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Theoretical Contribution

CUTTING NATURE AT ITS JOINTS: TOWARD AN EVOLUTIONARILY INFORMED THEORY OF NATURAL TYPES OF CONDUCT DISORDER

Kevin MacDonald
Department of Psychology, California State University–Long Beach

Abstract
This paper proposes a theory of different types of Conduct Disorder based on individual differences in five sex-differentiated evolved personality systems: The Behavioral Approach System (BAS) underlying sensation seeking and aggressive pursuit of reward and social dominance; the Nurturance/Pair Bonding System, low levels of which are linked to the callous-coldhearted personality trait associated with behavior that victimizes others; the Reactivity/Affect Intensity System underlying individual differences in emotional intensity, most notably, in proneness to anger; the Prefrontal Executive Control underlying the ability to control sub-cortical impulses related to behavioral approach and emotionality; and the Behavioral Inhibition System underlying fear and other reactions to personal threat. The most socially destructive combination of these traits appears in individuals who are callous-coldhearted and high on behavioral approach. When low in prefrontal executive control, such individuals are prone to impulsive, emotionally charged reactive and proactive aggression that victimizes others; when high in prefrontal executive control, such individuals are prone to well-planned, non-impulsive proactive victimization of others. Individuals who are not callous-coldhearted are low to moderate on behavioral approach and emotionality, and are high on prefrontal executive control are the least likely to be diagnosed with Conduct Disorder. Discussion emphasizes conceptualizing interactions between the BAS and the Nurturance/Pair Bonding System.

Keywords: Conduct Disorder, evolutionary psychology, personality

Introduction

Perhaps the most basic task for a science of psychopathology is classification. The bane of research on the causes of psychiatric disorders is that subjects grouped in the same diagnosis are often in fact quite disparate. The proposal here is that an evolutionary perspective is able to shed light on what might be termed natural categories of psychopathology.

The promise and challenge of evolutionary psychology are to chart the set of human psychological adaptations—mechanisms designed by natural selection over the

AUTHOR NOTE: Please direct correspondence to Kevin MacDonald, Department of Psychology, CSU-Long Beach, Long Beach, CA 90840-0901. Email: kevin.macdonald@csulb.edu

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 that humans evolved in and which presented the set of problems whose solutions are the set of human adaptations. 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 relations of mutual inhibition within individuals, resulting in System X System interactions and leading at times to psychological ambivalence (MacDonald, 2005).

Psychopathology as Extremes on Normal Variation in Evolved Systems

More than one model is needed for conceptualizing psychiatric diagnoses. Keller and Miller (2006) argue that certain highly debilitating psychiatric disorders (e.g., autism, schizophrenia, bipolar disorder) occur as the result of polygenic mutation-selection balance. However, they do not apply this model to aggression-related disorders or to psychopathy central to this paper, quite possibly because, as argued here, it is plausible that these disorders were adaptive in ancestral environments.

Adaptedness in the EEA versus Contemporary Environments. In thinking about the adaptiveness of psychiatric classifications, distinction should be made between current environments and the EEA. The present paper focuses on conduct disorder, an externalizing disorder. In the contemporary world, such disorders occur at rates (4-10% for boys; 1-5% for girls) that indicate selective processes maintaining genes influencing these traits to remain in the population (Wilson, 1993). Moreover, impulsivity, strong attraction to reward (including sexual reward), antisocial behavior, and aggression would have had adaptive effects in the environment of evolutionary adaptedness (EEA) (Daly & Wilson, 1997; Gerard & Higley, 2002; MacDonald, 1995). However, being extreme on these traits often limits cultural success in modern environments where drugs of abuse are easily available and physical aggression tends to have limited payoffs and is subject to high levels of social control.

Nevertheless, impulsivity (which is linked to aggression—an aspect of the Behavioral Approach System discussed below) is reasonably considered to have been adaptive, at least in the EEA. Duntley and Buss (2004) note that

> …effective strategies sometimes require immediate action. Ponderous time delays and real-time extended reflection would result in failure. Stated differently, we propose that "impulsivity" is actually a design feature of certain adaptations that promotes their tactical effectiveness. The fact that they appear to external observers to be products of the lack of judicious reflection may speak to the profound inability of human intuitions to grasp the logic of evolved design or to our moral judgments that classify certain strategies as good or bad. Speedy, immediate, real-time responses can be the product of adaptive design rather than "mechanical failure." (p. 118)

Impulsive aggression is likely to result in incarceration in contemporary societies, but negative results may have been much less likely in the EEA, and there is no indication that such individuals would suffer fitness deficits in the contemporary world. Similarly, the diagnostic criteria of ADHD in DSM-IV (American Psychiatric Society, 2000) involve difficulties in adapting to contemporary school environments (e.g., difficulty sustaining attention; easily distracted; excessively active in the classroom; acts as if "driven by a motor"). However, ADHD such traits may not have been at a similar disadvantage in the EEA.

Psychopathy and Frequency-Dependent Selection. Another mechanism that can result in genes for psychiatric disorder remaining in the population is frequency dependent selection. The present paper interprets the trait of callous-coldhearted (psychopathy) as being very low on the Nurturance/Pair Bonding system designed to cement close family relationships and investment in children. Glenn and Raine (2009) propose that psychopathy (involving lack of empathy and guilt) and proneness to instrumental aggression is an alternative life-history strategy for obtaining resources by exploiting others. Mealey (1995) proposed that psychopathy persists at a low base rate (~1%) because it brings high fitness benefits resulting from exploiting others when rare, but becomes less rewarding at higher frequencies because of increased anti-cheater vigilance. It should also be noted that if indeed the Nurturance/Pair Bonding system evolved in order to insure paternal investment under adverse environmental conditions (see below), the generous social safety net of many contemporary societies, in which children of non-investing fathers and mothers are placed in adoptive or foster homes, would facilitate psychopathy as a viable strategy for both sexes.

Psychopathology as Extremes on Personality Systems: Balancing Selection. 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 resulting in balancing selection (MacDonald, 1995; Nettle, 2006; Penke et al., 2007). This is well established in animal research where variation in personality (e.g., exploratory behavior) is associated with greater reproductive success in some environments but imposes costs in others (Carere & Eens, 2005; Dingemanse et al., 2004; Dingemanse & Réale, 2005; van Oers et al., 2005).

Basic to the present paper is the proposal that some types of psychopathology should be conceptualized as extremes on evolved personality systems. (Although not adopting an evolutionary perspective, Costa and McCrae (1994) propose that extremes on personality dimensions are linked to psychopathology.) Consistent with such a conceptualization, some types of psychopathology may be conceptualized as high risk strategies, where genetic load in some individuals is balanced by increased reproductive success in others (Crespi, 2006; Klimkeit & Bradshaw, 2006). Nettle and Clegg (2006) showed that individuals high on two components of schizotypy, including Unusual Experiences (i.e., perceptual aberrations and magical thinking which are positively correlated with creativity), have elevated mating success, thus resulting in retaining genes for these traits in the population. This occurs despite the fact that schizotypy also predicts schizophrenia, a severe mental illness associated with drastically reduced mating success. These genes may be seen as influencing a high-risk strategy in the sense that the negative effects of the genes influencing psychosis and other psychopathology are offset by enhanced mating success.

The behavioral approach systems central to some types of conduct disorder have important adaptive functions for children and adults. 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 system constitutes a 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, as in the case of schizotypy discussed by Nettle and Clegg (2006). Genes predisposing individuals, especially males, to be high on behavioral approach systems can 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, of their relatives.

One can think of these genes as underlying a high-risk evolutionary strategy. 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 successfully aggressive 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 and close relatives of these individuals would be expected to be at the pathological extreme for these traits (MacDonald, 1991). These genes would have an average effect, however, which would indeed make the offspring of these individuals more likely to be creative, enthusiastic, energetic, neophilic, assertive, and even aggressive, as well as strongly 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.

Relevant to the present discussion, Nettle and Clegg (2006) also found that Impulsive Non-conformity (violent and reckless behaviors) is also positively associated with reproductive success. In terms of the following discussion, such people are high on the Behavioral Approach System (BAS; see below) linked to aggression and strong attraction to reward, including having more than average numbers of sex partners. Aggression is a high-risk/high reward behavior. That is, aggression violates the interests of others and therefore invites retaliation—potentially a very high cost to an aggressor. However, successful aggression may have a very large positive payoff.

Successful aggression, even on a small scale, can benefit the aggressor by obtaining resources held by others, inflicting costs on intrasexual rivals, and negotiating status and power hierarchies (Duntley & Buss, 2004, 2005). Similarly, sensation seeking involves risky behavior and is linked psychometrically and at the level of brain mechanisms to aggression. 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 (Farley, 1981, 1985).

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

An evolutionary theory of psychopathology seeks to establish the set of adaptations that underlie the various disorders in order to provide a set of natural classifications. This is not the same as showing that a psychiatric disorder 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). Similarly, given the heterogeneous nature of conduct disorder (CD), a genetic analysis that included several of the proposed sub-types discussed here might well show heritability but would not be informative about the biological systems involved because people diagnosed with CD have very different traits (see below).

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 they 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 conduct disorder: Males are expected to take a more pro-active 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 non-social environment than females. In all of the traditional societies of the world, males who have had relatively high levels of control of social and non-social resources have had higher reproductive success because they have had access to additional mates (polygyny, extramarital 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.

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 behavioral approach adaptive space described above) 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.

Five Adaptive Systems Related to Psychopathology

This section sketches five adaptive systems derived from the temperament and personality literature (see MacDonald, 2012) and proposed as relevant to providing an evolutionary perspective on important psychiatric diagnoses, with an emphasis on

conduct disorder. The following section will present how these systems interact to produce various sub-types of conduct disorder.

The Behavioral Approach System (BAS)

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 systems (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).

Important components of the BAS are dopaminergic reward-seeking mechanisms (Depue & Fu, 2012; Gray, 1987, 2000; Panksepp, 1982**,** 1998; Panksepp & Moskal, 2008; Zuckerman, 1991). Evolution has resulted in affective motivational systems that are triggered by specific feeling states that motivate active interface with the environment (Wilson, 1975) (e.g., the taste of sweet foods, the pleasure of sexual intercourse, feelings of social domination).

The human BAS includes motivational mechanisms for seeking social dominance, sensation seeking, and reward-seeking—all of which show sex differences in accord with the evolutionary theory of sex (MacDonald, 2012). 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 (i.e., seeking rewards without attention to costs), "High Intensity Pleasure," and aggressiveness are components of behavioral approach in young children (Rothbart et al., 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.

Relevant to conduct disorder, there are evolutionarily expected sex differences in aggression (Eagly & Steffan, 1986), high-intensity pleasure, externalizing psychiatric disorders (conduct disorder, oppositional/defiant disorder), risk-taking and aggression (Klein, 1995; LaFreniére et al., 2002), and rough and tumble play (which is often associated with aggression [Collaer & Hines, 1995; Hines, 2011; MacDonald & Parke, 1986; Humphreys & Smith, 1987]). Beginning in infancy, boys engage in more large-motor, physically intense activity (Eaton & Yu, 1989; Else-Quest et al., 2006). Genetic females exposed to testosterone-like hormones prenatally are more aggressive (Matthews et al., 2009; Pasterski 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 (LaFreniére & Charlesworth, 1983; LaFreniére 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).

Importantly for the following discussion, the negative emotion of anger is associated with positive emotionality at the neurological level (Fox, 1991, 2001; Dawson, 1994; Harmon-Jones & Sigelman, 2001; Harmon-Jones et al., 2008). In terms of brain organization, anger is associated with left cortical activation, along with positive emotions of joy and interest, and therefore should be conceptualized as aspects of the BAS. This 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. On the other hand, right cortical activation is associated with fear, disgust, and distress—key components of behavioral withdrawal associated with the Behavioral Inhibition System (BIS).

Age changes in the BAS fit evolutionary expectations. Sensation seeking, including promiscuous sexual activity (which loads on the Disinhibition 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 above, this "young male syndrome" is highly compatible with evolutionary thinking: sex-differentiated systems are expected to be strongest at the time of sexual maturation and maximum divergence of male and female reproductive strategies.

The Nurturance/Pair Bonding System

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 that facilitate the transfer of resources to others, prototypically within the family.

The personality trait of Nurturance/Love is associated with relationships of intimacy and other long-term relationships, especially family relationships involving reciprocity and transfer of resources to others (e.g., investment in children) (Kiesler, 1983; Trapnell & Wiggins, 1990; Wiggins et al., 1988). Individual differences in warmth and affection observable in early 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, non-exploitative interpersonal relationships (Belsky et al., 1991). The physiological basis of pair bonding involves specific brain regions (Bartels & Zeki, 2000; Burkett et al., 2011) and the hormones oxytocin and vasopressin as well as opiates and dopamine (Atzil et al., 2011;

Burkett et al., 2011; Insel et al., 1998; Panksepp, 1998; Turner et al., 1999). This physiological infrastructure underlies the ability to find intimate relationships psychologically rewarding and pleasurable.

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 maters 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. In agreement with this theory, there are robust sex differences (higher in females) on the Nurturance/Love dimension (Trapnell & Wiggins, 1990).

This dimension involves the tendency to provide aid for those needing help, including children and people who are ill (Wiggins & Broughton, 1985. This dimension is strongly associated with measures of femininity, and is associated with warm, empathic personal relationships and dependence (Wiggins & Broughton, 1985). 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.

Relevant to CD, people who are low on Nurturance/Pair Bonding are prone to psychopathy—exploitative interpersonal relationships, lack of warmth, love and empathy, inability to form long term pair bonds and close, confiding relationships, and lack of guilt or remorse for violating others' rights. The finding that males in the general population are three times as likely as females to be categorized with Antisocial Personality Disorder (American Psychiatric Association, 2000; see also Cale & Lilienfeld, 2002) fits with the robust sex differences in this system. Moreover, Salekin et al. (2005) found that all of their measures of antisocial personality were associated with low levels of the Nurturance/Love dimension (termed "Affiliativeness," with low levels labeled "Coldheartedness" in their study) and, to a lesser extent, with the neighboring arrogant-calculating octant. Psychopathy, characterized by lack of empathy and social bonds, is associated with having many sexual partners, an uncommitted approach to mating, increased mating effort and sexual coercion (Lalumiere & Quinsey, 1996), many short sexual relationships, sexual promiscuity (Hare, 2003), and lack of nurturance of children (see Glenn & Raine, 2009). In the following the usage of research on the Interpersonal Circle (see Salekin et al., 2005), the term "callous-cold-hearted" will be used to refer to refer to individuals who are low on the Nurturance/Pair Bonding system.

The Reactivity/Affect Intensity System (RAIS)

A third important system for understanding different natural types of conduct disorder is reactivity (affect intensity). Arousal functions to energize people to meet environmental challenges or opportunities. In the absence of a reactivity system, there would be chronic arousal, which would needlessly consume resources, or there would be chronic underarousal, so that people would not be able to meet environmental challenges and opportunities. The RAIS occurs in all vertebrates. Thus Quinkert et al. (2011, p. 15617) identify generalized arousal mechanisms as "the most powerful and essential activity in any vertebrate nervous system."

Unlike most adaptations which are designed to solve specific problems, the RAIS functions to mobilize behavioral resources by increasing arousal in acutely demanding situations in the service of either approach or withdrawal. It is thus a generalized arousal system (Quinkert et al., 2011) that energizes a variety of systems so that responses are scaled to current environmental opportunities and threats. Rather than evolving a variety of arousal systems specific to each aspect of behavioral approach and withdrawal, all the evidence points to a single system underlying reactivity and affect intensity energizing a variety of systems.

Regarding conduct disorder, the most important emotions are anger, an emotion associated with the BAS, and empathy, an emotion associated with Nurturance/Pair bonding (see above). As discussed below, highly reactive, emotionally intense people are prone to reactive aggression and Oppositional Defiant Disorder. On the other hand, individuals who are callous-coldhearted as well as unreactive and not easily aroused emotionally fail to exhibit empathy and are prone to predatory instrumental aggression.

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 et al. (2011) conceptualize arousal as a generalized, valence-free force that supplies the energy for emotionally charged responses, thereby regulating their intensity (see also 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 (Quinkert et al., 2011; Posner, Russell, and Peterson, 2005; Posner et al., 2008). Freeman and Gosling's (2010) finding of an excitability dimension provides evidence for an individual-differences dimension of reactivity/affect intensity in primates. Garey et al. (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 which 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 1987; MacDonald, 2012). 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 to situations perceived as threatening as well as to potential rewards.

Prefrontal Executive Control (PEC)

A very basic trend in evolution, especially in the Primate line, has been the evolution of a centralized control system able to integrate and coordinate lower-level adaptations. This top-down Prefrontal Executive Control (PEC) system control enables

coordination of specialized adaptations, including all of the mechanisms associated with the BAS, behavioral withdrawal (see below), and the RAIS (MacDonald, 2008). PEC enables explicit construals of context in generating behavior, most notably linguistic and symbolic information. 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 behavioral approach adaptive space discussed above. However, whether or not aggression actually occurs may also be influenced, at least for people with sufficient levels of PEC, 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 PEC (also labeled "effortful control") is a fundamental aspect of temperament related to self-regulation (e.g., Posner & Rothbart, 1985; Rothbart, 2012). In 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 et al., 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 above. Males are expected to be higher on behavioral approach systems (sensation seeking, impulsivity, reward seeking, aggression) and therefore, on average, to be less willing and able to control prepotent approach responses.

Individual differences in PEC are most closely associated with conscientiousness in the Five Factor Model (FFM) (Caspi, 1998; Kochanska & Knaack, 2003; MacDonald, et al., 2007; Rothbart et al., 2000). Conscientiousness involves variation in the ability to defer gratification in the service of attaining long-term goals, persevere in unpleasant tasks, pay close attention to detail, and behave in a responsible, dependable, cooperative manner (Digman & Takemoto-Chock, 1981; Digman & Inouye, 1986). It is also associated with academic success (Digman & Takemoto-Chock; 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).

Conscientiousness refers to "*socially prescribed impulse control* that facilitates task and goal-directed behavior" (John & Srivastava, 1999, p. 121; italics in original) and is thus central to understanding undercontrolled behaviors central to some types of conduct disorder. Specifically, variation in PEC is central to understanding the difference between controlled and uncontrolled aggression (Raine, 1998; see below). Variation in PEC is also central to control of reward-oriented behavior, another central component of the BAS (see MacDonald, 2008 for a review). Individuals with low levels of prefrontal control are prone to impulsivity, substance abuse, and have low levels of emotional control, including relative inability to control anger, a prime motivator of some types of aggression.

The Behavioral Withdrawal System

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, 2000). Recent conceptualizations distinguish between a fear system and an anxiety system, with different neuropsychologies and adaptive functions (Depue & Fu, 2012). 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.

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., Weissman, 1985; American Psychiatric Association, 2000). 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).

The BIS has a central role in conceptualizing phobias and anxiety disorders but is not a factor in developing a theory of natural types of conduct disorder. Nevertheless, because of the possibility of retaliation and penalties at law, aggression is a high risk activity carrying the possibility of threat to personal safety and well-being which naturally trigger the BIS and which would in turn tend to inhibit aggression. That is, there are mutually inhibitory reflexive connections between behavioral approach and behavioral withdrawal (Fox, 1994), implying that high levels of fear and anxiety inhibit aggression. Thus being high on the BIS acts as a protective factor against aggression, so that phobias and chronic anxiety are unlikely to be comorbid with CD. On the other hand, being very low on the BIS would facilitate the BAS, making a diagnosis of CD more likely.

Natural Types of Conduct Disorder

It is well-recognized that children diagnosed with conduct disorder are a diverse group. This section provides a natural typology for CD derived from the evolved systems perspective described above.

A useful starting point is a large meta-analysis of studies on conduct disorder indicating four types (Frick et al., 1993): "Oppositional," characterized by intense emotionality (touchy, irritable, loses temper, angry); "aggression," characterized by overt proactive aggression and victimization (bullies, cruel, assaults, hurts animals); "Property violations"—covert behavior that compromises the rights of others (lies, vandalizes, steals, sets fires); and "status offenses" (truancy, swearing, running away, substance use). In the following, these four types will be integrated into the discussion of natural types of CD.

The Callous-Coldhearted Trait and CD

It is increasingly recognized that low levels on Nurturance-Pair Bonding specify an important subset of CD children. In the CD literature, research has centered on the personality trait of callous-unemotional (C-U) characterized by lack of empathy and

guilt—both associated with Coldheartedness in the Interpersonal Circle (see above) combined with low levels of emotionality.

Importantly for the present analysis in which the RAIS is an independent evolved system with a distinct set of influences on CD (see below), factor analytic research on the callous-unemotional trait has indicated that lack of emotional expressiveness is a separate subfactor from callous and from uncaring, the latter characterized by hurting others' feelings, and lack of empathy, guilt, and remorse for misdeeds (Essau, et al., 2006; Kimonis et al., 2008; Patrick et al., 2007; Roose et al., 2010). Nevertheless, in addition to finding separate subfactors of callous and unemotional, the C-U trait shows enough intercorrelation among the subfactors to form a unitary trait with a high degree of construct validity. From the present perspective, being low on the RAIS would prevent feelings of empathy and thus predispose people to exploitative, predatory aggression.

Consistent with the evolutionary perspective positing discrete systems, Roose et al. (2010) found that both the Callous and the Uncaring subfactors of Callous-Unemotional were correlated with Agreeableness in the Five Factor Model of personality. (Agreeableness in the FFM is the personality factor most closely related to Nurturance-Pair Bonding [MacDonald, 2012]). However, also consistent with the present theory, Roose et al. found no correlation between the Unemotional subfactor and Agreeableness.

Also consistent with an analysis separating callous-coldhearted from emotionality, Waldman et al. (2011) found separate factors of negative prosocial attitudes (lack of empathy and concern for others) and proneness to negative emotions in their analysis of genetic influences on CD (see discussion below).

Callous-coldhearted individuals are prone to exploitative interpersonal relationships and violating the rights of others. For example, Lawling, Frick & Cruise (2010) found that controlling for impulsive/antisocial behavior (e.g., pervasive anger, school problem behavior, arrests), adolescent sex offenders high on the trait of Callous-unemotional had a greater number of sexual offense victims, used more violence with their victims, and were more likely to plan their attacks. In general, individuals high in C-U are more likely to engage in instrumental, planned aggression that results in physical harm to victims. Such children also react less to cues of distress, indicating low empathy (Blair, 1999). This trait specifies a subgroup of antisocial children with a more severe, aggressive, and stable pattern of antisocial behavior (Frick & White, 2008). In the presence of C-U, antisocial behavior is substantially more heritable (h=.75, compared to h=.55), indicating that anti-social behavior with C-U is a valid sub-type (Viding et al., 2008).

The BAS and CD

As noted above, the BAS refers to a suite of traits that promote active interface with the environment, and at the extreme includes sensation seeking, risk-taking, strong attraction to reward (e.g., sexual pleasure) and aggression. This suggests two categories associated with quite different types of CD depending on whether they are also Callous-Coldhearted. In terms of the 4-fold typology of Frick et al. (1993), the Aggression and the Property Violations groups are both Callous-Coldhearted, because they are prone to violating the rights of others. However, they differ on their standing on the BAS: The Aggression type is prone to overt, proactive, physical aggression, while the Property Violations group is prone to covert, non-confrontational forms of victimization.

Children with a combination of high levels of the BAS with callous-unemotional personality are at especially high risk for overt forms of CD that victimize others. Nevertheless, these traits are independent psychometrically and have very different evolutionary history and adaptive function. Most fundamentally, the BAS is linked to externalizing disorders, including an intercorrelated set of traits classified as disinhibited: substance abuse (attraction to reward), aggression, risk-taking, sensation seeking, and neophilia (Castellanos-Ryan & Conrod, 2011). As expected on the basis of the evolutionary theory of sex, these behaviors are substantially more common among boys than girls.

Further, Krueger et al. (2007) discuss a genetically based "externalizing liability" linked to strong attraction to reward as indicated by various types of substance abuse (cocaine, alcohol, marijuana, nicotine), neophilia, aggression, excitement seeking and boredom proneness, impulsivity and an unconstrained, disinhibited personality style. Similarly, Epstein, Griffin and Botvin (2001) found links between excitement seeking, risk-taking, and substance abuse. The model of Kreuger et al. (2007) also includes lack of empathy and physical and destructive aggression that violates the rights of others. This quite possibly results because approximately half of the sample consisted of prisoners likely to combine high levels of behavioral approach with callousness (i.e., low on Nurturance/Pair bonding). From a systems perspective, these are psychometrically and evolutionarily separable traits.

On the other hand, an evolutionary perspective predicts that since there is a robust sex difference in the BAS favoring boys, girls who are callous-coldhearted will be more likely to engage in covert and non-confrontational behaviors that compromise the interests of others. DSM-IV (American Psychiatric Association, 2000, p. 88) notes that girls with CD use "non-confrontational aggression." In their review of the literature on CD in girls, Keenan, Loeber, and Green (1999) note that girls diagnosed as CD are less likely to inflict physical harm on others and are more likely than boys with CD to develop internalizing disorders (depression and anxiety disorders). Relational aggression, which is non-confrontational, is more common among girls and has many of the same correlates as childhood onset CD in boys, except for the lack of physical aggression, including the intention to harm others. Thus Marsee, Silverthorn and Frick (2005) found that the trait of callous-unemotional was linked with both relational and physical aggression and to both violent and non-violent delinquency in both boys and girls, but that relational aggression and non-violent delinquency were much more characteristic of girls. They suggest that in cases without overt physical aggression, relational aggression may serve as an alternative marker of CD risk for girls. Although relational aggression does not inflict physical harm, Crick, Casas and Ku (1999) note that relational aggression is an attempt to hurt others and that it has a significant negative effect on the psychological adjustment of the victims.

The theory proposed here also predicts that there will be a class of individuals who are high on the BAS but, in the absence of the callous-coldhearted trait, these individuals are prone to status offenses resulting from their strong attraction to reward and risk-taking but they are not prone to victimizing others. Research on adolescence has commonly emphasized risk-taking (e.g., Casey et al., 2008; Steinberg, 2007), and status offenses for adolescents often involve risky behavior related to substance use and sexual behavior linked to reward, as well as sensation seeking—all of which are far more robust tendencies in boys, as expected by the evolutionary theory of sex. The category of "socialized conduct disorder" from DSM-III (American Psychiatric Association, 1980)

includes behaviors indicative of risky, reward-oriented behavior combined with friendship to similar others (see Frick & Ellis, 1999, Table III). Such individuals have the ability to form social attachments to others (i.e., they are normal on Nurturance/Pair Bonding), but these relationships are expressed as loyalty to a deviant peer group with whom the child commits antisocial and aggressive acts. This fits with the finding that close relationships may be directed mainly toward ingroups. Indeed, recent research on the neuropsychology of affection and nurturance indicates that oxytocin facilitates close relationships, friendship, and altruistic relations within an ingroup but also facilitates lack of cooperation with outgroups (Declerck et al., 2010).

Reactivity/Affect Intensity and CD

The evolved systems perspective predicts that reactivity/affect intensity will make an independent contribution to CD typology. In terms of the Frick et al. (1993) 4-fold typology, the "Oppositional" quadrant, characterized by being touchy, irritable, and prone to anger and losing one's temper, has a surface plausibility as being high on the RAIS. While intensely emotional people have difficulty controlling all their emotions, inability to control anger is most relevant to CD. Many of the criteria of Oppositional Defiant Disorder involve high levels of reactivity and emotional intensity: "Often loses temper"; "Is often touchy or easily annoyed by others"; "Is often angry and resentful" (American Psychiatric Association, 2000). Other criteria indicate a low frustration tolerance also indicative of high reactivity ("Often actively defies or refuses to comply with adults' requests or rules"; "Often argues with adults").

Emotionality is also implicated in reactive, impulsive aggression. In both psychological research and legal practice, there is a distinction between planned aggression without emotional expression and unplanned, impulsive aggression motivated by anger (reactive aggression). Dodge et al. (1997; see also Crowe and Blair, 2008) distinguish proactive and reactive aggression based on the animal literature on aggression. Proactive aggression is characterized by coercion and the intent to harm others in the absence of any provocation—traits indicative of the callous-unemotional subtype. As discussed above, individuals low on the RAIS are expected to fail to show the emotion of empathy; their aggression is not motivated by anger, but by instrumental gains resulting from victimizing others (see Glenn & Raine, 2009). Reactive aggression, on the other hand, is emotionally driven, "hot-blooded" anger responding to threat or provocation. Such people are not necessarily callous and cold-hearted. Their aggression may be a reaction to events in their lives, such as frustrations and insults. Nevertheless, the present perspective expects to find callous-coldhearted individuals who are high on the BAS and the RAIS. Their aggression is emotionally charged, they are prone to victimizing others, and have low levels of empathy.

Waldman et al. (2011) showed three genetically and phenotypically independent traits related to CD: a negative association with prosociality (low on empathy, concern for others, and helping others—clearly compatible with being high on the trait of callous-coldhearted); negative emotionality (getting upset easily, emotional, reacting intensely—indicative of high emotionality); and daring (daring, adventurous, enjoying risky and dangerous things—indicative of strong behavioral approach tendencies).

These results indicate that differences in emotional reactivity define unique types of conduct disorder. Indeed, there is a very large literature showing that many people who are highly aggressive and prone to sensation seeking (i.e., they are high on the BAS) 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, anti-social behavior, and sensation seeking. As noted above, 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 direction expected by the evolutionary theory of sex: males are more likely to have low resting heart rate than females.

Such results are compatible with proposals that people low on autonomic arousal use aggression and sensation seeking to attain an optimal level of arousal (Eysenck, 1997; Raine, 1997; Quay, 1965). 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 are consistent with proposals for a specific subtype of aggression accompanied by anger ("hostile or reactive aggression"). For example, 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 are not only low on empathy, guilt, and concern for others (associated with low levels of Nurturance/Love), they are 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" (p. 160). This low-emotional subtype is also prone to sensation seeking and reward seeking—indicating that they 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 levels of callous-coldhearted and high reactivity/affect intensity are prone to emotionally charged, angry, hostile aggression that victimizes others; they are also prone to reward seeking accompanied by positive emotionality. On the other hand, the combination of callous-coldhearted and high behavioral approach with low reactivity/affect intensity is associated with aggression that victimizes others unaccompanied by anger (instrumental, proactive aggression) and reward seeking unaccompanied by strong positive emotionality.

This analysis thus distinguishes 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 above. As a result, people can score high on behavioral approach without being intensely emotional. This perspective is congruent with two-dimensional perspectives on affect which distinguish arousal components from valence components (Posner et al., 2005; Posner et al., 2008; Russell, 2003). Thus, as noted

above in the discussion of the RAIS, the reticular formation is central to arousal, while Posner et al. (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.

Prefrontal Executive Control

In general, individuals with high levels of PEC are able to control the BAS and emotionality. They are therefore unlikely to be diagnosed with CD with the important exception of individuals who are high on PEC and who exhibit the trait of callous-coldhearted. As discussed in the following, such people are prone to predatory instrumental aggression that shows a high degree of planning and control.

There are links between impulsive aggression and lowered functioning of the PFC (Oquendo & Mann, 2001; see Raine, 2002, for a review). Raine et al. (1998) found that impulsive murderers had relatively lower left and right prefrontal functioning and higher right hemisphere subcortical function. In contrast, predatory murderers whose crimes involved planning and deliberation had prefrontal functioning that was more equivalent to comparisons, while also having excessively high right subcortical activity. Results "support the hypothesis that emotional, unplanned impulsive murderers are less able to regulate and control aggressive impulses generated from subcortical structures due to deficient prefrontal regulation" (p. 319). However, predatory murderers are better able to control these impulses stemming from subcortical areas because of adequate prefrontal functioning. There are well-established links between predatory aggression and psychopathy (i.e., callous-coldhearted, lack of guilt, remorse, and empathy) (e.g., Glenn & Raine, 2009).

From the present perspective, it is also important to distinguish between the BAS and PEC. For example, Castellanos-Ryan and Conrod (2011) distinguish between lack of cognitive control (impulsivity) and strong behavioral approach tendencies. Finn et al. (2000) found that whereas impulsivity is linked to general deficits in self-regulation based on errors on the go/no-go task (a measure of cognitive control), sensation seeking was linked to attraction to pleasurable activities associated with behavioral approach. From the present perspective, this reflects the distinction between PEC and the BAS as well as the role of the PEC in controlling the BAS reviewed in MacDonald (2008). Individuals high on effortful control are not prone to externalizing disorders even when they have powerful behavioral approach tendencies.

Finally, it should be noted that the BAS and PEC have different developmental trajectories. PEC becomes stronger as children mature, paralleling developmental changes in the prefrontal cortex. In general there is linear development of prefrontal cortex 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 behavioral approach (Casey et al., 2008; see also Steinberg, 2007) (see Figure 1). Adolescents are thus relatively uncontrolled when the development of sub-cortical structures underlying risk-taking (a component of behavioral approach) outpaces the development of prefrontal control structures.

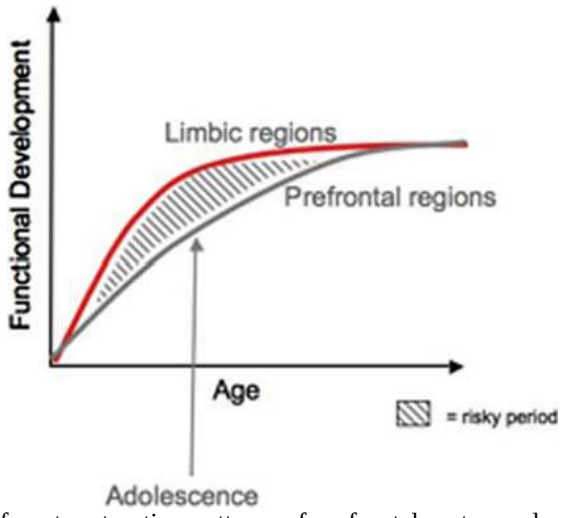

Figure 1. Illustration of different maturation patterns of prefrontal cortex and subcortical limbic regions (e.g., nucleus accumens and amygdala) implicated in adolescent risk-taking. (From Casey, Jones, & Hare, 2008).

These different developmental trajectories of the BAS and PEC may be important for understanding early versus late onset conduct disorder. The upsurge in the BAS associated with adolescence, particularly in boys as the result of the surge of testosterone, may outpace the development of PEC, thereby rendering some adolescents prone to forms of CD in which the BAS is particularly important (e.g., substance abuse and other types of reward seeking [e.g., sex], risky behavior). This is a biological version of the "maturity gap" hypothesis for adolescent-onset CD (see Moffitt, 2008, for a review). Individuals with adolescent-onset and childhood-limited forms of CD are known to fare quite well in later life in terms of education, health, occupation, and family life, although prone to substance abuse and minor law breaking (Moffitt et al., 2008).

Finally, it is well known that there is a strong co-morbidity between CD and ADHD. At the systems level, there is good evidence for separate hot and cold executive function systems, the former associated with emotional control and the latter with cognitive control (see review in MacDonald, 2008; see also Blaskey, Harris, & Nigg, 2008; Castellanos, Sonuga-Barke, Milham, & Tannock, 2006; Zelazo, Qu & Müller, 2005; Zelazo & Cunningham, 2007). This suggests natural typologies of ADHD in which lack of cognitive control, as indicated, for example, by poor performance on the Stop Signal task, is the central deficit seen in ADHD children. However, children with ADHD as well as a diagnosis of CD also have deficits in hot executive function involved in sensation seeking, impulsivity and lack of emotional control, including control of anger.

Discussion

The challenge of an evolutionary approach is to cut nature at its joints. The foregoing provides substantial support for providing a natural typology for CD based on a set of four evolved systems. Figures 2 and 3 provide a schematic overview of CD based on differences in the traits of callous-coldhearted, the BAS, and Reactivity/Affect Intensity. As a general control system exercising inhibitory control over emotions and behavior, lack of Prefrontal Executive Control is involved in behavior that is impulsive or

undercontrolled, such as occurs among people who cannot control anger and fail to attend to the likely consequences of action. However, as noted above, high levels of PEC may occur among people who plan aggressive acts and are entirely in control of their emotions when they carry them out.

Figures 2 and 3 show the proposed relationships of the Callous-Coldhearted personality trait to sub-types of CD based on individual differences in the BAS and emotionality. Not pictured is the role of PEC in controlling and modulating the BAS and Reactivity/Affect Intensity. The left side of Figure 2 illustrates proposed behavior in people who are high on the callous-coldhearted trait and high on the BAS. Such people are prone to victimizing others in aggressive pursuit of reward and social dominance; rape is a paradigmatic violation perpetrated by such people. They are also prone to risk-taking and excitement-seeking, resulting in dangerous, impulsive, overt aggression in pursuit of reward. Additionally, individuals high on the BAS and high on Reactivity/Affect Intensity are prone to angry, emotionally driven victimization, both proactive and reactive.

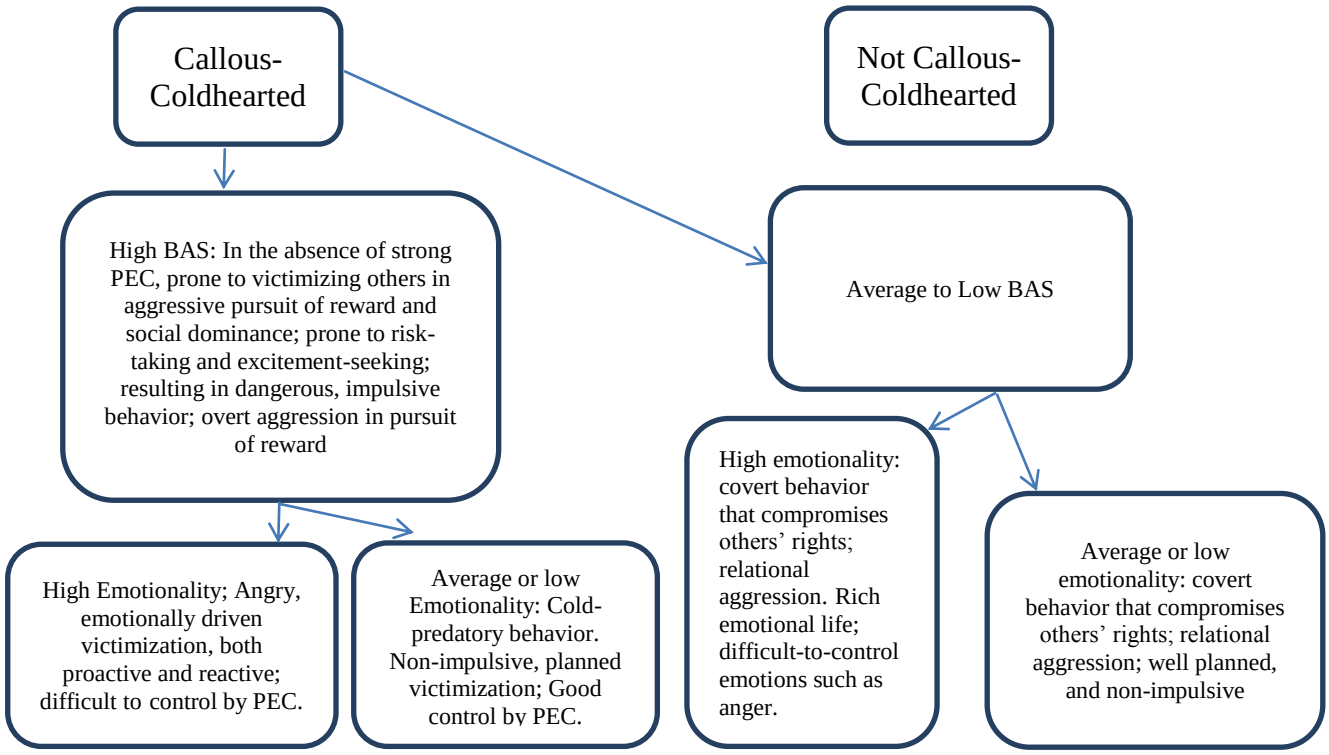

Figure 2. Relationship of the Callous-Coldhearted personality trait to sub-types of CD based on individual differences in the BAS and emotionality.

On the other hand, callous-coldhearted individuals who are low on the BAS (shown on the right side of Figure 2) are prone to covert, non-confrontational behavior that compromises others' rights, paradigmatically relational aggression. These individuals are also expected to vary depending on their degree of Reactivity/Affect Intensity, with callous-coldhearted individuals low on emotionality prone to engaging in well-planned, non-impulsive, non-confrontational behavior that compromises the rights of others (e.g.,

predatory aggression). The moderating role of PEC is not depicted in Figure 1 for the sake of simplicity. As noted above, low PEC is associated with undercontrol and with externalizing problems generally, with the exception of planned predatory aggression carried out by individuals with adequate or even high levels of PEC.

Figure 3 shows types of CD by individuals who are not callous-coldhearted. If high on the BAS (left side of Figure 3), such individuals are prone to status offenses involving aggressive pursuit of reward, social dominance, risk-taking and excitement, but they are not prone to proactive aggression that victimizes others. If high on the BAS and Reactivity/Affect Intensity, such individuals are prone to reactive aggression and ODD. Individuals who are not callous-coldhearted and are low on the BAS (right side of Figure 3) are least likely to be diagnosed with CD.

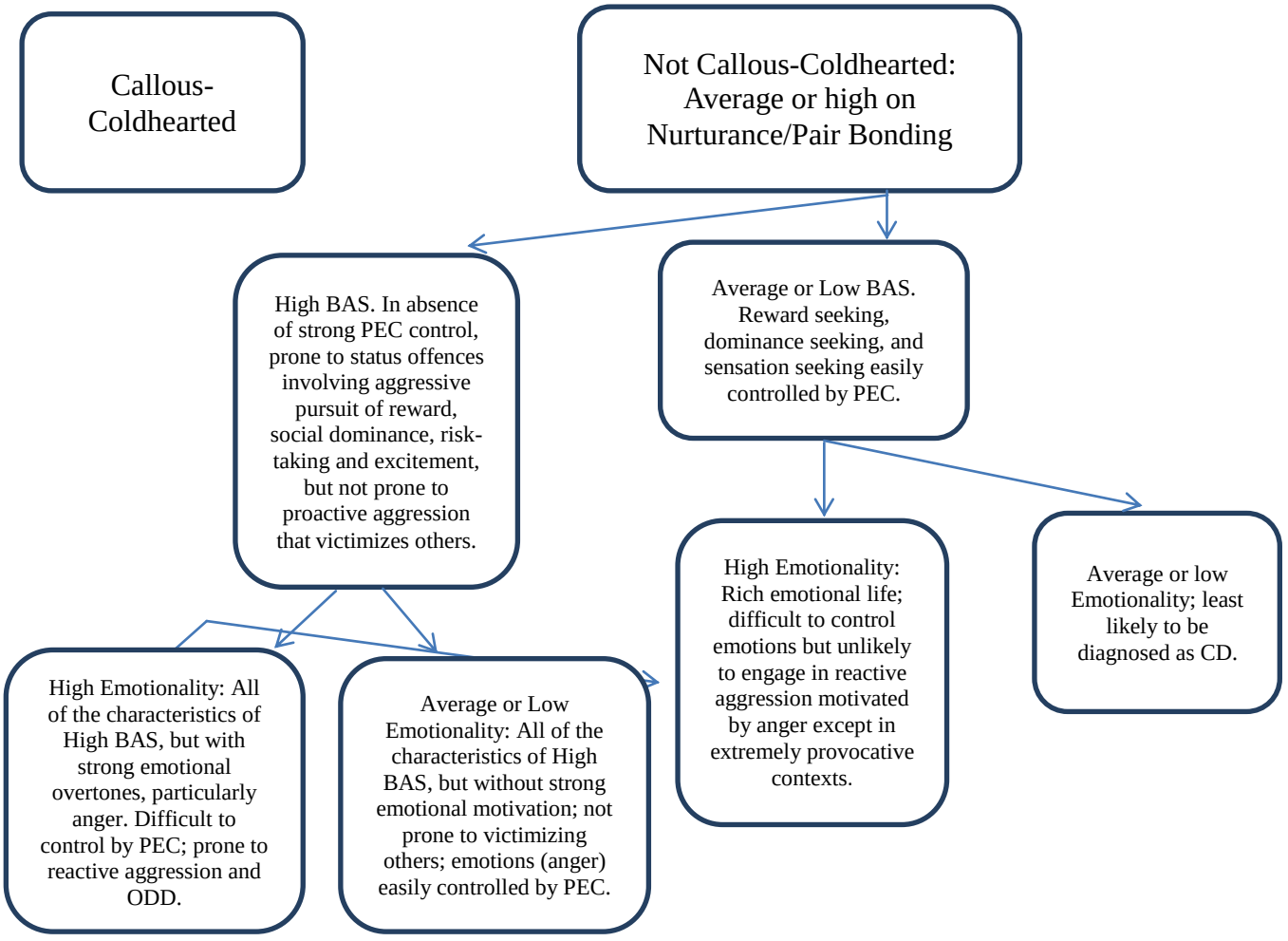

Figure 3: Sub-types of CD in children who are not callous-coldhearted, based on individual differences in the BAS and emotionality.

Implications for Clinical Practice

Clinical practice would benefit from a clear, simplified classifications based on individual differences in the systems discussed here. DSM-IV (American Psychiatric Association, 2000) continues the tradition of behaviorally based diagnosis for CD. This method certainly pinpoints children who are of concern for society, but the resultant diagnosis of CD may result in decidedly heterogeneous samples that would be of limited usefulness in designing interventions. Research conducted on the basis of a simple diagnosis of CD would be plagued by very large error variance because the category is so disparate.

From the present perspective, adding different age categories (Childhood-Onset and Adolescent-Onset) in DSM-IV is an improvement because, as noted above, there are important age changes in the systems reviewed here, particularly PEC and the BAS; moreover, in general, children develop greater emotional control as they get older, at least partly because of maturation of PEC. Children who are prone to aggression, attraction to reward, and lack of impulse control from an early age are indeed likely to present more persistent problems than children who have a temporary age-based mismatch during adolescence between the maturing PEC and its ability to control behavioral approach tendencies and emotionality.

However, because age-based categories are not based on evolved systems, they are not directed at certain critical distinctions. For example, the differences between CD with and without callousness, between CD with and without strong behavioral approach tendencies, and between CD with or without strong emotionality should be central to diagnosis. The result is likely to be highly heterogeneous categories even within age-of-onset classifications.

The recommendation that presents itself is to obtain independent assessments of each of the systems discussed here. Thus a measure of Sensation Seeking (Zuckerman, 1994) would be a good measure of the BAS, while the Inventory of Callous and Unemotional Traits (Roose et al., 2010) would be a good measure of callous-coldhearted and emotionality respectively, the latter trait perhaps supplemented by the Highly Sensitive Person Scale (Aron & Aron, 1997). Prefrontal Executive Control may be assessed by a variety of tests such as the Wisconsin Card Sort Task and the Stroop task (see Burgess, 2010). However, of particular relevance to CD are tests of "hot" executive function—that is, tests of the ability to control emotions and reward-related impulses, such as the Iowa Gambling Task and delay discounting tasks which measure tolerance to delayed reward (see Hosking & Winstanley, 2011).

The present perspective does not offer any panaceas for treatment. The evolved systems discussed here are rooted in specific brain systems that are typically difficult to alter, especially after early childhood. There is substantial evidence for heritabilities in the 0.50 range for all personality systems, indicating the importance of genetic variation, but also leaving room for substantial environmental influences. In the future it is quite possible that there would be effective neurochemical or genetic interventions.

Nevertheless, the evolved systems perspective is compatible with the concept of system-specific environmental influences—that is, environmental influences conceptualized as involving specific types of stimulation that strengthen or weaken particular evolved systems (MacDonald, 1998, 2005). Given that environmental influences are indicated by behavior genetic studies, it is important to ask what types of environments would be important for which specific systems.

An attractive general model incorporates feedback between behavior and specific neurological structures. Particularly well researched is the area of drug addiction, where data indicate that drug usage has feedback effects on specific brain regions linked to the regulation of reward seeking, an integral component of the BAS. Drugs of abuse typically activate dopamine reward systems, causing them to act as primary reinforcers. Drug dependency involves both an increased salience of the rewarding properties of drugs and also impairment in prefrontal executive control of limbic-striatal reward mechanisms, with the result that addicts are dominated by reward-seeking behavior and insensitive to future negative consequences of that behavior (Jentsch & Taylor, 1999). Compromised orbito-frontal cortex (which is the most important neural basis for prefrontal executive control of emotion and reward [see MacDonald, 2008]) emerges as a general aspect of disinhibitory/externalizing disorders of the BAS, including alcohol dependence, substance abuse/dependence and CD (Kendler, Prescott, Myers, & Neale, 2003).

Hosking and Winstanley (2011) propose a general feedback model in which drug use results in neuro-structural alterations in orbito-frontal mechanisms of prefrontal executive control as well as of areas such as the nucleus accumbens underlying reward which are controlled by these orbito-frontal mechanisms. Prefrontal executive control becomes weaker, and reward mechanisms become more powerful, with the result that the prospect of reward becomes more psychologically salient and less likely to be controlled by explicit construals of context, such as being aware of the negative consequences of drug use.

This model is congruent with feedback models of bipolar disorder (BD). (BD is likely a disorder of the BAS. The manic phase involves a hyper-activated BAS; symptoms include excessive involvement in pleasurable activities, grandiosity, intense goal-related activity. The depressive phase involves a hypo-activated BAS; symptoms include anhedonia, feelings of worthlessness, lack of engagement in goal-related activities [DSM-IV, American Psychiatric Association, 2000].) Post and colleagues (Post et al., 2001; Post & Miklowitz, 2010) summarize data indicating that each episode of depression and mania results alterations in brain neurochemistry in proportion to the severity of the episodes.

In the case of the BAS, the therapeutic problem is typically to decrease attraction to reward, prototypically reward associated with drug use and sexuality. In natural families there are likely to be invidious genotype-environment correlations such that parents who are high on the BAS impart genetic tendencies toward a powerful BAS in their children and also fail to monitor or punish these reward-oriented behaviors in their children. Children's successful reward seeking then likely feeds back and strengthens the reward systems as described above.

Such feedback effects may also operate with the other systems discussed here. The trait of callous-coldhearted is central to the most serious forms of CD. Given the status of the Nurturance/Pair Bonding system in promoting close relationships, the primary source of environmental influence that would serve to strengthen this system would typically be affection and love provided by adult caretakers, usually family members, at least in early childhood (MacDonald, 1992, 1997). Such environments stimulate pleasure centers in the brain and are perceived as naturally pleasurable (e.g., MacDonald, 1992), a process quite analogous to drug-induced stimulation of limbic-striatal reward centers (e.g., the nucleus accumbens) discussed above.

This would predict shared environmental influences in behavior genetic studies—a relative rarity in behavior genetic studies. Nevertheless, Agreeableness (the

trait most closely related to Nurturance/Love in the FFM) shows evidence of shared environmental influence as well as additive genetic influences (Bouchard, 1996; Tellegen et al., 1988). Similarly, shared environmental influence has been implicated in security of attachment (Bakermans-Kranenburg et al., 2004; Bokhorst et al., 2003; O'Connor & Croft, 2001; Roisman & Fraley, 2008).

Unfortunately, in natural families of children diagnosed as CD, as in the case of the BAS discussed above, there are likely invidious genotype-environment correlations driven by parents who are genetically inclined to be callous-coldhearted imparting similar genetic tendencies in their children and providing environments that do nothing to strengthen the Nurturance/Pair Bonding system in their children. Thus parents of CD children are more likely to have criminal backgrounds and a history of anti-social behavior (Silverthorn & Frick, 1999). The only viable source for positive environmental influences would be from non-family members, perhaps via adoption or residential treatment emphasizing love and affection, ideally begun at a very early age.

Strengthening the Nurturance/Pair Bonding system would be expected to result in motivation that conflicts with reward-oriented, impulsive behavior associated with the BAS. Individuals who are high on the trait of Nurturance/Love are strongly motivated to help others and feel empathy, traits that compete with externalizing disorders associated with the BAS. Because of the reward value of affection and love to individuals who are at least moderately high on the trait of Nurturance/Love, individuals are motivated to seek and maintain close relationships of intimacy and trust (MacDonald, 1992). Such people are therefore motivated to control reward seeking, impulsive behavior that interferes with ongoing intimate relationships. As noted above, they experience guilt and remorse if they harm others.

Strengthening the Nurturance/Love system by providing affectionate stimulation during childhood, especially early childhood, would thus strengthen a system that motivates people to subordinate the BAS to more socially constructive goals. Consistent with such findings, there is a large body of literature showing that children with genetic markers for externalizing disorders, such as certain variants of the DRD4 dopamine receptor gene, do not show externalizing disorders when reared in affectionate, loving environments. Thus differences in maternal sensitivity (a marker for maternal affection) observed when children were 10 months of age predict externalizing problems reported by mothers more than 2 years later, but only as a function of whether or not children carry the 7-repeat variant of the dopamine receptor D4 (DRD4) allele (Bakermans-Kranenburg & van IJzendoorn, 2006; see also Sheese, Voelker, Rothbart, & Posner, 2007). Children with this variant and without sensitive mothers displayed the most externalizing behavior, but such children with highly sensitive mothers showed the least externalizing behavior.

Although such studies are typically considered examples of Genotype X Environment Interaction (e.g., Ellis et al., 2011), from the present perspective the results may also be interpreted as due to the effects of the Nurturance/Love System moderating the behavioral consequences of genetic tendencies toward a powerful BAS by resulting in a relatively strong competing motivational system focused on developing and maintaining close relationships. The moderating effects of Nurturance/Love are the result of a phenotype resulting from both genetic and environmental sources of individual variation—an example of System X System interaction (see Introduction). On the other hand, children at the low end of Nurturance/Love (i.e., callous-coldhearted) who also

have a powerful BAS remain prone to socially and individually destructive reward seeking and impulsivity.

In conclusion, the evolved systems perspective provides a principled typology of CD based on a small set of adaptations that have been critical for survival and reproduction over evolutionary time. Taking account of the typologies resulting from individual differences on these systems offers the promise of far more precise diagnoses which are important for conducting research and for designing treatments. Further, this approach, combined with feed-forward models of environmental influence in which specific systems are targeted by system-specific environmental influences, hold considerable promise for designing appropriate environmentally-based interventions.

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