

Evolution, the Five Factor Model, and Levels of Personality

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Abstract

This paper interprets the Five Factor Model as subsuming variation in normative, species-typical systems with adaptive functions in the human environment of evolutionary adaptedness. It is argued that the evolutionary logic of personality systems is apparent in the patterning of mean sex differences in personality. Personality systems are conceptualized as evolved motivational systems with an affective core. The evolved motive dispositions at the core of personality anchor a hierarchy of levels of cognitive and behavioral functioning aimed at attaining or avoiding the affective states central to these personality systems. Personality systems are seen as often in dynamic conflict within individuals and as highly compartmentalized in their functioning between settings. While variation in personality consists of a range of viable strategies for humans, extremes on these systems tend to be maladaptive, although in at least some cases individuals who approach the maladaptive extremes of individual variation may be viewed as engaging in high-risk evolutionary strategies. Within this wide range of viable strategies, personality variation functions as a resource environment for individuals in the sense that personality variation is evaluated according to the interests of the evaluator.

The Five Factor Model (FFM) emerges from the English lexicon and can be understood as reflecting independent dimensions of human functioning from the point of view of an observer (Goldberg, 1981). The proposal is that the factors identified by the FFM denote variation in a set of semantically linked subsystems which evolved in order to solve adaptive problems. Human psychological adaptations underlying personality are thus conceptualized as a set of normative, universal mechanisms.

However, the present view also provides a robust role for individual differences in the universal adaptations underlying personality. Personality distributions are conceptualized as subsuming more than one viable adaptive strategy (Belsky et al, 1991; Gangestad & Simpson, 1990; MacDonald, 1991; Wilson, 1994; see also discussion in Buss, 1991). Rather than conceptualizing human psychological adaptations as unvarying ideal Platonic types, the present perspective proposes that personality variation represents a continuous distribution of phenotypes which matches a continuous distribution of viable strategies. Traits under selection in fluctuating (i. e., uncertain) environments show relatively high heritabilities (Burger et al, 1989), and Williams (1975) has provided evidence that some organisms facing uncertain environments and resource scarcity resort to sexual reproduction, a mechanism which maximizes variability. These results thus fit well with the idea that 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 non-human environment. There is abundant evidence that intraspecific genetic variation is associated with variation in habitat preference, and that genetic variation is linked with environmental heterogeneity (Futuyma & Moreno, 1988; Hedrick, 1986; Wilson, 1994). At different times different parts of a personality distribution may be favored by natural selection resulting, e.g., in separate niches for risk-takers and risk-avoiders. However, assuming fitness differences within the normal range of personality variation are not dramatic, the phenotypic distribution will be approximately normal, and the fitness distribution will in effect be something of a plateau because there are no consistent forces of selection getting rid of variation over the great majority of the distribution.

Within this perspective, while there is expected to be a wide range of adaptively viable personality variation, extremes on these distributions are expected to be maladaptive. This

approach is thus highly consistent with attempts to conceptualize psychopathology in terms of maladaptive extremes on FFM dimensions (e.g., Costa & Widiger, 1994). I propose here that the types of psychopathology associated with the FFM dimensions are an important clue as to the evolutionary function of the system.

One difficulty with establishing an evolutionary perspective is that it is conceivable that humans are interested in dimensions of individual differences which have no evolutionary basis at all, and there is undoubtedly variation in evolved systems which is completely irrelevant to human interests (e. g., variation in fingerprint ridge count). Nevertheless, the evolutionary perspective is strengthened by the following types of evidence: 1.) Evidence for similar systems in animals which meet obvious adaptive needs; 2.) Evidence for a structural basis for these systems in the brain; 3.) Developmental evidence that recognizable precursors of the five factors exist during infancy or early childhood when there is little *a priori* reason to suppose that such dimensions of individual variation would answer to adult interests in describing individual variation.

Evidence for the presence of the five factors cross-culturally in natural language is of less importance, although in fact there is considerable support for the widespread occurrence of the Five Factor Structure (Buss, 1991). An evolutionary perspective is not falsified by finding a language which does not label variation in one or more of the five factors. If a culture did not label variation in a Big 5 dimension, it could mean that such a culture was not interested in this variation (as, e.g., our culture is little interested in normal variation in the size of one's pancreas or fingerprint ridge count). Or it could mean that the culture failed to verbalize the trait variation (even though they might still react to the variation). Several animal species (rats [Gray, 1987a], wolves [MacDonald, 1983a], various primates [Suomi 1991], and even fish [Wilson 1994]) are known to vary in traits conceptually and/or neurophysiologically linked to the FFM dimensions, but the animals never verbalize about them and may not be much interested in the variation. Personality evaluation is a social act, and evolution may produce variation which is not important in social evaluation in particular societies. It does not follow that personality evaluations performed in Western cultures do not assess variation in evolved systems. Indeed, it is conceivable that another culture evaluates variation in an even wider set of adaptations.

The project of specifying personality dimensions linked to brain mechanisms has a fairly long history. Much of the discussion has centered around the work of Eysenck (Eysenck, 1967; 1982) and Gray (1982, 1983, 1987a,b). It is of interest in this regard that attempts to develop a model of this nature based only on the dimensions of Extraversion and Neuroticism have not uncommonly included a behavioral approach system, a behavioral inhibition system (BIS), as well as a separate arousal/reactivity system (e. g., Fowles, 1987; Gray, 1987b; MacDonald, 1988). This paper continues in that tradition but argues that the Five Factor model provides the basis for a more satisfactory theory of this nature.

In addition, however, the present attempt is firmly rooted in evolutionary biology, and particularly the evolutionary theory of sex differences. The evolutionary theory of sex differences has provided a robust framework for research on a wide range of human behavior (reviewed in Buss, 1994). I am proposing here that the personality systems identified by the FFM are sex differentiated in a manner which is predictable from the evolutionary theory of sex.

At a conceptual level, organisms need to perform two very broad types of functions. They must approach the world and obtain resources related to adaptive functioning (e.g., food and mating opportunities) and they must have mechanisms for avoiding threats (e.g., predators, environmental dangers). 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 to females, including being prone to risk taking, neophilia, and exploratory behavior. 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 (Buss & Schmitt, 1993; Symons, 1979; MacDonald, 1988; 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.

Mating for males is thus expected to be much more of a high stakes enterprise, with much more to gain and much more to lose than is the case with females. Risk taking directed at resource acquisition can therefore have very high payoffs for males compared to females, and, as a result, the evolutionary theory of sex makes predictions of sex-differentiated behavior which go well

beyond expected differences in mating strategies to encompass a wide range of behaviors which influence resource acquisition. In terms of the following discussion, males in general are expected to be higher than females on behavioral approach systems (including sensation seeking, risk-taking, and impulsivity) and lower on behavioral withdrawal systems (including caution and fear).

In addition, evolutionary theory predicts that in species with sex-differentiated patterns of parental investment, males, as the low investment sex, would gain more from aggression and social dominance because engaging in these behaviors would be more likely to lead to increased mating opportunities. For the same reason, males are also expected to be more attracted to low cost, short term mating opportunities. Females, on the other hand, are expected to adopt a more conservative strategy and benefit less from sexual gratification, aggression, and social dominance. Females are also expected to benefit more from long term mating relationships characterized by romantic involvement, trust, and empathy. These expectations refer to mean sex differences in trait distributions and are compatible with considerable overlap between the sexes, as occurs in personality trait distributions. As implied by the perspective sketched above, variation in personality may subsume more than one viable strategy within each sex which is nevertheless compatible with mean differences between the sexes in the frequencies of particular strategies.

The proposal here is that there are four independent evolved systems which are functional adaptations underlying four of the dimensions of the FFM: Dominance/Sensation Seeking, Conscientiousness, Nurturance/Love, and Neuroticism.¹ Dominance/Sensation Seeking and Nurturance/Love are conceptualized as sex differentiated sets of systems underlying behavioral approach; Conscientiousness is conceptualized as a set of correlated systems underlying behavioral avoidance/inhibition; and Neuroticism is complexly related to an activation/reactivity system underlying variation in affect intensity. The interactions among these systems are complex, and there is no one-to-one relationship among these adaptations and personality dimensions.

In the following I will attempt to develop an evolutionary perspective on the FFM as a set of affectively based motivational systems. I will then develop a hierarchical theory of levels of personality in which these affectively based mechanisms serve as the foundation or motivational core of personality upon which is built a superstructure of lower-level goals, cognitively mediated strategies and other types of self-regulatory behavior. Within this perspective, general-purpose

cognitive mechanisms function in the service of attaining these lower-level self-regulatory processes.

Conceptualizing Behavioral Approach, I: The Dominance/Sensation Seeking Dimension

Because of the central role of the evolutionary theory of sex differences in the present analysis, I will focus on available factor analytic rotations which maximize sex differences and note whether these sex differences conform to theoretical expectations. In adopting this procedure, there is no implication that traits which do not lie on directly on these dimensions are less "biological," since all phenotypes are subject to selective processes; it is simply that by focussing on these sex differentiated dimensions one can see that the FFM conforms to a fairly clear evolutionary logic.

In conceptualizing behavioral approach, it is instructive to compare the circumplex model of interpersonal descriptors (Trapnell & Wiggins, 1990; Wiggins, Trapnell, & Philips, 1988) to the NEO-PI-R (Costa & McCrae, 1992). The circumplex model results in the dimensions of Dominance and Nurturance/Love and covers the same domain as Extraversion and Agreeableness on other Five Factor Model (FFM) measures (Briggs, 1992; Trapnell & Wiggins, 1990). As Trapnell and Wiggins (1990) point 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 and Nurturance 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. Hogan (1983) notes that problems of status and popularity are central to survival and reproduction, and Wiggins (1991), on the basis of evolutionary theory, has noted that males and females would be expected to have different interests in agentic and communal interpersonal styles.

Within this perspective, Dominance as well as several other highly sex differentiated, non-interpersonal approach behaviors, including Sensation Seeking (see below), form one axis, while Nurturance/Love, including pair bonding and close emotional attachments (see below), forms the other. In accord with evolutionary expectations, men score significantly higher on the IAS-R-B5

DOM (Dominance) scale and significantly lower (by .88 Standard Deviations) on the IAS-R-B5 LOV (Love) scale (Trapnell & Wiggins, 1990).²

Theoretically expected sex differences are also pronounced on the Sensation Seeking Scale in studies performed in America, England, Scotland, Thailand, and Japan (Zuckerman, 1979). These scales tap variation in attraction to physically dangerous activities and lack of fear of physical harm, promiscuous sexual activity, disinhibition, and susceptibility to boredom. In factor analytic studies, Sensation Seeking, like IAS-R-B5 Dominance, lines up between Extraversion-Sociability and EPQ Psychoticism (Zuckerman, 1989), a measure which is conceptually associated with lack of nurturance and love. Indeed, Zuckerman (1984) notes that Sensation Seeking is associated with an "impulsive type of Extraversion" characterized by social dominance, surgency, and aggression. Taken together, the data indicate a highly sex differentiated interpersonal and non-interpersonal space tapped by IAS-R-B5 Dominance and several central aspects of Sensation Seeking.

The neuropsychology of personality remains a highly unsettled area, but one theoretically attractive line of research indicates that an important aspect of behavioral approach is dopaminergic reward mechanisms (Gray, 1987a; Cloninger, 1987; Gray et al, 1983; Panksepp, 1982; Zuckerman, 1983, 1984, 1991). The emphasis on reward mechanisms underlying behavioral approach reflects the typical manner in which evolution shapes the motivation to engage in behavior (see, e. g., Barash, 1977; Wilson, 1975). Evolution seems to have resulted in an array of affective motivational systems which 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 conceptualize how it could have done otherwise. At a basic level, motivation, virtually by definition, involves affect: "A goal may be defined as a mental image or other end point representation *associated with affect* toward which action may be directed" (Pervin, 1989; p. 474; my italics). The evolutionary basis of motivation is thus the evolution of affective systems underlying particular adaptive behaviors in the environment of evolutionary adaptedness.

Consistent with this perspective, Newman (1987; see also Derryberry, 1987) found that compared to 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 (1987a) proposes close linkages between behavioral approach mechanisms and positive emotions, and Heller (1990) notes 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 evolved basis of behavioral approach may also involve attentional mechanisms underlying sex differentiated patterns of neophilia and exploratory behavior. As indicated above, Boredom Susceptibility is a sex-differentiated component of Sensation Seeking, and Tucker and Williamson (1984) propose a diffuse attention system with a habituation bias underlying novelty seeking and exploratory behavior. In this regard it is important that the vast majority of children diagnosed as having Attention Deficit Hyperactivity Disorder (ADHD) are males. Males, as the high risk sex, are predisposed to diffuse attention underlying exploratory behavior and neophilia. This "extraverted attentional state" (Tucker & Derryberry, 1992) is present-centered, holistic, and easily habituates. Affect is positive due to the activation of the noradrenergic phasic arousal system. Underlying the role of positive affect in behavioral approach generally, Isen et al (1987) found that positive mood was associated with holistic, creative thought processes, and Schwarz et al (1991) found that positive mood resulted in looser, more diffuse information processing strategies, while negative mood resulted in more highly focussed strategies.

Developmentally there appears to be a pattern in which the most sexually-differentiated aspects of behavioral approach are maximized during late childhood and early adulthood while non-sex-differentiated aspects of behavioral approach appear early in infancy and are highly 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). In early infancy there are individual differences in the extent to which infants will approach rewarding stimulation, as indicated by attraction to sweet food, grasping objects, or attending to novel visual patterns. At around 4 weeks of age behavioral approach is accompanied by smiling and other indications of positive affect in both social and non-social situations. 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. Later in childhood sociability has been linked to the more general trait of extraversion (Buss & Plomin, 1984; John et al, 1994), and such a relationship continues during adulthood.

Although there is little evidence for age changes during adulthood in NEO-PI-R Extraversion (Costa & McCrae, 1990), it is of interest that 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. 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 be relatively problematic for males, it is during young adulthood, when males are attempting to establish themselves in the wider group and accumulate resources necessary for mating, that the male tendencies toward sensation seeking, risk taking and aggression are expected to be at their peak.

Nevertheless, 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; MacDonald & Parke, 1986; Humphreys & Smith, 1987; O'Brien & Huston, 1985). The social interactions of boys are also more characterized by dominance interactions and forceful, demanding interpersonal styles (Borja-Alvarez et al, 1991; Charlesworth & Dzur, 1987; Cowan & Avants, 1988; LaFrenière & Charlesworth, 1983; Savin-Williams, 1987). On the other hand, females are more prone to depression which clearly involves low levels of behavioral approach (Davidson, 1993). Indeed, anhedonia and negative mood are primary symptoms of depression within the DSM IV classification.

The sex difference in activity level (characterized by large-motor, physically intense activity) begins during infancy and is a particularly robust finding (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).

Taken together, the data on behavioral approach indicate that over development there is differentiation of behavioral approach from a relatively simple dimension characterized by differences in activity level, approach to novel objects, visual displays and sensory stimulation, to sociability and positive emotionality during early infancy, to aggression, dominance, and rough and tumble play during early childhood, and undergoing further differentiation and intensification as children approach reproductive competence and behavioral approach begins to include attraction to sexual gratification. There is some evidence that activity level appears to remain distinct from the less sexually differentiated aspects of behavioral approach until adulthood. John et al (1994) found that activity level and extraversion were differentiated in adolescence. John et al note that these findings may result from the particular item pool used and should be replicated with other measures, including, I would suggest, items related to the other sexually differentiated aspects of behavioral approach emphasized here.

An Adaptationist Perspective on Conscientiousness

The trait of Conscientiousness subsumes variation in the ability to defer gratification, persevere in unpleasant tasks, pay close attention to detail, and behave in a responsible, dependable manner. Wiggins and Trull (1992) find that the psychiatric disorder most associated with conscientiousness is obsessive-compulsive disorder, a disorder which 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; 1987a) 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.

A central feature of mechanisms designed to cope with threats is the behavioral inhibition system (BIS), conceptualized at a fundamental level as subsuming variation in sensitivity to

punishment (Gray, 1982; 1987a). 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). Children who are high on behavioral inhibition respond negatively to new people and other types of novel stimulation (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. Many behaviorally inhibited children have a very intense emotional response to novel situations, and in particular, they tend to be highly prone to tension, anxiety, and fear in these situations.

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 focussing 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. Further, Tucker and Derryberry (1992) review 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. Although Gray's (1982; 1987a) theory of the behavioral inhibition also emphasizes septo-hippocampal mechanisms, he also posits a prominent role for the frontal cortex, especially in primates. Consistent with an important role of the frontal cortex in the human behavioral inhibition system, Reiman et al (1989) found that individuals anticipating painful electrical shock had increased blood flow in the temporal anterior temporal lobes.

There is also evidence for mutual inhibitory influences between the mechanisms underlying Conscientiousness and behavioral approach. Mesulam (1986) describes reciprocal inhibition between frontal and the parietal lobes, the latter viewed as an approach system characterized by diffuse attention and impulsive responding. Gray (1987a) also notes reciprocal

inhibitory influences between the behavioral inhibition system and the reward-based approach system and that 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. Tucker and Derryberry (1992) also emphasize the inhibitory role of the frontal cortex. They note that individuals with frontal lesions are prone to impulsive responding and socially inappropriate behavior--the "disinhibition syndrome" (Luria, 1980), as well as inadequate anticipation of aversive outcomes.

This is an excellent model for conceptualizing conflicts between evolved systems as well as for situation specificity. The behavioral approach underlying Dominance/Sensation Seeking and the behavioral avoidance systems underlying Conscientiousness are psychometrically independent, implying that individuals can be more or less sensitive to rewards and more or less sensitive to punishments and deferring gratification. 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 Dominance/Sensation Seeking 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 by the mechanisms underlying Conscientiousness, such as Gray's Behavioral Inhibition System. On the other hand, a situation characterized overwhelmingly by potential danger activates the BIS, even for individuals moderately high on Dominance/Sensation Seeking; on the other hand, 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.**

As with behavioral approach, attentional mechanisms are implicated in Conscientiousness. Tucker and Derryberry (1992; see also Tucker & Williamson, 1984) propose that left frontal systems mediate attention which is tightly focussed on possible environmental threats as well as planning to meet these environmental contingencies. These findings are consistent with the findings of Zametkin et al (1993) of lower metabolic rates in the left frontal lobe area in

hyperactive children. Amphetamines are dopaminergic drugs which result in focussing attention. Amphetamine is typically prescribed for individuals with ADHD, and helps them engage in effortful, planned behavior, and focussing attention on important environmental cues. Large doses of amphetamine result in repetitive, stereotyped (i. e., novelty avoidant), overfocussed, hypervigilant, and eventually paranoid behavior. Tucker and Derryberry note that the compulsions of obsessive-compulsive disorder patients are stereotyped and often tightly focussed 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, focussed, and has a redundancy bias. As expected on the hypothesis that the negative emotions of fear and anxiety are central to Conscientiousness, Schwarz et al (1991) found that negative mood resulted in more highly focussed information processing strategies, presumably because such individuals are focussing their attention on possible sources of environmental threat.

While negatively-valenced emotions such as anxiety are central to Conscientiousness, positive emotions also appear to be involved. Gray (1982; 1987) postulates a second motivational system of the BIS in which the positive emotions of hope and relief are elicited upon signals of safety. The suggestion would be that the system works by triggering negative emotions (anxiety, fear) during the period of danger as well as feelings of relief after the danger had been successfully evaded.

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.

Females are indeed significantly higher on IAS-R-B5 Conscientiousness (Trapnell and Wiggins, 1990), although this is not the case for the NEO-PI-R (Costa & McCrae, 1992; see Note 3). Females are also more prone to most anxiety disorders, including agoraphobia and panic disorder (e. g., Weissman, 1985; DSM IV). It is also noteworthy that 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; Minton, Kagan & Levine, 1971; Pederson & Bell, 1970; Smith & Dagliesh, 1977), and girls are more prone to anxiety disorders (Weissman, 1985).

On the other hand, ADHD is overwhelmingly found among boys. As indicated above, ADHD is conceptualized by Tucker and Derryberry as involving the diffuse, extraverted attentional style which is the antithesis of the redundancy bias characteristic of the attentional style of obsessive-compulsive disorder. Indeed, the characteristics of ADHD children clearly place them low on all of the typical descriptors of conscientiousness: undisciplined, unplanful, unreliable, non-compliant, disorderly, impulsive, incautious, non-persistent in the face of difficulty, interested in immediate gratification, and lacking in neatness and tidiness (e. g., Shaywitz & Shaywitz, 1988).

The data reviewed above are compatible with the proposal that in the course of evolution the behavioral inhibition system differentiated to encompass not only the inhibition of behavior in anticipation of punishment, as envisioned by Gray (1987), but also to encompass planning and perseverance in difficult tasks. The system came to underlie the ability to flexibly plan strategies which would avoid long term dangers or would result in future rewards (Ingvar, 1985; Tucker & Derryberry, 1992). In order to obtain future rewards, the organism may need to inhibit impulsive responding, delay gratification, and carefully plan a strategy. While the goal may be to obtain an evolved reward (e. g., mating opportunities), the mechanism for obtaining the reward may involve systems which function partly by inhibiting immediate gratification.

Further evidence for differentiation of Conscientiousness is that factor analytic studies have found Conscientiousness items yield separate factors for what one might term Social Conscientiousness and several types of Asocial Conscientiousness (Lusk et al, 1993; Watson &

Clark, 1992). Thus the NEO-PI-R (Costa & McCrae, 1992) contains a "Dutifulness" facet of Conscientiousness consisting of items related to performing assigned tasks conscientiously, fulfilling commitments, fulfilling social obligations, and being dependable and reliable. At least some facets of Costa and McCrae's Conscientiousness appear to be asocial, including orderliness and lack of impulsivity. The primitive function of the system, checking for environmental threats, may well have been elaborated in social species to include attention to social obligations perceived as threats if not fulfilled. Indeed, Öhman (1993) suggests that there are evolved social fears associated with a dominance-submissiveness system.

The widespread occurrence of social phobias (Gray, 1987a; 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 evolutionary pressures on group-living males for status within the group may have resulted in sex-differentiated patterns of behavioral inhibition. In support of this proposal, Öhman (1993) summarizes data indicating that angry faces are among the potentially phobic stimuli (including also snakes and spiders) able to condition autonomic responses which are more resistant to extinction than are 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 which also fails to consistently show a sex difference (DSM IV; Weissman, 1985).

Threats emanating from the group may also result from cognitive appraisals by general purpose cognitive mechanisms. From this perspective, social threats may act like any other threat, so that individuals who are highly conscientious react intensely to perceived threats emanating from the group as they would from any other source. Tucker and Derryberry (1992) suggest that whereas more primitive animals have rigid connections between stimuli and specific affective responses, evolution has resulted in more open ended programs in humans, so that the sources of threat may not be rigidly programmed. Individuals high on conscientiousness may, however, be highly prone to reacting to perceived threats whatever their source.

Affect Intensity as an Evolved System: An Evolutionary Perspective on Neuroticism

A third adaptation important for conceptualizing approach and avoidance mechanisms is proposed to be affect intensity as described by Larsen and Diener (1987, 1993). Within an evolutionary framework, the activation system is an adaptation which functions to mobilize resources in order to confront dangers and opportunities in the environment. At a conceptual level, one might suppose that behavioral approach and behavioral avoidance mechanisms would each have their own set of activating mechanisms and that the systems would interact only to the extent of having inhibitory influences on each other.

It is remarkable, however, that affect intensity appears to be an independent system subsuming variation in the proneness to both positive and negative emotional experience. Larsen and Diener (1987) find a robust positive correlation between positive and negative affect intensity. Similarly, 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).

Larsen and Diener's (1993) circumplex model of emotions and their personality correlates indicate two orthogonal dimensions, high activation—low activation and Pleasant—Unpleasant affective tone. Within the circumplex, activated positive affect is associated with Extraversion, while activated negative affect is associated with Neuroticism. Heller (1990) notes that three separate regions of the brain underlie these two dimensions. An activation system centered in the parietal region of the right hemisphere plays a role in both cortical and autonomic arousal. Emotional valence involves the balance between the frontal regions of the left and right hemispheres of the brain, the former associated with positive emotions and the latter associated with negative emotions.

I propose that the evolutionary function of affect intensity is that of a general behavioral energizer—an engine that is utilized both in the service of behavioral approach and behavioral avoidance. It is behavioral a scaling system which allows the organism to scale its responses to current environmental opportunities and threats. This system is well studied by temperament

researchers (see, e. g., Strelau, 1989; Rothbart, 1989a,b; Thomas et al, 1968). 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, on the other hand, 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. These 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.

Reactivity as a temperament trait is conceptually related to the dimension of affect intensity in adults. Larsen and Diener (1987) note that emotionally intense individuals respond relatively strongly to emotional stimulation independent of the emotion involved, including both positive and negative emotions. They 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).

Larsen and Diener note that affect intensity should be related to "any temperament or personality trait which contains in its construct definition reference to heightened positive or negative affect" (1987; p. 20). Affect intensity may be viewed as a generalized motivation-enhancement system which can be directed toward behavioral approach as well as behavioral avoidance and checking for possible threats in the environment. Individuals high on affect intensity are thus highly motivated to intensive interaction with the environment and often have conflicting goals because, I would suggest, both behavioral approach and behavioral avoidance systems are prone to activation.

Affect intensity appears to be a primitive adaptive system in animals. Schrierla (1959) shows that an extremely wide range of animals, from amoebas to humans, intense stimulation

results in behavioral avoidance while low levels of stimulation are associated with behavioral approach, including behaviors related to obtaining food, shelter, and mating. For example, rapidly approaching objects augment arousal and result in an increasing retinal image and behavioral withdrawal, while retreating objects result in a decreasing retinal image, reduced arousal, and behavioral approach. Stimulus intensity can also facilitate the inhibitory effects of novelty, as in Broadhurst's (1975) finding that a bright light suppresses exploratory behavior in an open field test more than a dim light. Among human infants, McGuire and Turkewitz (1979) found that low intensity stimulation was associated with approach, while high intensity of stimulation is associated with withdrawal.

Based on Schrier's work, Fox (1991) has analyzed early emotional development in terms of approach/avoidance tendencies in response to stimulus intensity. Approach tendencies are associated with positive emotions and anger, while avoidance tendencies are associated with the negative emotions of distress, fear, and disgust. There is developmental evidence for differentiation of negative emotions over the first 2 years of life. Disgust and distress appear at birth, while sadness and fear develop in the second half of the first year (Izard, 1971). Guilt, embarrassment, and shame—emotions which are presumably important for Social Conscientiousness—do not emerge until approximately age 2 (Lewis & Michalson, 1983).

Reactivity therefore appears to have evolved as a primitive approach/avoidance mechanism motivated by positive emotional response at low levels of stimulation and negative emotional response to intense stimulation. Animals with highly reactive nervous systems are prone to withdrawing in the face of environmental stimulation but also prone to behavioral approach at low levels of environmental stimulation. In higher animals this primitive biphasic approach/avoidance patterns based on responses to intensity of stimulation has become progressively elaborated, leading in humans to the evolution of the elaborate independent mechanisms underlying the behavioral approach and behavioral avoidance systems described above. Nevertheless, reactivity and its link to both positive and especially negative emotional response has continued as a very basic adaptation underlying temperament and personality.

The developmental data taken together suggest a dimension ranging from individuals with low reactivity (prone to low levels of both positive and negative emotional response) to

individuals with moderately high levels of reactivity (prone to relatively high levels of both positive and negative emotions (Fox, 1989; Gunnar & Nelson, 1994; Porges, 1991); and finally, there are individuals who are very highly reactive and prone to intense negative emotional responding even under stimulus conditions which result in behavioral approach in most children—the latter often labeled "difficult temperament (Rothbart, 1989a; Strelau, 1989; Thomas et al 1968). Congruent with Schrierla's work on a wide range of animals, there is a general tendency for behavioral avoidance to occur at high levels of stimulus intensity, and individuals with very high levels of reactivity are thus expected to experience negative emotions and withdraw at lower levels of stimulus intensity than individuals with moderate or low levels of reactivity.

Distress proneness factors linked with reactivity have been found in older children as well. For example, the Teacher Temperament Questionnaire (Keogh et al, 1982) contains a factor of Reactivity which includes both negative affect and items indicating sensitivity to stimulation. Thomas et al (1968) also note a tendency for affect intensity to be associated with low thresholds for response to stimulation, and Miller and Bates (1986) found an association between temperature sensitivity and negative emotions.

The primitive function of the reactivity system as underlying behavioral avoidance and negative emotionality suggests that reactivity should be linked with the personality trait of neuroticism. Larsen & Diener (1993) show that affect intensity is indeed associated with neuroticism. Neuroticism in turn, is closely linked to a proneness to a wide range of negative emotions. Watson and Clark (1992) show that Neuroticism is associated with all four of their dimensions of negative affect—guilt, hostility, fear, and sadness. Several studies have found that the negative affect (tense arousal) dimension of mood is closely associated with Neuroticism (e. g., Larsen & Diener, 1993; Watson & Clark, 1992).

However, it is important to note that these negative emotions also tend to be associated with other of the FFM dimensions: hostility (negatively) with nurturance/love (see discussion below), sadness with introversion, fear with conscientiousness, and guilt with nurturance/love and conscientiousness. Neuroticism is thus a dimension underlying a general tendency for negative emotional response but the negative emotions are also integrally related to the more highly elaborated and independently evolved approach and avoidance mechanisms underlying

conscientiousness, sensation seeking, and nurturance/love. Consistent with this view, neuroticism also appears to be related to a wide range of personality disorders which also load on other systems (Costa & McCrae, 1986; Widiger & Trull, 1992). High reactivity thus energizes negative emotional responding in general—its primitive function. However, high reactivity also provides a powerful engine for negative emotional responses which are central to other physiologically and psychometrically independent systems underlying behavioral avoidance.

I propose that the primitive link between negative emotionality and reactivity accounts for the sex differences in affect intensity (Larsen & Diener, 1987) and neuroticism (e. g., Costa & McCrae, 1992; Trapnell & Wiggins, 1990). Negative emotionality predisposes individuals to behavioral avoidance and the suppression of behavioral approach, and is thus fundamentally a conservative response to environmental contingencies. Because females are expected to adopt a more conservative evolutionary strategy in general, they are expected to be more prone to negative emotions. Individuals high on affect intensity and neuroticism are highly motivated toward behavioral avoidance mediated by the negative emotions of the conscientiousness system (fear, anxiety), but are also less prone to behavioral approach because of their proneness to sadness which appears to inhibit behavioral approach mechanisms (see below).

Larsen and Diener's (1987) finding of strong positive associations between negative and positive affect intensity indicate that reactivity also functions to energize behavioral approach. Nevertheless, the results here are more complex, and there is excellent reason to suppose that high reactivity would tend to interfere with at least some aspects of behavioral approach. On the basis of above discussion, a primitive function of reactivity is to underlie negative emotional responding and behavioral avoidance. Critical to this perspective is that there is a general tendency to avoidance at high levels of stimulus intensity, so that individuals with highly reactive nervous systems are prone to avoidance at high levels of stimulus intensity, while low levels of stimulation are experienced as pleasurable (Tucker et al, 1990; Rothbart, 1989b; Strelau, 1989). Intense emotional reactivity is thus expected to actually inhibit behavioral approach at high levels of environmental stimulation.

At high levels of stimulus intensity, highly reactive individuals are prone to avoidance responses, while individuals with low reactivity would be more prone to continue behavioral

approach. The prediction is that the most sex-differentiated aspects of behavioral approach will be characterized by moderate or low levels of reactivity. Males, because of their greater tendency toward a high risk strategy weighted toward behavioral approach, are expected to have lower reactivity in general. The male tendency for lower reactivity should be particularly apparent on the cluster of traits associated with sensation seeking, aggression, impulsivity, social dominance, and sexual behavior described above.

In support of this perspective, Larsen and Diener (1987) note that, while extraversion is positively associated with affect intensity, sensation seeking is not. Moreover, there is independent evidence that sensation seekers have relatively strong nervous systems and thus low reactivity. Sensation seekers tend to be stimulus augmenters at high levels of stimulus intensity, while people low on sensation seeking tend to be stimulus reducers (Zuckerman, 1984; 1990). By having relatively strong, hypo-reactive nervous systems, a sensation seeker engaging in physically dangerous activity or other types of sensation seeking thus avoids triggering negative emotions of fear and anxiety which would result in behavioral avoidance and defensive reactions; they continue to engage in behavioral approach. Congruent with these expectations, the augmenting-reducing phenomenon has been found to correlate most strongly with the most highly sex-differentiated subscale of Sensation Seeking (Disinhibition), but not with Extraversion (Zuckerman, 1991).

Affect Intensity and Conscientiousness. Because of its motivational role, high reactivity is expected to be characteristic of individuals who are high on behavioral avoidance as well as some aspects of behavioral approach. We have already seen, however, that some elements of behavioral approach are characterized by relatively low reactivity. The highly elaborated nature of conscientiousness as a system underlying coping with environmental threat is also compatible with behavioral avoidance processes being activated without a strong emotional component. Indeed, Fowles (1987) notes that Tellegen's Constraint dimension, which is related to the Goldberg-Norman Conscientiousness factor in the Five Factor Model (Tellegen et al, 1988), is primarily a behavioral dimension, containing items such as cautious, restrained, avoidant, and timid, while Negative Emotionality (Neuroticism) is linked with the negative emotions associated with Conscientiousness. Similar comments could be made about other items in the

conscientiousness factor (e. g., Costa & McCrae, 1992; Goldberg, 1990; Trapnell & Wiggins, 1990). Kagan et al (1987) have shown that behavioral inhibition is independent of physiological measures of emotionality. Within their group of behaviorally inhibited children (defined by their behavioral responses to novel stimulation) there was a group who respond with high and stable heart rate (high reactive, and presumably experiencing high levels of anxiety and fear) and a group with low and variable heart rate (behaviorally inhibited but whose behavior is not energized by the emotions of anxiety and fear).

In summary, the functionalist account of Dominance/Sensation Seeking, Neuroticism, and Conscientiousness proposes that at the most basic level these dimensions reflect phenotypic variation in systems which serve three critical adaptive functions: 1.) the need to approach the world and accumulate resources, including sexual resources and, in social species, social dominance; 2.) the need to monitor the environment for dangers and impending punishments and to persevere in tasks that are not intrinsically rewarding; 3.) the need to mobilize behavioral resources in the service of both approach and avoidance behaviors. All of these systems have motivating properties. While the motivating properties of the affective systems underlying behavioral approach and avoidance are perhaps obvious, the affect intensity system functions to strengthen motivation by providing a strong emotional component to intensify motivation to confront environmental opportunities and dangers. Moreover, we have seen that individuals who are intensely reactive are prone to overstimulation and thus withdraw from highly stimulating environments, resulting in motivation which would result in relatively low levels of at least some aspects of behavioral approach.

Conceptualizing Behavioral Approach, II: An Adaptationist Perspective on Nurturance/Love

As indicated above, the circumplex model of interpersonal descriptors (Kiesler, 1983; Trapnell & Wiggins, 1990; Wiggins et al, 1988) results in a dimension of Nurturance/Love. Here Nurturance/Love is proposed to underlie adaptive relationships of intimacy and other long term relationships, especially family relationships, involving reciprocity and transfer of resources to others (e. g., maternal and paternal investment in children). This trait is not considered as 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, 1992a). 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, non-exploitative interpersonal relationships (Belsky et al, 1991).

The essential proposal here is that the human affectional system be conceptualized as an evolved reward system which functioned to facilitate intimate family relationships and parental investment. The stimuli which 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. The termination of intimate relationships is met with disappointment and grief, while there is eager anticipation of reunion with a loved one.

The view that the human affectional system constitutes a reward system fits well with several theoretical and empirical considerations (MacDonald, 1988; 1992a). The affectional system clearly constitutes a fairly powerful motivational system. In our culture parents express intense attachments and love toward their children, and attachment research has documented the effects of disruptions in children's affectional relationships, such as separation and loss (e. g., Bowlby, 1969; 1973), as well as the occurrence of affectively positive interactions between parents and securely attached children (e.g., Main & Cassidy, 1988). Attachment research and the research on early parent-child interaction clearly indicate highly pleasurable interactions to be characteristic of parent-child relationships labeled as warm and affectionate—the dance of affective modulation whose goal is "to be with and enjoy someone else" (Stern, 1977; p. 71) or to "maintain a relational state that is evaluated positively" (Tronick, 1982; p. 3).

The idea that reward systems underlie the evolved basis of human appetitive traits is central to the theory of the behavioral approach systems of dominance/sensation seeking discussed above, and Panksepp (1986, 1989, 1992) and Liebowitz (1983) provide evidence that reward systems underlie the emotions of social separation and social support in animals and humans respectively. Consistent with these findings, Fox and Calkins (1993) summarize data showing that

positive interactions with mothers result in left frontal activation associated with positive affect and activation of dopaminergic reward mechanisms (Heller, 1990). It is also of interest that sociopaths, conceptualized here as very low on Nurturance/Love do not seek out psychiatric help. If indeed, the Nurturance/Love system is a reward system, those low on the system would not feel they are missing anything by not having close relationships. Similarly, a person who cannot taste sweetness would not be distressed by the loss or absence of candy.

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, morphologically imposed investments in pregnancy and lactation are expected to be highly discriminating mothers compared to males (e. g., Buss & Schmitt, 1993; Symons, 1979; Trivers, 1972). It was noted above that females score higher on the IAS-R-B5 LOV scale by a very robust 0.88 standard deviations (Trapnell & Wiggins, 1990). Moreover, IAS Nurturance is conceptualized as involving 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 boys throughout development (Berndt, 1986; Buhrmester & Furman, 1987; Douvan & Adelson, 1966; Hunter & Youniss, 1982). Females also tend generally to place greater emphasis on love and personal intimacy in sexual relationships (Buss & Schmitt, 1993; Douvan & Adelson, 1966; Haas, 1979; Hinde, 1984; Lewis et al, 1978; Kenrick & Trost, 1989; Miller & Simon, 1980; Normal & Harris, 1981; Peplau et al, 1977). 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 (Aukett et al, 1988; Buhrke & Fuqua, 1987; Reis et al, 1985; Wright & Scanlon, 1991). Developmentally, sex differences related to intimacy peak during the reproductive years (Gutmann, 1977; Turner, 1981),

a finding that is compatible with the present perspective that sex differences in intimacy are related to reproductive behavior.

Females score higher than males on Reward Dependence (Sigvardsson et al, 1987) which is conceptually related to IAS Nurturance. Cloninger (1987) found that dependency disorder, characterized by extreme dependency on obtaining affection was associated with his dimension of Reward Dependence, and Wiggins and Pincus (1989) found that IAS-R-B5 Love was associated with dependency disorder. 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). 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).

Nevertheless, conceptualizing Nurturance/Love solely as a reward system is inadequate. One difficulty with developing an adaptationist perspective in personality is that there is no reason to suppose that the dimensions revealed by factor analysis map in a one-to-one manner with biological adaptations. In the case of Nurturance/Love, the "opposite" emotions of hostility and affection load on the same factor, and the dimension itself ranges from individuals who are prone to affection and empathy to individuals prone to sociopathy and hostility. The finding of Watson and Clark (1992) that hostility was not only negatively related to Agreeableness, but also related more strongly to Agreeableness than to Neuroticism in one sample, is particularly interesting. This suggests that this dimension reflects variation in two types of discrete emotion systems: affection/love/empathy and hostility. Since these are opposite emotions, this variation may not reflect a unitary biological system. Hostility as an emotion is linked to interpersonal aggression, while affection is associated with long term relations of trust and intimacy.

It may well be that in general people who are highly prone to intimacy are not prone to interpersonal aggression and hostility (thereby accounting for the patterns found in factor analytic studies). However, there is every reason to suppose that they may be. A discrete systems perspective suggests that people may be prone to both of these emotions, with the result that their

relationships are *compartmentalized*: people can have radically different relationships with others depending on the context, because different biological systems are involved (MacDonald, 1992a). The ability to form close family relationships and engage in high-investment parenting may be an extremely important aspect of adaptation, but being able to compartmentalize one's relationships is also a highly important skill. The ability to engage in close family relationships would thus be highly compatible with engaging in purely instrumental behavior toward other individuals outside one's family or ingroup, including behavior of an exploitative nature. The result is trait X situation interaction resulting from the fact that separately evolved systems associated with the same personality dimension can be recruited in different situations.

Data on cooperation and competition generally indicate that children are able to compartmentalize their relationships between setting (MacDonald, 1992a). For example, the classic study of Sherif et al (1961) showed that fostering competitive goals resulted in groups with strong ingroup, outgroup feelings. Reciprocated positive affective relationships within a group were not incompatible with a complete lack of empathy and high levels of brutality against outsiders, and, in evolutionary terms, the prototypical ingroup may be the family and other close relatives. Social identity theory (e. g., Hogg & Abrams, 1987) is highly compatible with high levels of positive affective regard and loyalty within the group combined with intense hostility versus outgroups. There is also evidence that parents may treat their children with mixtures of hostility and affection (MacDonald, 1992a), and this phenomenon can also be found in the ethnographic literature (see Zborowski & Herzog, 1952; pp. 332-337).

Discussion

The FFM and Levels and Domains of Personality. The scientific attractiveness of the FFM derives from several sources. Since it emerges from the lexicon, it has a claim to covering the entire domain of individual differences in human functioning. Moreover, it is able to incorporate rival theories of personality (Costa & McCrae, 1992) and presents a compelling perspective of personality disorders as extremes on normal personality distributions (Costa & Widiger, 1994). The perspective developed here indicates the FFM is also highly compatible with an adaptationist logic and with the existence of neuropsychological mechanisms underlying personality systems.

Indeed, given the power of the FFM, the presumption should be that any putative domain of personality or conceptualization of different levels of personality functioning be performed within the context of the FFM. The following provides a conceptualization of levels of personality functioning in terms of the FFM.

Within the perspective developed here, personality is intimately bound up with affect and motivation. While personality systems may sometimes be triggered by natural eliciting cues (e. g., an evolved tendency to fear heights or certain animals), there is every reason to suppose that, especially in the case of behavioral avoidance, the evolved systems underlying personality are not domain-specific mechanisms reacting to a narrow range of evolved cues. General purpose cognitive processes appear to have an important role in eliciting these systems (MacDonald, 1991). Thus in Gray's (1987a) theory, the behavioral inhibition system even in animals can be triggered in response to a wide range of learned contingencies and the system does not mediate any particular action to avoid threats.

Among humans this conceptualization would be compatible with a hierarchical model in Emmons' (1989) sense, in which behavior related to personality occurs at several levels based ultimately on the motivating aspects of evolved personality systems. For example, the emotions of anxiety and/or relief consequent to achieving safety are central to mechanisms designed to avoid perceived danger. Within Emmons' (1989) scheme, these emotions act as motive dispositions. People are able to engage in a wide range of lower-level behaviors directed at approaching or avoiding these affective motive dispositions. Thus humans are able to deduce imminent danger by using an elaborate array of open-ended, general-purpose information processing mechanisms and learning (e. g., uncovering an elaborate plot as a result of sophisticated knowledge of computers). This appraisal of imminent danger would then trigger the behavioral inhibition system, checking behaviors, and feelings of anxiety. Humans are also able to devise a variety of flexible, open-ended strategies which are not significantly constrained by evolutionary processes in an attempt to lower their anxiety (e. g., concocting an elaborate scheme to escape imminent danger).

A hierarchical model is also applicable in the case of behavioral approach and Nurturance/Love. Buss (1991) has emphasized the importance of evolutionary goals, such as acquiring mates, negotiating dominance hierarchies, and forming reciprocal alliances in

personality psychology. The goals of affiliation-intimacy and power have appeared as central to several important recent approaches to personality (e. g., McAdams, 1985). Variation in these systems appears to influence the extent to which people are motivated to seek out discrete types of stimulation which satisfy evolutionarily derived reward systems. Thus, an individual high on Nurturance/Love is motivated to seek out the rewards of intimate, long term relationships with family members and close friends; such a person values these relationships highly and actively maintains the relationships. Individuals high on Dominance are highly motivated to control others, while individuals high on Sensation Seeking are attracted to short term sexual relationships (presumably motivated at least in part by the pleasure of sexual intercourse), risk taking, and physically dangerous situations.

The result is a hierarchical model in which the highest levels often involve affective goals subsumed by the evolved systems underlying the FFM—what I have termed evolved motive dispositions (MacDonald, 1991). Such a perspective provides a robust role for general-purpose cognitive processes (schemas, tasks, and strategies) used in attempting to achieve these goals as well as in evaluating situations relevant to affective goals. Secondarily-reinforcing rewards such as money would then be conceptualized as lower level goals which can be utilized to facilitate the attainment of evolved motive dispositions at the highest level.

Within this perspective on the FFM, one way to conceptualize domains of personality is to ask whether there can be motive dispositions which are not linked to the evolved affective systems associated with the FFM. There is reason to suppose the existence of such non-evolved motive dispositions and to suppose that they can successfully compete with evolved motive dispositions. Richerson and Boyd (1989) have argued that personal ideologies and any associated behavior can depart radically from that predicted by an optimality model, and in previous work I have emphasized that personal ideologies are irreducible to evolved psychological traits of individuals, are underdetermined by biological theory, and interact with but are independent of social controls on individual behavior (MacDonald, 1983b**, 1988, 1990). Thus individual males and even entire cultures have adopted ideologies of male sexual restraint despite the apparent existence of evolved adaptations toward male sexual promiscuity and despite the fact that such behavior is not optimal for wealthy males.

These results suggest that ideologies can act as motive dispositions; i. e., that they can become goals on a par with evolved motive dispositions resulting from human adaptations and in potential conflict with them. As a result, there may be stable individual differences in the extent to which individuals pursue a variety of lower level goals (e. g., attending church) in order to satisfy the motive disposition of attaining religious salvation, despite the fact that such a belief is only weakly or not at all related to the evolved motive dispositions central to the FFM. Nevertheless, it should be noted that social attitudes, including religiosity, show considerable heritability (Eaves et al, 1989), suggesting that linkages with the lexical space encompassed by the FFM may occur. In general, one would expect that variation in the evolved systems underlying the FFM is likely to be least important in homogeneous, authoritarian societies, since under such circumstances external environmental pressures strongly restrict the range of individual differences (MacDonald, 1989). As Rowe (1994, p. 90) notes, "in an environment of greater choice and opportunity, genetic dispositions may begin to influence choice in a way they may not have before."

Discrete Systems Theory and the FFM. The FFM is derived from the lexicon, and because of this origin, the opposite poles of the dimensions tend to consist of semantic opposites. However, as suggested above in the case of Nurturance/Love, the psychometric dimension may actually reflect variation in more than one evolved system. It is possible that this occurs elsewhere in the FFM dimensional space. For example, there is overwhelming evidence that variation in the proneness to positive emotions is strongly associated with behavioral approach (e.g., Watson & Clark, 1992). If that is the whole story, then one would conceptualize the lower end of behavioral approach as simply the relative absence of this single motivational system, not as grounded in a separate motivational system which is negatively correlated with positive emotionality at the phenotypic level.

Factor analytic studies indicate that people are well aware that they can be both prone to high positive emotions and high negative emotions associated with behavioral approach and behavioral avoidance respectively, although Watson and Clark (1992) note a moderate correlation between sadness and low extraversion. People are apparently less aware of the independence of systems in the case of the emotions underlying Nurturance/Love, perhaps because of the de-contextualized nature of personality inventories, or because in fact most people really do tend to

be either highly prone to affection and nurturance or highly prone to hostility but not both. As indicated above, other data strongly suggest that people can compartmentalize the emotions associated with the opposite poles of this dimension, resulting in trait X situation interactions resulting from the fact that different systems associated with the same personality dimension can be recruited in different situations.

Another possibility is that there are evolved mechanisms which function to inhibit behavioral approach tendencies in particular situations. Watson and Clark (1992) found that sadness (= low positive affect) was negatively associated with Extraversion, and Tellegen (1985) found that low positive affect was associated with depression. Davidson (1993) summarizes evidence linking depression and low levels of behavioral approach, including a pattern of left frontal hypoactivation in formerly depressed individuals (Henriques & Davidson, 1990). Depression is also associated with anhedonia (DSM IV) and introversion, including the descriptors pessimistic, lacking in self confidence, unmotivated to obtain rewards (Hirschfeld & Klerman, 1979; Hirschfeld et al, 1983; McGuire & Troisi, 1994).

Ethological psychiatrists (Price et al, 1994; McGuire & Troisi, 1995) have argued that depression is an evolved adaptive response to acute instances of failure in social competition because it results in social support and other aid and enables the individual to accommodate to a low rank. Some instances of the inhibition of behavioral approach may thus be the result of a situationally dependent adaptation. Similarly, certain discrete classes of environmental events, such as loss of attachment objects (Bowlby, 1980), may be evolved triggers for inhibitory influences on behavioral approach mechanisms.

The discrete systems perspective proposed here is also compatible with complementary as well as conflicting interactions between evolved motivational systems. Approach/avoidance conflicts have been central to evolutionary perspectives beginning with the ethologists, but different evolved systems may also combine in influencing the phenotype and thus result in complementary motives. For example, Watson and Clark (1992) found that NEO-Achievement was related to positive affect and Extraversion as well as the Dependability and Orderliness facets of Conscientiousness. One would expect that actual achievement would require not only ambition (desire for resources and social status—related to behavioral approach), but also attention to detail,

perseverance in the face of difficulty, adequately dealing with possible threats, dependability, and perhaps orderliness (related to Conscientiousness).

An Evolutionary Perspective on Individual Differences in Personality. In the Introduction, I sketched the view that variation in evolved personality systems represents variation in a range of viable strategies. There are good theoretical reasons to suppose that humans will be greatly interested in the genetic and phenotypic diversity represented by this range of viable strategies. 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).

At a basic level, individual genetic and phenotypic variation constitutes the playing field on which the evolutionary game is played (MacDonald, 1991). Evolutionary theory implies that organisms will be keenly interested in genetic variation and its expression in a wide array of phenotypic traits. Indeed, if kin selection theory (Hamilton, 1964) is correct, genetic variation is always a potential resource for individuals. Individuals not only possess genetic variants but act differentially toward others depending on the extent to which they share genetic variants. In addition, the phenomenon of assortative mating attests to the keen interest humans have in individual variation. Assortative mating not only maintains genetic variation within the population but may itself be viewed as an adaptive process because it results in increased relatedness to children (Rushton, 1989; Thiessen & Gregg, 1980) and increases the probability that children will be high in adaptive traits such as intelligence or resource obtaining ability which are influenced by genetic variation.

Phenotypic variation must therefore be seen as containing cues which influence how people evaluate each other. Different evaluations will be made depending on the putative role of the other person in their lives. Individual differences in personality and other traits are thus conceived as a resource environment for individuals.

In support of this idea, Hogan (1983) has proposed that personality trait terms evaluate the potential of persons as resources to others. Individual differences in personality are thus viewed as indicators of whether individuals are suited for particular roles. Buss (1991) notes that the vast majority of personality trait terms are evaluative, indicating a person's potential value as a resource

to others, and Wicklund and Braun (1987) found that individuals are more likely to ascribe traits to others if evaluation is the goal. Finally, Borkeanu (1990) showed that personality traits are judged to be similar to the extent that they are similar to common extreme values on a trait dimension. This supports the idea that in making attributions of personality, individuals are not making attributions of how closely a person conforms to a central tendency for the trait, but are rather describing the individual in terms of ideal-based goal categories which represent the extreme values of the trait.

Thus even though some personality psychologists have shown that knowledge of a person's personality traits is often unpredictable, personality traits as summary measures of individual differences seem to be important information for the rest of us. Individuals are expected to develop beliefs about their own relative standing on individual difference dimensions. Each individual is expected to not only appraise the phenotypic traits of others, but to evaluate these traits differentially depending on the type of relationship entered into. Thus Graziano and Ward (1992) found that teachers perceived a stronger association between Conscientiousness and school adjustment than did school counselors, a finding which presumably reflects the greater interest teachers have in this trait as a component of children's adjustment. Similarly, Lusk et al (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 which 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 which 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 which they themselves rated highly.

The possible role of non-additive genetic variation in personality is particularly interesting in this regard. There is considerable evidence for non-additive genetic variation for extraversion, neuroticism and a variety of other personality traits as indicated by very low correlations between first-degree biological relatives combined with a pattern in which DZ twin correlations tend to be less than half the correlations for MZ twins (Plomin et al, 1990; Bouchard, 1994). This pattern

(which does not occur with intelligence data) suggests a mechanism in which parents are not putting all their eggs in one basket when it comes to the personality of their children. The non-additive variation would make the offspring relatively unpredictable from parents' personality, and indeed, parent-offspring correlations for personality traits tend to be approximately 0.15 (Plomin et al, 1990). The presence of non-additive genetic variation (and additive genetic variation) is highly compatible with the proposal that environmental heterogeneity and the niche complexity of human societies are important in maintaining adaptive genetic variation. The presence of non-additive genetic variation is also compatible with the emphasis here on interactive relationships among personality systems: E.g., the effect of genes underlying the structures related to behavioral approach may depend for their effect on the level of opposing systems related to behavioral avoidance.

Another aspect of an evolutionary perspective on individual differences is that psychopathology is associated with the extremes of the FFM (Widiger & Costa, 1994). While extreme levels of a personality system may be maladaptive, some of these individuals may also be seen as engaging in high risk evolutionary strategies (MacDonald, 1992b). For example, 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 et al, 1988), with creativity associated with the manic phase (Isen, Daubman, and Nowicki, 1987). As another example, it was noted above that ADHD children have difficulty focussing attention and obtaining important information for coordinating activities with others. ADHD children tend to be impulsive and aggressive, and they are often socially rejected (Shaywitz & Shaywitz, 1988). Adults formerly diagnosed as ADHD tend to exhibit more antisocial behavior than non-ADHD siblings (Mannuzza et al, 1991). However, Cantwell (1990; 1992) reports that some adults identified as having exhibited the symptoms of ADHD as children went on to achieve high levels of success as entrepreneurs and salesmen, and some had achieved success in the entertainment industry. These individuals exhibited a great deal of drive and an extraordinary amount of energy in pursuit of their goals. (Winston Churchill is often depicted as hyperactive as a child.) They were highly creative individuals who "marched to a different drummer". Their jobs were not characterized by a great deal of routine activity nor did their jobs require a great deal of precision or attention to

detail (as would jobs suited to individuals high on the consciousness system). Instead, their jobs allowed them to work at their own pace and according to their own rules. Similarly Farley (1981; 1985) notes 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.

Although the exceptionally successful individuals described by Cantwell are clearly not typical of ADHD children grown up, they are of considerable theoretical importance. The behavioral approach systems clearly have important adaptive functions for children and adults. The evidence shows that being extreme on these systems is associated with pathology, and this is the case with all of the systems underlying personality described here. Nevertheless, from an evolutionary perspective, it is not surprising that disorders of the approach systems are so prevalent, and especially so among male children and young adults. The behavioral approach systems constitute an extremely powerful engine for obtaining resources and interfacing with the environment. Therefore it is not surprising that there is a fairly high level of what population geneticists term "genetic load" associated with the system. Genetic load refers to a situation where genes which are highly adaptive in general (and therefore maintained in the population) can also actually decrease biological fitness in some situations or for some individuals with particular genetic backgrounds. Genes predisposing individuals, especially males, to be high on behavioral approach systems can clearly have a very high payoff and will be maintained in the population even if the result is pathology and lowered biological fitness in some, even many, individuals.

One can think of these genes as underlying a high risk evolutionary strategy. Being high in these systems is a high risk strategy, but it is not a strategy which is doomed to failure. Some subset of the individuals who are very high on this system will be extraordinarily successful and undoubtedly such individuals were able to sire a high number of offspring during human evolution, especially given the fact that polygyny and large numbers of offspring have typically been the reward of highly successful males in traditional human societies (e. g., Betzig, 1986). Moreover, given the complex, interactive nature of the biological systems underlying personality, not all, or even most of the children of these individuals would be expected to be at the pathological extreme for these traits (MacDonald, 1991). However, these genes would have an

average effect which would indeed make the offspring of these individuals more likely to be creative, enthusiastic, energetic, neophilic, and highly driven by the prospect of reward. Genes predisposing individuals, especially males, to be high on these traits will therefore stay in the population at quite high levels.

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1. This paper does not consider the Openness to Experience factor. Openness differs from the other factors in that there are no sex differences, there is little evidence linking extremes on the dimension to psychopathology (but see Costa & Widiger, 1994) and, like intelligence (to which it is related) but unlike the other factors of the FFM, there is no evidence for non-additive genetic variation (Rowe, 1994). The dimension would appear to tap variation in what one might term an optimal Piagetian learning device—i.e., intrinsically motivated curiosity and interest in intellectual and aesthetic experience combined with imagination and creativity in these areas. Although there are no emotional correlates for this factor (Watson & Clark, 1992), the intrinsically motivated nature of intellectual and artistic activity tapped by this dimension strongly suggests the existence of evolved affective mechanisms which facilitate the development of cognitive competence. Indeed, interest—which would appear to be central to this dimension—is viewed as an emotion within discrete emotions theory (Izard, 1971). In contemporary societies this factor is modestly correlated with intelligence and education (Costa & McCrae, 1992; John et al, 1994) and may thus reasonably be viewed as linked to resource acquisition and reproductive success in traditional societies. The importance of intrinsic motivation in cognitive development is recognized in Piagetian theory and its contemporary descendants within the information processing tradition, e. g., Case (1985).

². The NEO-PI-R generally minimizes sex differences in personality systems. Thus, within the NEO-PI-R, there are no significant sex differences in Extraversion, conceptualized as a combination of Nurturance and Dominance, although females score somewhat higher. Contributing to this pattern, the Warmth facet of NEO-PI-R Extraversion contains seven items conceptually related to general gregariousness and sociability (for which there is little theoretical reason to expect a sex difference) along with one item indicating strong emotional attachments to others ("I have strong emotional attachments to my friends"). Intimate relationships tapped by this latter item are of considerable theoretical importance on an adaptationist account and are expected to be a stronger tendency for females than males (see below). The Warmth facet is located between Extraversion ($r = .65$) and Agreeableness ($r = .40$), and females are higher on this facet than males. Although there is a theoretically expected sex difference in NEO-PI-R Agreeableness, the difference is much less robust than that found with IAS-R-B5 Nurturance.

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