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Effortful Control, Explicit Processing, and the Regulation of Human Evolved Predispositions

Kevin B. MacDonald
California State University–Long Beach

This article analyzes the effortful control of automatic processing related to social and emotional behavior, including control over evolved modules designed to solve problems of survival and reproduction that were recurrent over evolutionary time. The inputs to effortful control mechanisms include a wide range of nonrecurrent information—information resulting not from evolutionary regularities but from explicit appraisals of costs and benefits. Effortful control mechanisms are associated with the ventromedial prefrontal cortex and the ventral anterior cingulated cortex. These mechanisms are largely separate from mechanisms of cognitive control (termed executive function) and working memory, and they enable effortful control of behavior in the service of long range goals. Individual differences in effortful control are associated with measures of conscientiousness in the Five Factor Model of personality. Research in the areas of aggression, ethnocentrism, sexuality, reward seeking, and emotion regulation is reviewed indicating effortful control of automatic, implicit processing based on explicit appraisals of the context. Evidence is reviewed indicating that evolutionary pressure for cooperation may be a critical adaptive function accounting for the evolution of explicit processing.

Keywords: Effortful control, explicit processing, evolutionary psychology, conscientiousness, prefrontal cortex

Converging evidence in cognitive psychology and neuroscience supports the existence of two quite different types of cognitive processing: implicit and explicit processing. Implicit and explicit mechanisms may be contrasted on a number of dimensions (e.g., Geary, 2005; Lieberman, 2007; Satpute & Lieberman, 2006; Stanovich, 1999, 2004; see Table 1). Implicit processing is automatic, effortless, relatively fast, and involves parallel processing of large amounts of information. Implicit processing is characteristic of what Stanovich (2004) terms the autonomous set of systems (TASS), which responds automatically to domain-relevant information. In this article, I use the term *module* to refer to mechanisms characterized by implicit processing.

Evolved cognitive modules form an important subset of TASS. A fundamental premise of evolutionary psychology is that evolutionary adaptations equip animals to meet recurrent challenges of the physical, biological, and social environment (Tooby & Cosmides, 1992). When the environment presents long-standing problems and recurrent cues relevant to solving them, the best solution is to evolve modules specialized to handle specific inputs and generate particular solutions (Geary, 2005; Tooby & Cosmides). For example, the visual systems of monkeys and humans contain numerous areas specialized for different aspects of vision (e.g., Zeki, 1993). Areas specialized for color and for motion are sensitive to different aspects of visual stimulation; processing in these different areas occurs in parallel and results in a unitary image. Other modules proposed in the cognitive literature include modules for social exchange (Cosmides, 1989), theory of mind (Baron-Cohen, 1995), fear (Bowlby, 1969; Gray, 1987; LeDoux, 2000), folk physics (Povinelli, 2000), and grammar acquisition (Pinker, 1994).

Although implicit processing is characteristic of evolved modules, it is not restricted to evolved modules. It occurs in a wide range of circumstances, including skills and appraisals that have become automatic with practice or repetition, perceptual interpretations of behavior (e.g., stereotypes), and priming effects (Bargh & Chartrand, 1999). Modules, as defined here, therefore need not be domain specific; they may also result from domain general processes of associative and implicit learning (Stanovich, 2004, p. 39).

On the other hand, explicit processing is conscious, controllable, effortful, relatively slow, and involves serial processing of relatively small amounts of information. Such processing is characteristic of what Stanovich (2004) terms the analytic system characterized by context-free mechanisms of logical thought, planning, and cognitive control. The analytic system is sensitive to linguistic input that allows for explicit representations of the context, including hypothetical representations of the possible consequences of actions. Although language is unlikely to be the medium of thought (Pinker, 1994), explicit processing is “typically experienced as an internal linguistic monologue emerging in a freely chosen way from oneself and [is] associated with the experience of agency or will” (Satpute & Lieberman, 2006, p. 88).

There may be conflicts between TASS and the analytic system (Stanovich, 2004). The central purpose of this article is to develop theory and adduce data relevant to the control exerted by the

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Correspondence concerning this article should be addressed to Kevin B. MacDonald, Department of Psychology, California State University–Long Beach, Long Beach, CA 90840-0901. E-mail: kmacd@csulb.edu

Table 1
Characteristics of Implicit and Explicit Cognitive Systems

Implicit system	Explicit system
Not reflectively conscious	Conscious
Automatic	Controllable
Fast	Relatively slow
Evolved early	Evolved late
Parallel processing	Sequential processing
High capacity	Limited by attentional and working memory resources
Effortless	Effortful
Evolutionary adaptation or acquired by practice	Acquisition by culture and formal tuition

analytic system and explicit processing over TASS and implicit processing in the area of social behavior and emotions.

Implicit processing is evolutionarily ancient, whereas the control processes associated with explicit processing are centered in the prefrontal cortex (PFC), which is a late developing, relatively recent evolutionary innovation. In general the primate brain has moved away from massively parallel processing "with widely converging and diverging connections between individual neurons" to a more serial, hierarchical design (Striedter, 2005, p. 340).

Explicit processing involves executive functions that control and regulate thought and action. The PFC is involved in top-down processing utilized during attempts to match behavior to intentions or internal states. It is especially important when previous connections between inputs, thoughts, and actions are not well established, as in confronting novel problems, rather than either innate or well-established learned connections (Miller & Cohen, 2001). Particularly relevant to this article, executive control permits "goal-directed override of primitive and inflexible reactions to environmental stimuli" (Gazzaley & D'Esposito, 2008, p. 188). Executive control associated with the PFC enables top-down suppression and enhancement of neural activity in a wide range of brain areas, thereby influencing a wide range of functional systems: vision, physiological mechanisms (e.g., respiratory rate), emotion, long-term memory, motivation, cognition, and attention (Gazzaley & D'Esposito).

There are a variety of explicit processing mechanisms that parallel implicit processing mechanisms (Koch, 2004). For example, the bottom-up, saliency based vision-for-action system reflexively attends to evolutionarily prepotent stimuli, such as loud noises, snakes, or sexually attractive individuals. There is also a top-down conscious vision-for-perception system underlying detection of objects and other tasks requiring visual attention. Top-down attention is part of the serial processing system; it depends on effortfully sustaining attention to a focal attribute; it is task dependent and under voluntary control.

Explicit processing is called into play when confronting nonroutine tasks that require flexible responses, retention of information over time, and planning future courses of action (Dehaene & Naccache, 2001; Gray, 2004; Koch, 2004; Miller & Cohen, 2001). Explicit processing implies conscious awareness (Stanovich, 2004), and theories of conscious awareness have converged on the proposition that they are adaptive because they allow consideration of different kinds of information from systems with different functions and phylogenetic origins (Morsella, 2005). A paradigmatic example of an integrative prefrontal mechanism is general intelligence as a set of mechanisms (most notably the executive processes of working memory) useful for solving novel problems under conditions of uncertainty (Chiappe & MacDonald, 2005; Geary, 2005). Because the PFC is widely connected to sensory, cognitive, affective, and motor modalities, it is well suited to integrate information useful for making plans and for the production of skilled, intentionally controlled movements (Gazzaley & D'Esposito, 2008; Striedter, 2005).

As noted above, a goal of this article is to delineate the role of explicit processing in the regulation of implicit processing in the area of socioaffective behavior. The control function of explicit processing over implicit processing has become well established in the area of intelligence research. Unlike the vast majority of animals, humans can control automatic, heuristic processing and make decisions that depend on explicit processing. Controlling heuristic processing requires effortful, controlled problem solving and makes demands on attention and working memory resources. Stanovich (1999) provides evidence that people with higher general intelligence are better able to selectively control heuristic, automatic, socially contextualized processing. An example is evaluating a valid syllogism with a false premise. Consider the following:

> All blue people live in red houses.
>
> John is a blue person.
>
> John lives in a red house.

Drawing the correct inference requires decoupling from experience in which there are no blue people and forming a mental model of a hypothetical situation in which there are blue people, all of whom live in red houses. The mental models involved in explicit problem solving include explicitly represented information involving language or images (Johnson-Laird, 1983).

Effortful Control and Executive Function

Because this article deals centrally with the control of implicit processing characteristic of TASS by explicit processing characteristic of the analytic system, it bears on self-regulation. Research in the area of self-regulation identifies two broad areas of control: cognitive, termed executive function, and socioaffective, termed effortful control (Blair & Razza, 2007; see also Zelazo & Cunningham, 2007). Executive function involves controlling prepotent cognitive responses such as attention shifting and the executive processes of working memory. It is measured by tasks such as set shifting tasks, antisaccade tasks (in which subjects must suppress a reflexive eye-turning response), and Stroop tasks.

Effortful control is the focus of this article. Like executive function, effortful control also involves controlling prepotent responses, but the controlled responses are affectively charged responses. This article discusses effortful control of aggression, ethnocentrism, sexuality, reward seeking, and emotions. Individual differences in effortful control are typically measured via personality and temperament questionnaires or behavioral assessments of subjects' ability to control approach behaviors, avoidance behaviors, and emotional expression (Kochanska, Murray & Harlan, 2000; Rothbart, Ahadi, & Evans, 2000).

Effortful Control: Theory

As noted above, evolutionary psychologists have provided evidence that many mental adaptations evolved as adaptive responses to recurrent environmental regularities over evolutionary time. This leads naturally to the suggestion that evolutionary regularities result in affective states as a cue to action (Wilson, 1975). For example, evolutionary theories of fear propose that recurrent cues to danger (intense stimulation, such as loud noises, evolutionary dangers, such as snakes and heights, and social stimuli, such as strangers or being left alone during infancy) are natural cues producing the affective state of fear (Bowlby, 1969; Gray, 1987). These affective states are emotional reflexes—the result of implicit processing utilizing thalamic pathways directly to the amygdala (LeDoux, 2000). This article considers implicit processing in the areas of human aggression, reward-oriented behavior, ethnocentrism, and emotion regulation.

The proposal here is that a critical component of human evolution is that these affective adaptations came to be subject to effortful control via explicit processing and that the inputs to these explicit processing mechanisms include a wide range of nonrecurrent information—that is, information resulting not from evolutionary regularities (as in the prototypical modular mechanisms described by evolutionary psychologists) but from explicit appraisals of costs and benefits. These explicit appraisals are based on representations of context and they are sensitive to rapidly changing and unique environmental contexts rather than contexts that were recurrent over evolutionary time.

For example, affective states resulting from evolutionary regularities place people in a prepotently aggressive state. As discussed below, Buss's (2005) evolutionary theory of aggression proposes that evolutionary regularities in the context of mating result in affective cues of sexual jealousy and anger at romantic rivals that are prepotent cues for aggression. 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, etc.; see below). 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. An important goal of this article is to describe mechanisms of explicit control over the output of implicit socioaffective processing, especially the output of evolved modules.

As indicated above, general intelligence is associated with the ability to control automatic, heuristic processing, and this ability requires decoupling from experience and forming mental models of hypothetical situations (Geary, 2005). In the effortful control of socioaffective behavior, the mental models may involve explicit representations of the costs and benefits of behavior, and the prototypical conflict is between the phenomenal output of socioaffective implicit processing (e.g., a desire for revenge) and symbolic representations of the world (e.g., imagining life in prison). The latter are open-ended—constantly changing as a result of scientific advances, changes in laws and customs, and changes in beliefs and attitudes.

Consider Morsella's (2005) example of the conflict resulting from walking across hot sand to get water. For many animals, such conflict is resolved simply by the summed strength of the competing implicitly processed action tendencies (thirst versus pain avoidance)—a standard ethological account (e.g., Goetz & Walters, 1997; Lorenz, 1981; Tinbergen, 1951). For mammals, the PFC or its analogues underlie executive control of behavior that takes into account not only subcortically generated affective cues that are routed though the orbitofrontal cortex (OFC), but also sensory input and other information (e.g., learned contingencies) available to working memory (Uylings et al., 2003). For humans, the information available for executive control also includes explicit appraisals of the context: Is the water potable and, if not, could it be made potable using available technology? Will taking the water provoke an attack from those who currently possess it and, if so, could this attack be suppressed? Is the water part of a sacred ritual and therefore off limits for drinking? As this example indicates, conflict occurs not only because of conflicting signals from modules; there may also be conflicts between the output of modules and symbolic representations of the context.

Whereas evolved modules are adaptations to environmental recurrences over evolutionary time, these symbolic representations are not responses to recurrent environmental features over evolutionary time, nor are they typically constrained by natural selection. For example, the symbolic representations related to whether or not to walk over the hot sand to obtain the water (e.g., imbuing the water with religious or legal significance) are not adaptations resulting from environmental regularities over evolutionary time—the formal requirement for adaptations adopted by some evolutionary psychologists (e.g., Tooby & Cosmides, 1992). Unlike the affective consequences of thirst and fear of pain resulting from walking on hot sand (which presumably result from past evolutionary regularities), these symbolic representations have not been exposed to the forces of natural selection because variation in them does not have a strong genetic basis, and there is no recurrence over sufficient time for natural selection to operate. Effortful control of socioaffective behavior based on explicit representations of context therefore cannot be considered an adaptation resulting from natural selection responding to environmental regularities over time.

Similarly, general intelligence is not an adaptation resulting from natural selection responding to environmental regularities over time. As noted above, general intelligence involves the ability to override automatic, heuristic cognitive processing that evolved as responses to environmental regularities over evolutionary time (Stanovich, 1999). General intelligence results in creative, evolutionarily novel ways to achieve evolutionary goals, ranging from improved foraging techniques in the environment of evolutionary adaptedness to modern technological innovations (Chiappe & MacDonald, 2005).

This of course is compatible with supposing that, despite the fact that it was not shaped by past environmental recurrences, effortful control is the result of natural selection: The ability to behave on the basis of symbolic representations of context rather than recurrent environmental regularities resulted in fitness advantages in the environment of evolutionary adaptedness (see Discussion).

The subject of this article is effortful control of socioaffective implicit processing. The proposal is that with sufficiently strong mechanisms of effortful control, evolutionary prepotencies resulting from past environmental recurrences (e.g., sexual desire, homicidal ideation, and ethnocentric tendencies) may be effortfully controlled depending on one's assessment of a host of open-ended, symbolically represented costs and benefits that have not been subject to the forces of natural selection. These prepotencies are thus analogous to the water–hot sand example: Affective input from evolved mechanisms related to thirst and fear is only part of the input to effortful control mechanisms; also relevant are open ended, symbolic representations of context, particularly the perceived costs and benefits of behavior.

These explicit assessments need not be true. For example, in the water/hot sand example, explicitly held religious beliefs may be a reason for performing a certain behavior without the belief being true. More importantly, explicitly held motivations may also involve rationalization or self-deception and thus not be an accurate portrayal of a person's motives. For example, research indicates that motives for aggression or drug use may involve rationalization and self-deception (see, e.g., Beck, Wright, Newman, & Liese, 1993; James et al., 2005). Similarly, although it has not been researched, it is reasonable to suppose that people may not always be aware of their actual motives in the effortful control of socioaffective behavior discussed in this article. As a result, there is no requirement that people are always aware of their actual motives when engaging in effortful control. What is important for this article is that, at least some of the time, people do in fact attempt to control automatic processing related to social and emotional behavior and that explicit assessments of the costs and benefits of behavior are commonly involved.

Moreover, given that, as noted above, implicit processing may involve appraisals and skills that have become automatic with repetition or practice (Bargh & Chartrand, 1999), some instances of control over evolved modules may involve implicit processes that originated as explicit construals of context but became automatic with repetition or practice. This is suggested by the finding that verbal labeling of photos of African Americans by both African American and White subjects resulted in lowered amygdala response even though there was no intention to regulate their response and no instructions to do so (Lieberman et al. 2005).

Nevertheless, the prediction is that in regulating their impulses originating from evolved socioaffective modules, people do indeed take account of information that could only have been available as a result of explicit construals of context. This article therefore presents evidence that indeed there are socioaffective impulses stemming from the regularities of our evolutionary past; it also presents evidence that the effortful control mechanisms able to regulate these impulses function by taking account of information that is not the result of past evolutionary regularities but of explicit representations of open-ended, symbolically represented costs and benefits. In the areas of aggression, reward-related behavior, ethnocentrism, and emotional expression covered by this article, the prediction is that people behave differently depending on their awareness of the costs or benefits of the situation that could only have been available through explicit processing. Evidence in conformity with this prediction is presented below.

The general argument is as follows:

1. In animals and humans there are distinct prefrontal areas associated with working memory, with executive function, and with the effortful control of socioaffective behavior, respectively.

2. Implicit processing related to social behavior mainly involves a set of evolutionarily ancient mechanisms that result in affective signals and action prepotencies rather than overt behavior.

3. Explicit processing exerts a control function over implicit processing related to social behavior, including aggression, reward-related behavior, ethnocentrism, and emotional expression.

4. Explicit processing expands the universe of potential costs and benefits for behavior beyond evolutionarily recurrent implicit contexts (e.g., adulterous spouses, evolutionary dangers—snakes, loud noises—nonreciprocators) to include explicit representations of the context and explicit calculation of costs and benefits.

5. The Discussion section considers theory and data indicating that the evolutionary pressure for indirect reciprocity may be a critical adaptive function accounting for the evolution of explicit processing and prefrontal control of socioaffective behavior. The Discussion also touches on the issue of culture as aimed at explicit processing and its ability to control prepotent automatic responses.

The Neuropsychology of Control

Nonhuman Data

Among mammals generally, the PFC is linked to executive control—selecting and generating behavioral patterns and utilizing access to working memory and long-term memory. Uylings, Groenewegen, and Kolb (2003) reviewed data for rats indicating subdivisions of the PFC into a medial prefrontal area linked to working memory (e.g., delayed response tasks), executive function tasks (e.g., reversals, attention shifting), and the selection and ordering of behavioral sequences (including sequences of species-typical behavior, such as nest building). There is also an orbitofrontal area linked to socioaffective behavior and associations between behavior and reward. Rats with OFC lesions choose a small reward with a short delay over a large reward with a long delay (Rudebeck, Walton. Smyth, Bannerman, & Rushworth, 2006), and they fail to adjust their behavior to lowered reward values (Pickens et al., 2003). Both these results are compatible with human studies showing that compromised OFC is linked to impulsivity and inability to delay gratification (see below).

Moreover, given the proposed role of the OFC in regulating human evolved predispositions that is the central topic here, it is interesting that the rat OFC is involved in inhibiting species-typical behavior. OFC lesions result in the failure to inhibit the prepotent, presumably species-typical response of attempting to climb up the walls in a swimming pool (Kolb, 1984, 1990). (Normal rats will abandon the wall-climbing strategy if it is ineffective.)

Rolls (2000) notes evidence for separation of function among three different prefrontal areas in monkeys: areas associated with executive function tasks (inferior convexity, e.g., go/no-go and object reversal tasks), a working memory system for short-term spatial memories (dorsolateral PFC), and emotional control related to aggression, fear, and primary reinforcers (caudal OFC). Damage to the OFC causes a loss of inhibitory control in emotional processing (Dias, Robbins, & Roberts, 1996). Lesioned animals suffer impairment in the ability to alter their behavior in response to fluctuations in the emotional significance of stimuli.

In rhesus monkeys, the OFC is also involved in actions in response to specific reward contingencies and in inhibiting simple prepotent responses, such as reaching for a reward directly through a Plexiglas container (Roberts & Wallis, 2000; Wallis, Dias, Robbins, & Roberts, 2001). Orbital neurons are sensitive to the expected or preferred reward value of stimulation and are involved in altering behavior in response to changed reinforcement contingencies (Rolls, 1996, 2000; Rushworth, 2008). In animals and humans, the OFC is involved in reversal learning (Overman, Bachevalier, Schuhmann, & Ryan, 1996; Rolls, 2000), a process that requires flexible updating of reinforcement contingencies and the suppression of previously rewarded responses.

These findings indicate specialization of function among PFC areas specialized for working memory, executive function, and the control of evolutionarily prepotent species typical behavior and affectively tinged responding. The following section reviews similar data for humans.

Human Data

Reflecting the generally high degree of functional specialization within the cortex, there are distinct prefrontal areas for working memory, for executive function, and for the effortful control of socioaffective behavior. Regarding working memory, the dorsolateral PFC has been associated with working memory functions, including storage of representations (Goldman-Rakic, 1987) and selection of motor responses based on attention to representations stored elsewhere (Curtis & D'Esposito, 2003).

Regarding executive function, Aron, Robbins, and Poldrack (2004) reviewed a large number of studies indicating that the right inferior frontal gyrus (IFG), the dorsolateral PFC, and the dorsal anterior cingulated cortex (ACC) are involved in executive function tasks of the sort measured on the Wisconsin Card Sort Task, set switching, and suppressing target words when given a cue word. Aron et al. proposed that the involvement of the dorsolateral PFC is likely due to the task requiring vigilance and keeping the instructions in mind (i.e., working memory capacity; see also Casey et al., 1997; Durston et al., 2002), whereas involvement of the dorsal ACC likely results from conflict when the stimulus does not match goals (see also Bush, Luu, & Posner, 2000), and right IFG suppresses the irrelevant response—similar results were reported for a homologue of the right inferior PFC in monkeys (Nakahara et al., 2002). The dorsal ACC maintains strong reciprocal connections with lateral PFC but not to regions associated with emotion and the control of emotion (e.g., amygdala and OFC).

Nevertheless, Curtis & D'Esposito (in press) note that the right IFG may not be involved in all tasks of inhibitory control and that different executive function tasks involve somewhat different mechanisms. Further research is needed to show that the IFG is specialized for general inhibitory control; indeed, Curtis and D'Esposito interpreted presently available data to be compatible with a model in which subjects choose among available alternatives of various strengths rather than a mechanism specialized for inhibiting actions per se.

The main topic here is the effortful control of socioaffective behavior. In general, the prefrontal lobes exert tonic inhibitory control over subcortical emotion centers (Stuss & Benson, 1986). Research on the neuropsychology of traits related to control of socioaffective behavior has increasingly centered on the ventromedial PFC, particularly the OFC, and the ventral ACC.

Structurally, the ventromedial PFC is specialized for emotional processing with strong connections to the amygdala and ventral ACC (Banfield, Wyland, Macrae, & Heatherton, 2004; Bush et al., 2000; Drevets & Raichle, 1998; Humphreys & Samson, 2004). The ventral ACC is implicated in emotional Stroop tasks and in studies of symptom induction in psychiatric patients—for example, anxiety, depression, obsessive-compulsive disorder (Bush et al., 2000). Drevets and Raichle (1998) show that there is reciprocal suppression of regional cerebral blood flow during emotional and higher cognitive processes. That is, experiences that stimulate emotional processes increase blood flow in the amygdala, posteromedial OFC, and the ventral ACC, while decreasing blood flow to the dorsolateral PFC and the dorsal ACC. The ventral ACC is stimulated during both positive and negative emotional experiences. Performing cognitively demanding tasks without emotional overtones, such as those involved in working memory, antisaccades, and visuo-spatial tasks, has the opposite effects: increased blood flow to the dorsolateral PFC and dorsal ACC but decreased blood flow to the posteromedial orbital cortex, the ventral ACC, and the amygdala.

Research on humans with orbitofrontal lesions indicates that there is a general lack of control of social behavior. The classic example is Phineas Gage, who became impulsive, socially inappropriate, indifferent to social conventions, and lacking in conscientiousness after an iron spike destroyed his orbitomedial PFC as the result of an accident (Davidson, Jackson & Kalin, 2000; Dolan, 1999; Öngür & Price, 2000).

Patients with damage to the ventromedial PFC have normal sensitivity to reward and to punishment, but their behavior is controlled by immediate rewards or punishments rather than long-term prospects (Bechara, Damasio, Tranel, & Anderson, 1998; Bechara, Tranel, & Damasio 2000; Rolls, 1999, 2000; Rolls, Hornak, Wade, & McGrath, 1994). There is also some indication that at least a subset of patients with ventromedial PFC lesions are prone to risk taking, as indicated by choosing gambling outcomes with greater variance (Sanfey, Hastie, Colvin, & Grafman, 2003). Anderson et al.'s (1999) patients with ventromedial PFC damage originating in infancy exhibited a general lack of conscientiousness (lack of dependability, inability to plan for the future, proneness to immediate rewards rather than pursuit of long-term goals); impulsive aggression rather than instrumental, goal-directed aggression; and lack of guilt for transgressions against others. The two patients studied had an immature moral sense thought to be due to failure to learn moral contingencies during childhood.

Executive function and effortful control. The animal and human research reviewed thus far indicates anatomically separate brain areas associated with executive function and effortful control, respectively. These findings fit with proposals for separate "cool" and "hot" forms of executive control, the former involving control of cognitive processes under affectively neutral conditions and the latter involving control of socioaffective processes (Hongwanishkul, Happaney, Lee, & Zelazo, 2005; Kerr & Zelazo, 2004; Miller & Cohen, 2001; Zelazo & Cunningham, 2007; Zelazo, Qu,

& Müller, 2005; but see Unsworth, Heitz, & Engle, 2005). In addition to anatomical differences associated with cool and hot mechanisms of executive control, several lines of evidence support a separate system for control in emotionally charged contexts. Rolls et al. (1994) show that the ventral OFC is implicated in reversal learning involving rewards and punishments but not unmotivated category switching of the type measured by the Wisconsin Card Sorting Task or paired associate learning. Impairment on this motivated reversal learning task correlated with the sorts of undercontrolled social behavior discussed below (e.g., impulsive purchases of luxury items made without concern for the future).

At the level of individual differences, Kindlon, Mezzacappa, and Earls (1995) found that a stop task (in which subjects have to respond to a signal to withhold a prepotent learned response) and a Stroop task loaded on one factor, while tasks with reward motivation loaded on a second factor; children with externalizing disorders performed worse on both factors (Mezzacappa, Kindlon, & Earls, 1999). Further, Horn, Dolan, Elliott, Deakin, & Woodruff (2003) found that measures of trait impulsivity did not correlate with performance on a go/no-go task without reward motivation. These findings fit well with Hinshaw's (2003) proposal that although all ADHD children have deficits in executive function resulting in cognitive impulsivity, only the subset who are aggressive had problems with emotion regulation. This suggests that ADHD involves failures of executive function, whereas poor control of socioaffective responses is linked to the undercontrolled socioaffective behaviors that are central to this article.

Nevertheless, Blair and Razza (2007) found weak positive correlations between measures of executive function (e.g., set shifting) and measures of effortful control (factor score for teacher and parent reports on the Child Behavior Questionnaire Anger, Approach, Attention, and Inhibitory Control scales). However, each makes a unique contribution to academic performance even when controlling for general intelligence (Blair & Razza). Indeed, Ladd, Birch, and Buhs (1999) have shown that socio-emotional competence makes an independent contribution to academic performance, and effortful control has been shown to be related to academic achievement (Blair & Razza; Martin, Drew, Gaddis, & Moseley, 1988; Rothbart & Jones, 1998). These linkages indicate that these systems show considerable but not complete independence. As Zelazo and Cunningham (2007) note, some tasks require only emotional control; but, in many tasks, emotional control is in the service of other goals, so that both cold and hot executive control mechanisms are involved.

Working memory capacity and effortful control. As noted above, working memory and the dorsolateral PFC are activated during the performance of executive function tasks (Aron et al., 2004). Working memory and the dorsolateral PFC are also activated during effortful control tasks. For example, adequate decision making involving rewards and punishments involves both dorsolateral PFC areas linked to working memory as well as ventromedial PFC associated with effortful control (Davidson, 2002). Bechara et al. (1998) found that measures of working memory capacity (delayed response tasks) were affected by lesions in the dorsolateral PFC and these lesions affected decision making. Intact working memory is thus a necessary condition for normal decision making that takes into account long-term consequences rather than attending only to immediate rewards or punishments in a gambling game. However, intact working memory is not a sufficient condition: Subjects with intact working memory but impaired ventromedial PFC performed poorly on these decision-making tasks because of their lack of attention to long-term consequences.

Socioaffective output from the ventromedial PFC constitutes a load on working memory capacity and disrupts performance on executive function tasks. Performance on Stroop tasks is compromised if subjects are attempting to control socioaffective responding, for example, prejudicial attitudes (Unsworth et al., 2005). Moreover, effortful control itself is a resource-limited process that is depleted after a situation requiring effortful control, resulting in relative lack of self-control on later tasks (Richeson & Shelton, 2003; Richeson, Trawalter, & Shelton, 2005; Schmeichel & Baumeister, 2004). Based on findings that connections between the amygdala and the dorsolateral PFC are sparse, Hikosaka and Watanabe (2000) suggested that expectancies for reward originate in the OFC and are then transmitted to the dorsolateral PFC, where the integration of emotional and cognitive processing occurs (see also Davidson, 2002). These data show that the output of socioaffective processing enters consciousness and constitutes a load on working memory.

Indeed, socioaffective processing, working memory capacity, and executive function interact such that a load on any one of them disrupts processing in the others (Schmeichel, 2007). We have seen that the output of socioaffective processing constitutes a load on working memory. However, increased working memory load also results in less ability to suppress inappropriate responses on executive function tasks, including negative priming tasks and antisaccade tasks (Engle, Conway, Tuholski, & Shisler, 1995; Roberts, Hager, & Heron, 1994). And Schmeichel found that subjects who had recently completed executive function tasks were less able to control their emotional responses to a video of animals being slaughtered; moreover, subjects who had recently completed an emotional control task (intentionally exaggerating a negative emotional response) performed more poorly on working memory tasks (e.g., recalling test words paired with a series of math questions). Schmeichel interpreted the results as support for the hypothesis that executive processes are powered by a common, limited resource and reviewed data indicating that the common resource is brain glucose reserves.

Consistent with data reviewed above, these data indicate separate cognitive (cool) and social (hot) executive control mechanisms, both of which result in a load on working memory. This is illustrated in Figure 1 which is an elaboration of Unsworth et al.'s Figure 2.3. Cognitive load resulting from affective processing is influenced by effortful control, which is in turn influenced by individual differences in effortful control as well as individual differences in subcortical socioaffective modules. For example, highly prejudiced individuals (relatively prone to negative affect when responding to racial outgroups) have a large load on working memory capacity. If they also have strong effortful control, they are able to inhibit these feelings, but this also constitutes a drain on working memory resources. This proposal is compatible with the study by Richeson et al. (2003) showing that areas linked to executive processes of working memory (dorsolateral PFC and anterior ACC) are activated during interracial encounters and that performance on the Stroop declines after interracial encounters.

Given the interactions among working memory, executive function, and effortful control, it is not surprising that individual

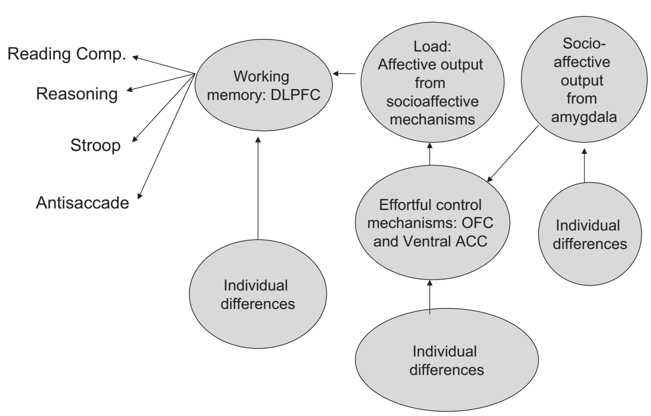

Figure 1. Proposed schematic representation of relationships among socioaffective output from the amygdala, effortful control mechanisms in the orbitofrontal cortex (OFC), and working memory in the dorsolateral prefrontal cortex (DLPFC); Reading Comp. = reading comprehension; ACC = Anterior Cingulated Cortex.

differences in these processes are modestly correlated. Unsworth et al. (2005) showed that individual differences in working memory capacity are positively correlated with measures of executive function (e.g., Stroop, antisaccade).

Effortful Control: Development, Sex Differences, and Links to Conscientiousness

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.; Lamb, Chuang, Wessels, Broberg, & Hwang, 2002; Olson, Sameroff, Kerr, Lopex, & Wellman, 2005). Developmentally, the increasing efficiency of effortful control parallels developmental changes in the 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 behavioral approach (Casey, Jones, & Hare, 2008).

Beginning at about 10 to 12 months of age, there are individual differences in focused attention and in the ability to inhibit inappropriate approach tendencies (Rothbart et al., 2000). Effortful control predicts ability to modulate anger (less angry reaction to tight seat belt restraint) and ability to modulate joy (less joyful reaction to a puppet show) (Kochanska et al., 2000).

The superior performance of girls on effortful control fits well with the evolutionary theory of sex (MacDonald, 1995, 2005). Evolutionary theory predicts that in species with sex-differentiated patterns of parental investment, the sex with the lower level of parental investment (typically the males) would pursue a more high-risk strategy compared to females, including being prone to risk taking and reward seeking and exhibiting less sensitivity to cues of punishment. This follows because the high-investment sex (typically the females) is expected to be able to mate relatively easily but is limited in the number of offspring (Trivers, 1972). However, mating is expected to be problematic for the low-investment sex, with the result that males typically compete with other males for access to females. Males are thus expected to be higher on behavioral approach systems (sensation seeking, impulsivity, reward seeking, aggression) and therefore on average be less prone to control prepotent approach responses.

Several authors have proposed that the personality system most closely associated with effortful control is conscientiousness (Caspi, 1998; Kochanska & Knaack, 2003; Rothbart et al., 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 effortful control of prepotent socioaffective responses. Conscientiousness emerges as a dimension in the Five Factor model of personality (Costa & McCrae, 1992; Digman, 1990, 1996; Goldberg, 1981; John, Caspi, Robins, & Moffitt, 1994) and refers to "*socially prescribed impulse control* that facilitates task and goal-directed behavior" (John & Srivastava, 1999, p. 121; italics in original). 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). Conscientiousness is associated with academic success (Digman & Takemoto-Chock; Dollinger & Orf, 1991; John et al., 1994), an area where 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. Similar correlations occurred for occupational status assessed when subjects were in their mid-20s.

At the conceptual level, these associations suggest that conscientious people are able to control short-term pleasure seeking and other types of impulsive, affectively tinged responding stemming from subcortical psychological adaptations. Conscientiousness does indeed predict actual performance tendencies related to impulse control. Persons low in conscientiousness tend to have worse job performance and proficiency (Barrick & Mount, 1991), less restraint from dishonest activities (Murphy & Lee, 1994), poorer health habits, and increased mortality (Friedman, 2000).

Psychopathology is associated with being extreme on personality systems (MacDonald, 1995; 2005; Widiger & Trull, 1992). The low end of conscientiousness is associated with a variety of sex-differentiated externalizing behaviors (Eisenberg et al., 2004), conduct disorder (Krueger, Caspi, Moffitt, White, & Stouthamer-Loeber, 1996), aggression (Krueger et al. Pulkkinen, 1986), adolescent drug use (Block, Block, & Keyes, 1988), delinquency (Krueger et al.; Robins, John, & Caspi 1994; White et al., 1994), and antisocial personality disorder—for example, irresponsible and delinquent acts, failure to honor obligations or plan ahead (Widiger, Trull, Clarkin, Sanderson, & Costa, 2002; Widiger & Trull), all of which are more common among males.

The greater involvement of males in such behavior is expected to be particularly acute in adolescence and young adulthood when evolutionarily prepotent behavioral approach tendencies related to aggression and sexuality mature and play a prominent role in sexual competition among males. Several theorists have proposed that adolescent antisocial behavior, reward seeking, and risk taking are at least partly caused by the relative underdevelopment of prefrontal mechanisms compared to behavioral approach mechanisms at this age (Casey et al., 2008; Raine, 2002).

Explicit Processing and Effortful Control of Implicit Socioaffective Processing

This section briefly reviews a variety of studies supporting the existence of modular systems related to behavioral approach systems (aggression, sexuality, reward seeking), ethnocentrism, and emotion regulation. Within each section, data are reviewed showing prefrontal effortful control of these evolved modular systems, explicit appraisals of potential costs and benefits, and links to variation in conscientiousness.

Effortful Control Over Behavioral Approach Systems: Aggression

Evolved mechanisms of aggression. Several theorists have called attention to evolutionary prepotencies for aggression. Berkowitz (1989, 1990, 1993; see also Anderson, Anderson, & Dueser, 1996) has provided extensive data indicating that negative affect resulting from various unpleasant experiences automatically stimulates fight or flight tendencies, including emotions (e. g., anger), motor reactions, and physiological responses. These unpleasant experiences may include provocation, frustration, pain and discomfort. Of these triggering influences of aggressive tendencies, the effects of discomfort (e.g., hot temperatures, physical pain, loud noises, foul odors) are likely evolutionarily ancient. Such effects can be found with animals, where the tendency toward aggression cooccurs with tendencies toward flight—the fight or flight syndrome. Aversive experiences result in angry facial expressions and may directly activate aggression-related motor programs (Berkowitz, 1993).

David Buss and his colleagues have proposed a modular architecture of aggression, proposing that humans have a specific adaptation for homicide (Buss, 2005; Buss & Shackelford, 1997; Duntley & Buss, 2004, 2005). There are several adaptive problems "to which aggression might have evolved as a solution" (Buss & Shackelford, p. 608): Coopting resources held by others, defending against attack, inflicting costs on intrasexual rivals, negotiating status and power hierarchies, deterring rivals from future aggression, deterring long-term mates from sexual infidelity, and reducing resources expended on unrelated children.

The prime examples of aggression stressed by Buss and colleagues are impulsive and accompanied by anger rather than deliberative and finely calibrated to potential costs. Duntley and Buss (2004) reject the idea that impulse control is a critical mechanism in understanding aggression:

> 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." (Duntley & Buss 2004, p. 118)

This proposed module is not a simple on–off switch responsive to a single factor. Rather, it is influenced by a variety of contextual cues, including status differences between killer and victim, issues of genetic relatedness and reproductive value, and the size and strength of the killer's and victim's families and social allies (Duntley & Buss, 2005). Thus, in large part, the assessment of costs and benefits is part of the modular architecture of aggression rather than the result of domain general, explicit processing mechanisms (Buss & Shackelford, 1997).

Explicit control of evolved mechanisms of aggression. Although impulsive aggression certainly does occur, impulsivity is unlikely to be a general evolutionary design feature of human aggression. Aggression, whether homicidal or nonhomicidal, has often been linked to poor impulse control (e.g., Seroczynski, Bergeman, & Coccaro, 1999), or in the terminology of the present article, to the inability of the prefrontal effortful control system to inhibit prepotent tendencies stemming from modular mechanisms operating via implicit processing. As indicated above, low conscientiousness is associated with conduct disorder (Krueger et al., 1996), aggression (Krueger et al.; Pulkkinen, 1986), delinquency (Krueger et al.; Robinset l., 1994; White et al., 1994), and antisocial personality disorder—for example, irresponsible and delinquent acts, failure to honor obligations or plan ahead (Widiger, Trull, Clarin, Sanderson, & Costa, 2002; Widiger & Trull, 1992). Impulsive aggression is thus an issue of individual differences rather than a universal feature of human psychology. The literature reviewed here indicates that low levels of prefrontal control mechanisms are linked to impulsivity and aggression.

Specifically, 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 functioning. 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). The authors propose that both impulsive and predatory murderers have "excessive subcortical activity" (p. 319)—what one might term "modular aggression." However, predatory murderers are better able to control these impulses stemming from subcortical areas because of adequate prefrontal functioning.

Woerman et al. (2000) found that episodes of impulsive aggression are sometimes observed in patients with temporal lobe epilepsy. These patients have a highly significant reduction (approximately 17%) in left prefrontal gray matter compared with temporal lobe epilepsy patients with no history of aggression or controls.

Congruent with these findings, Davidson, Putnam, and Larson (2000) note that the PFC contains a high density of serotonin type 2 receptors linked with inhibition of activity in the amygdala. They note that the OFC and the ACC have been particularly implicated in the ability to inhibit impulsivity through their connections to the amygdala. The general model is that activations in these areas serve to inhibit emotional behavior, whereas deficits in these areas increase the likelihood of impulsive aggression. Importantly, conscious effortful control associated with these same areas of the PFC, particularly the OFC, is able to inhibit the eye-blink startle response to negatively perceived information. This indicates a role for effortful control in suppression of negative affect associated with aggression (Davidson, Putnam, & Larson).

Explicit information processing and aggression. The planning and deliberation of predatory murderers noted by Raine et al. (1998) implies a role for explicit processing in aggression. Despite the emphasis on impulsivity as a design feature of aggression (see above), Buss (2005, p. 31) shows that most murderers construct homicidal fantasies before they murder, enabling them "to fashion alternative scenarios and evaluate the extended costs, benefits, and consequences of each." Evidence compiled by social interaction theory (Tedeschi & Felson, 1994) shows that instrumental aggression may involve decisions on how to achieve goals by making explicit cost–benefit analyses that take into account the probabilities of various outcomes. Aggressors often have explicit beliefs that aggression will be a successful means of attaining a particular outcome (Huesmann & Guerra, 1997), or they are inhibited from aggression because of explicit representations of the possible costs (Buss, 2005, p. 31). Explicit attitudes on the appropriateness of violence toward particular classes of people also facilitate aggression (Malamuth, Linz, Heavey, Barnes, & Acker, 1995). Aggression is also facilitated by explicit attitudes on the appropriateness of aggression, as in areas where there are codes of honor and personal respect (Nisbett & Cohen, 1996).

This fits well with models emphasizing the importance of explicit processing for aggression. An internal state of anger is produced, say, via an aversive experience that results in an automatic appraisal. However, as indicated in Figure 2 (Anderson & Bushman, 2002), whether these internal states result in aggression is determined, in the absence of impulsivity, by the outcome of conscious appraisal and decision processes enabled by the effortful control system.

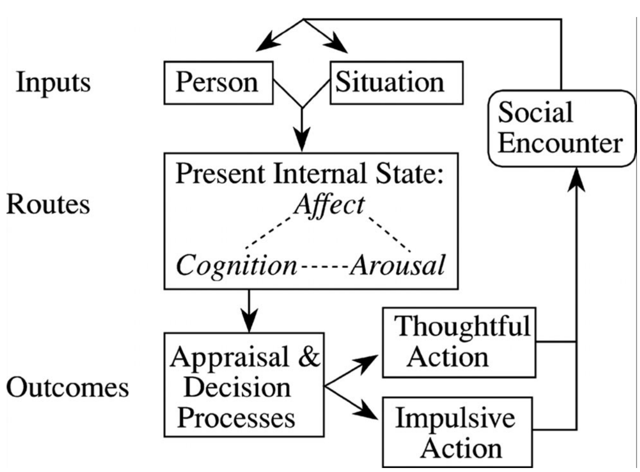

Figure 2. The general aggression model, from "Human Aggression," by C. A. Anderson and B. J. Bushman, 2002, *Annual Review of Psychology, 53,* p. 342. Copyright 2002 by the American Psychological Association.

Information that could only be available as a result of explicit processing rather than evolutionary regularities has been shown to influence the behavior of criminals. For example, studies on the effects on crime of closed-circuit television (CCTV) indicate that criminals are often aware of the cameras and alter their behavior accordingly; further, there is mixed evidence indicating that CCTV results in displacement effects in which crime is channeled into areas without surveillance (Ditton & Short, 1998; Phillips, 1999; Welsh & Farrington, 2003).

It is striking that most people do not commit physical aggression (especially homicide) even in contexts predicted, from an evolutionary perspective, to trigger aggression. One such context is reducing or eliminating resources expended on unrelated children (Buss & Shackelford, 1997, p. 608). Stepparents are much more likely to kill or abuse their children than are natural parents (Daly & Wilson, 1988). Based on Canadian data from 1974–1983, there were over 600 victims per million child-years of "parent"-child coresidence of children aged 0–2 years from stepparents compared to fewer than 10 for natural parents. Child abuse data present a similar picture: 13/1,000 children 0–4 years of age were abused in stepparent families, compared to fewer than 1/1,000 in natural families.

These are large differences, but these rates imply that the vast majority of stepparents did not kill or abuse their stepchildren. Therefore, to the extent that there is an evolved automatic tendency to kill or abuse unrelated children in order to reduce or eliminate resources expended on them, these results are consistent with actual violence as resulting from failure to control these evolved tendencies. Indeed, anthropological data suggest that the contexts for violence are more likely the result of explicit appraisals than adaptive design: Stepchildren are at higher risk if their mothers are relatively powerless, typically because they lack powerful male relatives (Flinn, 2006).

Impulsivity, like other traits linked to high levels of the behavioral approach system, can be seen as a high-risk evolutionary strategy with high potential costs and high potential benefits (MacDonald, 1995, 1998, 2005). One might speculate that impulsivity was more likely to be adaptive in past environments, but in the modern world of elaborate police and bureaucratic institutions, it is typically maladaptive: Hence the correlations among impulsivity, aggression, criminality, incarceration, and low levels of effortful control. Nevertheless, there are subcultures in the modern world where impulsivity and aggression in the service of short-term gains may be adaptive solutions to lack of access to resources (Daly & Wilson, 1997). In any case, given the empirically discovered architecture of aggression as typically involving explicit appraisals and decision making and the argument that natural selection has acted to bring aggression increasingly under the control of prefrontal control mechanisms and explicit processing, it is indeed likely that there has been a long evolutionary history of selection against impulsivity.

The adaptiveness of explicit processing for aggression. In general, aggression is a high-stakes behavior—potentially very costly but also potentially resulting in great benefits. Consider the difference between aggression and the fear system. It is well-established that the fear system results in reflexive defensive behavior prior to any conscious processing (LeDoux, 1996, 2000).

This low road of fear processing routes stimuli directly to the amygdala, bypassing the cortex entirely. For example, a loud noise or the sudden appearance of a threatening snake results in a reflexive response directly triggered through the amygdala. The high road to the cortex takes significantly longer to process this information, but the person is already engaged in defensive action, such as jumping back from the perceived source of danger: Time is of the essence in such situations. And it is better to err on the side of caution than to wait until the cortex figures out that the "snake" is actually a curved stick or that the loud noise was simply a backfire from a passing car.

Reflexive aggression certainly occurs among animals without prefrontal control over aggression; the actual occurrence of aggression then depends on the strength of competing action tendencies (e.g., Lorenz, 1974). However, such a system would be maladaptive for humans able to take advantage of explicit construals of context. Aggression, unlike the defensive responses programmed by the reflexive fear system, is much more likely to be costly, simply because retaliation or punishment is always a possibility. As indicated above, the probability and likely consequences of retaliation or punishment are not likely to be captured by recurrent regularities in the environment of evolutionary adaptedness. Responding to an insult or spousal infidelity or any of the other proposed evolutionary contexts of aggression with automatic, reflexive aggression has presumably been selected against because in the case of aggression it is always better to look before you leap—to determine via explicit processing the probable consequences in what is often a complex situation. In Morsella's (2005) terms, aggression is accompanied by phenomenal states because there is always the possibility of conflict with other skeletal muscle plans, whereas reflexive fear reflects an adaptive lack of cross-talk between systems. Reflexive fear is thus an adaptive response to evolutionary regularities, but a human aggression system that responded only to environmental regularities over evolutionary time would be unable to respond to opportunities or costs imposed by contemporary, rapidly changing environments.

Effortful Control Over Behavioral Approach Systems: Reward-Related Behavior

The general proposal here is that effortful control is particularly important for the adaptive control of behavioral approach tendencies, paradigmatically including aggression and reward-related behavior. This suggests that ventromedial PFC mechanisms will be involved in the control of reward-related behavior, including primary reinforcers, such as sex, food, and drugs of abuse, as well as secondary reinforcers, such as money.

Studies of drug addiction implicate dysfunctions in prefrontal cognitive control over implicit subcortical processing linked to drug craving (Curtin, McCarthy, Piper, & Baker, 2006). 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 active prefrontal control, with the result that addicts are dominated by reward-seeking behavior and insensitive to future negative consequences of that behavior (Jentsch & Taylor, 1999). Congruent with this, addicts have relatively little ability to persevere in cognitively demanding tasks, suggesting impaired effortful control (Brown, Lejuez, Kahler, & Strong, 2002; see also Curtin et al., 2006). These data fit well with findings that substance abuse and dependence have been linked to low conscientiousness scores (e.g., Roberts & Bogg, 2004; Trull & Sher, 1994).

Alcohol dependency, impulsivity, and other disinhibitory disorders are associated with deficits in ventromedial PFC regions (e.g., Carlson, Katsanis, Iacono, & Mertz, 1999; Chen et al., 2007; see Moselhy, Georgiou, & Kahn, 2001, for a review). These results are consistent with a study by London, Ernst, Rant, Bonson, & Weinstein (2000) of chronic drug abusers that found elevated risk taking in a gambling task previously found by Bechara, Damasio, Damasio, & Anderson (1994) to be sensitive to ventromedial PFC dysfunction. Compromised prefrontal control emerges as a general aspect of disinhibitory/externalizing disorders, including alcohol dependence, substance abuse/dependence, adult antisocial disorder, and conduct disorder (Kendler, Prescott, Myers, & Neale, 2003).

Several different psychotherapeutic methods have been developed that depend on explicit processing to lessen substance abuse behavior. For example, cognitive behavior therapy attempts to change distorted thinking about abused substances and develop conscious control strategies for coping with substance abuse situations (Beck et al., 1993; Wells, Peterson, Gainey, Hawkins, & Catalano, 1994). Motivational interview techniques attempt to develop a desire to change based on explicitly represented reasons followed by explicit strategies for change (Miller & Rollnick, 2002). Twelve-Step programs typically include explicit endorsement of abstinence goals and changing dysfunctional cognitions (Ouimette, Finney, & Moos 1997). These programs have shown some success in reducing remission rates and unemployment in a substantial percentage of patients (Morgenstern & McKay, 2007; Ouimette et al.; Wells et al.).

However, to date there is no evidence that improvement occurred because of the unique type of explicit cognitions proposed by each theory, suggesting that a generic process model of psychotherapy may be correct (Morgenstern & McKay, 2007). In terms of the present framework, this suggests that the effortful control system could be activated by a variety of motivating explicit cognitions, including rejecting dysfunctional attributions, explicit representations of the costs of addiction and the benefits of nonaddiction, endorsing abstinence as a goal, religious beliefs, or developing explicit control strategies. These data suggest that positive effects of explicit control strategies occur as a result of activation of prefrontal areas linked with effortful control. However, this issue has not been specifically addressed by research to date.

Regarding sexual arousal, Beauregard, Lévesque, and Bourgouin (2001) found that viewing erotic films activated the right amygdala, right anterior temporal pole, and hypothalamus. Subjects given explicit instructions to decrease their sexual arousal showed no activation of the subcortical structures, but activation was observed in the right dorsolateral PFC (superior frontal gyrus) and the right ventral affective subdivision of the ACC. Activation in the dorsolateral PFC is interpreted as an example of top-down explicit processing necessary for voluntary action. Activation of the right ventral ACC fits well with data reviewed above that the ventral ACC is implicated in emotionally charged tasks of effortful control (Posner & Rothbart, 1998; Bush et al., 2000; see above). This study is particularly interesting because the amygdala response to erotic films is an evolutionarily prepared reaction.

Finally, there is evidence for a role of prefrontal inhibitory control in regulating food intake. Obese subjects have less prefrontal activation when viewing high-calorie foods compared to normal subjects (Killgore et al., 2003; see also Del Parigi et al., 2002). Several studies have implicated the OFC in terminating feeding (Hinton et al., 2004; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001; Tataranni et al., 1999). These data are consistent with substantial evidence for a link between conscientiousness and health-related behaviors (e.g., Booth-Kewley & Vickers, 1994; Friedman et al., 1995; Friedman, 2000; Roberts & Bogg, 2004). On the basis of these well-established relationships, Friedman et al. (1995) hypothesized that low conscientiousness would be associated with poor dietary habits.

Prefrontal Control of Ethnocentrism

This section begins with a brief discussion of different types of models for ethnocentrism: Evolutionary models proposing dedicated, implicit processing mechanisms deriving from natural selection in our evolutionary past and learning models in which implicitly negative attitudes toward racial outgroups result from associations that become automatic with repeated exposure. Literature is then reviewed showing that explicitly conscious mechanisms of effortful control associated with the PFC are able to inhibit the output of implicit processing.

Mechanisms of ethnocentrism. There is good evidence for several different mechanisms related to ethnocentrism: social identity mechanisms (MacDonald, 2001; Tullberg & Tullberg, 1997; van der Dennen, 1999), genetic similarity mechanisms (Rushton, 1989), a human kinds module (Hirschfeld, 1996), and individualism/collectivism (Triandis, 1991, 1995). Research on social identity has repeatedly found that the stereotypic behavior and attitudes of the ingroup are positively valued, whereas outgroup behavior and attitudes are negatively valued (Abrams & Hogg, 1990; Brewer & Brown, 1998; Fiske, 1998; Hogg & Abrams, 1987). The tendency for bias in favor of ingroups arises automatically and implicitly (Otten & Wentura, 1999). Social identity processes occur very early in life, prior to explicit knowledge about the outgroup. Anthropological evidence indicates the universality of the tendency to view one's own group as superior (Vine, 1987). Social identity processes also occur among some animal species: Russell (1993, p. 111) notes that "chimpanzees, like humans, divide the world into 'us' versus 'them,'" and van der Dennen (1991, p. 237) proposes, on the basis of his review of the literature on human and animal conflict, that advanced species have "extra-strong group delimitations" based on emotional mechanisms. This results in the expectation that people will be biased toward associating outgroups with negative traits.

Genetic Similarity Theory is a biological/genetic theory aimed at explaining positive assortment on a variety of traits in friendships, marriage, and alliance formation. People not only assort positively for a wide variety of traits, they do so most on traits that are more heritable. Moreover, identical twins have more similar spouses and friends than do fraternal twins, indicating that individual differences in the tendency to assort with similar others are heritable (Rushton & Bons, 2005).

Kin recognition mechanisms are a possible mechanism for positive assortment. Animal research finds support for two general categories of kin-recognition mechanisms, direct and indirect. Direct mechanisms of phenotypic matching allow organisms to recognize relatives directly via self-referent phenotypic matching (Hauber & Sherman, 2001). For example, people respond to facial resemblance as a cue for kinship. DeBruine (2002) found that subjects showed greater trust of others in a two-person trust game if the other person's face resembled their own, results compatible with proposals that self-resemblance lowers the potential costs and increases the benefits of coalition membership. DeBruine (2004) showed that although both sexes preferred self-resembling faces of same and opposite-sex photos, they showed greater preference for same-sex faces. These results are interpreted as a nonsexual positive regard for persons resembling self.

On the other hand, indirect mechanisms of phenotypic matching take advantage of the fact that kin will be in a particular area. Such mechanisms may involve relatively specialized social learning confined to a particular developmental phase. For example, children are not sexually attracted to their coresident siblings even if their siblings are adopted nonrelatives (Lieberman, Tooby, & Cosmides, 2007). Indirect mechanisms of phenotypic matching may also be implicated in race preferences. Research on human infants indicates that preference for own race occurs by 3 months of age but is not present at 1 month (Kelly et al., 2005). However, racial ingroup preferences are weakened by exposure to outgroup faces during infancy (Bar-Haim, Ziv, Lamy, & Hodes, 2006; Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005).

Negative stereotypes of outgroups may also develop or be facilitated by domain-general association mechanisms, such as social learning or spreading activation—a standard view among social psychologists (e.g., Blair, 2001; Monteith & Voils, 2001). Theories based on social learning propose that people learn negative views of outgroups through socialization agents or media exposure. With repeated exposure, these stereotypes become automatic and implicit.

Whatever the exact combination of mechanisms underlying ethnocentrism, there is little doubt that attitudes related to ethnocentrism are automatic. For example, Olsson, Ebert, Banaji, and Phelps (2005) found that, for both Black and White subjects, faces of racial outgroup members acted as evolutionarily prepared fear stimuli: As in the case of evolved fear stimuli like snakes and spiders, subjects' conditioned fear responses did not extinguish after faces of outgroup members were no longer paired with shock. (Conditioned fear responses to racial ingroup faces rapidly extinguished when they were no longer paired with shock.) These results are consistent with an evolutionary basis for negative responses to outgroups or with overlearned automaticities resulting from individual experience (Öhman, 2005). Prepared learning effects were less for subjects with interracial dating experience, an effect that could be due to the effects of interracial contact on lessening amygdalar responses or to genetic or environmental differences affecting self-selection of dating partners.

Explicit control of evolved mechanisms of ethnocentrism. Explicitly represented goals are able to control implicit negative attitudes toward racial outgroups associated with activation of the amygdala (Wheeler & Fiske, 2005). Both Richeson et al. (2003) and Cunningham et al. (2004) found that activation in the dorsolateral PFC and the ACC was associated with diminished amygdala responsiveness to explicitly processed photos of Blacks. Thus, Cunningham et al. found that White subjects had a stronger amygdala response to photos of Blacks than Whites if the photos were displayed for a very short period of time (30 ms) insufficient to be represented explicitly in the prefrontal area. At longer periods (525 ms), this difference in reaction to Black and White faces decreased, and the prefrontal region was activated. "These results suggest that controlled processing can moderate, and even override, activity that would otherwise result from automatic processing" (Cunningham et al., p. 811).

Lieberman, Hariri, Jarcho, Eisenberger, & Brookheimer (2005) showed a role for the ventrolateral PFC in dampening negative responses in the amygdala to photos of Blacks acting by way of intermediate projections to the medial PFC. fMRI scans of Black and White subjects showed involuntary and unconscious activation of amygdala in a task requiring them to choose the face (from a pair of faces at the bottom of the screen) that was the same race as the photo of the person at the top of the screen. However, when subjects identified the race of the person by linking the verbal label "African American" to the photo, there was no response in the amygdala, but the right ventrolateral PFC was activated. These results were interpreted as indicating that explicit verbal processing suppressed impulses originating in the amygdala linked with subjective feelings of threat.

Finally, prefrontal effortful control of ethnocentrism is consistent with findings that older adults are less able to control ethnocentric attitudes than younger adults despite greater motivation to control such thoughts (von Hippel, 2007; von Hippel, Silver, & Lynch, 2000). Although based on correlations between stereotyping and low scores on an executive function task (reading passages while ignoring distracting information), these results are consistent with a general decline in prefrontal functions with age that would also include effortful control mechanisms emphasized here. Consistent with this, older subjects are generally less able to control socially inappropriate utterances and behavior (von Hippel, 2007).

Explicit information processing and ethnocentrism. Explicit cultural norms related to ethnocentrism and awareness of the costs involved in violating those norms are important input to the prefrontal control mechanisms. White subjects who are told they are violating cultural norms of racial egalitarianism inhibit ongoing behavior in an attempt to bring responses more in line with cultural and personal norms (Monteith, Ashburn-Nardo, Voils, & Czopp, 2002). Similarly, Amodio et al. (2004) found that subjects adopted a more controlled processing strategy following errors in object identification indicative of race bias. Subjects slowed their responses in order to avoid such errors.

As children mature, they become more aware of cultural norms and are better able to inhibit implicit processing with increasing prefrontal control. Explicit race bias emerges early, as young as 3 or 4 years of age, and peaks in middle childhood. It typically undergoes a gradual decline through adolescence and disappears in adulthood (Aboud, 1988; Augoustinos & Rosewarne, 2001; Davey, 1983). However, there is no such decline in implicit racial preferences (e.g., Dunham, Baron, & Banaji, 2005). The developmental continuity of implicit preferences combined with a decline of explicitly stated racial preference coincides with a decline in cross-racial friends and companions. Over the same period that explicit racial preference in White children declines, the rate of cross-race interactions and interracial friendships, even in racially mixed schools, declines precipitously. In effect, schools undergo a process of self-segregation (Moody, 2002; Smith, 2003). These findings are consistent with the general gap between people's explicitly stated reasons and their implicit gut feelings for liking or disliking people, for example, romantic partners, or objects, for example, houses, cars (Wilson, 2002).

Taken together with the results of the previous section, these results indicate control by explicit processing over automatic processing related to ethnocentrism. To date, these data have not been linked with individual differences in conscientiousness. Research indicates a weak positive association between conscientiousness and ethnocentrism (Altemeyer, 1996; Ekehammar, Akrami, Gylje, & Zakrisson, 2004; Heaven & Bucci, 2001). However, these self-report measures do not address the proposed greater ability of conscientious individuals to control evolved ethnocentric tendencies in contextually sensitive ways. This hypothesis awaits further study.

Prefrontal Control of Emotions

As noted above, effortful control predicts the ability to modulate anger and joy in children (Kochanska et al., 2000). There is considerable evidence that prefrontal control mechanisms are able to generate emotions via expectations and to regulate ongoing emotions via reappraisal or in response to placebo (Ochsner & Gross, 2005). For example, observing aversive images (a bottom-up task triggering automatic processing) and instructions to think of neutral images in negative ways (a top-down task requiring explicit processing) both triggered responses in the amygdala, but only the latter triggered a response in the PFC (Ochsner & Gross). Up-regulating and down-regulating negative emotion both involved the dorsolateral PFC and ACC, but down-regulation (implying inhibitory control) uniquely recruited the OFC (Ochsner et al., 2004).

Several studies illustrate the ability of explicit processing to inhibit emotional arousal. Explicit instructions to suppress emotional responses to unpleasant stimuli modulated the eyeblink startle response and the corrugator supercilii muscle, whereas instructions to enhance the emotional response had the opposite effect (Davidson et al, 2000; see also Jackson, Malmstadt, Larson, & Davidson, 2000). Subjects with greater relative left activation in prefrontal scalp regions (as measured by EEG recordings) showed greater startle attenuation in response to the suppression instruction. These findings are attributed, at least in part, to conscious efforts to control associated with the PFC, particularly the OFC.

Controlling negative emotions: depression and posttraumatic stress disorder (PTSD). As discussed in a previous section, people low on effortful control have difficulty controlling subcortical approach tendencies (aggression, reward seeking). However, effortful control is domain general, suggesting that people low on effortful control will also be found to have less ability to control negative emotions.

Davidson, Irwin, Anderle, & Kalin (2003) found that prior to treatment, depressed patients had relatively less left prefrontal activation in response to pictures producing negative affect (e.g., a mutilated face), suggesting that they are relatively less able to inhibit negative emotions stemming from the amygdala. Indeed, depression is associated with increased metabolism in the amygdala, whereas treatment with antidepressants correlates with decrements in amygdala activation (Drevets, Spitznagel, & Raichle, 1995, Drevets et al., 1992). Davidson et al. (2003) found that treatment resulted in increased left prefrontal activation, results interpreted as consistent with increased voluntary ability to control negative emotional responding.

Also consistent with a role for prefrontal effortful control mechanisms, late-onset depression among older adults is associated with lowered executive function, interpreted as a lack of inhibitory control over rumination (von Hippel, 2007; von Hippel, Vasey, Gonda, & Stern, in press). Although based on correlations between late-onset depression and low scores on executive function tasks (e.g., a Stroop task) and a working memory task, these results are consistent with a general decline and atrophy of effortful control mechanisms as an aspect of a general decline of prefrontal functioning with age.

Given the links between conscientiousness and effortful control, it is not surprising that several studies have found that depression is associated with low conscientiousness (Anderson & McLean, 1997; Costa & McCrae, 1992; Trull & Sher, 1994). This is a substantial effect. For example, Anderson and McLean (1997) found that depressives scored one standard deviation below the normative mean on conscientiousness. Improvements in conscientiousness scores combined with conscientiousness scores at discharge explained 29% of the variation in depressive symptoms. Conscientiousness explained an additional 11% of the variance in psychiatric symptomatology after removing the variance accounted for by life stressors, social support, and discharge level of psychiatric symptomatology.

PTSD is also associated with lack of prefrontal control over subcortical negative emotional responses. Viet Nam war veterans with PTSD had lowered blood flow to the medial prefrontal region compared to similar patients without PTSD (Bremner et al., 1999). Patients without PTSD had greater activation of ventral ACC in areas immediately adjacent to these medial prefrontal areas. Similarly, Shin et al. (2001) found diminished activation of the medial PFC in PTSD patients on an emotional Stroop test—a test that includes PTSD-relevant words ("bodybags," "firefight") as stimuli. Results were interpreted as "consistent with a neuroanatomic model of PTSD that posits a failure of medial PFC to inhibit a hyperresponsive amygdala" (Shin et al., p. 937). Shin et al. corroborated these findings using consciously processed images of faces expressing fear. Symptom severity was negatively correlated with medial PFC activation. Semple et al. (2000) found that PTSD patients with comorbid substance abuse had less blood flow in the frontal cortex and greater blood flow in the amygdala compared to normals, results consistent with "inhibition of amygdala function by the PFC and vice versa in a reciprocal interplay that contributes to the regulation of cognition, emotion, and affect" (p. 68). Finally, PTSD is associated with low conscientiousness (Trull & Sher, 1994).

Discussion

The data discussed above, and particularly the brain imaging data, indicate prefrontal control over implicit processing, including implicit processing resulting from evolved modules. This implies that the output from evolved modules, especially modules related to behavioral approach (i.e., aggression and reward-seeking behavior), is downgraded from an automatic response to recurrent features of the environment of evolutionary adaptedness to a prepotency capable of being controlled by explicit processing centered in the PFC.

An important adaptive feature of prefrontal control mechanisms is to expand the universe of potential costs and benefits for behavior beyond evolutionarily recurrent implicit contexts to include explicit representations of the context and the likely costs and benefits of behavior. These explicit representations need not be limited to those that were recurrent over evolutionary time but can rapidly respond to novel contingencies, including rapidly changing social norms and perceived cost–benefit outcomes of behavior. The use of explicit representations also intersects with human general intelligence to enable plans in the service of attaining evolutionary goals (Chiappe & MacDonald, 2005). In addition to evidence that human aggressors make explicit assessments of costs and benefits involved in aggression (Buss, 2005; Tedeschi & Felson, 1994), explicit processing is also presumably involved in the very rapid changes in sexual behavior that followed the introduction of safe, reliable, and legal contraception and abortion (e.g., Furstenberg, 1991)—changes too rapid to be due to natural selection.

The adaptedness of explicit processing is likely to extend well beyond the areas covered here. For example, humans have difficulty sustaining a public resource that is capable of overuse—the "tragedy of the commons" (Hardin, 1968). However, recent models of cooperation show that indirect reciprocity can evolve if people have access to explicit information on others' histories of interaction in cooperative situations (e.g., Milinski, Semmann, & Krambeck, 2003; Mohtashemi & Mui, 2003; Semmann, Krambeck, & Milinski, 2005; Smith, 2005). (Indirect reciprocators help others without expectation of reciprocity; but, as a result, they develop a good reputation, which benefits them in future interactions.) Information on the reputation of individuals may be the result of direct experience, verbal communication, or written records. As Mohtashemi and Mui (see also Panchanathan & Boyd, 2003) note, information on others' reputations constitutes a collective memory of the past history of individuals made possible by language—that is, explicit representations of the past history of individuals in cooperative situations. In fact, explicit agreements to cooperate made prior to the prisoner's dilemma game result in increases in cooperation and decreases in competition during the game (Orbell, van de Kragt, & Dawes, 1988).

This suggests the possibility that evolutionary pressure for cooperation may be a critical adaptive function accounting for the evolution of explicit processing and prefrontal control. The data reviewed here indicate that prefrontal mechanisms of effortful control are generally able to inhibit short-term gains for longer term payoffs resulting from reputation enhancement. Such a proposal fits well with arguments that humans have an evolved "need to belong" that functions to facilitate cooperation (Baumeister & Leary, 1995). Many of the descriptors of conscientiousness reflect long-term reputation as a cooperator: responsible, dependable, dutiful, and reliable. Indeed, responsibility emerges as a facet of conscientiousness defined as cooperative, dependable, being of service to others, and contributing to community and group projects (Roberts, Chernyshenko, Stark, & Goldberg, 2005). Among the lower-order facets of conscientiousness, responsibility correlates most highly ($r = .61$) with virtue, defined by adherence to standards of honesty and morality and behaving as a moral exemplar. The responsibility and virtue factors emerge as a factor in two-factor facet-level solutions of the inhibitory factor of conscientiousness. (The other factor of conscientiousness facets is a proactive factor concerned centrally with achievement-related items.)

The theoretical models of cooperation indicate that the responsibility and virtue facets of conscientiousness could not have evolved without the coevolution of explicit appraisals of reputation made possible by human language, representational ability, and long-term memory. Without such explicit appraisals, cooperators would be at an evolutionary disadvantage and vulnerable to a strategy of short-term exploitation rather than long-term cooperation with like-minded others.

There is an obvious sense in which the prefrontal control mechanisms are adaptive in the modern world. As noted above, people who are poor at controlling impulses stemming from our evolved modular psychology tend to do poorly in the educational system and are prone to a variety of externalizing behaviors (aggression, drug abuse) that are linked to significantly higher rates of incarceration, incapacitation, and mortality. Nevertheless, externalizing disorders occur at rates that indicate selective processes maintaining genes influencing these traits to remain in the population (Wilson, 1993). Impulsivity, strong attraction to reward, antisocial behavior, and aggression would have had adaptive effects in the environment of evolutionary adaptedness (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 available and physical aggression tends to have limited payoffs and is subject to high levels of social control.

Nevertheless, there are subcultures in which homicidal aggression may be a nonpathological solution to lack of access to resources and social support or cost–benefit appraisals (not necessarily explicit) in a high-mortality environment with restricted opportunities for upward social mobility (Daly & Wilson, 1997). Moreover, there is no indication of lowered fertility in this group. Indeed, Emery, Waldron, Kitzman, & Aaron (1999) found that age of first birth was negatively correlated with externalizing behavior in females.

Prefrontal effortful control also enables long-term planning in which present impulses are inhibited in favor of possible long-term gains. People low on effortful control have a relatively greater focus on immediate rewards compared to long-term consequences of their behavior, including, as noted above, their reputation. Adequate ability to control impulsive behavior is particularly important in contemporary culture because the long training period required for access to high-status occupations cooccurs with age-graded peaks in behavioral approach systems underlying aggression and reward-oriented behavior. Prefrontal effortful control mechanisms thus intersect with other domain general cognitive mechanisms, especially general intelligence, because of their usefulness in planning for complex contingencies and imagining and formally modeling the future.

This vast expansion of the universe of possible costs and benefits enriches and complicates an evolutionary analysis of culture. On one hand, most humans are equipped with mechanisms able to control evolved prepotencies; and, on the other, they are exposed to an often bewildering array of cultural messages that affect their explicit appraisals of costs and benefits and even their implicit appraisals of costs and benefits in situations where learning has become automatic with practice. These appraisals may be influenced by a wide range of competing interests. For example, media images, especially those aimed at explicit, conscious processing, have important effects on behavior even though people are often unaware that their behavior is influenced by the images (Wilson, 2002). These images are often engineered by advertisers who are consciously attempting to influence the recipients of the messages in ways that conform to the advertiser's interests, not the recipient's interests.

Because of the ability of explicit processes of effortful control to control automatic processing and because of the power of explicit cultural influences to shape behavior, the control of explicit cultural space assumes enormous importance in an evolutionary account. It has long been noted that the fundamental evolutionary goal of maximizing biological fitness has not been programmed into humans as a proximal mechanism—that is, there is no mechanism that directly tracks fitness over an individual's lifetime (e.g., Buss, 2004). Moreover, even modular mechanisms related to reproduction may be maladaptive in environments that depart from the recurrent invariances that shaped their evolution. (For example, mechanisms promoting male promiscuity may lead to maladaptive behavior in an environment with easily available contraception.) The conclusion is that even the proximal mechanisms that have resulted in the set of evolved prepotencies have come under the control of explicit processing and its ability to frame goals that may or may not converge on evolutionary interests. Explicit goals are influenced by a deluge of culturally available information and are often infused with political and religious ideologies. They need not be linked even remotely to evolutionary success.

The result is that there is an additional layer of uncertainty between evolutionary success and human evolved psychology. It is this additional layer that enormously complicates the evolutionary analysis of human behavior compared to that of animals.

Finally, these data also indicate that effortful control encompasses a set of nonmodular, domain-general control mechanisms. The domain generality of these systems is indicated by the evidence indicating prefrontal effortful control of a wide range of behaviors, ranging from aggression and other behavioral approach systems to ethnocentrism and both positive and negative emotions. Moreover, the personality trait of conscientiousness has a wide range of correlates, ranging from positive correlations with academic success and achievement to negative correlations with criminality and impulsive, reward-oriented behavior.

Although there is no doubt that prefrontal mechanisms are involved in effortful control, the exact mechanisms remain unsettled. For example, the specific prefrontal areas involved in emotion regulation have varied between studies (Ochsner et al., 2004). The data reviewed here point to important roles for the ventromedial PFC and the ventral ACC. In their discussion of prefrontal control of emotion regulation, Ochsner and Gross (2005, p. 246) note that "The consistent involvement of control–appraisal system dynamics in various forms of regulation [selective attention; reappraisal] suggests a common functional architecture that might be flexibly deployed to support multiple types of control strategies that regulate multiple types of emotional responses." A common functional architecture of effortful control that nevertheless shows stable individual difference is an important possibility for explaining the data reviewed here.

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