The Causal Role of Consciousness: A Conceptual Addendum to Human Evolutionary Psychology

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However, in certain cases, this approach may

By concentrating on the unconscious processes driving evolutionary mechanisms, evolutionary psychology has neglected the role of consciousness in generating human adaptations. The authors argue that there exist several "Darwinian algorithms" that are grounded in a novel representational system. Among such adaptations are *information-retention homicide*, the killing of others who are believed to possess information about the self that has the potential to jeopardize inclusive fitness, and those generating *suicide*, which may necessitate the capacity for self-referential emotions such as shame. The authors offer these examples to support their argument that human psychology is characterized by a representational system in which conscious motives have inserted themselves at the level of the gene and have fundamentally changed the nature of hominid evolution.

Evolutionary psychologists frequently recapitulate the theme that adaptive behaviors are guided by unconscious processes servicing genetic selection in individual organisms (Buss, 1995, 1999; Daly & Wilson, 1999; Dawkins, 1986; Leger, Kamil, & French, 2001; Symons, 1992). Among many other examples, such "blind" fitness-enhancing algorithms include those that are devoted to mate selection, child rearing, and altruism. For instance, individuals need not be consciously aware of the reasons they find pronounced interocular distance unattractive in a potential mate (Fink & Penton-Voak, 2002; Thornhill & Gangestad, 1993), are more likely to emotionally disengage from their infants born with chromosomal abnormalities than they are healthy children (Bjorklund, Yunger, & Pellegrini, 2002; Daly & Wilson, 1981, 1995), or are most likely to assist others when the costs of helping are relatively low and the likelihood of reciprocation is high (Axelrod & Hamilton, 1981; Tooby & Cosmides, 1992; Trivers, 1971) to directly and reliably engage in behaviors guided by these evolved heuristics.

not accurately capture the complexities of human evolution because it tends to ignore the role of consciousness in the emergence of unique human adaptations. We define consciousness as that naturally occurring cognitive representational capacity permitting explicit and reflective accounts of the—mostly causative—contents of mind, contents harbored by the psychological frame of the self and, as a consequence, the psychological frames of others. Because consciousness is often deeply interwoven with unconscious selection pressures, selection at the level of the gene cannot always be neatly cleaved off from intentionality at the level of the human organism. A new suite of adaptations may have been fostered by such higher order cognitive processes once they were in place, being uniquely plumbed from the metarepresentational abilities (i.e., cognitive resources enabling general perspective taking and access to epistemic positions) of early humans (Baron-Cohen, 1999; Bering & Povinelli, in press; Povinelli & Giambrone, 2000; Tomasello, 1999). This argument should not be confused with genetic teleology, as if the organism has any say in the instantiation of its own adaptations. Rather, it implies only that intentionality has played an important *causal* role in human evolutionary processes and is an integrative dynamic asserting itself at the level of the gene. That is, once the heritability for consciousness reached floor level, it began to exert a unique

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selective pressure on human behavior, serving essentially as an endogenous force that "rewrote" adaptations that had evolved before consciousness. In addition, consciousness may have precipitated new categories of ancestrally adaptive behaviors that had no precedent in evolutionary history.

If the foregoing analysis is correct, then human evolutionary psychology could be revised profitably to accommodate the unique selective forces driving human behavior, forces that have been overshadowed by the theoretical dominance of ultimate explanations of adaptation (i.e., blind mechanisms of genetic fitness). This strict attention to the blind mechanisms of genetic fitness is useful in dealing with the behavioral etiology of species that have not evolved the bundle of causal reasoning skills equated with "consciousness" or "intentionality," but it may not always be a successful strategy for addressing the origins of humans. This is because the appearance of such a representational system may be directly responsible for many qualitative differences in the behavioral motivations of humans and other species, and it is these conscious motivations that drive unique adaptations in the former.

Of course, even if this is the case, these large-scale differences mechanistically can only promote behavioral selection on the same ultimate scale of genetic selection as the behaviors of other species. The actual mechanisms of selection and genetic inheritance are firmly established and are not at issue (Alexander, 1987; Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Daly & Wilson, 1988; Dawkins, 1989; Williams, 1992). However, this model predicts that certain human adaptations, including suicide and certain forms of homicide, could not have evolved were it not for consciousness. Thus, we should find no homologous behaviors in closely related species. Other adaptive behaviors, including (among many other examples) altruism and cooperation (e.g., Johnson & Krüger, in press; Wedekind & Malinski, 2000), probably evolved before consciousness and are shared with other primate species but were dramatically reorganized in human brains to accommodate the new demands of an intentionality system. Evolutionary psychology must therefore begin to examine how consciousness built on ancient adaptations in the primate lineage to construct novel human adaptations. Darwinian algorithms are usefully exacted at the ultimate level of genetic selection, but for certain human adaptations, the evolution of such algorithms cannot be explained without invoking consciousness as an explanatory frame. Therefore, in the present article, we argue that consciousness has played an important causal role in ancestrally adaptive human behaviors. We concentrate on the evolution of ancestrally adaptive behaviors that arguably depend on the presence of consciousness to produce the associated genetic advantages. Indeed, consciousness was, in many respects, the "problem" that such adaptations were designed to solve. Without such a "problem," there would have been no selective pressure to have evolved mechanisms promoting specific solutions to the crisis of social knowledge.

Representational Discontinuity From Continuous Processes of Change

The central argument advanced here is that once an intentionality function was normatively entrenched in human cognition, a series of evolutionary adumbrations to initial low-level (i.e., unconsciously inspired) adaptive behaviors occurred, capitalizing on this new representational system and, in the process, establishing new heuristic strategies. These strategies can then be said to have opened up untrammeled tracts of genetic fitness. Much of this article is devoted to examples of these previously unexploited tracts, but for now it is important to recognize that throughout the 5 to 7 million year course of hominid evolution, neurocognitive changes underlying this representational system advanced rapidly and dramatically, ultimately leading to an evolutionarily novel system subserving abstract causal reasoning at least by the time modern humans arrived on the scene 150,000 years ago in sub-Saharan Africa (Povinelli, 2000; Povinelli & Bering, 2002; Povinelli, Bering, & Giambrone, 2000). The phylogenetic revamping of this primate neurocognitive apparatus was both quantitative and qualitative in nature: quantitative in the sense of physical expansion of the frontal cortex and increased brain mass and qualitative in the sense of reaching a critical threshold allowing genuine representational changes in the core cognitive system. These changes thus built on existing structures while simultaneously creating unprecedented psychological mechanisms (Povinelli et al., 2000; Tomasello, 1999; Tomasello & Call, 1997). What this means is that we should expect to find both similarities and legitimate differences in the cognitive and, accordingly, the behavioral assemblages between modern humans and their closest genetic relatives.

Accounting for Differences and Similarities Between Humans and Chimpanzees

Chimpanzees and humans possess a considerable degree of overlap in their cognitive and behavioral repertoire alongside formidable differences. Shared features between the two species are parsimoniously attributed to their recent shared ancestry (Bering & Povinelli, in press; Parker & McKinney, 1999; Suddendorf & Whiten, 2001; Tomasello & Call, 1997). Although the causes of differences between extant species are more difficult to identify, several investigators (e.g., Povinelli, 2000; Povinelli & Bering, 2002; Tomasello, 1999) have argued that these differences can be accounted for by relatively domain-general mechanisms of abstract causal reasoning that evolved in humans after the two primate clades diverged. According to this argument, behavioral and cognitive traits seemingly distinct to humans recruit a general explanatory drive serviced by abstract causes, whether these unseen causes are endemic to the social domain (e.g., desires, emotions, intentions, and beliefs) or the physical domain (e.g., mass, gravity, connectedness, and velocity).

Several models of the evolution of human cognition are based on this set of differences between humans and chimpanzees. One of the most notable is Tomasello's "ratchet effect" hypothesis of cultural origins (Tomasello, 1999, 2000; Tomasello, Kruger, & Ratner, 1993). According to this model, technological advances and cultural change emerge from a continuous process of human sociocultural scaffolding wherein the intellectual developments of each generation are transmitted to the next through metarepresentational functions such as imitation, pedagogy, and narrative discourse. Each generation can then be said to "ratchet" the foundations of those that come afterward by giving them a head start toward progressive improvements on the current cultural or temporal milieu. Chimpanzee societies, in contrast, as a result of the absence of these vehicles of information (an apparent symptom of metarepresentational deficit), appear to regularly undergo a "slippage" of cultural innovations in which new trends fail to be adequately transmitted between generations and each individual must start from scratch, "reinventing the wheel." Crucial to Tomasello's claim is the notion of a standard species-wide ontogenetic history of humans being treated as intentional agents and having their mental states demarcated by symbolic linguistic utterances (e.g., want, wish, believe, and know). A developmental context wherein children are as much behind the reigns of their own cognitive development as their caregivers (e.g., dialogic interchange in which children recognize that the same event can be represented differently), and wherein others are sensitive to these children's emotional, perceptual, intentional, and epistemic states from the start, is the condition under which an emergent, native intentionality prospers (Tomasello, 1999).

Although this capacity for representing unseen causes may be a cognitive specialization of humans, the success of this enculturation process demands a set of basic primate cognitive systems shared with chimpanzees, such as an appreciation of categorical social relations (tertiary and beyond); an understanding of others as animate, goal-driven agents; and a basic episodic memory. Evidently, Tomasello envisions human representational abilities as only quantitatively different from the systems of chimpanzees. Indeed, in a dynamic systems theory of "ape enculturation," Tomasello and his colleagues (Call & Tomasello, 1996; Tomasello, 1998; Tomasello, Savage-Rumbaugh, & Kruger, 1993) have speculated that chimpanzees reared by humans and treated in a manner similar to infants and young children may develop some degree of metarepresentational abilities, by implication suggesting that the chimpanzee neurocognitive substrate can potentiate evolved human competencies if subjected to the right epigenetic forces.

Although his ideas are not necessarily at odds with Tomasello's model, Povinelli, along with his colleagues (Bering & Povinelli, in press; Povinelli, 2000, 2001; Povinelli et al., 2000; Povinelli & Giambrone, 2000; Povinelli & Prince, 1999), has adopted a different explana-

tory skein to account for the evolution of similarities and differences between humans and chimpanzees. Whereas Tomasello's hypothesis emphasizes the categorical differences between the behaviors of the two species, Povinelli's hypothesis seeks to explain how structural similarities in behavior between chimpanzees and humans may not be driven by isomorphic cognitive processes. Dubbed the "reinterpretation hypothesis," Povinelli's model holds that the recent shared heritage between the two species guarantees an ensemble of behavioral homologies but that, with the evolutionary emergence of a new representational system serving to register the unseen causes of these behaviors, humans began to "redescribe" them in terms of the mental states generating actions (or inhibiting actions).

A key implication of Povinelli's model is that once the ability to represent underlying mental states was grafted onto the preexisting "lowlevel" (or first-order) representational system, which functioned by way of detecting statistical regularities in the social and physical worlds (i.e., propositional rules often acquired through association learning), the "high-level" system was in place to provide predictive and explanatory accounts whenever these rules were violated or when behaviors appealed directly to the higher order system. Because this model deals with progressive access to metarepresentation over evolutionary time, Povinelli et al. (2000) analogized their reinterpretation hypothesis to Karmiloff-Smith's (1992) representational redescription model of cognitive development, which is an ontogenetic model of similar representational change.

The Mind Matters, but so Do Genes

Such conceptualizations (particularly the reinterpretation hypothesis) of human cognitive evolution challenge traditional models of psychological continuity that can be traced back to Charles Darwin (1871/1982), whose proclamations that there can exist no legitimate psychological chasms between humans and other species have been something of an opiate to comparative psychologists bent on emphasizing the similarities between humans and other primates and something of an aching thorn in the sides of those scientists convinced of qualitative differences (Povinelli & Bering, 2002). On the matter

of the evolution of psychological mechanisms, however, Darwin may have been wrong, or, at least, not careful enough in his wording. As Tomasello's and Povinelli's models demonstrate, an integration of findings from comparative science, cognitive development, and evolutionary biology makes the strong case more for a genuine difference of *kind* between the representational systems of humans and their closet living relatives than one of *degree*.

These models, and other evolutionary accounts of metarepresentation, do not go far enough, however. Aside from brief mention of the "social adaptiveness" and "predictive and explanatory power" of this novel representational system, each fails to operationalize the actual mechanisms of selection that have resulted in adaptive human behaviors rooted either directly or indirectly in the system. Just as evolutionary psychology may have overlooked the role of intentionality in driving adaptive processes in humans, comparative science has not given sufficient insight into the role of intentionality at the level of the gene. Whereas the former can be seen as having compromised "content for process" in its theorizing of evolutionary mechanisms, the latter can be seen as having compromised "process for content." The basic premises of both fields can be combined to yield a more powerful analysis of human cognitive evolution than either might achieve alone.

Building New Intention-Based Adaptations Out of Low-Level Parts: Mechanisms of Change

Any inquiry into the role of intentionality at genetic levels of selection must begin with the identification of the actual mechanisms associated with this type of evolutionary change. Although there have probably been many different pathways of such adaptive processes linked to the presence of a metarepresentational system in the human brain, each pathway must sufficiently explain how particular human adaptations were *determined* by the system, taking into consideration several factors, including (a) which ancient psychological adaptations were co-opted by an intentionality system, (b) the actual means by which these ancient adaptations were exploited by this human cognitive specialization, and (c) the reproductive payoffs of behaviors caused by these coactions between

the old and new (or low- and high-level) systems that would have led to the selection of adaptive cognitive programs unshared by other species.

One of the central assumptions made here is that consciousness evolved in humans as a relatively domain-general operation at some point in hominid evolution, gearing the organism toward regular hypothesis formation and explanatory theorizing by appealing to the abstract causes of perceptually detectable events in the physical and social domains. Any later adaptations building on this representational structure can be said to have co-opted these general features of consciousness. The coordination of other adaptations, predecessors of this novel representational system and historically operating independently of the system, also was important in the evolution of these co-opted adaptations. Because adaptations are constrained by features of preexisting structures (Buss et al., 1998; Dawkins, 1986; Dennett, 1995; Williams, 1992), selection favors those traits that can exploit these more ancient designs (and especially those that also maximize the utility of these ancestral mechanisms) without interfering with the latter's adaptive functioning (see Buss et al., 1998; Gigerenzer, 2001).

Developmental and Contextual Influences on the Expression of the Metarepresentational System

The core modus operandi of evolutionary psychology is that organisms' behaviors are guided by "propositional algorithms" or implicit "adaptive heuristics," unconscious psychological operations that are activated by specific environmental stimuli impinging on evolved construals specializing in the domain of such stimuli (e.g., Cosmides & Tooby, 1992). The functioning of such adaptive heuristics is context sensitive. Nature does not countenance those genetic predispositions that cannot adequately adapt the organism to its regularly prevailing, but variable, social and ecological pressures. Indeed, advocates of the new subfield of "evolutionary developmental psychology" recently have established the ontogenetic bases of adaptive behavior as having played a major role in evolutionary change, with the particular features of developmental ecologies often determining the complexion of certain human adaptations (Bjorklund & Pellegrini, 2002).

Such thinking is important to keep in mind when considering adaptations borne of intentionality. Although adaptations are characterized by their insertion into the standard genotype of all individual members of a species (or subpopulations of a species), developmental plasticity can determine how they are manifest in individual organisms. Although intentionality appears fully developed by 4 to 5 years of age in human children (as demonstrated by the successful performance of children at this age on a range of "theory of mind" tasks, such as falsebelief and appearance-reality experiments; for reviews, see Flavell, 1999; Wellman, Cross, & Watson, 2001), there is evidence that particular social factors can serve to facilitate the precocious emergence of advanced metarepresentational abilities (Cutting & Dunn, 1999; Peterson & Siegal, 2002; Perner, Ruffman, & Leekam, 1994). For instance, preschool-aged children who have grown up with older siblings successfully pass these tasks, on average, earlier than same-aged peers who are single children or who are the oldest children in their families (Perner et al., 1994; Peterson, 2001). These results have been interpreted as arising through the competitive nature of sibling relationships; younger siblings able to "make the playing field level" by having their precursor representational competencies more rapidly transformed into higher order social cognition than is typical had adaptive advantage (Bjorklund & Pellegrini, 2002). Similarly, young children whose parents engage them in more dialogic narrative, enrich their conversations with more mental state terms, and make frequent reference to divergent viewpoints are also precocious in the domain of social cognition (Ruffman, Perner, & Parkin, 1999).

In addition, several investigators (Lillard, 1997, 1998; Schwanenflugal, Martin, & Takahashi, 1999) have argued that the metarepresentational system is invigorated not by a static regime of unobservable mental states, but instead that cultural influences can carve out the actual nature of explanatory appeals to unobservable forces, forces that may vary from culture to culture. For instance, Lillard (1997, 1998) reasoned that not only do individuals of different societies differ in the way they employ causal state terms (e.g., emphasizing emotions

over epistemic states when reasoning about the causes of behavior), but also this differential usage of such terms may reflect actual differential representational access to such states. That is, the developmental context may determine the way the intentionality system is experienced, with initial general capacities for a full representational range being progressively pruned in response to impoverished exposure to explicit appeals to certain causal states and frequent exposure to others. The result of these developmental trajectories may be that there is no singular theory of mind in adult humans but instead many different types of theories of mind, each the sociocognitive asymptote of particular epigenetic pathways. Although Lillard's claims of cultural variations in folk psychology have been criticized, most notably by Wellman (1998), who pointed out that "believing [mental states] is not the same thing as understanding [mental states]" (p. 36), her review of cultural differences in social cognition does show how development can exert pressure on the nature of representational processes.

This is an important issue when considering how specific adaptations that have co-opted the intentionality system to help individuals survive and reproduce in the past (and in current environments that simulate certain features of the environment of evolutionary adaptedness) may not be employed in some current social contexts and may even be assiduously inhibited as a defense against their present maladaptive consequences. This is not to say that the adaptation is not still present in modern minds. Rather, genetic variability in the capacity to harness cognitive resources, or in sensitivity toward domain-specific information offsetting Darwinian algorithms grounded in the intentionality system, may have led to diffuse handling strategies such that humans are not bound to a single expression of the adaptation irrespective of particular developmental and social contexts. Some examples of specific adaptive strategies associated with the intentionality system may help illustrate.

Infanticide and Metarepresentational Adaptation

As Lillard (1998) has shown, explanatory appeals to unobservable causal forces, even within the relatively narrow domain of social

cognition, can come in different culturally determined forms. The fact that each of these forms is evoked in diverse socioecologies suggests that they are not only embedded in cultural norms but are also selectively used to accommodate the genetic interests of individuals subscribing to such explanatory types. For instance, among many American Catholics and other religious adherents, the birth of deformed, retarded, or otherwise abnormal offspring is often interpreted as a special gift meant to test parents' faith in God (e.g., Hughes, McCollum, Sheftel, & Sanchez, 1994; Zuk, Miller, Bartram, & Kling, 1961). In Catholicism, abortion and infanticide of such children is strongly abhorred, and religious proscriptions forbid such practices. As Reynolds and Tanner (1995, p. 91) reported:

Not only is infanticide a crime in the affluent West, but Christian attitudes support this view, even in the case of [abnormal] children. Their presence in contemporary industrialized society in large numbers constitutes a considerable social and economic burden on both families and the state. Ethical abhorrence of infanticide occurs against a background of general affluence. In the Christian West, it is particularly among the more religiously motivated that survival of an abnormal child is more easily accepted.

Within societies in which the social and economic burdens of abnormal children can be shouldered by parents without incurring large genetic expenses (e.g., dampening the chances of survival of other, healthy offspring), parental investment in such children should not be uncommon. Indeed, in these societies, having unhealthy children may even cultivate unique selective advantages for parents in that, whereas investment in such children is possible but does come with some degree of apparent emotional and financial hardship, additional resources (e.g., societal support and pecuniary benefits) may be made more readily available to such families. When these favorable socioecological factors are compounded with a religious explanatory appeal to intentional agency (e.g., the will of God) as the causal force behind the event (i.e., the presence of the abnormal child), other nonrelated individuals subscribing to this same causal belief structure become increasingly likely to offer their support and thus contribute to the cumulative selective advantages of the natal family, who are believed to be doing "God's work." When the net genetic benefits

associated with rearing such children are coequal with or outweigh the potential costs to fitness, infanticide is less likely to occur. By drawing on the prevailing causal religious belief system in affluent societies, mothers of such infants can effectively strongarm their peers into providing them and their families with valuable resources. Without the intentionality system in place, however, this particular adaptive strategy seems unlikely to have been supported, as it is firmly planted in the set of metarepresentational competencies necessary for making theistic attributions (see Bering, 2002, in press). It is probably no coincidence that orphanages and institutions for sickly children have historically been governed by ecumenical organizations, and state agencies provide generous financial incentives for people willing to take on the burden of such children's care.

Different intention-related adaptive strategies may be used to deal with abnormal children in societies in which prevailing environmental factors do not favor parental investment in offspring unlikely to be reproductively successful. Scarcity of resources, economic and political instability, epidemiological diseases, malnutrition, and other environmental stressors associated with high infant mortality rates should contribute to the social, religious, and political endorsement of infanticide practices. Individuals in such societies cannot "afford" to invest in abnormal offspring because (a) parents would be unlikely to reap the genetic benefits of such investment because it is unlikely that such children would live to reach reproductive age; (b) the impoverishment of the current ecological conditions means that society cannot provide special assistance to the natal family; and (c) investment in such children demands reproductive and parental strategies that would be detrimental to the genetic fitness of the parents (e.g., deferred parturition involving future, healthy offspring and investment decrements in relationships with healthy, older offspring). In the face of such conditions, genes are best served by behaviors, such as infanticide, that address these impediments to fitness.

Evidence suggests that this is indeed the case. In many nonindustrialized and hunter-gatherer societies, infanticide of abnormal children is practiced regularly and receives strong cultural support (Langer, 1974). More often than not,

these practices are part of religious canon. Children born with birth defects, chromosomal disorders, and other serious maladies are regarded as symbolizing the special wrath of supernatural agencies. For example, infants born by breech presentation were believed to be evil tokens and immediately smothered with manure by the Kgatla peoples of South Africa (Schapera, 1966). In Sudan, the Mandari left male infants born with no testicles to die on anthills, and babies born with extensively marked bodies were also promptly destroyed (Buxton, 1973). The Sukuma of Tanzania developed religious practices to determine which of their ancestors were displeased enough to have caused such an inauspicious event (Cory, 1951). Attributing such events to the malicious intentions of supernatural agencies provides cultural support for infanticide and, subsequently, increases genetic fitness.

Daly and Wilson (1988) have explicitly rejected the importance of such causal ascriptions, reasoning that they play little or no role in promoting infanticidal behavior of abnormal offspring. Indeed, this general position is a common feature of evolutionary psychological models, wherein conscious beliefs are sometimes impugned for obscuring true causal processes (i.e., unconscious adaptive drives) and are seen either as epiphenomena or as proximal determinants of behavior servicing the ultimate unit of selection (i.e., the gene; Buss, 1995, 1999; Dawkins, 1989; French, Kamil, & Ledger, 2001; Tooby & Cosmides, 1992). For example, according to Daly and Wilson (1988, p. 50):

People dispose "superstitiously" of deformed or sickly babies in many societies, even though the expressed rationales and associated ideologies vary from place to place. It is hardly ever reported that people dispose "superstitiously" of well-formed, healthy babies, and when they do, they kill other people's babies, not their own. What explanatory force can we then grant to the concept of superstition?

In contrast to these authors, we believe that superstition can play a significant role in guiding ancestrally adaptive human behavior. In many cases, causal ascriptions are carefully tailored to the ecological contexts that dictate adaptive behaviors, promoting the relative pliability of behavior in the interests of genes. For some social behaviors, such as investing in a child when he or she is unlikely to convert

parental commitment into later reproductive payoffs, the capacity to attribute the birth of an abnormal child to divine intentions may be necessary. The immediate benefits associated with making such decisions will, of course, have their evolutionary impact at the ultimate level of genetic selection. However, these benefits may be solely determined by metarepresentational competency, what Daly and Wilson referred to simply as "superstition." For other adaptive stratagems, such as committing infanticide when offspring are unhealthy and when there is great instability and many environmental stressors, the capacity to attribute the unfortunate child to the malicious intentions of disgruntled gods or deceased ancestors should increase the likelihood of the behavior occurring, in that it can help override other adaptations such as mother-infant bonding as well as more evolutionarily novel intention-based mechanisms, such as empathy for a suffering infant, that might inhibit the adaptive behavior.

Ancestral Conspecific Killing

Although the killing of an abnormal infant may be *encouraged* by an intentionality system that has its representational processes developmentally defined by complex environmental factors, the system is not necessary for infanticide to have evolved as an adaptation in such cases. Indeed, most other mammalian species, including nonhuman primates, have been observed to kill their unhealthy offspring. For instance, Herrara, Knogge, and Heymann (2000) reported observing an adult female wild saddleback tamarin (Saguinus fuscicollis) kill its newborn infant after the infant expressed signs of possible neurological deficits by frequently falling from its carrier. Similarly, Fedigan and Fedigan (1979) reported observing a young Japanese macaque (Macaca fuscata) afflicted with cerebral palsy being pushed from a tree by its mother so that it fell a great height and was likely critically wounded. Such infanticidal incidents have been described by Hrdy (1979) as cases of "parental manipulation" in which mothers terminate their investment, which may up until the time of the infanticide occur at a normal level, when confronted with physical and behavioral signs that the infant has a low chance of survival. Such episodes need not involve metarepresentational abilities, as these

adaptive decisions are probably triggered by low-level detection mechanisms and cost-benefit analysis. Parental stratagems appear designed to be especially sensitive to features of offspring signaling reproductive or heritable deficiencies; when detected, and conditions do not favor investment, neglect or infanticide is likely to occur.

The subject of infanticide is one area of research that is part of a larger scientific program of evolutionary psychology: the nature of homicide. Since Daly and Wilson's (1988) seminal book on the topic, the study of murder, aggression, and abuse has led to dozens of empirical and theoretical publications by authors who have taken the strong position that such behaviors were selected because they led to fitness advantages throughout human evolutionary history (for a review, see Buss & Shackelford, 1997). To support this position, researchers typically develop metatheoretical models based on the central tenets of evolutionary psychology in relation to homicide, then make predictions about statistical probabilities of finding homicidal or aggressive behaviors occurring within specific social contexts and between individuals matching particular reproductive profiles, and finally assess the accuracy of these predictions by scouring criminal records and homicide reports filed in homicide databases to determine whether the hypotheses are supported by the data. For example, assuming an evolutionary psychological perspective, one can predict that stepchildren would be at a greater risk of abuse and homicide by their stepparents than would comparatively aged children reared by genetic parents (see Daly & Wilson, 1988; Davis & Daly, 1997). This is because unrelated adults can reap few selective advantages by investing in an unrelated individual's—indeed, a competitor's—offspring. In addition, stepfathers engaged in marital courtship with a reproductive-aged female presently raising young children from another male are at a select disadvantage. All of the female's maternal resources are currently invested in offspring that are "stealing" resources from the male's own future progeny, whose conception is delayed by these genetically unrelated children countermanding their mother's reproductive opportunities. Given these biological verities, nature would therefore be prone to select organisms that acted to remove such impediments to their own fitness interests by killing the unrelated young of mating partners.

The data marshaled by evolutionary psychologists suggest the presence of just such an evolved mechanism. The rates of child murder are significantly higher among stepparents than genetic parents (see Daly & Wilson, 1988; Davis & Daly, 1997), and the likelihood of such killings increases when the child is 2 years of age or younger (Daly & Wilson, 1988, 1995). The risk of a preschool-aged child being murdered by his or her stepparent is 40 to 100 times greater than that for children living with both genetic parents (Daly & Wilson, 1988, 1995). Cross-cultural evidence further supports the ancestrally adaptive nature of this behavior. For example, as a condition of marriage, Yanomamö males often insist that their future wives' current children be killed if such children were sired by a previous husband (Daly & Wilson, 1988).

Similar support for the ancestral adaptiveness of homicide has been found in a variety of other categories. Among many such examples, uxoricide (wife killing) is most likely to occur when husbands suspect that their young wives are involved in extramarital affairs, thereby increasing the risk of cuckoldry (Daly & Wilson, 1988; Shackelford, 2001; Shackelford, Buss, & Peters, 2000); the risk of being murdered by one's children increases with age, as adolescents and adults become increasingly self-sufficient (Daly & Wilson, 1988); and rates of physical violence and murder are highest among young adult males, who are engaged in intrasexual competition over females and are especially sensitive to status-related threats (Daly & Wilson, 1988; Mesquida & Wiener, 1996; Patton, 1997; Wilson & Daly, 1985). In light of evolutionary psychological metatheory, what appear to be senseless acts of violence begin to reveal predictable patterns of aggression and conflict. Although such behaviors are rightfully maligned and constitute an enormous societal ill in most parts of the world today, frequently underlying homicidal behaviors and ideation are fitnessenhancing mechanisms designed to increase the replication of the perpetrator's genes. The fact that these basic behavioral patterns are found across human societies and are only superficially influenced by legal deterrents reflects the unconscious character of these mechanisms. As such, none of these behaviors require the presence of intact metarepresentational abilities lending *meaning* to human actions (although they may very well be influenced by such processes), but are rather instantiated by the coordination of low-level adaptations (e.g., social awareness of tertiary relations, male proprietariness over females, status striving amid social hierarchies, social cue—driven emotionality), which serves to trigger violent behaviors.

Given that comparative research with nonhuman primates has shown that many of these low-level adaptations do not hinge on the presence of the intentionality system, it is not surprising that chimpanzees display an assortment of conspecific killing behavior closely resembling the pattern found among humans. Recent DNA evidence comparing hair samples of infants with those of in-group males suggests that a high proportion of births in wild chimpanzees are the result of "furtive mating" of female chimpanzees with out-group males (Gagneux, Boesch, & Woodruff, 1999). This has been used to account for the increased probability of aggression displayed toward reproductive-aged females discovered at territorial borders by ingroup males during routine "boundary patrols" (Arcadi & Wrangham, 1999; Newton-Fisher, 1999; Watts & Mitani, 2001). In these cases, violent attacks toward such peripheral females are probable, and several lethal attacks have been reported. The infants of such females are at even greater risk, because they may have been sired by foreign males of rival, neighboring groups (Arcadi & Wrangham, 1999; Boesch & Boesch-Achermann, 2000; Newton-Fisher, 1999; Nishida & Kawanaka, 1985; Watts & Mitani, 2000). When groups are disbanded through intergroup warfare and new reproductive females are incorporated into the successful community, these females' infants are promptly destroyed. In addition, intragroup infanticide has been linked to the mother's periodic absences from the community during oestrus periods around the time of conception (Sakamaki, Itoh, & Nishida, 2001), hinting at males' sensitivity to the possibility of unrelated males' insemination of females. Conspecific killing also occurs with some regularity in the context of sexual competition between in-group males for ascendance in the social hierarchy, which will ultimately lead to greater reproductive potential (Fawcett & Muhumuza, 2000). Complex social behaviors involving coalition formation, agonistic encounters, and reconciliation can instigate fatal attacks on individuals occupying positions of dominance or those whose social alliances threaten status maintenance or enhancement.

Information-Regulatory Mechanisms and Homicide

In Dostoyevsky's (1880/1950) The Brothers Karamazov, the Russian monk, Father Zossima, recalls the tale of a contrite and troubled middle-aged man hopelessly attempting to expiate his sin of murdering a young woman many years prior after she refused his marriage offer. The woman's innocent serf had been arrested for her murder, subsequently fell sick in prison, and died shortly thereafter. Plagued by guilt, the man, who "was in a prominent position, respected by all, rich and had a reputation for benevolence" (p. 360), confesses to the priest but soon comes to regret this public revelation and considers killing Father Zossima: "The thought was unendurable that you were alive knowing everything ... let me tell you, you were never nearer death" (p. 374).

This fictional scenario is useful insofar as it allows us to distinguish between the low-level mechanisms driving conspecific killing behavior that are deeply embedded in our primate ancestry, on the one hand, and the evolutionarily novel, high-level mechanisms promoting new classes of adaptive homicidal behaviors characteristic only of humans, on the other hand. The murder of the young woman was sparked by feelings of male proprietariness and jealousy over the woman's engagement to another man. As such, the proximal determinants (i.e., conscious motives) of the murderer's behavior are inconsequential to evolutionary analyses and probability estimates of violence and homicide; no matter what *meaning* the assailant attributes to his murderous actions, his behavior meshes well with the predicted pattern of mate killing and is analogous to similar patterns of aggression and violence in chimpanzees. However, the homicidal ideation underlying the second incident, in which the man considers murdering the priest after confessing to the first murder, seems a qualitatively different case in that such thinking demands an appreciation of the mental states of others. Here the motivation behind such premeditation is important; should

these fantasies have taken shape and the man decided to kill the priest, the murder would be beyond the explanatory power of an evolutionary psychological stance that discounts the proximal determinants—or conscious motives—of homicidal behavior. Although both homicidal stratagems were selected because they ultimately increased the likelihood of genetic transmission and, at this level, it matters little the actual means by which nature makes this happen, we cannot begin to understand human cognitive evolution until we specify how the intentionality system came to change preexisting adaptations or to establish entirely new adaptive behaviors.

Evaluating the evolution of homicide-related behaviors is one promising way in which investigators can begin to reveal how the bidirectional relationship between low- and high-level systems is responsible for establishing new adaptive strategies in humans. Primate evolution has been characterized by increased social complexity, with specific adaptations emerging to effectively process information from many different social domains. Recurrent exposure to information within each of these domains has resulted in neurocognitive faculties in different primate species specialized for producing ancestrally adaptive behavior fitted to their social environments. Although species-atypical experiences can lead the developmental emergence of such adaptive behaviors astray and suggest considerable neural plasticity (an integral part of selective processes; see Bjorklund, 1997; Bjorklund & Pellegrini, 2002), throughout evolutionary history organisms were faced with species-typical experiences that served to carve out psychological adaptations designed to respond to particular environmental contingencies.

In human societies, which consist of fluid polities wherein one's social position is never entirely stable, variables correlated with aggression and violence, and oftentimes implicated in cases of homicide, include status- and reputation-related threats (Daly & Wilson, 1988). Because increased status is linked to greater acquisition of resources that facilitate greater reproductive opportunities (e.g., higher status males are likely to have economic incentives that attract the sexual interest of females), assaults to one's reputation and status are likely to engender feelings of hostility and vengeance that may be channeled into actual aggression. Although

female-female physical violence is less frequent in humans, when it does occur, it is often precipitated by one individual seeking to undermine the reproductive opportunities of another by spreading rumors about her sexual infidelity or her otherwise "loose" behavior with males (Ahmad & Smith, 1994; Buss & Dedden, 1990; Campbell, 2002). By physically assailing the source of these rumors, the aggressor may be reducing the likelihood of such insults occurring in the future and thus preserving her genetic interests. Similarly, among males, barroom brawls and schoolyard fights are often precipitated by personal slights, homophobic remarks, and insulting comments regarding relatives, each of which is designed to affect (or establish) dominant and subordinate relations (Ahmad & Smith, 1994; Atzwanger, 1995; Buss & Dedden, 1990; Daly & Wilson, 1988; Gladue, 1991); if not sufficiently crestfallen, the receiving party may retaliate against this threat to his social position.

The importance of language in directing these status-related threats is deliberately underscored in the previous examples. Along with its capacity to threaten one's standing in a social community, the evolution of a natural language system provided individuals with social information that could not be directly inferred through first-person access to behaviors (Dunbar, 1993). With the appearance of language, social information could be rapidly dispersed among interested parties, and the amount of information potentially harbored about others was significantly increased. Knowledge about specific others ("Jim said that Mary cheated on John while they were dating") could be effectively stored in "social data files" and retrieved when determining one's behavior toward these others ("Therefore, if Mary asks me out on a date, I'll turn her down"). In general, the more knowledge one has of the behavioral and personality characteristics of specific others, the more adaptive one's behaviors concerning these individuals (e.g., because Mary has expressed signs of infidelity in the past, establishing a long-term relationship with her is risky owing to an increased possibility of cuckoldry). Although repeated encounters with others in a variety of situational contexts can help individuals assess the type of person someone is, the possibility of intentional deceit threatens the reliability of such first-person character judgments. Therefore, the ability and strong compulsion to detect hidden, deleterious traits in others—traits that may seriously jeopardize one's genetic fitness (e.g., a prospective job applicant's history of tax evasion, a potential mate's questionable sexual orientation, or allegations of child abuse from a previous spouse)—involve (a) gathering information "through the grapevine," (b) responding emotionally to such information and (c) subsequently putting such information to use in the social domain through ancestrally adaptive behavior.

This also expresses the bidirectional nature of low- and high-level cognitive systems involved in adaptive processes in humans. The appearance of such a strategy involved, first, the pilfering of ancestral primate adaptations involving social organization and relying on firstorder representational access, and, second, building on these adaptations by extracting additional knowledge of others from second-, third-, fourth-, and higher order sources of representation. With the coevolution of the intentionality system and natural language, our evaluative judgments of others were no longer confined to who we saw grooming whom, who we noticed was absent during oestrus, or who we observed attempting to steal food; rather, we could be informed of these activities (and others) even if they occurred during our absence. Dunbar (1993) has reported that as much as 60% of human conversation involves social gossiping, and other investigators have shown that people are primarily interested in the misdeeds and misfortunes of others, especially when these others are in positions of authority (McAndrew & Milenkovic, 2002). In addition, this pattern appears early in development, with school-aged children frequently participating in name-calling and rumor transmission, each of which has real consequences for a child's popularity and the number of friends he or she has (Crozier & Skliopidou, 2002). Mechanisms designed to monitor or control the flow of selfrelated information also seem at play early in development, for example in children's denouncement of others as "blabbermouths" and "tattletales" when their misdeeds are exposed.

The obvious selective advantage of accruing information about (potentially) significant others is the increased likelihood of evading threats to genetic fitness before they happen (see Shackelford & Buss, 1996). Having knowledge

of a dating partner's history of alleged physical abuse against his ex-wife, a pattern that did not appear until 3 years into the marriage, can help a woman to make an informed (i.e., ancestrally adaptive) decision when this man decides to propose to her. Indeed, much like Pascal's wager, even if such information is potentially unreliable, the risks associated with ignoring such facts should be, under normal conditions, much greater than the risks of allowing them to influence one's behavioral decision making. In addition, having knowledge of such information about others can provide a considerable degree of social leverage in the context of status-striving and resource acquisition, affording power over others who fear their social exposure (e.g., blackmail).

Consequently, however, this selective strategy of deriving fitness-related "negative" information about others can also have a tremendous impact on one's own genetic fitness when others' attention homes in one's traits, some of which may be undesirable from the perspective of a mate or social partner. Others' solicitation of negative information about the self can pose an enormous threat to one's genetic interests. If such information becomes public, or is otherwise revealed to sources whose knowledge of such matters can either reduce one's reproductive opportunities or diminish current and potential levels of fitness, individuals should have evolved strategies designed to conceal those personal attributes that others are, by design, driven to detect.

The result of this evolutionary dynamic can be envisioned as an arms race occurring between individuals coexisting in social communities where information-gathering mechanisms (those mechanisms designed to collect information about social others) become in conflict with information-retention mechanisms (those mechanisms designed to block others' access to negative information about the self). Each adaptation therefore occurs simultaneously as both defensive and counterdefensive strategies involving social exposure. Deficiencies in either regard would be maladaptive. The individual with deficient information-gathering mechanisms runs the formidable risk of engaging in social behaviors with dire genetic consequences, and the individual with deficient information-retention mechanisms runs the risk of being excluded from forms of social courtship

associated with reproductive opportunities (e.g., an individual known to abuse children is unlikely to attract many future mates). In addition, failure to protect such sensitive information from public exposure can have many indirect effects on one's fitness. For example, social stigmas often adhere to entire families rather than to the sole family member who originally provoked such public aversion through his or her faulty traits or moral transgressions. Because social dissidence is often perceived as sanguineous in nature, related individuals are also likely to bear the expense of having the self's negative attributes socially exposed. Among other examples, evidence of experiencing social stigma as a function of a family member's undesirable traits or behaviors has been found among individuals with mentally ill relatives (Choi, 1996; Veltman, Cameron, & Stewart, 2002), children whose mothers are HIV positive (Murphy, Roberts, & Hoffman, 2002), children and adults whose family members were murdered or committed suicide (Clements & Burgess, 2002; Dunn & Morrish-Vidners, 1988), those whose family members committed homicide (May, 2000), adult daughters of battered women (Humphreys, 2001), family members of homosexuals or bisexuals (Hammersmith, 1987; Herek, 1998), adoptive families (Miall, 1987), and children whose fathers are incarcerated (Gabel, 1992). Such information can constitute the anatomies of a family's closeted skeletons; from an evolutionary perspective, reluctance to make this information public occurs because the content of such secrets can have deleterious effects on reproductive potential.

However, revealing certain kinds of sensitive information, particularly information involving the personal commission of serious moral transgressions, can be especially damaging to one's genetic interests. Because the civil punishments for some transgressions can be extreme, involving such things as execution, torture, imprisonment, castigation, and isolation, the risks associated with exposing one's involvement in these transgressions are, as a consequence, considerably elevated. In such cases, engaging the information-retention mechanism as a counterdefense against others' information-gathering mechanisms becomes critical for preserving fitness. Therefore, the lengths to which an individual goes to protect him- or herself from social exposure of these misdeeds should notably expand. With so much on the line, individuals might resort to behaviors that, under any other condition, they would refrain from. Perhaps the most salient example of such behaviors, explicitly governed by information-retention mechanisms, is homicide in the service of protecting confidential information about oneself. Once such sensitive details have been revealed to someone else, and if no other evolved tactics are available to prevent the social transmission of this information, the extreme behavior of murder may occur.

Co-Optation of Mechanisms Motivating Conspecific Killing by the Intentionality System

The old proverb states that "dead men tell no tales." Nature, as well, seems to have capitalized on this fact by designing strategies for terminating the lives of those who possess highly damaging knowledge concerning the self. Because these strategies command the resources provided by the intentionality system, which allow for representation of epistemic states such as knowledge and ignorance, the evolutionary scenario provided in this article holds that this adaptation is a recent innovation in homicidal behavior and is exclusive to humans. Unlike the types of conspecific killing in the foregoing discussion, which are found in nonhuman primates and humans alike, the evolution of information-retention homicide was dependent on the presence of the intentionality system. As such, a true "Machiavellian intelligence" and the evolved heuristics bootstrapped to it do not seem to have come onto the evolutionary scene until humans appeared (cf. Byrne & Whiten, 1988).

We have identified four broad categories of information-retention homicide, each of which was designed to protect the self from the genetic consequences of social exposure in the environment of evolutionary adaptedness. The first is first-person exposure, victim-centered homicide: The perpetrator directly violates another individual, such as through rape or burglary, and murders the victim to prevent the victim from implicating the perpetrator in the transgression. The likelihood of homicide occurring in such cases should be a function of the seriousness of the offense, the reaction of the victim

during the course of the offense, and the perpetrator's perceived or actual exposure of his or her identification during the course of the offense. For example, although rape-murder occurs with some infrequency, it does occur. From an evolutionary psychological perspective that strictly discounts proximal motives, such a strategy is maladaptive in that it directly countermands the adaptive mechanisms involved in rape. However, the adaptiveness of rape-murder becomes clear in light of the current model, which holds that the risk of detection from committing the crime of rape outweighs the fitness advantages of impregnating a rape victim (see Shackelford, 2002a, 2002b). The second is second-person (or higher) exposure, witness-centered homicide: As a consequence of committing some offense, other individual(s) who are not directly victimized in the original offense are exposed (or believed to be exposed) to the transgression and to the identity of the perpetrator. Because of this incidental exposure, the perpetrator murders the witness(es) to prevent them from implicating the perpetrator in the transgression. For example, convenience store robbery-homicides may involve the killing of not only store clerks but anyone else in the store at the time who happens to see the thief.

The third category is defection from mutual criminality, informant-centered homicide: Two or more individuals participate in a transgression, and one (or more) individual(s) either defect from the criminal relationship or threaten to confess to the transgression. The defector(s) are murdered by the other perpetrator(s) to prevent implication in the socially maligned activity. For example, mafia-related killings frequently involve the murder of former business partners who became "turncoats" or "stool pigeons" or otherwise threatened to testify, or "squeal," against current members. The final category is confessional-regret, confessor-centered homicide: A perpetrator confesses a social transgression to a confidant and then comes to regret divulging this sensitive information. The perpetrator murders the confidant to prevent this individual from socially transmitting the information. For example, in the context of a marriage, an individual may confess a serious social transgression, come to regret this admission when the marriage dissolves, and then decide to murder his or her spouse.

There are interesting implications here for the evolution of confession, as well. It seems, for example, somewhat counterintuitive that individuals would be inclined to engage in confessional behavior when others have no knowledge of their transgressions. Because confession guarantees social exposure, it consequently threatens genetic fitness. However, confession may actually serve to ameliorate the fitnessrelated blows stemming from social exposure. Gold and Weiner (2000) have shown that when confession occurs with remorse signals (such as those accompanying feelings of guilt), others are more likely to infer that the transgression will not occur again, thus promoting forgiveness and a reduction in retributive behavior. Other authors have speculated that when such signals are in place, people are increasingly prone to decide that the party has suffered enough through his or her guilty feelings, thus making punishment unnecessary. We argue, therefore, that confession should be most likely to occur when individuals perceive the likelihood of social exposure to be high enough that "preemptive strikes" will be launched against them. Also, because of inclusive fitness issues, individuals should be most likely to confess to those who share some stock in their own genetic interests, such as parents and siblings. When confessions are made to those who do not hold such stock, they frequently involve conditions of anonymity (as in the Catholic church) or confidentiality (as in clinical therapy), both of which are designed to defend against social exposure. In addition, we believe that confession can also serve as a signal of commitment to others because it reduces the likelihood of defection from a relationship (e.g., Hong, 1998; Rogers & Holloway, 1993; Shackelford & Buss, 1996; Ting-Toomey, 1991). For instance, by confessing, one puts oneself at increased risk of being blackmailed and will therefore be more likely to be complicit in social arrangements dealing with those individuals possessing such knowledge (see also Schelling, 1960). As another example, a husband's confession to his wife about a previous affair may be interpreted as a gesture of current emotional commitment, in that if he intended to continue with his extramarital relationship(s) he would not be revealing the indiscretion.

In regard to homicide, the current position holds that although not all cases involve instantiation of such information-retention mechanisms, many cases of murder do involve such evolved strategies. Individuals who were able to employ these strategies under the threat of social exposure of serious transgressions or otherwise undesirable personal traits were more likely to pass on their genes than individuals who were not able to do so. With advances in security systems (e.g., video cameras), forensic science, and communication systems (e.g., telephone, media, the Internet)—each of which can be considered a technological arm of information-gathering mechanisms—the strategy may not be as successful in modern times as it was in the evolutionary past. In addition, even in the environment of evolutionary adaptedness, information-retention homicide demanded retention of information above and beyond the original motive; the murder episode presents the individual with new (and perhaps even weightier) information to conceal from others. This is highly risky. Still, if the murder is *not* committed, social exclusion may become an unavoidable reality. In this sense, covering up by killing, and then covering up the killing, is a more effective strategy than trusting others with sensitive information. Because perpetrators are *cer*tain to face grave genetic consequences if implicated in serious transgressions (such as rape or murder), committing information-retention homicide at least gives their genes a fighting chance of survival.

Social Learning and Developmental Modifiability of Information-Retention Mechanisms

Human cultures (as the aggregate output of evolved psychologies operating in interacting individuals; see Tooby & Cosmides, 1992) must "define" for individuals what it is that they abhor. Given regular variance in human socioecologies, Darwinian algorithms, to have been ancestrally adaptive, must first have been afforded sufficient slack in ontogeny to enable individuals to meet the culture-specific demands of particular social environments. This can account for why children, and in Western society even adolescents, are much less likely to be harshly penalized for committing serious social transgressions than adults involved in the same behavior, or are at least more likely to be given opportunities for redemption. Natural selection has made adults sensitive to the naïveté of children, permitting room for error during cultural "morality imbibing," a social luxury that becomes increasingly scarce as an individual ages.

As in the case of infanticide, which, depending on ecological constraints, is either culturally expected or culturally demonized, developmental acculturation involves the psychological internalization of composite features of moral systems. Although there are probably broadly based default system features, such as the general characteristics of information-retention mechanisms concerning disease or sexual behavior, that are characteristic of all human minds, social learning also plays a role in programming these default systems with the specific demands of different cultural forms, such as what behavioral content will actually trigger information-retention mechanisms. Therefore, to a reasonable extent, the information-regulatory systems of gathering and retention will be carved out through developmental processes lending social evaluative weight to particular behavioral types, working on a gradient scale of acceptable and unacceptable behavior. The result of such processes is a cognitive–emotional tautology of rule-based behavioral norms that both establishes the emotional currents underlying the self's and others' actions and, as a consequence of these affective determinants, helps to guide an individual's actions in the social world. Transgressing these behavioral norms should give rise to shame, the emotional determinant of information-retention mechanisms. Likewise, others' transgressions of these behavioral norms should give rise to anger, disgust, and vengeance, the emotional determinants of mechanisms devoted to retributive justice. This position does not question the existence of "deep structures" of "moral syntax" (Costanzo, 2002) but, rather, holds that evolved strategies dealing with information regulation are developmentally based, are initially openended but within the boundaries of general constraints, and ultimately become specialized to local social conditions and resistant to further modifications.

Suicide and Intentionality

Under certain conditions, information-retention mechanisms fail to protect sensitive per-

sonal information from being publicly disclosed, and the individual is faced with the reality of social exclusion (e.g., Leary, Tambor, Terdal, & Downs, 1995). In such situations, the information-gathering mechanisms of others have won out over the self's retention mechanisms, placing the self's negative attributes on public display. Although some degree of perseverance of the retention mechanisms is apparent (e.g., "hiding one's face in shame"), the damage has been done, and there is demand for alternative evolved strategies. The critical evaluations of others, or the anticipation of such evaluations, engender intense anxiety (Gilbert, 1998), which is scaffolded by negative self-appraisal and shame in response to the internalization of cultural mores. This negative affect is confounded with the fact that additional sociocognitive strategies involving changing the way others perceive the commission of the social transgression (e.g., rationalization and external attributions) are substantially less effective than information retention, thus fostering hopelessness. The confluence of these social, emotional, and cognitive factors has been identified as the proximal cause of suicide and suicidal ideation (Baumeister, 1990; Kalafat & Lester, 2000; Smith & Hackathorn, 1982).

From an evolutionary perspective, suicide is an especially challenging area because, at least on the surface, it appears fundamentally at odds with evolved decision making. Above all else, evolutionary processes involve fitting the organism with behaviors enabling it to survive and reproduce. However, if the self's survival comes at the expense of inclusive fitness—or, in other words, of genetic kin's ability to pass on genes-then "sacrificing" one's life for ultimate genetic gain may have been adaptive ancestrally (de Catanazaro, 1992). There are numerous cases of "suicide" in other species, particularly among insects, that are compatible with Hamilton's principle of inclusive fitness. For example, it may have been adaptive ancestrally for male Australian redback spiders (Latrodectus hasselti) to comply with sexual cannibalism for paternity reasons; males that are cannibalized copulate longer and fertilize more eggs than males that are not cannibalized, and, also, females that have cannibalized males are more likely to reject future suitors than those that have not (Andrade, 1996). The suicidal behavior of pea aphids (Acyrthosiphon pisum)

parasitized by Braconid wasps (Aphidius ervi) is context sensitive, involving calculations of reproductive potential (McAllister & Roitberg, 1987; McAllister, Roitberg, & Weldon, 1990). As reproductive opportunities diminish, pea aphids become more likely to modify their escape behavior when faced with predators such that there is an increased risk of mortality, thus increasing parasite transmission to subsequent hosts in multihost systems (Holmes & Bethel, 1972). These findings support the "host suicide hypothesis," which "presumes that the cost of 'suicide' may be overridden by the reduced death rate of closely related individuals due to the death of the parasite" (McAllister et al., 1990, p. 167).

Another example is the case of bumblebees (Bombus lucorum), a species parasitized by conopid flies inserting their larva in the host's abdomen, killing the bumblebee in about 12 days and then pupating until their emergence the following summer (Poulin, 1992). Poulin (1992) has presented evidence that parasitized bumblebees alter their behavior by abandoning the colony and spending all of their time in flower meadows outside the colony where they are susceptible to further parasitoid attacks. By doing so, the affected host leads the flies away from nonparasitized kin, thus increasing inclusive fitness by protecting the colony from infestation. Similar arguments have been posited for suicidal behaviors of birds (e.g., O'Connor, 1978). However, Poulin (1992) cautioned against use of the term suicide when describing the self-disadvantageous behaviors of other species, particularly insects. "The adoption of a more dangerous lifestyle by an insect that is bound to die shortly may be adaptive in terms of inclusive fitness, but no more suicidal than, for instance, an ageing animal taking risks to reproduce in the presence of a predator as its inevitable death approaches" (p. 175).

There are no confirmed cases of such behaviors among nonhuman primates. Although there are instances of self-injurious behaviors, usually conflated with stereotypies occurring in abnormal social environments such as laboratories (e.g., Lam, Rupniak, & Iverson, 1991), there is no evidence of behavioral modification leading to increased risk of mortality or direct self-inflicted lethal displays in monkeys and apes. In stark contrast to these closely related species,

suicide accounts for a significant minority of deaths in humans, and in certain age categories, such as adolescence and senescence, it is among the leading causes of death (Pampel & Williamson, 2001; Robbins, Angel, & Kumar, 1981). According to deCatanzaro's mathematical model of self-destruction and preservation (see deCatanzaro, 1992; see also Brown, Dehlen, Mils, Rick, & Biblarz, 1999), patterns of suicide in humans can be deciphered by applying principles of inclusive fitness. Individuals are most likely to commit suicide when direct reproductive prospects are discouraging and, simultaneously, their survival reduces inclusive fitness by posing a burden to close kin and interfering with their reproductive opportunities. For example, across age groups, deCatanzaro reported strong correlations between suicidal ideation and individuals' self-reports of such things as burdensomeness to families, success in heterosexual relations, health problems, homosexuality, number of children, number of friends, loneliness, frequency of sex in the past month, and future financial problems. With increasing age, the disposition of these correlations changes, such that health problems and burdensomeness replace reproductive potential as primary causal factors in suicidal ideation.

Such evolutionary reasoning casts muchneeded light on one of the darkest areas of human behavior. Although it successfully interprets suicidal behavior and ideation within an evolutionary framework, it fails to explain the evolutionary processes underlying human suicide adaptations. This is because it does not consider how the proximal cognitive determinants of suicide are deeply embedded in the intentionality system. Again, the question that we have focused on throughout this article is how a comprehensive evolutionary account of human behaviors can ever be achieved without paying attention to the unique cognitive processes underlying them, processes that are unshared by other species.

In the case of suicide, self-awareness involving the capacity to attribute unobservable characteristics to the self is a necessary cognitive component underlying the arguably ancestrally adaptive behavior. One of the consequences of having information-regulatory mechanisms becoming progressively specialized and resistant to change is that an individual comes to confuse the social jurisdiction of his or her local ecology

for a much more abstract deontological system in which culture-based rules of ought and should become the crucible of moral behavior. Therefore, the self's violation of the rules making up this system encourages a view of the self as inherently base, particularly in regard to transgressions or traits for which social repercussions are severe. As noted by Shreve and Kunkel (1991, p. 307), "Shame centers the psychological focus on the self, rather than on the behavior." Or, as according to Lester (1997, p. 353), the distinction between guilt, which seeks restitution, and shame, which seeks secrecy, can be made as follows: "I can't believe that I did that" (guilt) and "I can't believe that I did that" (shame; see also Gilbert, 1998; Tangney, 2001).

Empirical findings of Lester suggest that shame is a better predictor of suicide than guilt. Similarly, Baumeister (1990, p. 91) described the causal pathway toward suicidal behavior as including "unfavorable self-attributions, which are broadly meaningful interpretations of self as having stable, undesirable qualities, especially ones that may be predictive of additional difficulties in the future." Other evidence suggests that particularly heightened displays of self-awareness precipitate suicidal behavior. Baumeister (1990) has even referred to suicide as "escape from self." For instance, suicide notes are notorious for containing firstperson-singular pronouns, and when suicide note writers do mention significant others, they speak of them as being cut off or distant (see Baumeister, 1990). What seems to distinguish suicide in humans from the self-disadvantageous behaviors of other species is that only the former occurs in the context of social relations and is not caused by threats of interspecies predation. Rather, it is the threat of intraspecies negative social appraisals and the self's agreement with these appraisals that lead to the majority of suicidal behavior and ideation in humans. As in the case of information-retention homicide, however, conscious motives are important rather than inconsequential to evolutionary models of suicide. The chronic and acute dysphoric anguish resulting from these sociocognitive processes was designed to promote suicide, a behavior that ultimately led to inclusive fitness in the environment of evolutionary adaptedness.

Concluding Comments

In several ways, contemporary versions of evolutionary psychology are similar to the behaviorism of the mid-20th century. This is ironic considering that one of behaviorism's most notorious claims was that differences in the psychological systems between species were negligible because there exists only a single domain-general learning mechanism. This argument is antithetical to the position held by evolutionary psychologists, who argue for (and have empirically demonstrated) specialized psychological functions in different species that are dedicated to solving specific problems in the species' recurrent environments. But consider the following. Both behaviorism and evolutionary psychology are primarily concerned with how observable behaviors are affected by local environments over time; both fields either reject or do not attend to the influence of intentional motives and consciousness in general, arguing that mental states obscure true causal processes; and, by neglecting the role of consciousness, both fields treat the emergence of human behavior no differently than they treat the emergence of behaviors in other species.

Evolutionary psychology is unlikely to suffer the same fate as the now defunct behaviorism of old. Its explanatory relevance is significant and decisive, providing a unifying metatheoretical framework within which all of psychological science can be organized (Buss, 1999). However, to provide a comprehensive account of human behavior and psychology, evolutionary psychology must begin grappling with the cascading effects that one cognitive system, the intentionality system, had on the evolution of the species. If it is truly to become "the new science of the mind," the field is obliged to evaluate how behaviors exclusive to humans, such as information-retention homicide and suicide, came about through the intentionality system and also how more ancient behaviors embedded in our primate ancestry were influenced or changed by the evolution of this distinctive system. To date, the field has paid only lip service to the intentionality system, usually referring to it as a "theory of mind module" used to generate inferences about other people's behavior and therefore as adaptive in ancestral social contexts. Although this is accurate, it does not penetrate the issue deeply enough.

Part of the reason that evolutionary psychologists have been reluctant to acknowledge the role of conscious mechanisms in human evolution may be that they are averse to the concept of motive, whose semantic meaning is often conflated with teleological purpose, as if people deliberately engage in particular behaviors because they are adaptive. In this article, we have used the term only to refer to the psychological product of the intentionality system that serves as the proximal determinant of ancestrally adaptive behavior. Such motives are conscious in the sense that they are manufactured by the intentionality system, and thus individuals do have representational access to them. For instance, in information-retention homicide, an individual knows that he or she wants to kill another person because that person possesses harmful knowledge regarding the self. The individual knows what his or her motive is for committing homicide and therefore is aware of the content of his or her own evolved algorithms. This is not the same as saying that the individual knows that he or she wants to kill someone because that person's death may promote the killer's genetic fitness. Nevertheless, this is a qualitatively different motive category than those involved in more ancient design mechanisms, wherein the Darwinian algorithms feeding into ultimate genetic levels of selection are blind to individuals possessing them. For example, there is evidence that women's judgments of male facial attractiveness vary as a function of ovulatory status, such that women who are closer to ovulating prefer men with masculine facial characteristics (which are reliable indexes of "good genes"), whereas women who are earlier in their cycles are much less sensitive to these indexes, suggesting that women are more concerned at this stage with other male characteristics such as economic resources or parental contributions (Gangestad & Cousins, 2001). There is no reason to believe that women are aware of these motives at either the algorithmic level or the ultimate level of selection.

We are not claiming that all ancestrally adaptive human behaviors stem from the intentionality system, or even that all were influenced by the evolution of the system. Indeed, the majority of human adaptations may have nothing at all to do with metarepresentational abilities or abstract causal reasoning. But there is compelling

reason to suspect that everything that makes us uniquely human does.

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