect of the child's life (e.g., children's progress in school, children's peer relationships) (Belsky et al., 1991). From a theoretical perspective, the best evidence that the environments provided by high-investment parents must have benefits is the very clear evidence that they are costly to provide. Theoretically, it is difficult to conceive of a

behavior with clear costs remaining in a population without some compensating benefits. For example, if children do not benefit from paternal investment, it is difficult to conceptualize why either males or females would seek such investment. Under these circumstances, males would be better off competing with other males for access to additional females (i.e., increasing their mating effort) than to invest in the offspring of one female (i.e., maintaining high levels of parenting effort). Minimal parenting effort by males is a common pattern in nature, especially among mammals (e.g., Kleiman, 1977, 1981).

While the foregoing argues for the importance of children's environments, it is not inconsistent with evidence that high-investment parenting is itself genetically influenced. There is evidence for reasonably high heritability of all of the behaviors related to parental investment. Thus, measures of parents' and children's perceptions of parental control, and especially parental warmth, are genetically influenced (Rowe, 1994). Parental stimulation and involvement (including measures of parental warmth and control) as measured by the Home Observation for Measurement of the Environment (HOME) and the Family Environment Scale (FES) also have a considerable genetic component (Plomin, 1994). These measures of parental investment covary to a considerable degree with high IQ, which is itself substantially heritable (Plomin 1994; see also below). There is a substantial covariation among the HOME subscales of emotional and verbal responsiveness, provision of play materials, maternal involvement, and opportunities for variety of stimulation (Bradley & Caldwell, 1984). Parents who provide verbal stimulation and monitor their children closely also tend to have close emotional relationships with them.

Within an evolutionary paradigm, parental investment is an important aspect of life history theory. Life history theory attempts to understand variation in the reproductive strategies adopted by different life forms. Life history theory implies considerable coherence to individual development because a reproductive strategy involves a coordinated response to the organism's environment resulting from the need to optimally partition mating effort (i.e., the effort expended in attracting mates) and parenting effort (i.e., the effort devoted to nurturing children). The fundamental dimension of reproductive strategies may be construed as a dimension that ranges from a high-parental-investment/low-mating-effort strategy to a low-parental-investment/high-mating-effort strategy.

A reproductive strategy involves a response to a central external ecological contingency that selects for optimum levels of partitioning mating effort and parenting effort. The result is that variables such as mortality rates, longevity, pair bonding, age of first reproduction, period of preadult

dependency, and levels of paternal and maternal investment evolve as a coordinated response to the environment. Thus, for example, species adapted to environments where there is a relatively stable, predictable resource base tend to have a suite of traits allowing them to produce highly competitive offspring. Such species would be likely to have traits such as pair bonding between parents, high-investment parenting (including paternal provisioning of the young), low fertility, and delayed maturation of the young.

Theoretically, high-investment parenting is associated with adaptation to ecologically adverse or highly competitive environments where high levels of parental investment are critical to rearing successful offspring (Kleiman, 1977, 1981; Southwood, 1981). This makes intuitive sense because in ecologically adverse or highly competitive situations, male provisioning of food or other resources might tip the balance in favor of offspring compared with the offspring of males who do not provision their young. Indeed, several theorists have proposed that the adverse environment created by the Ice Age had an important role in shaping the intelligence and high-investment reproductive behavior of northern populations (Lynn, 1991; Miller, 1994a, 1994b; Rushton, 1995). Within this framework, natural selection resulted in a uniform tendency toward high-investment parenting as a result of long-term resource scarcity: Males who did not provision their young left few descendants. Long-term selection in resource-scarce environments is therefore expected to lead to high-investment parenting.

The data reviewed by Belsky et al. (1991) illustrate the utility of a life history perspective. They especially note the large intercorrelations among spousal harmony, parent-child relationship quality, children's interpersonal style, timing of puberty, sexual behavior, and level of parental investment. These qualities would be expected to be most closely related to the Nurturance/Love system discussed here; Figueredo et al. (2004) found that a single "K-factor" composed of measures of these qualities correlated -0.67 with the closely related factor of Psychoticism. The coherence of individual development also appears to involve measures of intelligence (e.g., Rushton, 1995) related to the Openness factor of the FFM. IQ is the single most powerful measure of individual differences psychologists have developed and is related to variation in a very wide range of human activities. Recent studies suggest that variation in life history strategy is influenced genetically (Moffitt, Caspi, Belsky, & Silva, 1992; Rowe, 2000; Comings, Muhlman, Johnson, & MacMurray 2002). Comings et al. (2002) report that father-daughter transmission of a specific X-linked androgen receptor gene is associated with early menarche as well as with parental divorce. Age of menarche is highly heritable; there is no evidence for shared environmental influence as would be expected in a father absence model (Rowe, 2000).

Evolution and Group Differences in Personality Systems

Several personality systems show systematic, theoretically expected differences between groups, the most important being sex and age differences noted above. Furthermore, because different human groups evolved in somewhat different EEAs, it is not surprising that there is between-group variation on personality systems. For example, children from the Mongoloid gene pool are lower on affect intensity, aggression, and disruptiveness, and tend to be more cooperative than Caucasian children (Brazelton, Robey, & Collier, 1969; Freedman & Freedman, 1969; Orlick, Zhou, & Partington, 1990). For adults, Vernon (1982), using a variety of standard personality instruments, found that Mongoloids were more introverted, more anxiety prone, less aggressive, and lower on social dominance than Caucasians, while Rushton (1995) found that Mongoloid samples were less extraverted and more neurotic than Caucasians. Also noting various physical adaptations for extreme cold typical of Mongoloids, including flattened face, narrow eyes, shortened limbs, and the epicanthic fold, Lynn (1991) and Rushton (1995) have theorized that this suite of traits resulted from selection for behavioral restraint during the Ice Age.

Birth order is another source of systematic group differences in personality. Sulloway (1996, 1999; see also Paulhus, Trappnell, & Chen, 1999; Rohde et al., 2003) has provided evidence for modest birth order effects on the five-factor dimensions and rebelliousness, and he has provided a compelling evolutionary interpretation of these differences. Firstborns have been found to be lower on Openness, higher on Conscientiousness, lower on Agreeableness, higher on negative emotionality (Neuroticism), higher on social dominance, lower on sociability (a facet of Surgency/Extraversion related also to Agreeableness), and lower on rebelliousness. Birth order—conceptualized as a proxy for differences in age, size, power, status, and privilege—is proposed as the most important systematic unshared environmental influence on personality. Each child attempts to occupy a niche within the family. The oldest child occupies the first available niche, identifies more strongly with parents and with authority, and tends to reject new ideas. Younger children identify less with their parents and are more open to new experience and ideas.

Sulloway's evolutionary perspective draws on parent-offspring conflict theory (Trivers, 1974). Parents tend to favor older offspring because they have a higher reproductive value (i.e., they are closer to reproducing themselves), particularly in situations where resources are limited. This is

theorized to increase firstborns' identification with adult values and facilitate the Conscientiousness system. Because they share only half their genes, siblings also have conflicts with each other over resources, and older siblings are typically able to dominate their younger siblings because of their advantages in size and strength. This strengthens the trait of Social Dominance. Laterborns, on the other hand, resent this domination and develop a suite of strategies that enable them to occupy other niches within the family dynamic, including higher levels of sociability and agreeableness.

Evolutionary Perspectives on Individual Differences in Personality Systems

Despite the claims that individual differences in personality are without adaptive significance (Tooby & Cosmides, 1990), evolutionary perspectives on individual differences is an active area of research and theorizing (Figueredo et al., 2004). A basic idea shared by several writers is that personality distributions imply more than one viable adaptive strategy (Belsky et al., 1991; Figueredo & King, 2001; Figueredo et al., 2004; Gangestad & Simpson, 1990; MacDonald, 1991; Wilson, 1994; see also discussion in Buss, 1991). Genetic variation in personality and other valued traits serves to facilitate the production of a wide range of variation (within a delimited range), which facilitates the occupation of a wide range of possible niches in the human and nonhuman environment.

One way that this variation could be maintained is via frequency-dependent selection, selection in which relatively rare phenotypes have an advantage while more common phenotypes have a disadvantage because they must compete with each other in the same niche (Figueredo & King, 2001; Gangestad & Simpson, 1990; Mealey, 1995). Another possibility is that stabilizing selection (i.e., selection against extremes) occurred (MacDonald, 1995, 1998). Personality systems fundamentally motivate people to approach the world and avoid dangers. Unlike the case with intelligence, it is intuitively plausible that being very high or very low on personality systems is maladaptive. For example, people must be motivated to approach rewards and take some risks in obtaining them, but being foolhardy is dangerous. On the other hand, there is a broad range of genetic variation in the middle of the distribution underlying a range of viable strategies. This approach is consistent with attempts to conceptualize psychopathology in terms of maladaptive extremes on FFM dimensions (e.g., Costa & Widiger, 1994).

Recent evidence suggests the importance of both frequency dependent selection and stabilizing selection for the 7R allele of the D4 dopamine

receptor gene linked with novelty seeking, impulsivity, and attention deficit disorder hyperactivity (ADHD). Harpending & Cochran (2002) interpret available data as suggesting natural selection for this allele up to a certain point followed by stabilizing selection. Despite their extreme behavior, children with this gene did not show common neurological abnormalities related to attention deficits (Swanson et al., 2000), suggesting that this variant of the D4 gene was adaptive during evolutionary history (Harpending & Cochran, 2002; see Ding et al., 2002). Data for this allele are also relevant to group differences in personality systems: This gene is common among South American Indians, occurs at intermediate levels in Europeans and in most African groups, and is non-existent among East Asians and the African !Kung (Harpending & Cochran, 2002).

The finding that a gene linked with psychopathology in contemporary environments was adaptive during evolutionary history is consistent with Farley's (1981, 1985) comment that individuals high on sensation seeking are overrepresented in prison populations, but sensation seekers who are well socialized are also overrepresented among highly creative people, including highly successful scientists, artists, political leaders, and entertainers. Similarly, several authors have noted that bipolar affective disorder is linked with creativity in normal or mildly affected relatives of psychiatrically impaired individuals (Andreasen, 1978; Richards, Kinney, Lunde, Henet, & Merzel 1988), with creativity associated with the manic phase (Isen, Daubman, & Nowicki, 1987). Evolutionists have also theorized that some psychopathology results from the differences between modern environments and the environments humans evolved in (e.g., Nesse & Williams, 1996). For example, rates of depression may be influenced by contemporary trends toward families removing themselves from close kinship ties as a source of social support. In addition, particular cultural contexts may render certain behavior pathological and maladaptive that would be quite adaptive in a different cultural setting. For example, it has often been informally suggested that although there are exceptions, the behavior of children with ADHD tends to be maladaptive in contemporary societies where children are expected to adjust to educational settings. However, such children may be well-adapted to life in societies where the aggressiveness and high-energy level of these children would be valued traits.

Personality and Social Evaluation

People are greatly interested in the genetic and phenotypic diversity represented by this range of viable strategies (MacDonald, 1995, 1998). As Buss (1991) notes, personality is an adaptive landscape in which "perceiving,

attending to, and acting upon differences in others is crucial for solving problems of survival and reproduction” (p. 471). Hogan’s (1996) socioanalytic theory emphasizes social evaluation as central to personality psychology. Individual differences in personality are thus viewed as indicators of whether individuals are suited for particular roles. Each individual is expected to not only appraise the phenotypic traits of others but also to evaluate these traits differently depending on the type of relationship entered into. For example, Lusk, MacDonald, and Newman (1993) found that ideal leaders were expected to be higher than ideal friends in scales intended to tap variation in physical attractiveness, intelligence, conscientiousness, activity, and sociability, but lower in emotionality and disabilities—a trait profile that presumably reflects individuals’ criteria for being a good leader. Ideal friends, on the other hand, were expected to be higher than prospective leaders in athletic ability and Intimacy/Warmth, traits that are presumably more important for a successful friendship. Moreover, subjects expected ideal friends to be more similar to self than to ideal leaders, and subjects rated themselves as more similar to prospective ideal leaders and ideal friends on categories that they themselves rated highly. Because of the importance of social evaluation of personality, people are motivated to adopt personality profiles that are appealing to other people: the job candidate who attempts to appear conscientious, the suitor who tries to appear loving and nurturing.

Conclusion

The foregoing illustrates how evolutionary theory is able to make an important contribution to personality research. The main contributions are to provide a powerful theory for a great many age and sex differences in personality and to think of personality variation as serving adaptive functions. Another contribution, much stressed here, is to emphasize the central importance of personality systems. In my view, the most neglected area is the failure to think of personality and temperament traits as reflecting variation in evolved systems serving adaptive functions. For historical reasons stemming from the fact that personality research originated long before a solid base in evolution and biological research was possible, we tend to think about variation but not about systems. We therefore miss the complex interactions among systems as being at the heart of personality—interactions that go a long way toward placing personality at the forefront of how people confront their social and nonsocial environments.

References

- Andreasen, N. C. (1978). Creativity and psychiatric illness. *Psychiatric Annals*, *8*, 113–119.
- Aron, E. N., & Aron, A. (1997). Sensory-processing sensitivity and its relation to introversion and emotionality. *Journal of Personality and Social Psychology*, *73*, 345–368.
- Avila, C. (2001). Distinguishing BIS-mediated and BAS-mediated disinhibition mechanisms: A comparison of disinhibition models of Gray (1981, 1987) and of Patterson and Newman (1993). *Journal of Personality and Social Psychology*, *80*, 311–324.
- Bartels, A., & Zeki, S. (2000). The neural basis of romantic love. *NeuroReport*, *11*(17), 3829–3834.
- Bates, J. E. (1989). Concepts and measures of temperament. In G. A. Kohnstamm, J. E. Bates, & M. K. Rothbart (Eds.), *Temperament in childhood* (pp. 3–26). Chichester, UK: John Wiley & Sons.
- Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development*, *62*, 647–670.
- Berndt, T. J. (1986). Children's comments about their friendships. In M. Perlmutter (Ed.), *Minnesota Symposia in Child Development: Vol. 18. Cognitive perspectives on children's social and behavioral development* (pp. 189–212). Hillsdale, NJ: Erlbaum.
- Bokhorst, C. L., Bakermans-Kranenburg, M. J., Pasco Fearon, R. M., van Ijzendoorn, M. H., Fonagy, P., & Schuengel, C. (2003). The importance of shared environment in mother-infant attachment security: A behavioral genetic study. *Child Development*, *74*, 1769–1782.
- Buhrmester, D., & Furman, W. (1987). The development of companionship and intimacy. *Child Development*, *58*, 1101–1113.
- Bowlby, J. (1969). *Attachment and loss: Vol. I. Attachment*. London: Hogarth Press and the Institute of Psychoanalysis.
- Bouchard, T. J. Jr. (1996). The genetics of personality. In K. Blum & E. P. Noble (Eds.), *Handbook of psychoneurogenetics* (pp. 267–290). Boca Raton, FL: CRC Press.
- Bradley, R. H., & Caldwell, B. (1984). Children: A study of the relationship between home environment and cognitive development during the first 5 years. In A. W. Gottfried (Ed.), *Home environment and early cognitive development: Longitudinal research*. Orlando, FL: Academic Press.
- Brazelton, T. B., Robey, J. S., & Collier, G. A. (1969). Infant development in the Zinacanteco Indians of Southern Mexico. *Pediatrics*, *44*, 274–290.
- Brennan, K. A., Clark, C. L., & Shaver, P. R. (1998). Self-report measurement of adult attachment. In J. A. Simpson & W. S. Rholes (Eds.), *Attachment theory and close relationships*. New York: Guilford Press.

- Buss, D. M. (1991). Evolutionary personality psychology. *Annual Review of Psychology*, 42, 459–491.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, 100, 204–232.
- Caspi, A. (1998). Personality development across the lifespan. In N. Eisenberg (Ed.), *Handbook of child psychology* (Vol. 3, pp. 105–176). New York: John Wiley.
- Charlesworth, W., & Dzur, C. (1987). Gender comparisons of preschoolers' behavior and resource utilization in group problem solving. *Child Development*, 58, 191–200.
- Christopherson, E. R. (1989). Injury control. *American Psychologist*, 44, 237–241.
- Cloninger, C. R. (1987). A systematic method for clinical description and classification of personality. *Archives of General Psychiatry*, 44, 573–588.
- Comings, D. E., Muhleman, D., Johnson, J. P., & MacMurray, J. P. (2002). Parent-daughter transmission of the androgen receptor gene as an explanation of the effect of father absence on age of menarche. *Child Development*, 73, 1046–1051.
- Costa, P. T., & McCrae, R. R. (1986). Personality stability and its implications for clinical psychology. *Clinical Psychology Review*, 6, 407–423.
- Costa, P. T., & McCrae, R. R. (1992). *NEO-PI-R professional manual*. Orlando, FL: PAR.
- Costa, P. T., & Widiger, T. A. (1994). Summary and unresolved issues. In P. T. Costa & T. A. Widiger (Eds.), *Personality disorders and the five-factor model of personality*. Washington, DC: American Psychological Association.
- Cowan, G., & Avants, S. K. (1988). Children's influence strategies: Structure, sex differences, and bilateral mother-child influences. *Child Development*, 59, 1303–1313.
- Davidson, R. J. (1993). The neuropsychology of emotion and affective style. In M. Lewis & J. M. Haviland (Eds.), *Handbook of emotions* (pp. 143–154). New York: Guilford Press.
- Depue, R. A., & Collins, P. F. (1999). Neurobiology of the structure of personality: Dopamine facilitation of incentive motivation and extraversion. *Brain and Behavioral Sciences*, 22, 491–569.
- Depue, R. A., & Morrone-Strupinsky, J. V. (2005). A neurobehavioral model of behavioral bonding: Implications for conceptualizing a human trait of affiliation. *Behavioral and Brain Sciences*, 28(3), 313–378.
- De Raad, B. (1992). The replicability of the Big Five personality dimensions in three word-classes of the Dutch language. *European Journal of Personality*, 6, 15–29.
- Derryberry, D. (1987). Incentive and feedback effects on target detection: A chronometric analysis of Gray's theory of temperament. *Personality and Individual Differences*, 8, 855–865.
- Diagnostic and Statistical Manual of Mental Disorders: DSM-IV* (1994). Washington, DC: American Psychiatric Association.

- Digman, J. M., & Shmelyov, A. G. (1996). The structure of temperament and personality in Russian children. *Journal of Personality and Social Psychology, 71*, 341–351.
- Ding, Y. C., Chi, H. C., Grady, D. L., Morishima, A., Kidd, J. R., Kidd, K. K., Flodman, P., Spence, M. A., Schuck, S., Swanson, J. M., Zhang, Y., & Moyzis, R. K. (2002). Evidence of positive selection acting at the human dopamine receptor D4 gene locus. *Proceedings of the National Academy of Science, 99*, 309–314.
- DiPietro, J. A. (1981). Rough and tumble play: A function of gender. *Developmental Psychology, 17*, 50–58.
- Douvan, E. A., & Adelson, J. (1966). *The adolescent experience*. New York: John Wiley.
- Draper, P., & Harpending, H. (1988). A sociobiological perspective on the development of human reproductive strategies. In K. MacDonald (Ed.), *Sociobiological perspectives on human development* (pp. 340–372). New York: Springer-Verlag.
- Eagly, A. H., & Steffan, V. J. (1986). Gender and aggressive behavior: A meta-analytic review of the social psychological literature. *Psychological Bulletin, 100*, 283–308.
- Eaton, W. O., & Enns, L. R. (1986). Sex differences in human motor activity level. *Psychological Bulletin, 100*, 19–28.
- Eaton, W. O., & Yu, A. P. (1989). Are sex differences in child motor activity level a function of sex differences in maturational status? *Child Development, 60*, 1005–1011.
- Ehrhardt, A. A., & Baker, S. W. (1974). Fetal androgens, human central nervous system differentiation, and behavioral sex differences. In R. C. Friedman, R. M. Rickard, & R. L. Van de Wiele (Eds.), *Sex differences in behavior*. New York: John Wiley.
- Ehrhardt, A. A. (1985). The psychobiology of gender. In A. S. Rossi (Ed.), *Gender and the life course*. New York: Aldine.
- Eysenck, H. J. (1967). *The biological basis of personality*. Springfield, IL: Charles C Thomas.
- Eysenck, H. J. (Ed.) (1982). *Personality, genetics, and behavior*. New York: Praeger.
- Farley, F. H. (1981). Basic process individual differences: A biologically-based theory of individualization for cognitive, affective, and creative outcomes. In F. H. Farley & N. H. Gordon (Eds.), *Psychology and education: The state of the union*, (pp. 7–31). Berkeley, CA: McCutchan Publishing Corp.
- Farley, F. H. (1985). The Big T in personality. *Psychology Today, 20*, 44–52.
- Figueredo, A. J., & King, J. E. (1996). The evolution of individual differences in behavior. *Western Comparative Psychological Association Observer, 2*(2), 1–4.

- Figueredo, A. J., & King, J. E. (2001). *The evolution of individual differences*. In S. D. Gosling & A. Weiss (Chairs), Symposium on Evolution and Individual Differences, Annual Meeting of the Human Behavior and Evolution Society, London, UK.
- Figueredo, A. J., Sefcek, J.A., Vasquez, G., Brumbach, B. H., King, J. E. & Jacobs, W. J. (2005). Evolutionary personality psychology. In Buss, D.M., (Ed.), *Handbook of evolutionary psychology*. Pp. 851–877. Hoboken, NJ: Wiley.
- Fisher, H. (1992). *The anatomy of love*. New York: Norton.
- Flinn, M. V., & Low, B. S. (1986). Resource distribution, social competition, and mating patterns in human societies. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecological aspects of social evolution: Birds and mammals* (pp. 217–243). Princeton, NJ: Princeton University Press.
- Fox, N. A. (1989). Psychophysiological correlates of emotional reactivity during the first year of life. *Developmental Psychology*, 25, 364–372.
- Fox, N. A. (1994). Dynamic cerebral processes underlying emotion regulation. In N. Fox (Ed.), *The development of emotion regulation: Biological and behavioral considerations*. *Monographs for the Society for Research in Child Development*, 59(2/3, Serial No. 240), 152–166.
- Fox, N. A., Henderson, H. A., Rubin, K. H., Calkins, S. D., & Schmidt, L. A. (2001). Continuity and discontinuity of behavioral inhibition and exuberance: Psychophysiological and behavioral influences across the first four years of life. *Child Development*, 72, 1–21.
- Freedman, D. J., & Freedman, N. C. (1969). Behavioral differences between Chinese-American and European-American newborns. *Nature*, 224, 1227.
- Gangestad, S. W., & Simpson, J. A. (1990). Toward an evolutionary history of female sociosexual variation. *Journal of Personality*, 58, 69–96.
- Garey, J., Goodwillie, A., Frohlich, J., Morgan, M., Gustafsson, J.-A., Smithies, O., Korach, K. S., Ogawa, S., & Pfaff, D. W. (2003). Genetic contributions to generalized arousal of brain and behavior. *Proceedings of the National Academy of Science*, 100, 11019–11022.
- Geary, D. (1998). *Male-female: The evolution of human sex differences*. Washington, DC: American Psychological Association.
- Ginsburg, H. J., & Miller, S. M. (1982). Sex differences in children's risk-taking behavior. *Child Development*, 53, 426–428.
- Goldberg, L. R. (1990). An alternative “description of personality”: The Big-Five factor solution. *Journal of Personality and Social Psychology*, 59, 1216–1229.
- Gosling, S. D., & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, 8(3), 69–75.
- Gray, J. A. (1982). *The neuropsychology of anxiety*. New York: Oxford University Press.

- Gray, J. A. (1987). *The psychology of fear and stress*. Cambridge, UK: Cambridge University Press.
- Graziano, W. G., & Ward, D. (1992). Probing the Big Five in adolescence: Personality and adjustment during a developmental transition. *Journal of Personality, 60*, 425–439.
- Gunnar, M. R., & Nelson, C. A. (1994). Event-related potentials in year-old infants: Relations with emotionality and cortisol. *Child Development, 65*, 80–94.
- Harpending, H., & Cochran, G. (2002). In our genes. *Proceedings of the National Academy of Science, 99(1)*, 10–12.
- Heller, W. (1990). The neuropsychology of emotion: Developmental patterns and implications for psychopathology. In N. L. Stein, B. Leventhal, & T. Trabasso (Eds.), *Psychological and biological approaches to emotion*. (pp. 167–211). Hillsdale, NJ: Erlbaum.
- Hogan, R. (1996). A socioanalytic perspective on the five-factor model. In J. S. Wiggins (Ed.), *The five-factor model of personality: Theoretical perspectives* (pp. 163–179). New York: Guilford Press.
- Humphreys, A. P., & Smith, P. K. (1987). Rough and tumble, friendship, and dominance in school children: Evidence for continuity and change with age. *Child Development, 58*, 201–212.
- Insel, T. R., Winslow, J. T., Wang, Z., & Young, L. J. (1998). Oxytocin, vasopressin, and the neuroendocrine basis of pair bond formation. *Advances in Experimental Medicine and Biology, 449*, 215–224.
- Isen, A. M., Daubman, K. A., & Nowicki, G. P. (1987). Positive affect facilitates creative problem solving. *Journal of Personality and Social Psychology, 52*, 1122–1131.
- John, O., Caspi, A., Robins, R. W., Moffitt, T. E., & Stouthamer-Loeber, M. (1994). The “little five”: Exploring the nomological network of the five-factor model of personality in adolescent boys. *Child Development, 65*, 160–178.
- Kagan, J., Reznick, J. S., & Snidman, N. (1987). The physiology and psychology of behavioral inhibition. *Child Development, 58*, 1459–1473.
- Kagan, J., & Snidman, N. (1991). Infant predictors of inhibited and uninhibited profiles. *Psychological Science, 2*, 40–44.
- Kernberg, O. F. (1986). Hysterical and histrionic personality disorders. In R. Michaels (Ed.), *Psychiatry, Vol. 1 (19)*: 1–11. Philadelphia: J. B. Lippencott Co.
- Kiesler, D. J. (1983). The 1982 interpersonal circle: A taxonomy for complementarity in human transactions. *Psychological Review, 90*, 185–214.
- King, J. F., & Figueredo, A. J. (1994, April). *Human personality factors in zoo chimpanzees?* Paper presented at the Western Psychological Association Convention, Kona, Hawaii.
- Klein, Z. (1995). Safety-seeking and risk-taking behavioral patterns in *Homo Sapiens*. *Ethology and Sociobiology*.

- Kochanska, G., & Aksan (1995). Mother-child mutually positive affect, the quality of child compliance to requests and prohibitions, and maternal control as correlates of early internalization. *Child Development*, 66, 236–254.
- Kohnstamm, G. K., Halverson, C. F., Mervielde, I., & Havill, V. L. (1998). *Parental descriptions of child personality: Developmental antecedents of the Big Five*. Mahwah, NJ: Erlbaum.
- Kleiman, D. G. (1977). Monogamy in mammals. *Quarterly Review of Biology*, 52, 39–69.
- Kleiman, D. G. (1981). Correlations among life history characteristics of mammalian species exhibiting two extreme forms of monogamy. In R. D. Alexander & D. W. Tinkle (Eds.), *Natural selection and social behavior* (pp. 332–344). New York: Chiron Press.
- LaFreniere, P. J., & Charlesworth, W. R. (1983). Dominance, affiliation and attention in a preschool group: A nine-month longitudinal study. *Ethology and Sociobiology*, 4, 55–67.
- Lamb, M. E., Chuang, S. S., Wessels, H., Broberg, A. G., & Hwang, C. P. (2002). Emergence and construct validation of the Big Five factors in early childhood: A longitudinal analysis of their ontogeny in Sweden. *Child Development* 73, 1517–1524.
- Lancaster, J. B., & Lancaster, C. S. (1987). The watershed: Change in parental-investment and family-formation in the course of human evolution. In J. B. Lancaster, J. Altman, A. S. Rossi, & L. R. Sherrod (Eds.), *Parenting across the life span: Biosocial dimensions* (pp. 187–205). New York: Aldine de Gruyter.
- Lang-Takoc, E., & Osterweil, Z. (1992). Separateness and connectedness: Differences between the genders. *Sex Roles*, 27, 277–289.
- Larsen, R. J., & Diener, E. (1987). Affect intensity as an individual difference characteristic: A review. *Journal of Research in Personality*, 21, 1–39.
- Larsen, R. J., & Diener, E. (1993). Promises and problems with the circumplex model of emotion. In M. S. Clark (Ed.), *Review of personality and social psychology: Vol. 13. Emotion* (pp. 25–59). Newbury Park, CA: Sage.
- LeDoux, J. (1996). *The emotional brain: The mysterious underpinnings of emotional life*. New York: Simon & Schuster.
- Lovejoy, O. (1981). The origin of man. *Science*, 211, 341–350.
- Lucas, R. E., Diener, E., Grob, A., Suh, E. M., & Shao, L. (2000). Cross-cultural evidence for the fundamental features of extraversion. *Journal of Personality and Social Psychology*, 79, 452–468.
- Luria, A. R. (1980). *The higher cortical functions in man*. New York: Basic Books.
- Lusk, J., MacDonald, K., & Newman, J. R. (1998). Resource appraisals among self, friend and leader: Implications for an evolutionary perspective on individual differences and a resource/reciprocity perspective on friendship. *Personality and Individual Differences*, 24, 685–700.

- Lynn, R. (1991). The evolution of racial differences in intelligence. *Mankind Quarterly*, 32, 99–173.
- MacDonald, K. B. (1983). Stability of individual differences in behavior in a litter of wolf cubs (*Canis lupus*). *Journal of Comparative Psychology*, 2, 99–106.
- MacDonald, K. B. (1988). *Social and personality development: An evolutionary synthesis*. New York: Plenum.
- MacDonald, K. B. (1991). A perspective on Darwinian psychology: Domain-general mechanisms, plasticity, and individual differences. *Ethology and Sociobiology*, 12, 449–480.
- MacDonald, K. B. (1992). Warmth as a developmental construct: An evolutionary analysis. *Child Development*, 63, 753–773.
- MacDonald, K. B. (1995). Evolution, the five-factor model, and levels of personality. *Journal of Personality* 63, 525–567.
- MacDonald, K. B., & Parke, R. D. (1986). Parent-child physical play: The effects of sex and age of children and parents. *Sex Roles*, 15, 367–378.
- MacDonald, K. B. (1997). The coherence of individual development: An evolutionary perspective on children's internalization of cultural values. In J. Grusec & L. Kuczynski (Eds.), *Parenting strategies and children's internalization of values: A handbook of theoretical and research perspectives* (pp. 321–355). New York: Wiley.
- MacDonald, K. B. (1999a). Love and security of attachment as two independent systems underlying intimate relationships. *Journal of Family Psychology*, 13(4), 492–495.
- MacDonald, K. B. (1999b). What about sex differences? An adaptationist perspective on “the lines of causal influence” of personality systems. Commentary on “Neurobiology of the Structure of Personality: Dopamine Facilitation of Incentive Motivation and Extraversion,” by R. A. Depue & P. F. Collins. *Behavioral and Brain Sciences*, 22(3), 530–531.
- Marks, I. (1987). *Fears, phobias, and rituals: Panic, anxiety, and their disorders*. Oxford, UK: Oxford University Press.
- McCrae, R. R., & Costa, P. T. (1990). *Personality in adulthood*. New York: Guilford Press.
- McCrae, R. R., Costa, P. T., Terracciano, A., Parker, W. D., Mills, C. J., De Fruyt, F., & Mervielde, I. (2002). Personality trait development from age 12 to age 18: Longitudinal, cross-sectional, and cross-cultural analysis. *Journal of Personality and Social Psychology*, 83, 1456–1468.
- Mealey, L. (1995). The sociobiology of sociopathy: An integrated evolutionary model. *Behavioral and Brain Sciences* 18, 523–599.
- Mesulam, M. M. (1986). Frontal cortex and behavior. *Annals of Neurology*, 19, 320–325.
- Miller, E. M. (1994a). Paternal provisioning versus mate seeking in human populations. *Personality and Individual Differences*, 17, 227–255.
- Miller, E. M. (1994b). Optimal adjustment of mating effort to environmental conditions: A critique of Chisholm's application of life history theory, with

- comments on race differences in male paternal investment strategies. *Mankind Quarterly*, 34, 297–316.
- Moffitt, T. E., Caspi, A., Belsky, J., & Silva, P. A. (1992). Childhood experience and the onset of menarche: A test of a sociobiological model. *Child Development* 63, 47–58.
- Nesse, R. M., & Williams, G. C. (1996). *Why we get sick: The new science of Darwinian medicine*. New York: Vintage Books.
- Newman, J. P. (1987). Reaction to punishment in extraverts and Psychopaths: Implications for the impulsive behavior of disinhibited individuals. *Journal of Personality Research*, 21, 464–480.
- Nigg, J. T., Blaskey, L. G., Huang-Pollock, C. L., Hinshaw, S. P., John, O. P., Willcutt, E. G., & Pennington, B. (2002). Big Five dimensions and ADHD symptoms: Links between personality traits and clinical symptoms. *Journal of Personality and Social Psychology*, 83, 451–469.
- O'Brien, M., & Huston, A. C. (1985). Development of sex-typed play in toddlers. *Developmental Psychology*, 21, 866–871.
- O'Connor, T. G., & Croft, C. M. (2001). A twin study of attachment in preschool children. *Child Development*, 72, 1501–1511.
- Öhman, A. (1993). Fear and anxiety as emotional phenomena: Clinical phenomenology, evolutionary perspectives, and information-processing mechanisms. In M. Lewis & J. M. Haviland (Eds.), *Handbook of emotions* (pp. 511–536). New York: Guilford Press.
- Orlick, T., Zhou, Q., & Partington, J. (1990). Co-operation and conflict within Chinese and Canadian kindergarten settings. *Canadian Journal of Behavioural Sciences*, 22, 20–25.
- Ostendorf, F. (1990). Sprache und persönlichkeitsstruktur: Zur validität des fünf-faktoren-modells der persönlichkeit [Language and personality structure: On the validity of the five-factor model of personality]. Regensburg, Germany: S. Roderer Verlag.
- Panksepp, J. (1982). Toward a general psychobiological theory of emotions. *Behavioral and Brain Sciences*, 5, 407–422.
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. New York: Oxford University Press.
- Paulhus, D. L., Trapnell, P. D., & Chen, D. (1999). Birth order effects on personality and achievement within families. *Psychological Science*, 10, 482–488.
- Pfiefer, M., Goldsmith, H. H., Davidson, R. J., & Rickman, M. (2002). Continuity and change in inhibited and uninhibited children. *Child Development*, 73, 1474–1485.
- Pickering, A. D., Diaz, A., & Gray, J. A. (1995). Personality and reinforcement: An exploration using a maze learning task. *Personality and Individual Differences*, 18, 541–558.
- Plomin, R. (1994). *Genetics and experience: The interplay between nature and nurture*. Thousand Oaks, CA: Sage.

- Porges, S. (1991). Vagal tone: A mediator of affect. In J. A. Garber & K. A. Dodge (Eds.), *The development of emotion regulation and dysregulation* (pp. 111–128). New York: Cambridge University Press.
- Ramsey, D., & Lewis, M. (2003). Reactivity and regulation in cortisol and behavioral responses to stress. *Child Development, 74*(2), 456–464.
- Richards, R., Kinney, D. K., Lunde, I., Henet, M., & Merzel, A. P. C. (1988). Creativity in manic-depressives, cyclothemes, their normal relatives, and control subjects. *Journal of Abnormal Psychology, 97*, 281–288.
- Rohde, P., A., Atzwanger, K., Butovskaya, M., Lampert, A., Mysterud, I., Sanchez-Andres, A., & Sulloway, F. J. (2003). Perceived parental favoritism, closeness to kin, and the rebel of the family: The effects of birth order and sex. *Evolution and Human Behavior, 24*, 261–276.
- Rothbart, M. K. (1989a). Temperament in childhood: A framework. In G. A. Kohnstamm, J. Bates, & M. K. Rothbart (Eds.), *Temperament in childhood* (pp. 59–73). Chichester, UK: John Wiley & Sons.
- Rothbart, M. K. (1989b). Biological processes in temperament. In G. A. Kohnstamm, J. Bates, & M. K. Rothbart (Eds.), *Temperament in childhood* (pp. 77–110). Chichester, UK: John Wiley & Sons.
- Rothbart, M. K., & Bates, J. E. (1998). Temperament. In N. Eisenberg (Ed.), *Handbook of child psychology* (Vol. 3, pp. 105–176). New York: John Wiley.
- Rothbart, M. K., Ahadi, S. A., & Evans, D. (2000). Temperament and personality: Origins and outcomes. *Journal of Personality and Social Psychology, 78*, 122–135.
- Rothbart, M. K., Ahadi, S. A., Hershey, K. L., & Fisher, P. (2001). Investigations of temperament at three to seven years” The Children’s Behavior Questionnaire. *Child Development, 72*, 1394–1408.
- Rowe, D. C. (1994). *The limits of family influence: Genes, experience, and behavior*. New York: Guilford Press.
- Rowe, D., C. (2000). Environmental and genetic influences on pubertal development: evolutionary life history traits? In J. L. Rodgers, D. C. Rowe, & W. B. Miller (Eds.), *Genetic influences on human fertility and sexuality*. Boston: Kluwer.
- Rushton, J. P. (1995). *Race, evolution, and behavior*. New Brunswick, NJ: Transaction.
- Savin-Williams, R. (1987). *Adolescence: An ethological perspective*. New York: Springer-Verlag.
- Southwood, T. R. E. (1981). Bionomic strategies and population parameters. In R. M. May (Ed.), *Theoretical ecology: Principles and applications* (pp. 30–52). Sunderland, MA: Sinauer Associates.
- Srivastava, S., John, O. P., Gosling, S. D., & Potter, J. (2003). Development of personality in early and middle adulthood: Set like plaster or persistent change? *Journal of Personality and Social Psychology, 84*, 1041–1053.

- Sulloway, F. J. (1996). *Born to rebel: Birth order, family dynamics, and creative lives*. New York: Pantheon.
- Sulloway, F. J. (1999). Birth order. In M. A. Runco & S. R. Pritzker (Eds.), *Encyclopedia of creativity (Vol. 1)* (pp. 189–202). San Diego, CA: Academic Press.
- Swanson, J., Oosterlaan, J., Murias, M., Schuck, S., Flodman, P., Spence, M. A., Wasdell, M., Ding, Y. C., Chi, H. C., Smith, M., Mann, M., Carlson, C., Kennedy, J. L., Sergeant, J. A., Leung, P., Zhang, Y. P., Sadeh, A., Chen, C., Whalen, C. K., Babb, K. A., Moyzis, R., & Posner, M. I. (2000). Attention deficit/hyperactivity disorder children with a 7-repeat allele of the dopamine receptor D4 gene have extreme behavior but normal performance on critical neuropsychological tests of attention. *Proceedings of the National Academy of Science*, *97*(9), 4754–4759.
- Tellegen, A., Lykken, D. T., Bouchard, T. J., Wilcox, K. J., Segal, N., & Rich, S. (1988). Personality similarity in twins reared apart and together. *Journal of Personality and Social Psychology*, *54*, 1031–1039.
- Tooby, J. & Cosmides, L. (1990). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality*, *58*, 17–67.
- Trapnell, P. D., & Wiggins, J. S. (1990). Extension of the Interpersonal Adjective Scales to include the Big Five dimensions of personality. *Journal of Personality and Social Psychology*, *59*, 781–790.
- Trivers, R. (1972). Parental investment and sexual selection. In R. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Chicago: Aldine-Atherton.
- Trivers, R. (1974). Parent-offspring conflict. *American Zoologist*, *14*, 249–264.
- Trull, T. J., & Geary, D. C. (1997). Comparison of the Big-Five factor structure across samples of Chinese and American adults. *Journal of Personality Assessment* *69*, 324–341.
- Tucker, D. M., & Derryberry, D. (1992). Motivated attention: Anxiety and the frontal executive functions. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology*, *5*, 233–252.
- Tucker, D. M., & Williamson, P. A. (1984). Asymmetric neural control systems in human self-regulation. *Psychological Review*, *91*, 185–215.
- Turner, B. (1981). Sex-related differences in aging. In B. B. Wolman & G. Stricker (Eds.), *Handbook of developmental psychology*. Englewood Cliffs, NJ: Prentice Hall.
- Turner, R. A., Altemus, M., Enos, T., Cooper, B., & McGuinness, T. (1999). Preliminary research on plasma oxytocin in normal cycling women: investigating emotion and interpersonal distress. *Psychiatry*, *62*, 97–113.
- Vernon, P. E. (1982). *The abilities and achievements of Orientals in America*. New York: Academic.

- Watson, D., & Clark, L. A. (1992). On traits and temperament: General and specific factors of emotional experience and their relation to the five-factor model. *Journal of Personality, 60*, 441–476.
- Weissman, M. M. (1985). The epidemiology of anxiety disorders: Rates, risks, and familial patterns. In A. H. Tuma & J. Maser (Eds.), *Anxiety and the anxiety disorders*. Hillsdale, NJ: Erlbaum.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York: Oxford University Press.
- Widiger, T. A., & Trull, T. J. (1992). Personality and psychopathology: An application of the five-factor model. *Journal of Personality, 60*, 363–393.
- Widiger, T. A., Trull, T. J., Clarkin, J. F., Sanderson, C., & Costa, P. T. (2002). In P. T. Costa & T. A. Widiger (Eds.), *Personality disorders and the five-factor model of personality* (pp. 89–99). Washington, DC: American Psychological Association.
- Wiggins, J. S. (1991). Agency and communion as conceptual coordinates for the understanding and measurement of interpersonal behavior. In W. M. Grove & D. Cicchetti (Eds.), *Thinking clearly about psychology: Vol. 2. Personality and Psychopathology*. Minneapolis: University of Minnesota Press.
- Wiggins, J. S., & Broughton, R. (1985). The interpersonal circle: A structural model for the integration of personality research. *Perspectives in Personality, 1*, 1–47.
- Wiggins, J. S., & Pincus, A. (1989). Conceptions of personality disorders and dimensions of personality. *Psychological Assessment: A Journal of Consulting and Clinical Psychology, 1*, 305–316.
- Wiggins, J. S., & Trapnell, P. D. (1996). A dyadic-interactional perspective on the Five-Factor Model. In J. S. Wiggins (Ed.) *The Five-Factor Model of Personality: Theoretical Perspectives*, pp. 88–162. New York: Guilford Press.
- Wiggins, J. S., Trapnell, P., & Phillips, N. (1988). Psychometric and geometric characteristics of the Revised Interpersonal Adjective Scales (IAS-R). *Multivariate Behavioral Research, 23*, 517–530.
- Wilson, D. S. (1994). Adaptive genetic variation and human evolutionary psychology. *Ethology and Sociobiology, 15*, 219–235.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge: Harvard University Press.
- Wilson, M. A., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology, 6*, 59–73.
- Wright, P. H., & Scanlon, M. B. (1991). Gender role orientation and friendship: Some attenuation, but gender differences abound. *Sex Roles, 24*, 551–566.
- Zuckerman, M. (1979). *Sensation seeking: Beyond the optimal level of arousal*. Hillsdale, NJ: Erlbaum.
- Zuckerman, M. (1991). *Psychobiology of personality*. Cambridge, UK: Cambridge University Press.