

CHAPTER 14

Temperament and Evolution

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The promise and challenge of evolutionary psychology are to chart the set of human psychological adaptations—mechanisms designed by natural selection over the course of evolution that solve particular adaptive problems. These mechanisms are conceptualized as adaptive systems that served a variety of functions in the environment of evolutionary adaptedness (EEA)—the environment in which humans evolved and which presented the set of problems whose solutions are the set of human adaptations (also see Depue, Chapter 18, this volume). 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 (see Buss, 2008, for a review focused on personality psychology). It expects that each system will be responsive to particular environmental contexts, and that different temperament and personality systems will be in competition with each other within individuals, leading at times to psychological ambivalence (MacDonald, 2005).

Here I review theory and data on temperament from an evolutionary perspective. Standard definitions of temperament

acknowledge the centrality of biology. Rothbart's definition focuses on the two broad functional domains of temperament: constitutionally based individual differences in reactivity and in self-regulation (see Rothbart & Bates, 2006; also see Rothbart, Chapter 1, this volume). Rothbart and Bates distinguish temperament from personality by defining *temperament* as the affective, activation, and attentional core of personality—all of which are strongly biological, while *personality* is a larger category that includes also beliefs, social cognition, morals, skills, habits, and so forth, and is more characteristically human.

Evolution and Individual Differences

The term *trait* implies that individual differences are critical to temperament. In general, evolutionary psychologists regard adaptations as specieswide universals. However, genetic variation is ubiquitous, even for adaptations (e.g., West-Eberhard, 2003), leading to the evolution of appraisal mechanisms in which the value of different personality traits may be appraised differently depending on the perceived interests of evaluators—potential spouses, lovers, employees, employers,

friends, leaders, and so forth (Lusk, MacDonald, & Newman, 1998). For example, finding mates is an evolutionarily ancient problem for both sexes, resulting in substantial cross-cultural commonality in how people evaluated variation in the personality trait of ambition-industriousness in potential spouses, with theoretically expected sex differences whereby females valued this trait more highly in a potential spouse than males (Buss, 1989). In turn this suggests an evolutionary basis for valuations of personality, similar to Singh's (1993) findings for male appraisals of waist-hip ratio in females.

From an evolutionary perspective, individual differences within the normal range are seen as variation in evolved systems. The most accepted proposal for why genetic and phenotypic variation in adaptive systems remains in populations is environmental heterogeneity (MacDonald, 1995; Nettle, 2006; Penke, Denissen, & Miller, 2007). This is well established in animal research (Carere & Eens, 2005; Dingemanse, Both, Drent, & Tinbergen, 2004; Dingemanse & Réale, 2005; Van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005). For example, Dingemanse and colleagues (2004) found that exploratory males (but not females) had higher fitness in a year with high resource availability, but the reverse pattern occurred in resource-poor years. Thus, there are tradeoffs such that beneficial traits in some environments impose costs in others, depending on local environmental conditions—results compatible with models of fluctuating selection due to rapid changes in the physical and biotic environment (Bell, 2010). Dingemanse and Réale (2005) reviewed data indicating that the fitness of a personality trait may depend on sex, age, and the ecological quality of the environment. In most years, an intermediate phenotype had the highest fitness; interestingly, birds with extreme phenotypes mated disassortatively, thereby producing intermediate phenotypes in their offspring, suggesting that this is an adaptive strategy.

A Top-Down Perspective Aimed at Carving Nature at Its Joints

An evolutionary theory seeks to establish the set of adaptations that underlie tempera-

ment and personality. This is not the same as showing that a temperament trait has a biological basis, or that it is genetically influenced. An evolutionary theory seeks to “carve nature at its joints” on the basis of functional units—systems that have been the focus of natural selection. An illustrative example of a trait that shows genetic variation but is not an adaptation is proneness to divorce. McGue and Lykken (1992) found that proneness to divorce is heritable. However, proneness to divorce does not reflect variation in an adaptation. Different people are prone to divorce for different reasons (e.g., emotional instability [high neuroticism], selfishness, or proneness to philandering).

The standard psychometric approach is not ideal for discovering the adaptations underlying personality and temperament. For example, Freeman and Gosling's (2010) review of studies of primate personality found 14 categories: sociability, fearfulness, playfulness, confidence/aggression, activity, excitability, curiosity, dominance, agreeableness, irritability, intelligence, impulsiveness, anxiousness, and independence. Support for putative personality dimensions depends on interrater reliability, as well as convergent and discriminant validity, all of which are at least promising. From an evolutionary perspective, however, discerning reliable and valid traits is only an essential first step. In addition, an evolutionary analysis requires evidence that these traits are real foci of natural selection. Ideally, one would need to find independent evidence that the traits represent variation in adaptive systems designed to solve particular problems. Was variation in curiosity or playfulness a focus of natural selection or is it simply “noise”—nonadaptive genetic variation that is not undergoing natural selection and does not contribute to fitness, as Tooby and Cosmides (1990) proposed for personality variation in general? Are these traits like the divorce example—complexly influenced by a variety of evolved systems, in which different animals may be playful or curious for different reasons? Is the variation linked to differences in adaptive outcomes in the different environments that the animal's ancestors encountered over evolutionary time, or is it merely variation that human observers find interesting?

In general, evolutionary psychologists are

“splitters” in studying adaptations; that is, they study each putative adaptation separately. The emphasis is on universality rather than on correlations among individual differences among different adaptations. For example, evolutionary psychologists study anger as an adaptation (Sell, Cosmides, & Tooby, 2009), without considering how individual differences in anger are correlated with individual differences in other traits. Because of the centrality of individual differences, personality psychology has naturally been interested in the correlational patterns among traits, leading to an important role for higher-order factor analyses, such as the five-factor model (FFM). This review proposes that several general adaptive spaces can be meaningfully related to the FFM if not in a 1:1 manner. As Dingemanse and Réale (2005, p. 1180) point out, “Functional explanations for personality variation (i.e., *consistent* individual differences in suites of *correlated* behavioural traits) would require insight into conditions favouring phenotypic (or genetic) correlations among behavioral traits” (emphasis in original). The proposal in the following is that the concept of adaptive space provides a rationale for why there are correlations among particular suites of behavioral traits.

The concept of an adaptive space is an abstraction in the sense that it refers not to a particular adaptation but to a suite of adaptations with the following attributes:

- There are phenotypic correlations among individual differences in the traits detectable by factor analysis.
- There is shared genetic variation among the traits.
- There are broadly similar functions among this suite of adaptations.
- There are shared motivational, attentional, perceptual and, in addition for personality, cognitive mechanisms (there may also be motivational, attentional, perceptual, and cognitive mechanisms that are unique to a particular subsystem).
- This suite of adaptations results from an evolutionary history of elaboration and differentiation from systems that existed in common ancestors.

The adaptive space idea proposes that personality systems should be conceptual-

ized hierarchically, from more specific to more general, within a generally defined adaptive space. For example, the behavioral approach adaptive space (BAAS) is at the highest level of evolutionary analysis—the highest level of meaningful adaptive space, with more specific systems arrayed beneath it. As described more fully below, the BAAS functions to motivate animals to interface actively with the environment. Research on animal personality supports correlations and genetic overlap among functionally distinct behavioral traits related to behavioral approach. For example, Dingemanse and Réale (2005) describe suites of “autocorrelated traits” based on the finding that animals that are relatively aggressive toward conspecifics are also bolder in exploring novel environments and predators; they are more prone to taking risks, more liable to scrounge during foraging, and are more responsive to stress. The correlations among these conceptually related traits are typically based on strong underlying genetic correlations (Dingemanse & Réale, 2005; van Oers et al., 2005), for example, a genetic correlation of .84 between early exploratory behavior and risk taking in laboratory conditions in great tits (*Parus major*). Reported genetic correlations for boldness and aggression ranged from .37 in German shepherd dogs to .84 in three-spined stickleback fish (*Gasterosteus aculeatus*) (see van Oers et al., 2004). Thus Barr (Chapter 13, this volume), discussing Korte, Koolhaas, Wingfield, and McEwen (2005), notes that traits of aggression and exploration likely did not evolve in isolation, but rather as a package of traits resulting from genetic linkage. Similarly, Hur and Bouchard (1997) found a genetic correlation of .55 between sensation seeking and impulsivity in a sample of identical twins reared apart, with the remaining genetic variance unique to impulsivity.

An evolutionary interpretation proposes that these different subsystems accrued over evolutionary time as primitive foraging and mate attraction systems became elaborated and somewhat differentiated in response to specialized features of the “approach” adaptive space, effectively resulting in subsystems or “facets” of temperament and personality. These subsystems share anatomical and neurological structures, as well as genetic and phenotypic variance, and may therefore be

nested under one or more of the superfactors of higher-order models, prototypically the FFM. Thus, for example, testosterone influences aggression, dominance, sexual activity, mating effort, antisocial behavior, rough-and-tumble play, and personality traits (extraversion, sociability, disinhibition, sensation seeking, and instrumental effort) (Archer, 2006). Despite important differences among these behaviors and dispositions, as well as the mechanisms underlying them, they also share common mechanisms.

All of these characteristics of an adaptive space are falsifiable empirical propositions. Evidence against genetic correlations for traits that are phenotypically correlated would be evidence that two traits are not part of the same adaptive space. As discussed below, phenotypic overlap in the absence of genetic correlations could occur if people tended to group quite different types of negative affect together (e.g., fear and anger) even though fear and anger are quite different in terms of evolutionary function and in their neuropsychology.

Tools of an Evolutionary Theory: Evolution, Sex, Age, and Life History Theory

An important tool for carving nature at its joints is the evolutionary theory of sex (Trivers, 1972). The sex with the higher level of parental investment (typically the females, especially for mammals) is expected to be relatively more discriminating in choosing mates because the typically greater female investment implies that females will be a valued resource in the mating game. 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. This results in a large number of predictions related to personality: Males are expected to take a more proactive approach to the environment, whereas females benefit from a more conservative strategy. This is because males have more to gain by controlling the social and nonsocial environment than females. In all of the traditional societies of the world, males who have had relatively high levels of control of social and nonsocial resources have had higher

reproductive success because they have had access to additional mates (polygyny, extra-marital relationships) and to higher-quality mates (Betzig, 1986). Females, because they do not similarly benefit from additional matings, are predicted to adopt a more conservative strategy, primarily because, since mating is less problematic for females under conditions of sexual competition, there is less benefit of engaging in risky, dangerous strategies. Thus, by conquering most of Asia (a risky endeavor), Genghis Khan was able to have millions of descendants in the contemporary world because his conquests enabled intensive polygyny by himself and his male descendants (Zerjal et al., 2003). Because of inherent reproductive limitations, no female could have benefited to a similar extent by pursuing such a strategy.

The evolutionary theory of sex also has implications for age-related changes in at least some personality systems. The *young male syndrome* describes the pattern in which sensation seeking, impulsivity, and aggression (all associated with the BAAS described earlier) peak in young adulthood at the time when young males must compete for mates and establish themselves in the dominance hierarchy (Wilson & Daly, 1985). Similarly, sex differences related to intimacy peak during the reproductive years (Turner, 1981), that is, during the period when sex differences are maximally divergent, and when finding a spouse who is loving and empathic is a critical adaptive challenge, particularly for females.

Life history theory attempts to explain the evolution of *resource allocation strategies* that optimize the utilization of resources over the life course and across varying ecological conditions. Life history traits are characteristics that determine rates of reproduction and associated patterns of growth, aging, and parental investment, including current versus future reproduction, short versus long period of preadult dependency, and offspring quality versus quantity (Charnov, 1993; Roff, 1992; Stearns, 1992).

Animal research has shown that individual differences in the systems underlying a species' life history profile become intercorrelated because they constitute a coherent manner of responding to the exigencies of life—survival, development, and reproduction. For example, Mehlman and colleagues

(1997) found a variety of personality- and life history-related responses in rhesus macaques that varied depending on levels of serotonin. Males with low serotonin levels were more violently aggressive and dispersed at an earlier age. They were also more likely to engage in risky behavior and to suffer premature death, but less likely to be sexually involved with females. Thus, variation in serotonin levels is associated with a wide range of phenomena expressed in different ways at different ages throughout the lifespan.

Research on humans inspired by life history theory has focused on finding evidence for a general personality factor. Rushton and colleagues have provided evidence for a general factor of personality using FFM questionnaires (Rushton, Bons, & Hur, 2008; Rushton & Irwing, 2009). Figueredo and colleagues have linked this general personality factor to what is termed a *K-style reproductive strategy*, defined as relatively late reproduction, strong pair-bonds, and high parental investment (Figueredo, Vásquez, Brumbach, & Schneider, 2007; see also Figueredo et al., 2006; Figueredo, Vásquez, Brumbach, & Schneider, 2004). (The opposite of a K-style reproductive pattern is labeled an *r-style reproductive pattern*, characterized by relatively early reproduction, weak pair bonds, and minimal parental investment.) A single factor emerged from 20 scales of personal, familial, and social functioning. Subjects with high factor scores reported higher quality of relationship with their parents, spouse, and children; they provided and received greater support from friends and relatives; and they scored higher on measures of long-term planning, impulse control, relationship stability, and degree of community organization or involvement. This K factor was correlated with a general personality factor characterized by relatively high scores on Extraversion, Agreeableness, Emotional Stability (the inverse of Neuroticism), Conscientiousness, and Openness to Experience.

The finding of a single personality factor implies that traits become intercorrelated because of the need to develop a coordinated life history response to the environment; that is, a mix of traits, some of which fit into a K-style life history pattern (e.g., long-term planning) and some of which fit into an r-style reproductive pattern (e.g., low

impulse control), would be maladaptive. This coordinated response cuts across the adaptive space concept; that is, the emergence of a single personality factor implies intercorrelations among all the systems related to personality, including systems designed to solve very different adaptive problems. On the other hand, the adaptive space concept rests on the possibility of finding correlations based on a common evolutionary history of elaboration and differentiation of adaptations that existed in common ancestors. These are mutually compatible ways of conceptualizing personality from an evolutionary perspective.

Six Adaptive Spaces

The following sketches six adaptive spaces reflected in the temperament and personality literature. The procedure is to sketch out these adaptive spaces, then, by using the evolutionary tools mentioned earlier, discuss how the results of factor-analytic studies map onto these adaptive spaces.

The BAAS

Among even the most primitive mammals, there must be systems designed to approach the environment to obtain resources, prototypically foraging and mate attraction systems. As used here, a temperament/personality system includes a specific neuropsychological substrate influencing motivation, perception, and behavior. For example, Panksepp (1998) has argued that the mammalian brain contains a "foraging/exploration/investigation/curiosity/interest/expectancy/SEEKING" system (p. 145; see also Panksepp & Moskal, 2008). Thus, the SEEKING system includes neuropsychological substrates for motivational mechanisms that make curiosity and exploration psychologically rewarding, as well as perceptual biases toward attending to novel stimuli and specific exploratory behaviors, such as smelling novel aspects of the environment, seen in many mammals.

The behavioral approach system (BAS; Gray, 1987, 2000) evolved from systems designed to motivate approach toward sources of reward (e.g., sexual gratification, dominance, control of territory) that

occurred as enduring and recurrent features of the environments in which animals or humans evolved. These systems overlap anatomically and neurophysiologically with aggression, perhaps because aggression is a prepotent way of dealing with the frustration of positive expectancies (Panksepp, 1998, p. 191). Several of the primate traits studied by Freeman and Gosling (2010; confidence/aggression, dominance, impulsiveness, activity, curiosity, and perhaps playfulness) have a surface plausibility as components of the BAAS for primates (see also Barr, Chapter 13, this volume, on confidence/aggression as a consensus temperament trait in rhesus). Furthermore, the auto-correlated traits of aggression, exploratory behavior, and risk-taking revealed in animal research (see Dingamane & Réale, 2005; van Oers et al., 2005; see earlier discussion) all concern traits conceptually related to behavioral approach. Similarly, working with human data, De Pauw, Mervielde, and Van Leeuwen (2009) found that activity level loads on the same factor as impulsivity and high-intensity pleasure, and in Larsen and Diener's (1992) study, activity level appears in the same factor-analytic space as dominance and sensation seeking.

Important components of the BAAS are dopaminergic reward-seeking mechanisms (Gray, 1987, 2000; Panksepp, 1982, 1998; Panksepp & Moskal, 2008; Zuckerman, 1991; see also Putnam, Chapter 6, and Depue, Chapter 18, this volume). Evolution has resulted in affective motivational systems triggered by specific feeling states that motivate active interface with the environment (e.g., the taste of sweet foods, the pleasure of sexual intercourse, the joy of the infant in close intimate contact with its mother; E. O. Wilson, 1975). For example, in rats, these mechanisms underlie energetic searching, investigating, and sniffing objects in the environment as possible sources of reward (Panksepp, 1998).

There are species differences in behavioral approach related to the animal's ecology. For example, predatory aggression is a component of behavioral approach in cats, but not in rats (Panksepp, 1998, p. 194). Over evolutionary time, the BAAS has become elaborated and differentiated according to the unique adaptive demands of each species. As a result, carnivores seek different sorts of

food than do herbivores, with the former requiring mechanisms involved in stalking and taking down prey, and the latter requiring mechanisms for locating edible plants. Dominance mechanisms are an important component of behavioral approach for many social species, but not for solitary species.

The behavioral approach system is related to Surgency/Extraversion in the FFM (see also Rothbart, Putnam, Chapter 1, and Putnam, Chapter 6, this volume) and Dominance in the circumplex model of interpersonal descriptors (Trapnell & Wiggins, 1990; Wiggins, 1991; Wiggins & Trapnell, 1996). 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. Newman (1987; also see Derryberry, 1987) found that compared to introverts, extraverts have a stronger response to reward. Among human adults, behavioral approach is also associated with aggressiveness and higher levels of sexual experiences (Gray, 1987, 2000; Zuckerman, 1991) and positive emotionality (Gray, 1987, 2000; Heller, 1990), while impulsivity, "high-intensity pleasure," and aggressiveness are components of behavioral approach in young children (Rothbart, Ahadi, Hershey, & Fisher, 2001).

Sensitivity to reward emerges very early in life as a dimension of temperament (Bates, 1989; Rothbart, 1989b; Rothbart & Bates, 2006). 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 facet of positive emotionality" (Pfeifer, Goldsmith, Davidson, & Rickman, 2002, p. 1475; see also Fox, Henderson, Rubin, Calkins, & Schmidt, 2001). Children who score high on behavioral approach are prone to positive emotional responses, including smiling, joy, and laughter available in rewarding situations and in the pleasant social interaction sought by sociable children (see Putnam, Chapter 6, this volume).

Sensation seeking, including promiscuous sexual activity (which loads on the Disin-

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hibition subscale of the Sensation Seeking Scale; Zuckerman, 1979), and aggression (Wilson & Daly, 1985) peak in late adolescence and young adulthood, followed by a gradual decline during adulthood. As noted earlier, 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 male and female 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 score higher on behavioral approach even during infancy in cross-cultural samples (reviewed in Rothbart, 1989b). Furthermore, sex differences in aggression (Eagly & Steffan, 1986), high-intensity pleasure (see Else-Quest, Chapter 23, this volume), externalizing psychiatric disorders (conduct disorder, oppositional defiant disorder), risk taking and aggression (Klein, 1995; LaFrenière et al., 2002), and rough-and-tumble play (which is often associated with aggression [Collaer & Hines, 1995; Hines, 2011; Humphreys & Smith, 1987; MacDonald & Parke, 1986]) can first be seen in early childhood. Beginning in infancy, boys engage in more large-motor, physically intense activity (Eaton & Yu, 1989; Else-Quest, Hyde, Goldsmith, & Van Hulle, 2006). Genetic females exposed to testosterone-like hormones prenatally are more aggressive (Matthews, Fane, Conway, Brook, & Hines, 2009; Paster-ski et al., 2007) and more active than girls without such exposure (Ehrhardt, 1985). Moreover, the social interactions of boys are more characterized by dominance interactions and forceful, demanding interpersonal styles (LaFrenière & Charlesworth, 1983; LaFrenière et al., 2002). 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* (lack of ability to experience pleasure) and negative mood are primary symptoms of depression within the *Diagnostic and Statistical Manual of*

Mental Disorders (DSM-IV) classification (American Psychiatric Association, 2000).

In general, the results for behavioral approach fit well with the idea of an adaptive space of approach traits linked psychometrically and neurophysiologically, and showing evolutionarily expected sex differences and developmental trajectories (i.e., the young male syndrome).

The Behavioral Withdrawal Adaptive Space

While behavioral approach systems motivate active engagement with the environment, specialized systems are required to respond to environmental threats, prototypically by withdrawal or defensive aggression. The behavioral inhibition system (BIS) functions to monitor the environment for dangers and impending punishments (Gray, 1987, 2000; LeDoux, 1996). Recent conceptualizations distinguish between a fear system and an anxiety system, with different neuropsychologies and adaptive functions (see Depue & Fu, Chapter 18, this volume). The fear system is designed to respond to unconditioned (e.g., pain, snakes, spiders) or conditioned aversive stimuli, while anxiety is designed to respond to situations of uncertainty and unpredictability.

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, 2006). Children who score high on behavioral inhibition respond negatively to new people and other types of novel stimulation (Fox et al., 2001; Kagan, Reznick, & Snidman, 1987; also see Kagan, Chapter 4, and White, Lamm, Helfinstein, & Fox, Chapter 17, this volume).

Fearfulness is a well-established temperament trait in children (see Kagan, Chapter 4, this volume) and in primates (Freeman & Gosling, 2010), and, indeed, in all animals studied (see Barr, Chapter 13, this volume). It is most closely related to Neuroticism in five-factor personality scales (see below). The evolutionary theory of sex predicts that females will be more sensitive than males to signals of personal threat. Females are more prone to most anxiety disorders, including agoraphobia and panic disorder (e.g., Amer-

ican Psychiatric Association, 2000; Weissman, 1985). Girls report being more fearful and timid than boys in uncertain situations and are more cautious and take fewer risks than boys (Christopherson, 1989; Ginsburg & Miller, 1982).

The Reactivity/Affect Intensity Adaptive Space

A third important adaptive space is reactivity (affect intensity). Arousal functions to energize the animal to meet environmental challenges or opportunities. In the absence of such a system, the animal would either be permanently overaroused, which would needlessly consume resources, or permanently underaroused and less able to meet environmental challenges. Indeed, Quinkert and colleagues (2011, p. 15617) identify generalized arousal mechanisms as "the most powerful and essential activity in any vertebrate nervous system."

Affect intensity functions to mobilize behavioral resources by increasing arousal in acutely demanding situations in the service of either approach or withdrawal. 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; research implicates systems that energize both positive and negative emotion systems. Thus, Schiff and Pfaff (2009) and Quinkert and colleagues (2011) conceptualize arousal as a generalized, valence-free force that supplies the energy for emotionally charged responses, thereby regulating their intensity (also see Panksepp, 1998, pp. 109–110, 117). These generalized arousal mechanisms utilize a variety of neurotransmitters (Quinkert et al., 2011). Anatomically, the reticular formation is critical for regulating arousal levels of the central nervous system through its connections with the limbic system and thalamus (Posner, Russell, & Peterson, 2005; Posner et al., 2008; Quinkert et al., 2011). Freeman and Gosling's (2010) finding of an excitability dimension provides evidence for an individual-differences dimension of reactivity/affect intensity in primates. Garey and colleagues (2003) identified a generalized arousal component in the behavior of mice across experiments, investigators, and mouse populations.

Reactivity, along with self-regulation, is one of the two fundamental realms of temperament in Rothbart's scheme (see, e.g., Rothbart & Bates, 2006). Children who are highly reactive respond intensely to stimulation, reach peak arousal at lower stimulus intensity, and have a relatively low threshold for arousal (Rothbart, 1989a, 1989b; Strelau, 1989). Low-reactive children have a relatively high threshold of stimulation and do not become aroused by stimulation that would overwhelm a high-reactive individual. Emotionally intense individuals respond relatively strongly to emotional stimulation, independent of the emotion involved, including both positive and negative emotions (Aron & Aron, 1997; Benham, 2006; Larsen & Diener, 1992). Smolewska, McCabe, and Woody (2006) found that people who score high on the Highly Sensitive Person Scale (a measure of reactivity; Aron & Aron, 1997) also scored higher on measures of Neuroticism, Behavioral Inhibition (which measures proneness to fear), and Responsiveness to Reward (a component of the behavioral approach system). Highly reactive individuals thus react intensely both to situations perceived as threatening and potentially rewarding.

An independent arousal regulation system is also implied in two-dimensional models of mood that distinguish between activation (arousal) and valence (Russell, 2003; also see Posner et al., 2005). Nevertheless, it should be noted that acknowledging the independence of arousal and valence need not entail a rejection of discrete negatively valenced emotions energized by the generalized arousal system. Here evidence is provided that fear and anger are associated with different adaptive spaces (Behavioral Withdrawal and Behavioral Approach, respectively) and have different neuropsychologies (see below).

Larsen and Diener (1992) found that affect intensity is most closely associated with Neuroticism in the FFM; similarly, Smolewska et al. (2006) found that reactivity to stimulation as measured by the Highly Sensitive Person Scale was most strongly correlated with Neuroticism in the FFM. Similarly, Depue and Fu (Chapter 18, this volume) analyzes neuroticism as reactivity to stressful situations and "labile, reactive moods." Watson and Clark (1992) show that Neuroticism is

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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 associated with the FFM: hostility (negatively) with Nurturance/Love, sadness with Introversion, 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; see below). 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; Benham, 2006; Panksepp, 1998, p. 117; Smolewska et al., 2006; see below).

The Nurturance and Pair-Bonding Adaptive Space

Mammalian females give birth to and suckle their young. This has led to a host of adaptations for mothering, an outgrowth of which are pair-bonding mechanisms present also in males (MacDonald, 1992). 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. The adaptive space of nurturance/pair-bonding therefore becomes elaborated into a mechanism for cementing adult relationships of love and empathy, prototypically within the family.

Variation in Nurturance/Love, the second factor emerging from the circumplex model, is associated with 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, 1996; Wiggins, Trapnell, & Phillips, 1988). Recently, models of temperament have included a temperament dimension of Affiliativeness (Rothbart, 1994; see also Evans & Rothbart, 2007; Rothbart & Bates, 2006, also see Knafo, Chapter 9, this volume). Affiliativeness involves warmth, love, closeness, empathic concern, and a desire to nurture others. Individual differences in warmth and

affection observable early in parent-child relationships, including secure attachments, are conceptually linked with Nurturance/Love later in life (MacDonald, 1992, 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 pair-bonding involves specific brain regions (Bartels & Zeki, 2000; Burkett, Spiegel, Inoue, Murphy, & Young, 2011) and the hormones oxytocin and vasopressin, as well as opiates and dopamine (Atzil, Hendler, & Feldman, 2011; Burkett et al., 2011; Insel, Winslow, Wang, & Young, 1998; Panksepp, 1998; also see Barr, Chapter 13, and Depue & Fu, Chapter 18, this volume). In prairie voles (*Microtus ochrogaster*), a monogamous species with paternal involvement in provisioning the young, oxytocin receptors (Insel et al., 1998) and opioid receptors (Burkett et al., 2011) are found in brain regions associated with reward and with pair-bonding, supporting the proposal that pair-bonding is a reward-based system that functions to facilitate intimate family relationships and parental investment (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 nurturance of the objects of affection are pleasurable, and such relationships are sought out by those sensitive to the reward value of this stimulation.

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. The evolutionary theory of sex implies that females are expected to be highly discriminating mothers compared to males and more committed to long-term relationships of nurturance and affection; cues of nurturance and love in males are expected to be highly valued by females seeking paternal investment.

There are robust sex differences (higher in females) on the Interpersonal Adjective Scale—Big Five version (IAS-R-B5) (LOV)

scale, which measures the Nurturance/Love dimension of the circumplex model (Trapnell & Wiggins, 1990). This dimension involving the tendency to provide aid for those needing help, including children and people who are ill (Wiggins & Broughton, 1985), would therefore be expected to be associated with high-investment childrearing. This dimension is strongly associated with measures of femininity, and with warm, empathic personal relationships and dependence (Wiggins & Broughton, 1985). Girls are more prone to engage in intimate, confiding relationships than boys throughout development (Berndt, 1986; Buhrmester & Furman, 1987; Douvan & Adelson, 1966). Females also tend to place generally greater emphasis than males 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). Females exposed prenatally to testosterone-like hormones show reduced empathy (Mathews et al., 2009), and testosterone measured in amniotic fluid relates negatively to empathy in both boys and girls (Chapman et al., 2006). 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.

The Prefrontal Executive Control Adaptive Space

Top-down control enables coordination of specialized adaptations, including all of the mechanisms associated with the four general adaptive spaces discussed earlier (MacDonald, 2008). For many mammals, the prefrontal cortex or its analogues underlie executive control of behavior that takes into account not only subcortically generated affective cues routed through the orbitofrontal cortex (OFC) but also sensory input and other information (e.g., learned contingencies) available to working memory (Uylings, Groenewegen, & Kolb, 2003).

Humans have greatly elaborated this general adaptive space, resulting in top-down effortful mechanisms able to control not only a very wide array of mechanisms encompassed in the four general adaptive spaces mentioned earlier, but also capable of incorporating explicit construals of context in generating behavior, most notably linguistic and symbolic information (MacDonald, 2008). For example, affective states resulting from evolutionary regularities place people in a prepotently aggressive state energized by anger—an emotional state that is one of the subsystems of the BAAS discussed earlier. However, whether or not aggression actually occurs may also be influenced, at least for people with sufficient levels of effortful control, by explicit evaluation of the wider context, including explicit evaluation of the possible costs and benefits of the aggressive act (e.g., penalties at law, possible retaliation). These explicitly calculated costs and benefits are not recurrent over evolutionary time but are products of the analytic system evaluating current environments and producing mental models of possible consequences of behavior.

Rothbart has pioneered the idea that effortful control is a fundamental aspect of temperament related to self-regulation (e.g., Posner & Rothbart, 1998; also see Rueda, Chapter 8, this volume). In human children, there is increasing coherence between 22 and 33 months of age among a variety of tasks assessing the ability to suppress dominant socioaffective responses—for example, waiting for a signal before eating a snack, not peeking while a gift is wrapped, not touching a wrapped gift until the experimenter returns (Kochanska, Murray, & Harlan, 2000). In general, effortful control increases with age, with girls superior to boys (Kochanska & Knaack, 2003; Kochanska et al., 2000). The superior performance of girls on effortful control fits well with the evolutionary theory of sex discussed earlier. Males are expected to score higher on behavioral approach systems (sensation seeking, impulsivity, reward seeking, aggression) and therefore, on average, to be less prone to control prepotent approach responses.

The increasing efficiency of effortful control with advancing age parallels developmental changes in the prefrontal cortex

(PFC). In general there is linear development of PFC from childhood to adulthood; however, age changes in sensation-seeking and reward-oriented behavior are nonlinear because behavior is also influenced by the degree of maturation of limbic structures underlying the behavioral approach (Casey, Jones, & Hare, 2008) (see Figure 14.1). Adolescents are relatively uncontrolled when the development of subcortical structures underlying risk taking (a component of behavioral approach) outpaces the development of prefrontal control structures. This illustrates the complex, dynamically interactive nature of temperament systems, as well as normative changes over age in the relative strength of temperament systems.

Several authors have proposed that the personality system most closely associated with effortful control is Conscientiousness (Caspi, 1998; Kochanska & Knaack, 2003; Rothbart, Ahadi, & Evans, 2000). The only temperament factor of Rothbart's Adult Temperament Questionnaire that is correlated with Conscientiousness is the effortful control factor, which includes measures of attention shifting from reward and from punishment (MacDonald, Figueredo, Wenner, & Howrigan, 2007; Rothbart et al., 2000).

There are also strong conceptual links between Conscientiousness and the effort-

ful control of prepotent socioaffective responses. Conscientiousness is a dimension in the FFM of personality (Costa & McCrae, 1992a; Digman, 1990, 1996; Goldberg, 1981; John, Caspi, Robins, Moffitt, & Stouthamer-Loeber, 1994) referring to "socially prescribed impulse control that facilitates task and goal-directed behavior" (John & Srivastava, 1999, p. 121; emphasis in original). Conscientiousness involves variation in the ability to defer gratification in the service of attaining long-term goals; to persevere in unpleasant tasks; to pay close attention to detail; and to behave in a responsible, dependable, cooperative manner (Digman & Inouye, 1986; Digman & Takemoto-Chock, 1981).

Conscientiousness is associated with academic success (Digman & Takemoto-Chock, 1981; Dollinger & Orf, 1991; John et al., 1994), an area in which there are sex differences favoring females throughout the school years, including college (King, 2006). Correlations between high school grades and assessments of Conscientiousness performed 6 years previously were in the .50 range. There are similar correlations between higher Conscientiousness and higher occupational status and income assessed when subjects were in their mid-20s.

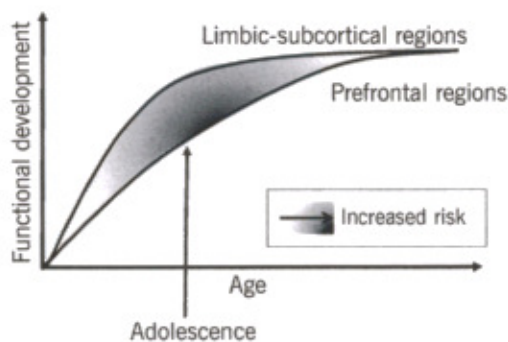


FIGURE 14.1. Illustration of different maturation patterns of prefrontal cortex and subcortical limbic regions (e.g., nucleus accumbens and amygdala) implicated in adolescent risk taking. From Casey, Jones, and Hare (2008). Copyright 2008 by the New York Academy of Sciences. Reprinted by permission.

The Orienting Sensitivity Adaptive Space

Evans and Rothbart (2007) propose that the temperamental basis for Openness is *Orienting Sensitivity*, a trait that taps perceptual sensitivity and is substantially correlated with standard personality measures of Openness. Markon, Krueger, and Watson (2005) show that Openness splits off from Positive Emotionality when moving from a four-factor to a five-factor solution. Moreover, Openness and Extraversion appear on the same factor in two-, three-, and ~~4~~ ^{four}-factor models, but they split off in the five-factor solution (Caruso & Cliff, 1997; DeYoung, 2006; Digman, 1997; Rushton & Irwing, 2009).

This suggests that Openness is part of the BAAS, but that it became an adaptive space of its own as a result of differentiation and elaboration. This is intuitively plausible because people who score high in Orienting Sensitivity are intensely engaged with the

environment in a positive manner. As with Behavioral Approach generally, people who score high on Orienting Sensitivity approach rewarding stimulation. In the case of Orienting Sensitivity this involves approaching novel aesthetic, perceptual, and intellectual experience characteristic of Openness.

Fitting the Adaptive Spaces to the Results of Factor-Analytic Studies

Animal Research

Individual differences in personality among chimpanzees can be understood within the FFM framework (Figueredo & King, 1996; King & Figueredo, 1994). Reviewing 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 nine 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 (also see Barr, Chapter 13, this volume).

As noted earlier, Extraversion is associated with the BAAS. Gosling and John's (1999) results 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 (a system common to all animals studied; Barr, Chapter 13, this volume) or systems of arousal regulation (reactivity/affect intensity, a system common to all vertebrates; Quinkert et al., 2011). These findings may indicate that although these animals have these systems, individual differences are not conspicuous enough to be captured by the observer rating methodology.

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 the ecology of these animals. Nor is it surprising that only humans and chimpanzees showed differences in Conscientiousness, since these species are involved in long-term projects requiring delay of gratification and close attention to detail; less cognitively advanced species (i.e., species that respond

to environmental challenges mainly via pre-programmed 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.

Human Research

Rothbart and Bates (2006) review studies that yielded from two to eight factors, depending on the items in the item pool. They note support for strong conceptual similarities between three of the dimensions of the FFM: Negative Emotionality (Neuroticism), Positive Emotionality (Extraversion), and Effortful Control (Conscientiousness). Subsequently, Rothbart has added items intended to tap the other dimensions of the FFM, as reviewed earlier: Affiliation, tapping the Nurturance/Pair-Bonding Adaptive Space, and Orienting Sensitivity, intended to tap the temperamental basis for Openness on the FFM (see Evans & Rothbart, 2007).

These developments indicate a powerful convergence between research on temperament and personality centered around the FFM. In seeking to determine how this factor-analytic research fits with an adaptationist perspective, I consider an important paper by Markon and colleagues (2005), which may be considered paradigmatic of a factor-analytic approach that could potentially be incorporated into an evolutionary account. This is because it shows an orderly sequence in factor solutions, from two factors to five factors. The question is: Is it reasonable to view this result as mapping a 1:1 congruence between adaptive spaces and personality factors? In particular, could the branching pattern noted in Figure 14.2 reflect a real evolutionary sequence of elaboration and differentiation of primitive structures?

The Markon and colleagues (2005) α - and β -factors refer to withdrawal (Negative Emotionality) and approach (Positive Emotionality), respectively. The three-factor solution adds Disinhibition, and the four-factor solution distinguishes between Disagreeable Disinhibition and Unconscientious Disinhibition. As mentioned earlier, the fifth factor arises when Openness splits off from Extraversion. The differentiation of Negative Emotionality into Nega-

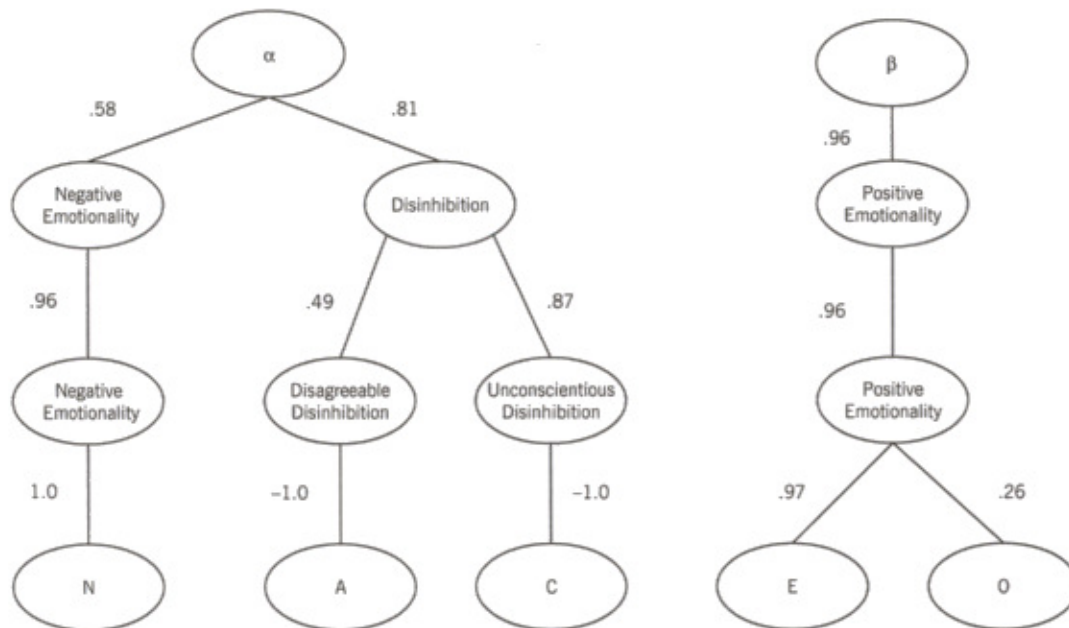


FIGURE 14.2. Correlations between subordinate and superordinate factors. From Markon, Krueger, and Watson (2005). Copyright 2005 by the American Psychological Association. Reprinted by permission.

tive Emotionality, Disagreeable Disinhibition, and Unconscious Disinhibition reflects clinical categorizations rather than a reasonable interpretation of evolutionary adaptive spaces. Disagreeable Disinhibition is related to the reverse of the Nurturance/Pair-Bonding Adaptive Space, and Unconscious Disinhibition is the reverse of Effortful Control/Conscientiousness within the prefrontal executive control adaptive space. Evolution has likely selected for these positive traits rather than their reverse. In the case of pair-bonding, there is a clear evolutionary rationale for the development of nurturance and pair-bonding mechanisms derived from parental investment theory, as noted earlier. In the case of effortful control, the prefrontal machinery of top-down control has clear adaptive benefits deriving from planning and impulse control.

One gap between an evolutionary perspective and factor analyses such as the one presented by Markon and colleagues (2005) is that an evolutionary perspective is more compatible with a factor rotation yielding factors of Dominance/Sensation Seeking and Nurturance/Love rather than Extra-

version and Agreeableness (MacDonald, 1995, 1999a,b). The Markon and colleagues five-factor solution is typical of many others emphasizing Extraversion-like traits as a basic factor. For example, Depue and Collins (1999) advocate Gregarious/Aloof and Arrogant/Unassuming as fundamental causal dimensions of personality covering the same factor space. Extraversion is also a factor in the NEO Personality Inventory (Costa & McCrae, 1992b) and the Schedule for Nonadaptive and Adaptive Personality (SNAP; Clark, 1993) utilized by Markon and colleagues (2005).

As Trapnell and Wiggins (1990) note, the difference amounts to a rotational difference between two 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. As noted earlier, evolutionary theory predicts that in species with sex-differentiated patterns of

parental investment, the sex with the lower level of parental investment (typically males) is expected to pursue a more high-risk strategy compared to females, which includes being prone to risk taking and reward seeking, and less sensitive to cues of punishment. Depue and Collins (1999) claim that the traits associated with Behavioral Approach (i.e., dominance, aggression, sensation seeking, 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 indeed heterogeneous at the level of mechanism, but they also have mechanisms in common, notably testosterone (Archer, 2006). As noted earlier, testosterone is implicated in sex differences both in Behavioral Approach (aggression, activity level) and in empathy, a central emotion of the nurturance/pair-bonding adaptive space. These mechanisms are thus much more likely to be the focus of natural selection than are Extraversion and Agreeableness. And, as noted earlier, there is a clear evolutionary logic in supposing mechanisms that promote parental investment are a critically important adaptive space, with clear implications for sex differences favoring females.

Whereas 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 in some studies (McCrae et al., 2002; Srivastava, John, Gosling, & Potter, 2003). These results are compatible with Else-Quest's review of data indicating inconsistent and negligible sex differences in Extraversion and Surgency (Chapter 23, this volume).

This pattern of results occurs 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). A good example of this is the Markon and colleagues (2005) study in which warmth loaded approximately equally on Extraversion and (negatively) on Disagreeable Disinhibition;

similar results were obtained by Evans and Rothbart (2007). From the evolved systems perspective developed here, it is unlikely that combining warmth and affiliation with Dominance, Sensation Seeking, and Exploratory Behavior cuts nature at its joints.

Moreover, at the level of brain functioning, these systems are quite separate: There are unique neurochemical and neuroanatomical substrates for Nurturance/Love and Behavioral Approach, respectively (Archer, 2006; Bartels & Zeki, 2000; Depue & Morrone-Strupinsky, 2005; Panksepp, 1998; Depue & Fu, Chapter 18, this volume). The highly sex-differentiated traits of dominance, aggression, and sensation seeking on the one hand, and nurturance and love on the other, are thus compatible with neurological findings.

A related reason for focusing on these highly sex-differentiated traits is that they exhibit theoretically expected age changes, whereas 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.

An important part of current-day personality psychology is based on ratings of people by themselves and others, so that the most socially salient features of people are emphasized. These may bear only indirectly on the underlying systems. For example, the factor of Neuroticism refers to a tendency toward negative emotionality, but at the systems level, the research discussed earlier reveals separate systems of reactivity/affect intensity (involving a general tendency toward both positive and negative emotionality) and the behavioral withdrawal adaptive space dominated by the emotions of fear and anxiety. Reactivity/Affect Intensity should be understood to be a separable component of temperament systems apart from motivation (MacDonald, 1988; Rothbart & Bates, 2006). At the motivational core of behavioral withdrawal are the emotions of fear and anxiety, whereas reactivity/affect intensity makes an independent contribu-

tion, heightening these emotions in people who score high on Reactivity/Affect Intensity.

This implies that the psychological salience of Neuroticism in everyday evaluations of self and others provides an imperfect guide to the underlying adaptations. Indeed, Vaish, Grossmann, and Woodward (2008) review data showing that, beginning early in life, people have a negativity bias whereby they attend to, learn from, and use negative emotional expressions more than positive emotional expressions in evaluating people. This is evolutionarily adaptive because cues to danger are often of immediate and irreversible relevance to survival, whereas missed opportunities are often reversible. This would result in emotional reactivity tending to be conflated with negative emotionality, so that positive emotional expressions by highly reactive, emotionally intense people are not given equal weight. The result is a temperament trait dominated by negative emotionality (Neuroticism), while positive emotionality is a much less dominant characteristic associated with Extraversion.

Moreover, the fact that the negative emotion of anger is associated with positive emotionality at the neurological level (Dawson, 1994; Fox, 1991; Fox et al., 2001; Harmon-Jones, Peterson, Gable, & Harmon-Jones, 2008; Harmon-Jones & Sigelman, 2001; see below) makes excellent sense within an evolved systems perspective where these emotions are linked to a variety of approach behaviors underlying reward (e.g., sexual gratification), aggression, social dominance, risk taking, and sensation seeking.

Similarly, the emergence of Extraversion in factor analysis may well reflect combinations of socially valued traits: Extraverts combine warmth and gregariousness with assertiveness and excitement seeking (see, e.g., the Markon et al. [2005] five-factor solution, Table 10, p. 151; Else-Quest, Chapter 23, this volume).

Moreover, in the model presented by Markon and colleagues (2005), the reactivity/affect intensity adaptive space is split into Positive Emotionality and Negative Emotionality. Negative Emotionality includes hostility and aggression, both loading on the Disagreeable Disinhibition (reverse of Agreeableness) factor in the five-factor solution.

However, this is unlikely to reflect neurological structure. Fox (1991; Fox et al., 2001; see also Dawson, 1994; Harmon-Jones & Sigelman, 2001; Harmon-Jones et al., 2008) has shown that in terms of brain organization, anger is associated with left cortical activation, along with positive emotions of joy and interest, and therefore is categorized as part of the behavioral approach adaptive space (discussed earlier). On the other hand, right cortical activation is associated with fear, disgust, and distress—key components of the behavioral withdrawal adaptive space (White et al., Chapter 17, and Depue, Chapter 18, this volume).

Furthermore, Evans and Rothbart (2007) found that aggressive and nonaggressive negative affect scales loaded on the same general Negative Affect factor, while Saucier's (2003) Multi-Language Seven Questionnaire separates Neuroticism into aggressive components ("angry" and "irritable" vs. "calm" and "patient") and nonaggressive components ("fearful" and "scared" vs. "tough"). The separation of aggressive and nonaggressive negative affect is consistent with an evolutionary perspective, since anger-type emotions (conceptually and neuropsychologically linked to the behavioral approach adaptive space) are vastly different functionally from fear-type emotions (conceptually and neurologically associated with the behavioral withdrawal adaptive space). However, the results from the Markon and colleagues (2005) study indicate that these traits load on the same factor in higher-order analyses all the way up to the two-factor solution, implying that anger never appears along with the positive emotionality cluster. This conflicts with the data on the neuropsychology of anger cited earlier (Dawson, 1994; Fox, 1991; Fox et al., 2001; Depue, Chapter 17, this volume), indicating that anger is associated with positive emotionality as an aspect of behavioral approach at the level of neuropsychology. It also conflicts with the data reviewed earlier indicating close ties between reward-seeking mechanisms and aggression at not only the level of neurobiology but also in terms of individual differences: People who are prone to aggression are also prone to strong attraction to reward. Again, the results of factor analyses of questionnaire-based data are

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poor guides to carving nature at its joints. These results suggest that people mistakenly tend to group all negative emotionality together. A more appropriate classification is based on individual differences in reactivity/affect intensity: People who score high on affect intensity tend toward intense emotions of all types, including anger, fear, and anxiety, therefore scoring high on measures of Neuroticism. It would be expected that some of these people would also score high on measures of Positive Emotionality, but, as noted earlier, this would be less salient as an aspect of personality because of the negativity bias.

As noted, at the level of neuropsychology, reactivity/affect intensity is a general behavioral energizer, with connections to both behavioral approach mechanisms and behavioral withdrawal mechanisms. This suggests that at the level of phenotypic temperament and personality descriptions, affect regulation will not appear as a separable component but will be intertwined with approach and withdrawal tendencies, respectively (see Figure 14.3). Individuals who score high in reactivity/affect intensity and behavioral approach also score high on measures of Positive Emotionality; individuals who score high in reactivity/affect intensity and behavioral withdrawal also score high on measures of negative emotionality (Neuroticism).

The intertwining of reactivity with approach and withdrawal mechanisms, respectively, is compatible with Larsen and Diener's (1992) findings that activated positive affect is associated with Extraversion, while activated negative affect is associated with Neuroticism. Furthermore, Heller (1990) notes that 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, with the former associated with positive emotions and the latter with negative emotions.

Again, it is important to distinguish the arousal component of temperament systems as separate from motivational components (MacDonald, 1988, 1995; Rothbart & Bates, 2006). For example, motivation for behavioral approach includes mechanisms such as sensitivity to reward, discussed ear-

lier. As a result, people can score high on behavioral approach without being intensely emotional. This perspective is congruent with two-dimensional perspectives on affect that distinguish arousal components from valence components (Posner et al., 2005, 2008; Russell, 2003). Thus, as noted earlier in the discussion of the reactivity/affect intensity adaptive space, whereas the reticular formation is central to arousal, Posner and colleagues (2005, 2008) show that valence is linked to the mesolimbic dopamine reward system activated with pleasurable stimulation and the mesolimbic ventral striatum activated with aversive stimulation.

Indeed, a very large literature shows that many people who are highly aggressive and prone to sensation seeking are emotionally hyporeactive. For example, Adrian Raine and colleagues (e.g., Ortiz & Raine, 2004; Raine, 2002) have provided evidence that reduced adrenergic function as indicated by low resting heart rate, is the best biological correlate of aggression, antisocial behavior, and sensation seeking. As noted earlier, the biological substrate of reactivity/affect intensity is the adrenergic arousal system, indicating that these children score low on reactivity/affect intensity, while nevertheless scoring high on behavioral Approach. Deficits in prefrontal structures associated with Effortful Control/Conscientiousness are also implicated. Low resting heart rate at age 3 predicts aggressive behavior at age 11 and is heritable. Furthermore, sex differences are in the expected direction: Males are more likely than females to have low resting heart rate.

Such results are compatible with proposals that people who score low on autonomic arousal use aggression and sensation seeking to attain an optimal level of arousal (Eysenck, 1997; Quay, 1965; Raine, 1997). These results are also compatible with the idea that people high in Reactivity/Affect Intensity would avoid sensation seeking and aggression because these activities would be emotionally overwhelming (MacDonald, 1995); that is, highly reactive people—people with weak nervous systems (Strelau, 1989)—withdraw in the presence of even moderate levels of stimulation. These findings fit well with the common distinction between aggression accompanied by anger (“hostile or reactive aggression”). For exam-

ple, Frick and Ellis (1999) show that children with reactive aggression are prone to anger and emotional dysregulation, but this is not the case for children diagnosed with proactive aggression. Children labeled as callous/unemotional were found to have the most severe type of conduct disorder. Such children score low on not only empathy, guilt, and concern for others (associated with low levels of Nurturance/Love), but also generally low on emotional expressiveness ("does not show emotion"), including fearfulness and anxiety. Similarly, psychopathic adults show a pattern of "lower anxiety, less fearfulness, and other evidence for deficits in their processing of emotional stimuli" (Frick & Ellis, p. 160). This low-emotional subtype is also prone to sensation seeking and reward seeking, indicating that such people score high on behavioral approach.

Bushman and Anderson (1999; see also Anderson & Bushman, 2002) note that emotionally charged, angry aggression and aggression unaccompanied by anger may have similar motives (e.g., harming another, reclaiming self-esteem). In terms of the present framework, people who combine high levels of behavioral approach with high reactivity/affect intensity are prone to emotionally charged, angry, hostile aggression; they are also prone to reward seeking accompanied by positive emotionality. On the other hand, the combination of high behavioral approach with low reactivity/affect intensity is associated with aggression unaccompanied by anger (instrumental, proactive aggression) and reward seeking unaccompanied by strong positive emotionality.

An Evolutionary Proposal

Ideally, one would be able to trace the evolution of these systems over time and chart their differentiation in different lineages, for example, as approach systems originally designed for foraging and mating become linked with social dominance and intraspecific aggression in social species, and with systems assessing risk (impulsivity, sensation seeking, etc.), self-confidence, and sociability. Figure 14.3 provides an illustration of the proposed evolutionary lineages of the six adaptive spaces discussed here, based partly on MacLean's (1990, 1993) work on the tri-

une brain. MacLean shows that the reptilian brain included mechanisms of behavioral approach, while the distinguishing feature of the paleomammalian brain was adaptations for nurturance; these later evolved into pair-bonding mechanisms in some lineages, including humans (MacDonald, 1992). The neomammalian brain is dominated by the cortex, with top-down processing utilizing prefrontal control mechanisms exerting inhibitory control over the more evolutionarily ancient subcortical areas. In humans these are elaborated in the prefrontal executive control adaptive space. The figure suggests that prefrontal executive control shares some mechanisms with Nurturance/Pair-Bonding. This fits with the Markon and colleagues (2005) findings that Disinhibition (Eysenck's Psychoticism) breaks down into Disagreeable and Unconscientious Disinhibition in the four-factor solution. Watson and Clark (1992) found that guilt was an emotion common to the two systems. Figure 14.3 also illustrates the orienting sensitivity adaptive space branching off from the behavioral approach adaptive space, as discussed earlier.

Figure 14.3 also illustrates the proposed linkages between the six adaptive spaces to personality factors as delineated in the FFM, a six-factor model based on Saucier (2003), in which Neuroticism is broken down into Nonaggressive Negative Emotionality (i.e., Saucier's Self-Assured reversed: e.g., fearful, scared, cowardly) and Aggressive Negative Emotionality (i.e., Saucier's Temperamental: e.g., hot-tempered, short-tempered, impatient; Freeman & Gosling's [2010] trait of irritability would seem to tap this aggressive negative emotionality in primates generally). Figure 14.3 also illustrates the linkages between evolved systems and an evolutionarily informed factor analysis with Dominance/Sensation Seeking, Nurturance/Love and Behavioral Withdrawal as primary factors, as discussed earlier.

Conclusion

The fundamental goal of an evolutionary approach is to cut nature at its joints. The foregoing shows that doing so requires an integration at several levels—the neuropsychological (e.g., how behavioral approach

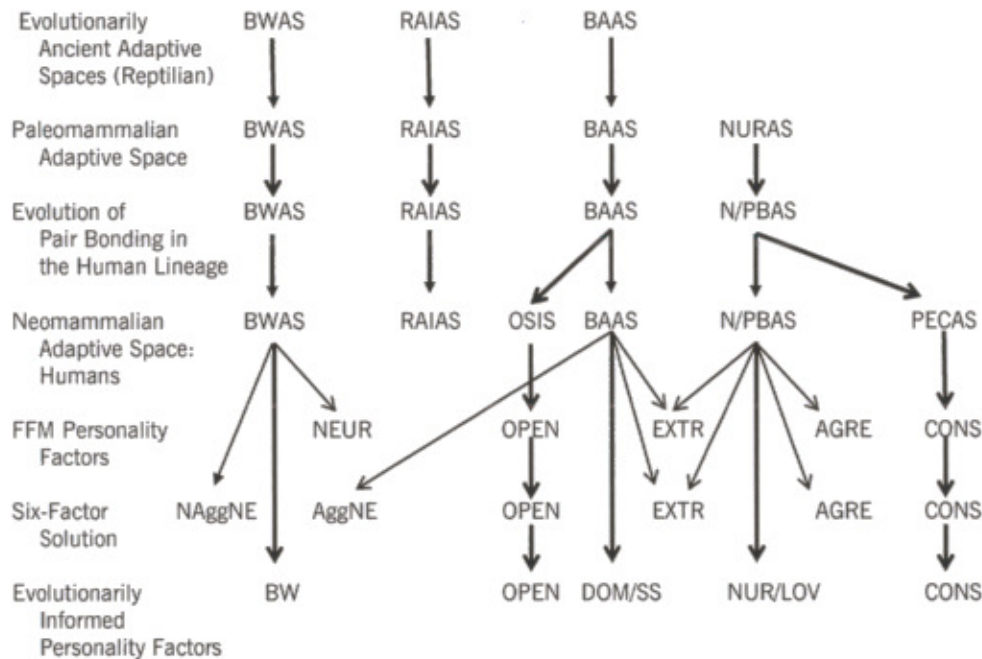


FIGURE 14.3. Illustration of the proposed evolutionary history of the adaptive spaces and their relation to personality factors. The thick arrows indicate evolutionary relationships of homology (identity by common descent). The thin arrows indicate influences of neomammalian adaptive systems on personality. Individual differences in reactivity/affect intensity influence all personality factors; the lines connecting the reactivity/affect intensity adaptive space (RAIAS) and the personality factors are not drawn for reasons of clarity. BWAS, behavioral withdrawal adaptive space; BAAS, behavioral approach adaptive space; NURAS, nurturance adaptive space; N/PBAS, nurturance/pair bonding adaptive space; OSAS, orienting sensitivity adaptive space; PECAS, prefrontal executive control adaptive space; NEUR, Neuroticism; EXTR, Extraversion; OPEN, Openness; AGRE, Agreeableness; CONS, Conscientiousness; AggNE, Aggressive Negative Emotionality; NaggNE, Nonaggressive Negative Emotionality; BW, Behavioral Withdrawal; DOM/SS, Dominance/Sensation Seeking; NUR/LOV, Nurturance/Love.

and emotionality are organized in the brain), the comparative (species differences in adaptations related to temperament and personality), the theoretical (e.g., the evolutionary theory of sex, life history theory), and the results of factor analysis of temperament and personality questionnaires. While much remains to be learned in all these areas, it is clear at this point that an evolutionary perspective provides novel insights into the structure of personality.

Further Reading

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